Flexibility in avian migration across scales

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He’s a birder—briefly, a student of birds—
Noting those he sees in his mind or his
camera, items found for collection, the many
made more by research, or his travels.

They’re his science, he says, telling you, if you
listen, of habits and rarity, but what you see
are the colors and shapes, the moments of
movement he captures, showing themselves.

Devoted to kinds beyond counting, he includes
what’s sweet, fierce, often unseen but yet heard,
the breathtakingly beautiful stars of his sky.

From *Birder*, by John Van Doren (1928–2019),
who loved hemlock trees and waterfalls.

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Author Contributions

Benjamin Van Doren had independent intellectual input into all aspects of the thesis. He conducted and oversaw blackcap fieldwork in the UK over four winters, analyzed data for all studies, drafted chapters, and incorporated co-author comments to produce final manuscripts.

Ben C. Sheldon (supervisor, co-author of chapters 3 and 6) secured funding and provided intellectual input, guidance, and feedback.

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Greg J. Conway (co-author of chapters 3 and 6) secured funding and helped oversee blackcap fieldwork. Provided guidance and intellectual input for co-authored chapters.

Kira Delmore (co-author of chapter 3) coordinated and conducted blackcap fieldwork in continental Europe. Contributed data, analysis, and writing to chapter 3.

Andrew Farnsworth (co-author of chapter 5) provided guidance and intellectual input. Contributed oversight and writing to chapter 5.

Kyle G. Horton (co-author of chapters 4 and 5) provided intellectual input, writing, and data analysis for co-authored chapters.

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Abstract

Migratory birds form a network of organisms that connect the world, serving as indicators of ecosystem health and biodiversity on a hemispheric scale. Unfortunately, avian migrants are threatened by the rapidly increasing pressures of global change. Understanding the capabilities of migratory birds to respond to established and emerging challenges requires knowledge of the complex interactions among individuals, populations, species, and natural and built environments. In this thesis, I surveyed the drivers of bird migration across scales. I focused on the contributions of the innate migratory program, birds' responses to environmental cues and conditions, and the influence of human activity on migratory behavior.

First, I investigated birds' innate migratory programs. I demonstrated that stonechats (genus *Saxicola*) possess inherited programs that vary among taxa according to migratory tendency, but also readily interact with environmental factors to influence migratory phenotypes (Chapter 1). Next, I combined field and laboratory studies to show that ongoing responses to climate change in a long-distance migrant, the pied flycatcher (*Ficedula hypoleuca*), involve not only phenotypic plasticity, but microevolutionary change as well (Chapter 2). I then shifted to a wild context and examined the migration of the Eurasian blackcap (*Sylvia atricapilla*) across its European range, illustrating two different ways that natural selection can act on migratory strategies (Chapter 3). Expanding to a continental perspective, I showed that migratory flexibility is important not only on evolutionary timescales, but also to enable short-term responses to variable environmental conditions during active migratory flights—and that these responses are predictable enough to reliably forecast avian movements (Chapter 4). Finally, I focused on human impacts on migration, showing that artificial light at night can drastically affect migratory journeys (Chapter 5). Human activity can impact not only migrants' in-flight behaviors, but also their broader ecology (Chapter 6). Overall, this thesis shows that the flexibility we observe in migratory birds stems from a range of sources, innate and external, and that variation in migratory phenotypes may be key to responding to environmental change.

Contents

General Introduction 1

I The innate migratory program 19

1 Migratory behavior of stonechats in a common garden 20

2 Evolutionary response to climate change in pied flycatchers 39

II A continental perspective 57

3 Versatile migratory strategies in blackcaps 58

4 A continental system for forecasting bird migration 88

III Migration in the Anthropocene 110

5 High-intensity artificial light alters bird migration 111

6 Human activity shapes the winter ecology of blackcaps 133

General Discussion 168

Appendices

A Supplementary material for chapter 1 182

B Supplementary material for chapter 5 202

C Timing and intensity of bird migration over the Gulf of Mexico 248

D Avian flight behaviors across a North American flyway 262

E Migratory birds' exposure to artificial light at night 273

General Introduction

Movement links the lives of animals, plants and people to the ever-changing environments of our planet. Migratory birds embody this essence, captivating human imagination and study for millennia while conveying important information about the natural world. People have wondered about the comings and goings of migratory birds since the days of Aristotle (Walters 2003), and such long-running fascination is well-founded. Migratory birds engage in breathtaking feats of navigation, endurance, social coordination, and physiological transformation—often multiple times per year—culminating in one of nature's most inspiring phenomena (Alerstam 1990; Newton 2008).

Today, birds serve as charismatic and accessible indicators of ecosystem health and biodiversity on a hemispheric scale (Butchart et al. 2010; Canterbury et al. 2000; Gregory et al. 2005; O'Connell et al. 2000). In recent decades, birds' responses to pesticides, invasive species, human development, and climate change have afforded detailed insight into the impacts of human activity on natural systems (Butchart et al. 2010; Gregory et al. 2009; Rosenberg et al. 2019; Wurster et al. 1965). Birds provide key ecosystem services, transport nutrients and propagules, and participate in important trophic interactions (Bauer and Hoye 2014; Whelan et al. 2008).

Unfortunately, these travelers are disappearing under rapidly increasing pressures of global change (Bairlein 2016; Rosenberg et al. 2019; Sanderson et al. 2006). Understanding the capabilities of migratory birds to respond to established and emerging challenges requires knowledge of the complex interactions among individuals, populations, species, and natural and built environments. Despite millennia of human fascination with migratory birds, we lack important understanding of the flexibility of avian migration across spatial and taxonomic scales.

Challenges of a changing world

Migrants' finely tuned, worldwide existence makes them susceptible to rapid global change. Migratory birds must contend with a diverse array of challenges: navigating through a dynamic atmosphere; accurately timing departures, stopovers, and arrivals; efficiently locating resources *en route*; and thriving in diverse ecological contexts (Newton 2008).

Migratory birds face a variety of threats. The habitats birds evolved to occupy are undergoing rapid alterations caused by habitat loss, climate change, and a proliferation of vehicles, built structures, and artificial lighting. Major drivers of terrestrial land cover change include agriculture, deforestation and urbanization (Lambin et al. 2001). Aerial habitats are also changing, as the numbers of airplanes and skyscrapers rise and populations of insects dwindle (Diehl et al. 2017; Hallmann et al. 2017; Stepanian et al. 2020). For the billions of migratory birds that migrate at night (Newton 2008), light pollution compounds this crisis; artificial lighting draws migratory birds into urban areas and is directly responsible for fatal collisions with built structures (Allen 1880; Lao et al. 2020; Loss et al. 2015; McLaren et al. 2018). Climate change transforms habitats and causes mismatched breeding attempts (Dunn and Møller 2019). All of these forces have fundamental consequences for migratory birds, contributing to direct and indirect mortality and threatening the integrity of ecosystems (Kirby et al. 2008). As environmental change proceeds and humans modify both the landscapes through which birds pass and the areas where they breed and winter, a migratory strategy may become increasingly untenable (Runge et al. 2015; Wilcove and Wikelski 2008).

Fortunately, many of these indicator species are responding to global change in detectable ways, providing evidence for ecosystem flexibility. As warming temperatures have advanced the annual arrival of spring, the migrations of many bird species have shifted forward (Usui et al. 2017). As locations with suitable climatic conditions have changed, so have birds' geographic ranges (Devictor et al. 2008; La Sorte and Thompson III 2007; Tingley et al. 2012). In some cases, migratory routes have changed or individuals have stopped migrating entirely, as birds take advantage of new resource regimes (Cheng et al. 2019; Elmberg et al. 2014; Visser et al. 2009). It is evident that many bird species possess an ability to rapidly respond to environmental change (Usui et al. 2017). At the same time, other species appear to be relatively rigid in their behavior, raising concerns that even some of the world's most mobile animals will fail to adapt in time (Both and Visser 2001; Crick 2004; Sutherland 1998). These observations prompt an important question: what drives flexibility in bird migration?

Flexibility in migration

The migrations of birds are highly diverse journeys, undertaken by individuals responding to—and perhaps predicting—changing conditions. Variation in migratory behavior is present at all taxonomic levels, including within species and populations. Movements may be long- or short-distance, diurnal or nocturnal, obligate or facultative, regular or irregular, performed singly or in groups, and rigidly timed or conditions-dependent (Newton 2008). This diversity in migratory strategies mirrors large variation in the degree of flexibility migrants demonstrate as they interact with and respond to the natural world. Flexibility makes successful migration possible, and it manifests at multiple levels: migrants must interact with the atmosphere during active flight (Richardson 1990), find suitable terrestrial conditions during stopover (Alerstam 2011), and match the timing of breeding to local resource availability (Charmantier and Gienapp 2014). Over the long term, populations and species must also respond to environmental change (Dunn and Møller 2019).

Interacting with a dynamic atmosphere

Migratory birds respond to variation in their environment in a variety of ways. During active migration, birds move through a dynamic atmosphere, a flowing medium that may move faster than a bird can fly (J. W. Chapman et al. 2011). Atmospheric dynamics are highly changeable, and they can strongly influence a bird's flight trajectory, energy expenditure, and ultimately its survival (Richardson 1990). All avian navigators must possess the capability to effectively and efficiently interact with a variable atmosphere, or risk costly detours. Indeed, birds are frequently selective with the time, direction, and altitude of their movements (Dokter et al. 2013; Schmaljohann et al. 2009). Wind and weather conditions strongly influence the decision to migrate, as birds select departure times with favorable or even optimal conditions for progress towards their goal (Åkesson and Hedenström 2000; Erni et al. 2002). Yet prevailing wind regimes and constraints on annual cycle timing (e.g. the need to match the timing of reproduction to resource availability) mean that birds cannot always be selective. Crosswinds may drift birds off of their intended courses; whether and how much to actively compensate for drift is an important consideration for migrants (Liechti 2006). As powered fliers, birds can partially or fully compensate for wind drift, and they show complex interactions with moving atmospheric flows. Birds frequently adopt a compensatory strategy, and the degree to which migrants fight the wind is influenced by a range of factors, including age, body size and condition, time pressure, wind conditions, and the potential dangers of being drifted off course (Alerstam 2011; J. W. Chapman et al. 2016; Horton et al. 2016; Liechti 2006). Migrants respond not only to wind but also to temperature, precipitation, and atmospheric pressure (Richardson 1990), cues that may contain predictive information about the conditions they will experience *en route* and on arrival. As weather conditions may change quickly, migrants must be flexible enough to stay on course and minimize delays.

Adjusting to a variable environment

The seasonal return movements that characterize classic migratory behavior are an adaptation to variable environments, where fluctuations in resource availability are regular, predictable, and severe (Winger et al. 2019). Indeed, annual cycles are one of few truly predictable phenomena on earth. However, there is considerable variation from year to year in how seasonal patterns manifest: in their exact timing, their harshness, and the biotic responses of plant and animal communities.

Moreover, recent climatic changes have brought on increased volatility in seasonal patterns and more frequent extremes (IPCC 2014).

Migratory birds thrive by using movement to escape harsh environments. For example, some species move extreme distances to experience perpetual summer (Newton 2008; Shaffer et al. 2006). In order to track seasonal changes that are themselves variable, migrants must demonstrate sufficient flexibility. Such phenotypic plasticity manifests in the adjustments birds make to the timing of migration and breeding in order to match faster or slower spring phenology (Charmantier and Gienapp 2014; Charmantier et al. 2008; Horton et al. 2020; Usui et al. 2017), as well as in range shifts in response to variable conditions (e.g. Bateman et al. 2015). In partially migratory populations, some individuals migrate while others stay on the breeding grounds year-round. The drivers of these decisions are not always clear, but they may relate to a suite of environmental, social, and demographic factors (B. B. Chapman et al. 2011). A suite of Australian species takes rapid responses to variable conditions to the extreme, reacting to distant precipitation events by engaging in long movements to exploit ephemeral wetlands (Pedler et al. 2018). A number of patterns emerge from this wide continuum of variation: for example, long-distance migrants, which rely on programmed circannual clocks to time migration, are generally less flexible than short-distance migrants that typically time their movements in response to environmental cues (Newton 2008).

Adapting to long-term change

To cope with long-term environmental modifications, such as climate change and habitat transformation, migrants cannot generally rely on phenotypic plasticity. In many bird species, including passerine migrants, the innate circannual clock exerts substantial control over the timing of annual cycle events such as molt, migration, and reproduction (Gwinner 1996). In long-distance migrants, endogenous control of these events is particularly strong, and these species often show remarkable consistency in migration timing among years, even in the face of varying conditions. In addition, the juveniles of most migratory species are not accompanied by experienced individuals on their first migration and must rely on some degree of genetic programming to find their way (Newton 2008). The suite of endogenous mechanisms that control migration is known as the migratory program, and adjustment of this innate system requires evolutionary change. It is easy to observe the footprint of evolutionary change on migration today, in routes that recapitulate post-glacial expansions (e.g. Ruegg et al. 2006); sedentary species with migratory ancestors (e.g. Winger et al. 2012); and innate timing and navigation programs. However, because adjustment of the migratory program requires hard-coded evolutionary change, it is unclear whether rigidly-timed species will be able to match the current pace of environmental shifts, and whether microevolution is at work in the responses we observe today (Charmantier and Gienapp 2014; Gienapp et al. 2007; Van Buskirk et al. 2012).

Migration across scales

Understanding multifaceted natural processes is best approached from multiple perspectives, and avian migration is no exception. Migratory birds form an interconnected network with multiple layers of complexity. The migratory phenotype of an individual is influenced by a range of internal and external factors, from genes and developmental processes to social environments and atmospheric conditions. At the same time, a population of migratory birds might occupy habitats across the world at different times of year, and hundreds of species interact to form hemispheric migration systems. Understanding bird migration requires that we think across scales, from individuals to systems.

The individual is the fundamental unit of a migration system. It is important to recognize that each individual will possess an underlying migratory program, influenced by a suite of factors. The most obvious determinant of its innate migratory tendency is species identity and the genetic architecture shared with conspecifics. Population identity may also be important in certain cases, especially for species that show strong migratory connectivity by breeding population (see Webster et al.

2002). Individuals are influenced by their immediate social and kin relations as well as individual experience, health, and demographics (Briedis and Bauer 2018; Newton 2008). Finally, each individual experiences a unique combination of environmental conditions, dictated by location, behavior, and physical traits. All of these factors contribute to the migratory phenotype of an individual. An individual perspective is therefore essential to understanding the drivers of variation in migratory behavior.

At the same time, an individual-based perspective is insufficient to address some of the most pressing scientific questions of today, which require a wider view on natural systems. Widespread and ongoing population declines among migrants warrant species-level perspectives. In addition to direct conservation, simply understanding how populations interact with human society and respond to global change will require studies with global scope, as environments and the changes they are experiencing are resoundingly heterogeneous. A wider view on bird migration is necessary to capture continental movement patterns, study how migration networks behave in the face of habitat loss, identify conservation bottlenecks, and quantify demographic trends (see Dokter et al. 2018).

Therefore, a modern understanding of bird migration requires a holistic view that incorporates the behavior of individuals, populations, species, and even entire hemispheric migration systems. Migratory systems facilitate large-scale fluxes of biomass and transport of nutrients, with consequences for ecosystem services, nutrient cycling, pathogen and parasite transport, and biotic interactions ranging from competition to pollination. In addition, migratory bird species are vastly interconnected (Cohen and Satterfield 2020). Migrants form mixed species groups both during active flight (Larkin and Szafoni 2008) and during foraging and stopover periods (Rodewald and Brittingham 2002). Many species give vocalizations in both contexts (Farnsworth 2005), but the extent of their function is poorly known. What is clear is that migratory bird species form an interconnected, global system that requires study across scales. Furthermore, avian migration should not be thought of from exclusively ecological, behavioral, or evolutionary points of view. In this thesis, I attempt to improve our understanding of the flexibility of avian migration across spatial scales, taxonomic groups, and disciplines.

Approaches to studying migration

The methods used to study migration are nearly as diverse as the phenomenon itself. Ringing is one of the oldest means of tracking individual birds. In the United Kingdom alone, millions of birds have been ringed since 1909, and these individually-marked birds have been recaptured over 500,000 times (Wernham et al. 2002). Around the world, ringing has led to invaluable insight into the movements, longevity, and ecology of countless bird species. In addition, colorful rings designed to be read in the field by observers—not only on a bird in the hand—allow marked individuals to be monitored in their element without disturbance, making possible detailed observations of behavior.

Tracking devices that use Global Positioning System (GPS) receivers and smaller light-level geolocators (Ekstrom 2004; Lisovski et al. 2012; Rakhimberdiev et al. 2016) are well enough miniaturised to enable the tracking of all but the very lightest bird species. However, for birds under 20 g, representing thousands of species, only archival light-level geolocators are sufficiently lightweight (López-López 2016). These devices must be physically recovered to obtain data, posing an additional challenge for study. Nevertheless, these devices allow scientists to monitor migratory birds daily in the wild and have led to a multitude of invaluable insights (McKinnon and Love 2018).

Tracking technology allows scientists to study migratory phenotypes as they manifest in wild populations. Yet, migratory phenotypes may be strongly influenced by environmental conditions that can vary widely in the wild. Some questions therefore require experimental approaches in a laboratory setting, especially those pertaining to the innate migratory program. Lab-based studies of migratory restlessness assay the behavior of migrants in captivity, and their behavior is well correlated with activity in the wild (Berthold 2001). The major advantage of a laboratory approach is that investigators can place birds under standardized, "common garden" conditions in order to remove environmental variation as a source of observed phenotypic differences.

Today, biologists are making increasing use of large datasets to study animal behavior and ecology. For decades, ornithologists have used various types of radar to study birds in active migration (Gauthreaux and Belser 2003). Doppler weather surveillance radars scan huge regions of airspace and form the basis of many governmental weather monitoring and prediction networks. In the United States, the Next-Generation Radar (NEXRAD) network has been operating since the mid-1990s, and analyses of these data have yielded important insights into the North American bird migration system (Dokter et al. 2018; Farnsworth et al. 2016; Gauthreaux and Belser 2003).

In this thesis, I bring together a suite of approaches to study avian migration. I use data from captive studies to study the migratory program, data from radar and individual tracking devices to explore the variation and flexibility of migration at local and continental scales, and ringing recovery and visual resight data to study migrants' movements and ecology.

Geographic and taxonomic scope

Like so many migratory birds, this thesis connects disparate regions of the world. I focus on representatives of two hemispheric migration systems, the Palearctic-Afrotropical and Nearctic-Neotropical migration systems. From the Palearctic-Afrotropical migration system, I study three migratory passerine songbirds: stonechats (genus *Saxicola*, family Muscicapidae), pied flycatchers (*Ficedula hypoleuca*, family Muscicapidae), and Eurasian blackcaps (*Sylvia atricapilla*, family Sylviidae). Stonechats and blackcaps show large variation in migratory strategies across populations and subtaxa, making them useful study systems for understanding migratory flexibility. Pied flycatchers are obligate long-distance migrants and are therefore ideal for studying migratory evolution in a rigidly timed species. My studies of the Nearctic-Neotropical migration system focus on understanding the ecology of entire migration assemblages and are not taxon-specific.

Thesis outline

The aim of this thesis is to investigate the drivers of change and flexibility in avian migration across scales, from the individual bird to the hemispheric migration system. I focus on three themes, each comprising two chapters: (1) the innate migratory program and its potential for evolutionary change; (2) continent-scale perspectives on processes driving flexibility and evolution in migration systems; and (3) the impact of human activity on migratory birds' behavior, both in flight and across generational timescales.

All characteristics of species and systems are emergent properties of their constituent individuals. For migratory birds, knowledge of the drivers of behavior at the individual level is a prerequisite to understanding the flexibility of entire species and assemblages. Therefore, in **Chapter 1**, I investigate individual variation in the innate migratory program in closely related stonechat taxa that show divergent migratory strategies. I use data from laboratory studies of individuals raised in a common garden setting and develop an objective analysis approach based on changepoint analysis for quantifying restlessness data. I compare results from lab-based assays to migratory behavior in the wild, including study of a partially migratory taxon. I also examine flexibility and evolutionary potential in this phenotype by investigating how restlessness behavior varies across age and sex classes and comparing phenotypes of hybrid individuals with those of their parents.

A large component of songbirds' migratory behavior is under genetic control, especially for obligate long-distance migrants with rigid timing programs (Liedvogel and Lundberg 2014). Although these species have shown evidence of recent climate-linked changes in migration, the role of microevolution in these adjustments is poorly understood. In most instances, climate-related shifts can be explained by phenotypic plasticity alone (Charmantier and Gienapp 2014). Knowing whether microevolution also plays a role is vital to the conservation of long-distance migrants, whose adaptation to climate change may be constrained by rigid timing programs. The pied flycatcher is a well-studied example of a long-distance migrant responding to climate change, yet the answer to this question is unclear even in this species (Both 2010). In **Chapter 2**, I use data from a common garden study replicated in 1981 and 2002 to test whether pied flycatchers have evolved changes in their innate timing program. I then compare the results in laboratory-tested birds to timing advances documented in a local wild breeding population, with the goal of understanding whether the internal clock of this long-distance migrant may be more flexible than previously believed.

Although studies in the laboratory are unique in their ability to control for environmental variation, it is equally important to understand variation in migratory behavior in wild populations. In **Chapter 3**, I retain a focus on individual behavior but shift to a wild context. I use the blackcap, a species with a long history of migration study and broad variation in migratory phenotype across its range (Cramp and Brooks 1992). I use light-level geolocators to examine migratory behavior across the European continent, focusing on two salient features of blackcap migration. The first is a migratory divide—a zone of contact between populations with opposing autumn migratory directions—that exists in central Europe (Helbig 1991a; Helbig 1991b; Helbig 1992). I investigate patterns of migratory behavior at the divide to understand how migratory direction varies across the contact zone and how natural selection may be operating on different phenotypes. The second salient feature of blackcap migration is the recent emergence of a new wintering population in the British Isles, a potential consequence of human activity (Bearhop et al. 2005; Berthold et al. 1992; Berthold and Terrill 1988; Leach 1981). I use geolocators to identify the source areas of these British winterers, compare their novel migrations to those of birds wintering in traditional Mediterranean areas, and examine the potential for reproductive isolation based on the timing of migration.

Chapter 3 illustrates how studies across large spatial scales can reveal important insight into the processes governing transgenerational migratory evolution in a bird species. Yet the avian assemblages that traverse continents must also respond rapidly to changeable conditions *en route*. In **Chapter 4**, I focus on capturing how an entire migration system comprising billions of individuals actively responds to environmental conditions. Using a 23-year dataset derived from Doppler weather surveillance radars, I train a machine learning model to learn associations between migration and weather conditions across the contiguous United States. I examine the accuracy with which this model can forecast migratory movements days in advance, and I interpret learned associations to reveal the factors birds respond to most readily during spring migration. I also discuss the potential conservation and outreach applications of migration forecasting. **Appendix C** uses the Doppler radar dataset to assess the timing, intensity, and distribution of bird migration through the Gulf of Mexico region in North America, and **Appendix D** examines flight behaviors through the Great Plains region.

As nocturnally migrating birds traverse the landscape, they are increasingly exposed to a stimulus virtually unknown in their evolutionary histories: artificial light. Inputs of artificial light affect a range of taxa (Gaston et al. 2013). For passerine migrants, this new stimulus may dramatically affect their ability to interact with their environment, causing many migrants to approach and potentially collide with man-made structures. Light pollution may influence how migratory birds interact with the landscape across broad scales (McLaren et al. 2018). In **Chapter 5**, I investigate how a single extremely bright light source in an urban area can drastically alter birds' migratory behavior, and I give recommendations for mitigating these negative effects. **Appendix E** further explores the contributions of urban areas to light pollution in the context of bird migration.

As Chapter 5 demonstrates, the influence of the Anthropocene on migratory birds can be profound. Not only does human activity affect migratory birds during active migration, but it can shape the ecology of entire populations—provided they are able to take advantage of new resources and opportunities. The blackcap is one of few migratory species thriving in today's changing world, and the recently established population of blackcaps wintering in the British Isles demonstrates the species' ability to rapidly take advantage of newly suitable areas. In **Chapter 6**, I discuss the broad footprint of human activity on the wintering ecology of blackcaps in the British Isles. I investigate the associations between blackcaps and humans on a landscape scale, and I analyze a large dataset of observations from British gardens to study how these migrants interact with supplementary food provided by people.

In the **General Discussion**, I synthesize the work presented in Chapters 1–6 and discuss promising avenues for further study.

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Part I

The innate migratory program

Van Doren, B.M., *Liedvogel, M., and Helm, B. (2017). Programmed and flexible: long-term Zugunruhe data highlight the many axes of variation in avian migratory behaviour.*
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Migratory behavior of stonechats in a common garden

Articles

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Programmed and flexible: long-term *Zugunruhe* data highlight the many axes of variation in avian migratory behaviour

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Studies of *Zugunruhe* – the ‘migratory restlessness’ behaviour of captive birds – have been integral to our understanding of animal migration, revealing an inherited propensity to migrate and an endogenous timing and navigation system. However, differences between *Zugunruhe* in captivity and migration in the wild call for more data, in particular on variation within and among taxa with diverse migration strategies. Here, we characterise *Zugunruhe* in a long-term dataset of activity profiles from stonechats (genus *Saxicola*) with diverse migratory phenotypes (976 migration periods from 414 birds), using a flexible and consistent quantitative approach based on changepoint analysis. For east African, Austrian, Irish, and Siberian stonechats and hybrids, we report key inter-population differences in the occurrence, timing, and intensity of *Zugunruhe*. In line with expectations, we found the highest *Zugunruhe* intensity in the longest-distance migrants, more variable patterns in short-distance migrants, and intermediate characteristics of hybrids relative to their parental groups. Inter-population differences imply high evolutionary lability of *Zugunruhe* timing within a robustly structured annual cycle. However, counter to theory, Irish partial migrants showed no segregation between migrant and resident individuals, and previously reported nocturnal restlessness was confirmed for resident African stonechats. Further features of nocturnal restlessness that did not align with migratory behaviour of stonechats were juvenile nocturnal restlessness even prior to postjuvenile moult, and protandry in spring, although stonechats winter in heterosexual pairs. Importantly, *Zugunruhe* of all populations declined with age, and the intensity of an individual bird’s *Zugunruhe* was correlated with activity levels during other parts of the annual cycle. Our results confirm endogenous, population-specific migration programmes but also reveal apparent discrepancies between *Zugunruhe* and migration in the wild. We thus highlight both the continued potential of *Zugunruhe* study and the need for circumspect interpretation when using migratory restlessness to make inferences about migration in the wild.

The phenomenon of bird migration, particularly regular biannual movements, has captured human interest throughout recorded history (Alerstam 1990, 2011). How do birds know when to depart, which direction to fly, when to stop, and when to return? Given that migration takes place in midair and often spans continents, answering these questions based solely on observations of free-living birds has been intrinsically difficult (Birkhead 2008). Although new tracking technologies are beginning to overcome this challenge, they are limited in their potential to answer fundamental questions because each bird’s journey is a unique experience under a particular suite of environmental conditions (Delmore and Irwin 2014, Bäckman et al. 2016). Much of our understanding of the regulation of migration therefore continues to be based on studies of songbirds in captivity. These studies leverage the fact that many nocturnally migrating species spontaneously modify their activity patterns during the migration seasons of wild conspecifics, even when kept under constant conditions in captivity. Instead of their usual rest at night, captive migratory birds extend their activities after sunset, flying, hopping and whirring their wings often until the morning (Berthold 2001, Birkhead 2008). This behaviour, called migratory restlessness, or *Zugunruhe*, has been extensively used as a proxy for studying migration. In general, intensity and/or duration of *Zugunruhe* increases with the ‘migratoriness’ of a population, measured for example by the distance covered by wild migrants or by the proportion of individuals that migrate. The behavioural phenomenon of migratory restlessness is not restricted to birds and has also been characterised in, for example, fish and insects (Leverton 1997, Mouritsen and Frost 2002, Sudo and Tsukamoto 2015).

However, the comparability between *Zugunruhe* and actual migration in the wild is not always clear (Farner 1955, Helms 1963, Berthold 1988a, b, Newton 2008). For example, resident populations of otherwise migratory species can show apparent *Zugunruhe* (Chan 2005, Helm and Gwinner 2006), and juvenile birds of some migratory species display nocturnal restlessness well in advance of actual migration (Mukhin 1999). Migratory songbirds in captivity often extend *Zugunruhe* far beyond the seasonally appropriate migration time window (e.g. summer restlessness, Gwinner and Czeschlik 1978) and are often restless every night, whereas wild birds typically migrate for single nights and then refuel at stopover sites (Bäckman et al. 2016 compared to Gwinner and Biebach 1977). In light of these discrepancies, there is a need for more information on the relationship between *Zugunruhe* and diverse migratory phenotypes in the wild, and on the factors associated with variation in *Zugunruhe* within and between populations. Here, we investigate a long-term nocturnal activity dataset from several taxa of the stonechat complex (genus *Saxicola*), providing new insight into the variation and regulation of this migratory trait. Furthermore, comparison of *Zugunruhe* across studies and taxa has been hampered by heterogeneous and sometimes subjective quantifications. To address this issue, we propose a single quantitative approach to analyse nocturnal activity data in the phenotypically diverse stonechat system.

Stonechats are a well-studied taxon in avian biology (Gwinner et al. 1983, Wikelski et al. 2003, Illera et al. 2008, Helm 2009, Zink et al. 2009, Versteegh et al. 2014). These widespread songbirds breed across an unusually extensive latitudinal range, from ca 70°N in Siberia to 30°S in South Africa (Fig. 1A, Urquhart 2002). Within this range, they show large variation in morphology, physiology, and life history, including a broad spectrum of migratory behaviours from resident to long-distance migrant. Therefore, studies on stonechats offer opportunities to examine variation in these traits within a single species complex, with the benefit of reduced cross-species comparative noise. Extensive studies in the field and laboratory have compared stonechats from various environments with different migratory phenotypes. The least migratory population in our dataset comprises residents from east Africa (Kenya), followed by partial migrants from the British Isles (Ireland), obligate short-distance migrants from central Europe (Austria), and the most migratory population, long-distance migrants from west Siberia (Kazakhstan) (Helm 2009).

Stonechats included in this study were raised under common garden conditions in decades-long captive breeding studies, which collected data on a broad range of traits. To examine patterns of inheritance, birds were selectively bred within and crossbred between populations (Helm et al. 2005, Helm 2009). Key findings demonstrated a high degree of inheritance of annual cycle organization and physiological traits (Wikelski et al. 2003, Helm 2009, Tieleman et al. 2009, Versteegh et al. 2014). Stonechats generally displayed distinct population-specific phenotypes, even under common-garden conditions, and F1 hybrids mostly exhibited intermediate trait values (Gwinner 1996, Helm et al. 2009, Tieleman et al. 2009, Versteegh et al. 2014). Variation in many traits was associated with migratoriness, including dimensions of wing (Baldwin et al. 2010) and brain (Fuchs et al. 2014).

Nonetheless, the strengths of the stonechat system for advancing migration research have hardly been fully played out (Zink 2011, Ketterson et al. 2015), and analyses of nocturnal activity profiles collected within the experimental breeding scheme have only been touched upon (Helm and Gwinner 2005, 2006, Helm et al. 2005, Helm 2006). One striking finding was that resident Kenyan stonechats display *Zugunruhe*: lower in intensity compared to short-distant migrants from Austria, but with similar timing characteristics (Fig. 1B, Helm and Gwinner 2006). Here, we present a more complete analysis of *Zugunruhe* in stonechats. Our long-term data, which for many birds started soon after fledging, enable us to compare population-specific programmes and address open questions in *Zugunruhe* research: do *Zugunruhe* patterns remain consistent as birds age? Are differences between spring and autumn migration seasons consistent among migratory species (e.g. *Zugunruhe* timing and intensity, and effects of age and sex)? Are birds that display high *Zugunruhe* generally more active birds, or is migratory activity a completely independent activity trait?

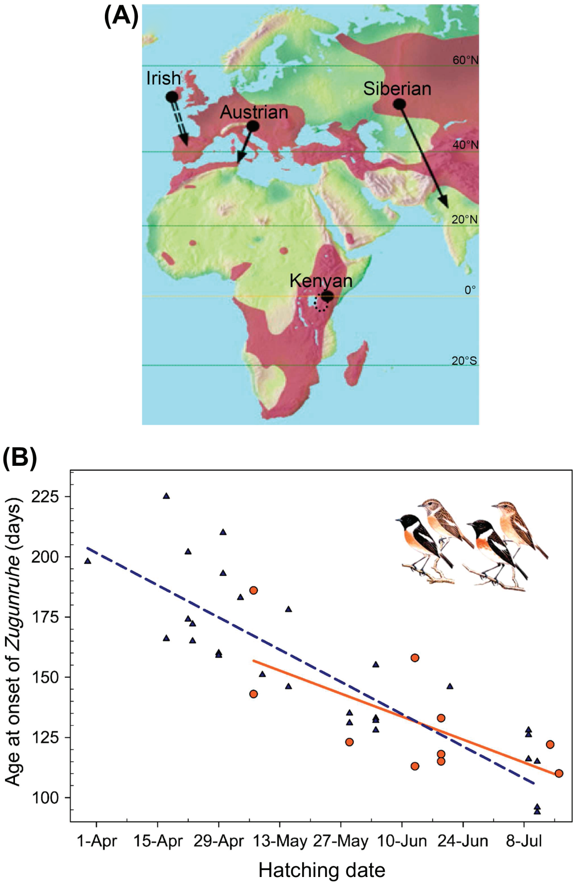

Figure 1. (A) Stonechat range map highlighting the locations and migratory phenotypes of the four populations: partially migratory Irish stonechats *Saxicola rubicola hibernans*, medium distance migrants *S. rubicola rubicola* from Austria, resident *S. torquatus axillaris* from Kenya, and long-distance migrants *S. maurus* from Siberia (Kazakhstan). Arrows indicate migratory routes between breeding and wintering grounds. We further included the following two hybrid groups: Austrian × Siberian and Austrian × Kenya. (B) Adjustment of the timing of *Zugunruhe* in response to the day lengths experienced over a bird's posthatching period, for captive Austrian and Kenyan stonechats. The onset ages of *Zugunruhe* for Austrian stonechats are shown as blue triangles (dashed blue line); the onset ages for Kenyan stonechats are shown as orange dots (solid orange line). Stonechats hatching later in the breeding season compensated for this by commencing *Zugunruhe* at earlier ages. Inlay: pairs of Austrian (left) and Kenyan (right) stonechats. Modified after Helm and Gwinner (2006).

In our efforts to answer these questions, our first objective is to develop robust analysis methods for *Zugunruhe* data. When looking at nocturnal activity data, researchers are often faced with noisy time series that contain putative migration-related signals whose clarity varies among species and individuals. In particular, it has been challenging for existing methods to simultaneously.

a) Determine the presence or absence of *Zugunruhe* in the nocturnal activity profile of a bird. In many studies, some proportion of birds may show very little or inconsistent bouts of nocturnal activity. Depending on study-specific criteria, records of these birds could get dropped completely from the study, remain included in population measures of 'migratoriness' (e.g. for average *Zugunruhe* profiles; Berthold 1988a), or be assigned the status of 'non-migrants' (e.g. in studies of partial migrant populations).

b) Define the onset, completion and duration of the *Zugunruhe* period. Nocturnal activity frequently also occurs outside of the migration period of wild conspecifics. *Zugunruhe* has often been distinguished from other nocturnal activity by thresholds and cut-off practices based on informed guesses or varying subsidiary criteria (e.g. occurrence of moult) that are not always comprehensively reported.

c) Assess the consistency of *Zugunruhe* estimates when measured over more than one migration period. Data from individuals are often presented only for a single migration period, leaving open whether the behaviour is a stable, age-independent trait – expected, for example, for some genetic studies (Berthold 1988a).

d) Distinguish inter-individual differences in *Zugunruhe* from differences in activity that may be unrelated to migration. Many studies have quantified activity only for seasonal time windows designated as migration periods, and during the night but not the day. While it is likely that inter-individual variation in nocturnal activity during the migration season correlates with variation in migratory disposition, alternative explanations are possible and should be accounted for. For example, such variation may be explained by individual differences in overall activity levels, which have been reported across animal species (van Oers and Naguib 2013).

Although most studies address a subset of these issues in some manner, analytic processes have often lacked robust, objectively defined, and thus transferrable criteria (Pulido et al. 1996, Helm and Gwinner 2006). Considerations of how to process the data substantially influence the outcome of a study. For example, the results of studies using *Zugunruhe* to classify captive birds as putative migrants or residents will vary depending on the choice of time windows, threshold levels, and processing of noisy *Zugunruhe* profiles.

We address these analytical issues by presenting an automated procedure based on changepoint analysis. Using a single algorithm for birds of all migratory phenotypes, we determine presence, timing and intensity of *Zugunruhe* on an individual level. Specifically, we assign presence or absence of *Zugunruhe* to all individuals, thereby deriving proportions of putative migrants based on *Zugunruhe* for all populations, and we use activity data from the full annual cycle of individuals to obtain robust estimates of the timing of *Zugunruhe*.

Using these quantifications, we then analyse activity data of the stonechat populations and their hybrids with the following objectives.

1) Examine population-level variation in the occurrence, timing and intensity of *Zugunruhe*. Based on field-derived differences in migratoriness, we test the prediction that birds originating from resident and partially migratory populations (Kenyan and Irish) are more likely to refrain from engaging in *Zugunruhe*; if they do show *Zugunruhe*, we expect intensities to be lower than in obligate short- and long-distance migrants (Austrian and Siberian). We therefore anticipate that intensity and duration will increase in the following sequence: Kenyan < Irish < Austrian < Siberian. We expect this pattern to hold for both spring and autumn seasons. Likewise, we test the prediction that timing of *Zugunruhe* relates to reported population differences in annual cycles, phenology, and migratory strategy (Helm 2009). In spring, we expect partially migratory populations to engage in *Zugunruhe* earlier than obligate short- and long-distance migrants. Conversely, for autumn we expect that long distance migrants will be the first, and partial migrants the last, to leave the breeding grounds.

2) Examine hybrid phenotypes. We investigate whether timing, prevalence, and intensity of *Zugunruhe* in hybrids are intermediate relative to parental phenotypes.

3) Identify differences between autumn and spring migration periods. Based on field evidence that migration is often more compressed and intense in spring than autumn (Alerstam 2011), we predict that *Zugunruhe* profiles are also more intense in spring than in autumn. We expect this pattern to be consistent among the three migratory populations, and possibly also in residents.

4) Examine the consistency of activity with age. Based on the premise that *Zugunruhe* reflects genetically programmed migratory traits, we test the prediction that *Zugunruhe* is consistently displayed over the lifetime of a bird. Because in weakly migratory species patterns may be flexible (Schwabl and Silverin 1990, Hegemann et al. 2015), we also test the prediction that *Zugunruhe* traits should have lower consistency in partial and short-distance migrants compared to the most migratory population. We first examine nocturnal restlessness during the postfledging phase, before the end of postjuvenile moult (referred to as 'juvenile restlessness'). Then, we focus on *Zugunruhe* and test for changes in timing, intensity, and frequency of occurrence with age, whether such changes differ among populations, and whether they also apply to year-round diurnal and nocturnal activity.

5) Compare analyses based on assignment of individuals as either migrants or residents to population-wide analyses. Classification of birds as either showing *Zugunruhe* (i.e. putative migrants) or not showing *Zugunruhe* (i.e. putative residents) filters nocturnal restlessness data prior to further analysis. *Zugunruhe* studies differ in whether or not individuals are divided by behaviour in this manner. To assess the effects of this classification on conclusions about *Zugunruhe* in stonechats, we compare outcomes of our analyses of birds identified as showing *Zugunruhe* to overall population-wide analyses of diurnal and nocturnal activity.

6) Examine the relationship between Zugunruhe and daytime activity. The few studies that have investigated how daytime activity changes during *Zugunruhe* suggest that birds compensate for sleepless nights by slight increases in daytime rest (Rattenborg et al. 2004, Fuchs et al. 2006). We therefore quantify the extent to which increased nocturnal

activity will be partially compensated by reduced daytime activity.

7) Examine whether more intense *Zugunruhe* is a characteristic of generally more active birds. We test whether activity levels of birds covaried between migratory and non-migratory contexts. We compare nocturnal activity levels of individuals during migration seasons (*Zugunruhe*) to a) nocturnal activity levels during 'neutral', non-migratory seasons, and to b) diurnal activity levels during non-migration seasons. We posit that a positive correlation between activity levels of these periods will weaken the assumption that individual variation in *Zugunruhe* uniquely represents individual variation in migratory propensity.

Methods

Birds and experimental setup

Origin and maintenance of birds

We present data from 976 migration periods (minimal duration 90 d) from 414 stonechats of the following four population groups: *S. rubicola rubicola* from Austria (hereafter referred to as 'Austrian' or by code A; n = 147; 48.0°N); *S. rubicola hibernans* from Ireland (hereafter 'Irish' or I; n = 83; 52.0°N); *S. torquatus axillaris* from Kenya (hereafter 'Kenyan' or K; n = 25; 0°N); and *S. maurus* from Kazakhstan (hereafter 'Siberian' or S; n = 53; 51.5°N) (Fig. 1A). We also included hybrid Austrian × Kenyan stonechats (n = 16, all A × K F1) and Austrian × Siberian stonechats (A × S; n = 80). Austrian × Siberian included F1 crosses (n = 56) and backcrosses (A × S with Austrian parent: n = 16; A × S with Siberian parent: n = 8). Hereafter, we refer to the four populations and the hybrid groups simply as 'populations' (for details see Supplementary material Appendix 1, and Helm 2003, 2009).

For the birds in this study, the sex ratio was consistently nearly balanced in all groups (overall: 193 females, 221 males). The vast majority (330) were offspring of captive stonechats from our breeding scheme (i.e. at least 2nd generation in captivity), and were born between 1998 and 2006. Between 1997 and 2004, 84 birds were taken from the field, usually as nestlings, with the exception of two Irish stonechats that were collected as wintering adults in January 2003. After fledging, birds were housed individually indoors in recording cages (60 × 40 × 40 cm) (Gwinner et al. 1995). Birds were kept under constant mild temperatures (ca 20°C) and under light exposure of ca 300 lx during daytime and 0.01 lx at night, simulating natural photoperiodic change as described below. We assessed postjuvenile moult by inspection of wing and 19 defined body areas (Helm and Gwinner 1999). To focus on the main phase of moult, we defined its onset and end when birds crossed a threshold of at least 5 simultaneously moulting body areas.

Photoperiodic conditions

A main purpose of the breeding experiments were comparisons of the stonechat populations under identical conditions (i.e. 'common garden', Noordwijk et al. 2006). Birds were kept indoors under one of three photoperiods that all simulated naturally fluctuating photoperiods. The vast majority (n = 356) were kept under conditions that simulated day length experienced by Austrian stonechats around the annual cycle; two Irish birds experienced summer day lengths mimicking those of their native location (52.5°N). A further 37 birds were exposed to simulated day length experienced by Siberian stonechats (Siberian and Austrian stonechats and their hybrids). Finally, 8 birds were exposed to both European and Irish day lengths during different years, and 11 were exposed to both European and Siberian day lengths during different years. In our analyses, if data were used from day length simulations other than those of Austrian stonechats, we included photoperiod as a covariate. The data reported are numbers of daily or nightly 10-min intervals during which activity was detected by passive infrared detectors.

Data preparation and processing

Data preparation

For our primary *Zugunruhe* analysis, we only analysed nocturnal activity data after a bird had started postjuvenile moult (Fig. 2). Overall, missing data represented 1.0% of our dataset and were handled as explained in Supplementary material Appendix 1. We split the annual cycle into two halves to quantify spring and autumn migration periods separately. To do so, we determined population-specific cut-off dates as the mid-points of summer and winter periods when nocturnal activity was minimal (for details, see Supplementary material Appendix 1).

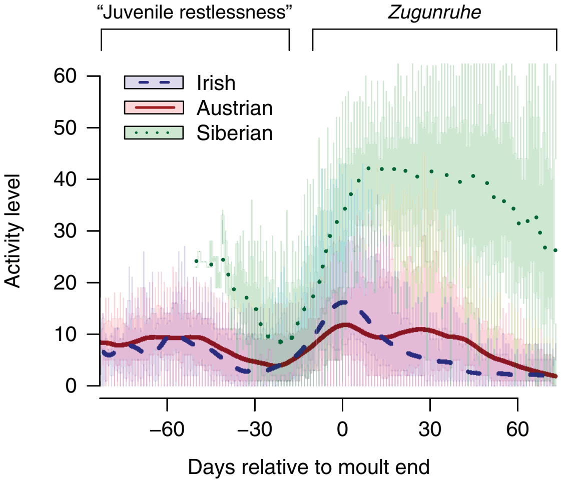

Figure 2. Nocturnal activity relative to moult completion in juvenile Irish, Austrian and Siberian stonechats. Although stonechats do not migrate until after the completion of postjuvenile moult, young birds showed 'juvenile restlessness' before this time, especially 50 or more days before moult completion (negative values along the x-axis). This activity typically reached a minimum 20–30 d before moult completion, after which *Zugunruhe* began. Activity level is defined as the number of active ten-minute periods during the night for an individual bird. For each day, curves show medians, and a boxplot describes the activity levels of birds in each population. Wide coloured bars corresponding to a given day represent the interquartile range (middle 50%) of activity values for stonechats on that day. Thin coloured lines extend outwards to the most extreme data point that is not an outlier, where an outlier is defined as exceeding a distance of 1.5 times the interquartile range from the bar. For clarity, outlier points are not shown.

Changepoint analysis for identifying and characterising periods of Zugunruhe

We applied changepoint analysis, developed to identify changes in the statistical properties of time series data, in the R package 'changepoint' (Killick and Eckley 2014). This algorithm assesses the mean and variance of time series data and identifies any changes in these properties (or absence thereof). Accordingly, we classified a migration period of a given bird as showing *Zugunruhe* if at least one changepoint was identified. A changepoint is identified if its addition to the model sufficiently improves the log-likelihood enough to overcome a penalty value used to prevent too many changepoints from being identified. Changepoint analysis of spring and autumn data provided us with one or more time segments for each migration period (Supplementary material Appendix 2, Fig. A1). When the analysis identified one or more changes, we classified a contiguous sequence of elevated segments as *Zugunruhe* (Supplementary material Appendix 2, Fig. A1).

Defining timing and intensity of Zugunruhe

For each migration period, we calculated several *Zugunruhe* timing metrics. Onset and end dates were given by the starting and ending dates of the contiguous elevated *Zugunruhe* period (Supplementary material Appendix 2, Fig. A1); duration was inferred as the number of days between start and end dates. We defined 'Mean day' as the average day from the elevated period, weighted by nightly activity levels. To derive a consistently defined measure of intensity, we first calculated the mean activity level during the contiguous 15-d period with highest overall activity (hereafter 'uncorrected peak intensity'). We then calculated 'corrected' peak intensity as the difference between uncorrected peak intensity and the mean of winter and summer baseline activity levels flanking the migration period. This correction accounts for consistent, year-round inter-individual differences in activity levels. We also calculated a bird's overall mean intensity as the average activity level over an entire elevated *Zugunruhe* period. Lastly, for comparability with the practice of some studies on *Zugunruhe*, we conducted a supplemental analysis in which we normalized our data according to the concurrent length of night (Owen and Moore 2008); we illustrate some comparative findings in Supplementary material Appendix 1.

Statistical analyses

Factors affecting occurrence of Zugunruhe

To identify which factors influence *Zugunruhe*, we modelled the proportion of spring and autumn migration periods with and without *Zugunruhe* by an analysis of deviance with binomial errors ('glm' function in the R base 'stats' package). The initial model comprised the categorical predictors of population (including hybrid groups), sex, age (first year or older), migratory season (spring or autumn), and all possible interactions. See Supplementary material Appendix 1 for details.

Consistent individual propensity to engage in Zugunruhe

We additionally examined intra-individual patterns of *Zugunruhe* for birds with activity data for more than two periods (spring or autumn). We analysed variation in the proportion of birds that always, sometimes, or never engaged in *Zugunruhe* during the periods for which they were monitored. We compared proportions using the 'pairwise.prop.test' function in R and corrected for multiple comparisons with the Holm–Bonferroni method (Holm 1979).

Variation in Zugunruhe timing and intensity

We examined overall variation in timing and intensity of *Zugunruhe* using linear mixed models (packages lme4 and lmerTest in R; Bates et al. 2015, Kuznetsova et al. 2015) as detailed in Supplementary material Appendix 1.

Population-wide nocturnal and diurnal activity during the migration periods

In addition to the procedure described above, we analysed overall nocturnal and diurnal activity levels during the migration periods of all individuals, regardless of the *Zugunruhe* status assigned to them by changepoint analysis, for compatibility with earlier analyses (e.g. blackcaps *Sylvia atricapilla*, Berthold 1988a). This required definitions of migration periods that were independent of changepoint analysis, as explained in Supplementary material Appendix 1. Diurnal activity of this data set was used to test for age-related changes in activity levels during the migration seasons. We also analysed these data by an approach that has sometimes been used in the literature, correcting the amount of nocturnal activity for the length of night. This follows the rationale that activity levels may be limited by night length, but it has the disadvantage of confounding activity level with time of year, which determines night length.

Covariation of diurnal and nocturnal activity levels

To examine how daytime activity varied relative to *Zugunruhe* (defined using changepoint analysis), we tested diurnal activity levels before, during, and after birds engaged in *Zugunruhe* with linear mixed models. We also studied the association between nocturnal and diurnal activity levels within individuals during both migration seasons and the 30-d neutral summer and winter periods (Supplementary material Appendix 1).

Covariation of activity between migratory and non-migratory contexts

We used two approaches to test whether high nocturnal activity levels during *Zugunruhe* periods were specific to a migration context, or, alternatively, reflected generally elevated activity levels of populations or individuals. First, we compared nocturnal activity during and outside of migration periods to test whether individuals with higher *Zugunruhe* activity were generally more active at night. Secondly, we compared *Zugunruhe* to diurnal activity during the non-migration seasons to test the hypothesis that individuals with high *Zugunruhe* were generally more active birds. We used linear mixed models (Supplementary material Appendix 1).

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.484m0> (Van Doren et al. 2016).

Results

Using changepoint analyses on a total of 976 migration periods (autumn: 552; spring: 424) from 414 individual birds, we detected *Zugunruhe* in 80.9% migration periods (autumn: 396; spring: 394, excluding 17 periods that were ambiguous).

Occurrence of *Zugunruhe* in different populations

Our final model predicting the frequency with which birds engaged in *Zugunruhe* comprised population, age, season, and the population × season interaction.

Effect of population and season

We found significant differences in *Zugunruhe* frequency among populations, and these varied between seasons. In autumn, Kenyan, Austrian and Irish populations showed a significantly lower proportion of periods with *Zugunruhe* than Austrian × Siberian and Siberian birds. In spring, the proportion of migration periods showing *Zugunruhe* was significantly elevated compared to autumn for Austrian ($z = 2.66$, $p = 0.0078$) and Irish ($z = 3.31$, $p = 0.0009$) stonechats. Figure 3 details these patterns.

Effects of age and sex

The proportion of periods during which birds engaged in *Zugunruhe* was significantly lower for older birds during both spring and autumn ($z = -7.43$, $p < 0.0001$). This observation was consistent across all populations. There was no significant effect of sex on frequency of *Zugunruhe* (Fig. 3C, D).

Consistency of *Zugunruhe* within individuals

We examined whether birds monitored for two or more migration periods (counting spring or autumn; $n = 296$ birds) always, sometimes, or never engaged in *Zugunruhe* (Fig. 4). Pooling all population groups, 63.9% of individuals always engaged in *Zugunruhe* and only 3.0% of birds never exhibited *Zugunruhe*. The remaining 33.1% were mixed records, when birds changed between showing and not showing *Zugunruhe*. Among birds with mixed records and data from their first autumn, 62.0% (49/79) showed

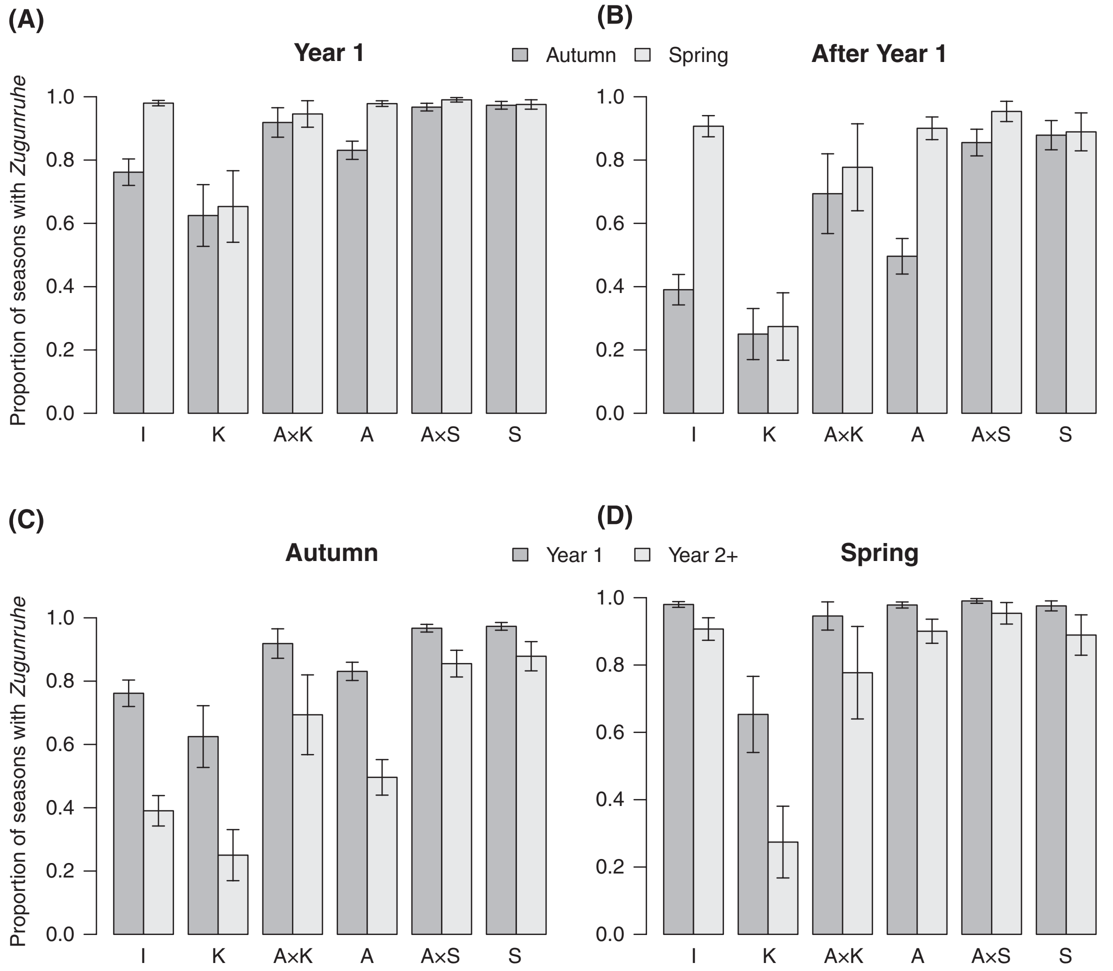

Figure 3. The proportion of seasons during which stonechats showed *Zugunruhe*, by population and age. Proportions were analysed with binomial errors; error bars show one standard error. Bar charts in the top row (A, B) directly contrast autumn and spring seasons side-by-side, while the bottom row (C, D) directly contrasts birds in their first year from older birds. Kenyan stonechats frequently abstained from *Zugunruhe* (spring and autumn), as did Irish and Austrian populations (autumn only).

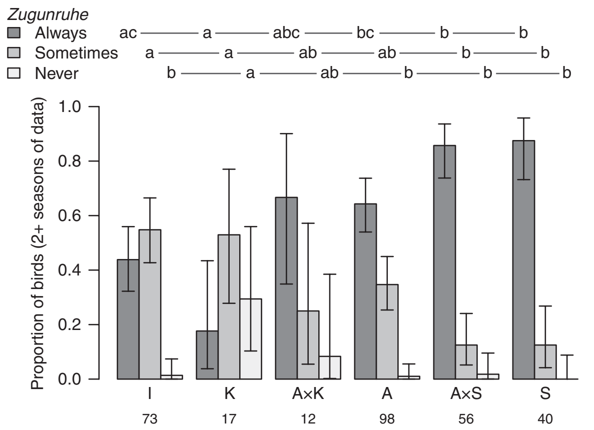

Figure 4. Consistency of individual birds' *Zugunruhe* behaviour by population. Shown are the proportions of birds for each population that engaged in *Zugunruhe* always (i.e. 'migrants'), sometimes (middle row: 'mixed') and never (bottom row: 'residents'). Included are birds for which data were available for at least two seasons (spring or autumn); numbers on the x-axis are total numbers of birds included from each group, and error bars are 95% confidence intervals. Letters shown above bars indicate significant pairwise differences: groups that do not share a letter are significantly different. For example, in the 'Always' category, Kenyan stonechats share an 'a' with Irish birds and Kenyan–Austrian hybrids, but not with the remaining groups, from which they differ significantly. Among non-hybrid groups, Siberian stonechats had the highest proportion of migrants and Kenyan stonechats had the highest proportion of 'residents'. Irish, Kenyan, and Austrian groups all had substantial numbers of 'mixed' individuals that sometimes engaged in *Zugunruhe*.

Zugunruhe during that first autumn (significantly different from 50% by Binomial test, $p = 0.042$). Patterns also differed starkly among populations, with the lowest proportions of consistent *Zugunruhe* in Kenyan (18%) and Irish (44%) stonechats and the highest in Siberian and Siberian × Austrian stonechats (86–88%). The proportion of birds showing mixed patterns was highest in Kenyan and Irish stonechats (53–55%) and lowest in Siberian and Siberian × Austrian stonechats (13%). The proportion of birds that never engaged in *Zugunruhe* was significantly greater than zero only in the Kenyan group (29%).

Timing of *Zugunruhe*

Effect of population

Populations varied significantly in all aspects of *Zugunruhe* timing (Fig. 5A, B). Among migratory populations, Siberian stonechats began autumn *Zugunruhe* earlier than all other groups; Irish birds started afterwards, followed by Austrian birds. Kenyan stonechats, with a small sample size ($n = 8$), had start dates not significantly different from Irish or Austrian birds. Irish and Siberian stonechats all showed mean autumn *Zugunruhe* at approximately the same time, but Austrian birds had significantly later mean dates; Kenyan stonechats were similar to all three. Irish stonechats ended *Zugunruhe* significantly earlier than Austrian and Siberian birds (which themselves had similar end dates); Kenyan stonechats showed intermediate end dates that did not significantly differ from those of the other populations. Irish, Kenyan, and Austrian birds all showed relatively short autumn *Zugunruhe* durations compared to Siberian stonechats.

In spring, onset, mean, and end dates were earliest for Irish stonechats, followed by Austrian stonechats. Kenyan and Siberian populations showed *Zugunruhe* periods that were later than those of the other two populations but not significantly different from one another. The duration of the spring *Zugunruhe* period was longest in Irish birds, significantly shorter in Austrian stonechats, and significantly shorter still in Siberian stonechats. For Kenyan stonechats, duration did not significantly differ from Austrian or Siberian birds, possibly because the sample size for Kenyan stonechats was small ($n \geq 6$). Within populations, the dates of *Zugunruhe* onset were generally more synchronous than the dates of *Zugunruhe* completion. Compared to autumn, duration of spring *Zugunruhe* was significantly longer for Irish (effect = 51.06 d, $t = 12.03$, $p < 0.0001$) and Austrian stonechats (effect = 27.51 d, $t = 7.66$, $p < 0.0001$), but shorter for Siberian birds (effect = –49.62 d, $t = -10.63$, $p < 0.0001$). Thus, in autumn, Siberian long-distance migrants started *Zugunruhe* earliest and showed the longest durations, while in spring, Siberian birds started among the latest and showed the shortest durations.

Hybrids

Austrian × Siberian hybrids generally showed intermediate timing relative to parental birds. In autumn, onset dates, mean dates, and durations of Austrian × Siberian stonechats were intermediate and significantly different from parental values, but end dates were all similar. In spring, timing of onset and mean *Zugunruhe* were intermediate and significantly different from parental values; the end date for hybrids was not significantly different from Siberian birds and duration was not significantly different from Austrian birds. Austrian × Kenyan stonechats showed autumn timing characteristics that were similar to those of both parental groups; spring timing was not significantly different from Austrian birds but significantly earlier than Kenyan birds. *Zugunruhe* profiles of hybrids are shown in Fig. 5C–F.

Effects of age and sex

Young stonechats showed high levels of juvenile nocturnal restlessness before they finished postjuvenile moult (Fig. 2). Nocturnal activity beginning after moult start was interpreted as *Zugunruhe*. In autumn (Supplementary material Appendix 2, Fig. A2), the onset, mean, and end dates of *Zugunruhe* of young birds occurred 2–3 weeks later than those of older birds (onset: effect = –14.08 d, 240.72 DF, $t = -5.05$, $p < 0.0001$; mean: effect = –19.19 d, 195.11 DF, $t = -8.11$, $p < 0.0001$; end: effect = –22.25 d, 355 DF, $t = -8.35$, $p < 0.0001$). There was no significant main effect of age on autumn duration (189.78 DF, $t = -0.02$, $p = 0.9872$), but there was a significant interaction for Siberian birds, which showed shorter *Zugunruhe* periods in older birds (effect = –25.44 d, 162.96 DF, $t = -2.6$, $p = 0.0101$). In spring, older birds of all groups had slightly later *Zugunruhe* start dates (effect = 4.98 d, 283.8 DF, $t = 4.73$, $p < 0.0001$), earlier end dates (non-significant; effect = –7.12 d, 105.9 DF, $t = -1.72$, $p = 0.0875$), and shorter durations (effect = –15.29 d, 113.2 DF, $t = -3.01$, $p = 0.0032$). Mean

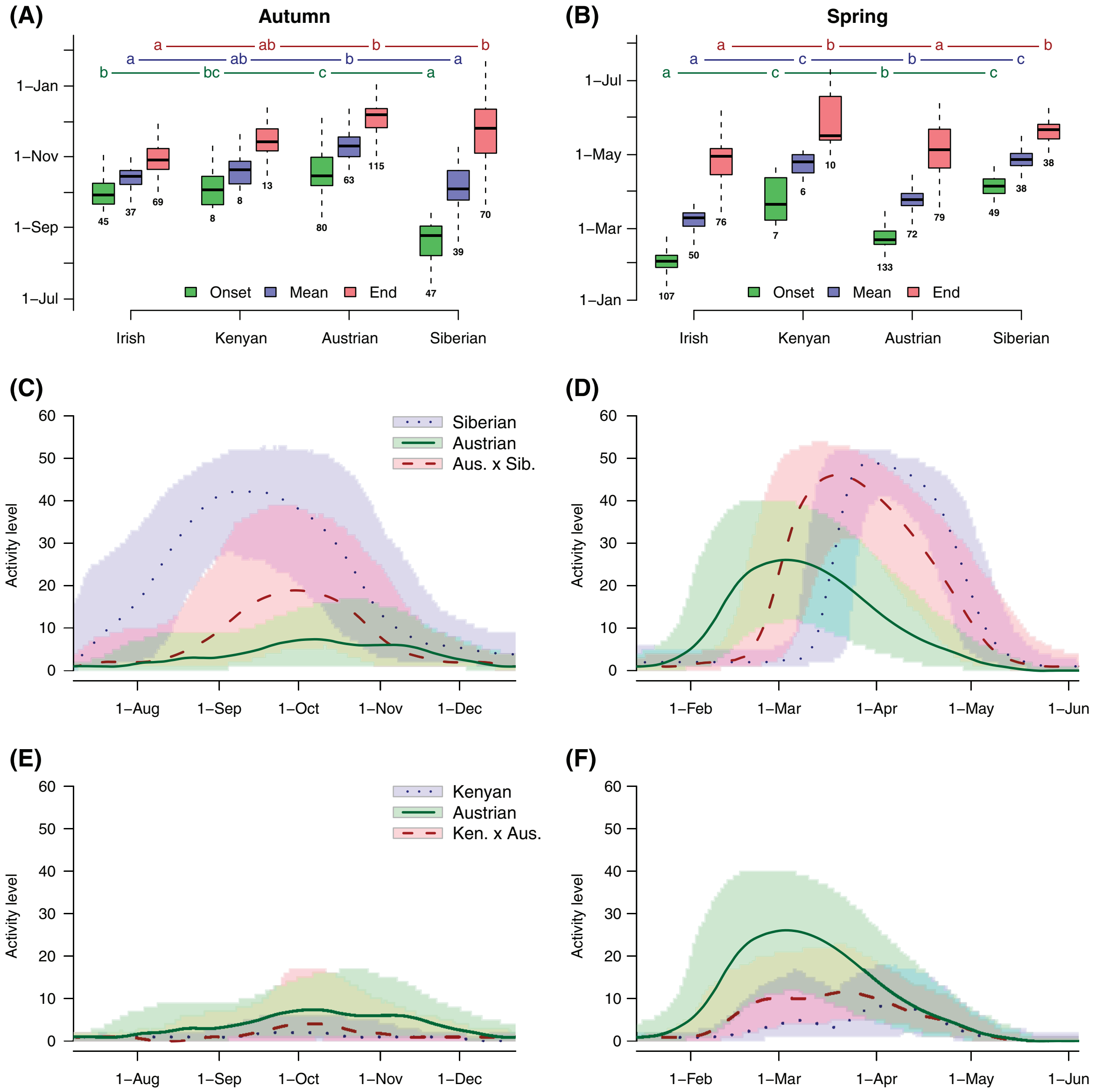

Figure 5. Timing of *Zugunruhe* by population. (A) and (B) show the dates of onset, mean, and end of autumn and spring *Zugunruhe*, respectively, determined with changepoint analysis. Numbers under boxplots show the number of migration periods in the given category; there are multiple migration periods for some birds with multiple years of data. Boxplots show interquartile range, and whiskers extend to the most extreme data point that is not an outlier (see legend of Fig. 2). Outliers are not shown for clarity. Rows of letters at the top of plots indicate significant pairwise differences within each timing category: groups that do not share the same letter are significantly different. (C) to (F): population level activity profiles of hybrids and their parental populations during autumn (C, E) and spring (D, F) migration periods. Activity level is quantified as the number of active ten-minute periods during the night for an individual bird. (C) and (D) compare nocturnal activity in Siberian stonechats, Austrian stonechats, and Austrian × Siberian hybrids. (E) and (F) compare nocturnal activity in Kenyan stonechats, Austrian stonechats, and Austrian × Kenyan hybrids. Lines show medians, and coloured bars show the interquartile ranges (middle 50%) of activity values corresponding to that day. Data shown are smoothed by fully overlapping 30-d windows, incremented by one day.

date did not change with age (effect = 0.24 d, 167.46 DF, $t = 0.19$, p = 0.8477).

In autumn, sex had no effect on timing. In spring, we found an effect of sex on onset date, with females showing significantly later onset (effect = 4.57 d, 171.01 DF, $t = 4.46$, p = 0.0001) and later mean *Zugunruhe* dates (effect = 2.95 d, 161.28 DF, $t = 2.24$, p = 0.0265), but no difference in end dates; overall, females therefore showed shorter spring durations (effect = –6.64 d, 163.39 DF, $t = -2.27$, p = 0.0247). We tested for an interaction between sex and population and found that the difference between male and female spring *Zugunruhe* onset dates in Kenyan stonechats was significantly greater than that of the other populations (effect = 30.3 d, 349.66 DF, t = 4.03, p < 0.0001). There was no significant interaction between population and sex for mean date or duration.

Intensity of *Zugunruhe*

We quantified *Zugunruhe* intensity as both the mean level of nocturnal activity (Supplementary material Appendix 2, Fig. A3) during a given *Zugunruhe* period and the peak nocturnal activity relative to a bird's winter and summer levels (Fig. 6). The two metrics yielded similar results.

Effect of population

Populations differed significantly in ways that generally aligned with their approximate degree of migratoriness (Fig. 6). Surprisingly, Irish stonechats, which are partial migrants, showed peak *Zugunruhe* intensities that were greater than or similar to those of obligate Austrian migrants in both autumn and spring and comparable to long-distance Siberian migrants in spring (Fig. 6A, B). For some, but not all, groups, intensity was significantly greater in spring compared to autumn: Irish (corrected peak: effect = 16.90, $t = 10.54$, $p < 0.0001$; overall mean: effect = 11.7, $t = 9.37$, $p < 0.0001$), Austrian (corrected peak: effect = 12.49, $t = 9.70$, $p < 0.0001$; overall mean: effect = 9.32, $t = 8.76$, $p < 0.0001$), and Austrian × Siberian (corrected peak: effect = 9.05, $t = 5.27$, $p < 0.0001$; overall mean: effect = 7.91, $t = 6.03$, $p < 0.0001$).

Hybrids

Austrian × Siberian stonechats showed corrected peak intensities that were significantly higher than the intensities of Austrian birds but not significantly different from those of Siberian stonechats (Fig. 6C, D). Like their Austrian parents (and unlike their Siberian parents), Austrian × Siberian hybrids showed a significant difference between levels of autumn and spring *Zugunruhe*. Austrian × Kenyan stonechats showed spring peak intensities lower than Austrian birds, and not significantly different from those of Kenyan birds; autumn intensities of all three groups were similar.

Effects of age and sex

Average autumn peak *Zugunruhe* intensity and mean intensity were generally significantly lower after the first year (corrected peak: effect = –4.55, 303.58 DF, $t = –3.36$, $p = 0.0009$; overall mean: effect = –3.06, 262.97 DF,

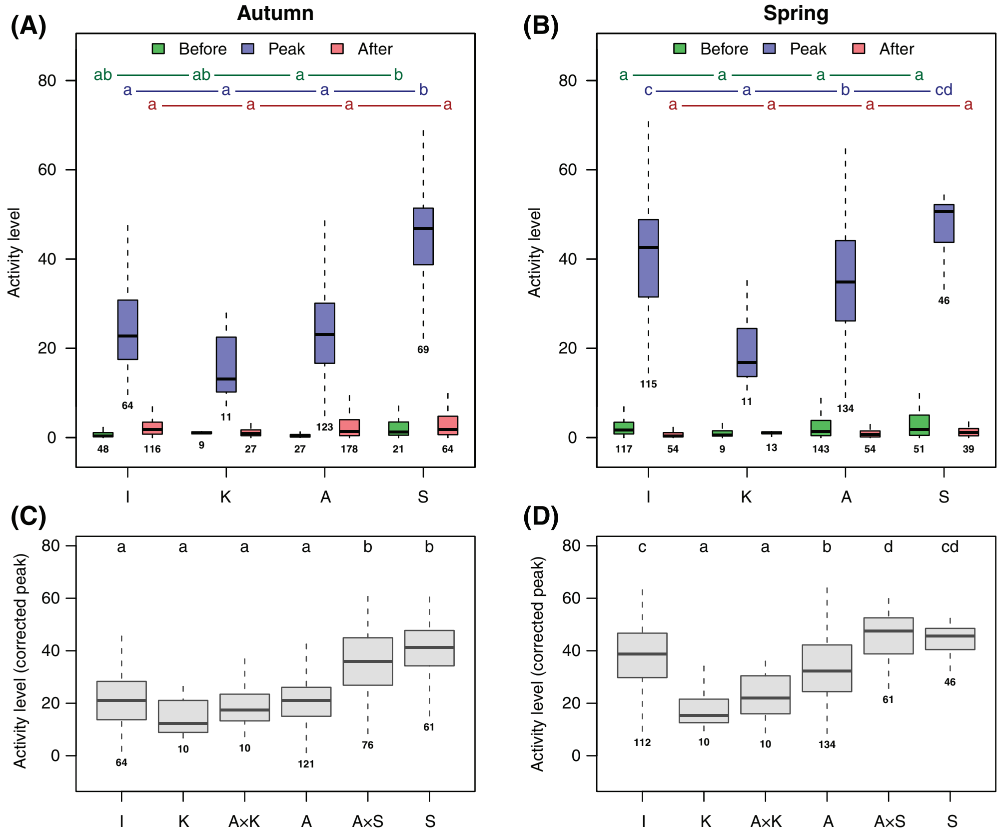

Figure 6. Intensity of *Zugunruhe* by population. (A) and (B) compare *Zugunruhe* with nocturnal activity during summer and winter ((A): autumn, (B): spring). (C) and (D) compare hybrids with their parental populations ((C): autumn, (D): spring). Activity level is defined as the number of active ten-minute periods during the night for an individual bird. Intensity of *Zugunruhe* (i.e. peak intensity) values are calculated as the mean activity level during the most-active 15-d period of *Zugunruhe*, as identified by changepoint analysis. Summer and winter values are the mean level of nocturnal activity across the least-active 30-d periods for each population. In (C, D), we show individual-specific corrected peak, calculated by subtracting the mean activity of flanking summer and winter periods from peak intensity. Numbers under boxplots show the number of migration periods in the given category; there are multiple periods for some birds with multiple years of data. Boxplots as in Fig. 2. Letters shown at the top of plots indicate significant pairwise differences: groups that do not share a letter are significantly different.

$t = -3.13$, $p = 0.002$). There was no significant overall population × age interaction. We found no effect of age on spring intensity (corrected peak: effect = –0.80, 260.01 DF, $t = -0.67$, $p = 0.5025$; overall mean: effect = –0.25, 267.55 DF, $t = -0.26$, $p = 0.7929$), nor an effect of sex on intensity during either migration period in any population (Supplementary material Appendix 2, Fig. A3).

Age effects on nocturnal and diurnal activity

Migration periods

Across all populations, the intensity of diurnal activity during the migration periods showed declines after the first year. Paralleling the patterns in nocturnal activity, these declines occurred both in autumn (effect = –11.00, 344.66 DF, $t = -9.41$, $p < 0.0001$) and spring (effect = –5.88, 158.44 DF, $t = -3.26$, $p = 0.0014$). There were no significant interactions between population and age in these models.

Winter

Nocturnal activity during winter was subtly but significantly lower after the first year (effect = –0.97, 268.32 DF, $t = -3.5$, $p = 0.0005$); diurnal winter activity showed a stronger reduction (effect = –12.02, 348.59 DF, $t = -8.43$, $p < 0.0001$) (Supplementary material Appendix 2, Fig. A3).

Summer

The first summer for which we have sufficient data was the summer approximately one year after hatching. Comparing activity levels during this summer to those during subsequent years revealed no effects of age on nocturnal activity (effect = 0.5, 215.06 DF, $t = 1.58$, $p = 0.1154$), but a significant drop in diurnal activity (effect = –10.29, 106.89 DF, $t = -4.68$, $p < 0.0001$) (Supplementary material Appendix 2, Fig. A3).

Within-individual effects

We examined the consistency of *Zugunruhe* measurements in the same individual in different years, although we were constrained by the small number of same-bird measurements in our dataset (sample size from 20–67, depending on the measurement). Overall, subsequent *Zugunruhe* patterns were correlated within individuals, but these patterns were largely driven by population differences (Supplementary material Appendix 2, Fig. A4). After standardizing for population, individual consistency was much lower (Supplementary material Appendix 2, Fig. A5). Our data suggest that spring *Zugunruhe* intensities show the highest within-individual consistency of all our timing or intensity metrics (Supplementary material Appendix 2, Fig. A5 and A6).

Population-wide nocturnal activity during the migration periods

Comparison between populations

Using the complete dataset of all populations, we visually compared activity profiles of hybrids with those of their parental populations (Fig. 5C–F) and those of the three migratory populations (Fig. 7). Although birds without assigned *Zugunruhe* were included in this data set, all main patterns persisted, including distinctly elevated nocturnal activity in Irish, relative to Austrian, birds. In some cases, reductions of activity over age were accentuated by inclusion of assigned non-migrants. In autumn, population-level nocturnal activity was most apparent in first-year birds (Fig. 7A) but decreased drastically in later years in Austrian and Irish individuals (Fig. 7C). In contrast, Siberian birds continued to show autumn nocturnal activity at levels on par with their first year. In spring, all migrant populations showed little appreciable change in nocturnal activity with age (Fig. 7B, D).

Quantitative comparisons of population-wide activity levels during the most active two-month periods of each population yielded results that were similar to those of peak intensity (Supplementary material Appendix 2, Fig. A6, top row). In particular, Irish partial migrants showed high mean and peak activities in spring that were not significantly different from those of Siberian long-distance migrants, and also significantly higher than those of Austrian short-distance migrants. In autumn, however, Irish stonechats showed mean and peak activities that were significantly lower than those of Siberian birds and similar to those of Austrian birds.

Nocturnal activity as proportion of night length

We detected generally minor differences in results when analysing *Zugunruhe* activity as a proportion of night length as opposed to in absolute units of time (Supplementary material Appendix 2, Fig. A6, bottom row). The exception was that Siberian stonechats, and to a lesser extent Austrian × Siberian stonechats, showed a higher relative peak activity level compared to the original analysis. This is because Siberian stonechats began *Zugunruhe* relatively late in spring and relatively early in autumn, when the nights were shorter than in the other populations. Some birds were active for nearly 100% of certain nights in spring.

Covariation of diurnal and nocturnal activity

Across all birds, we observed distinct differences in a bird's mean diurnal activity depending on whether it was also engaging in *Zugunruhe*. In the first 15 d of *Zugunruhe*, diurnal activity was significantly lower than in the 15 d preceding *Zugunruhe* onset in autumn (effect = –7.74, 844.04 DF, $t = -5.1$, $p < 0.0001$); in spring, however, this effect was much reduced, suggesting that birds compensated less for their nocturnal restlessness (interaction effect = 6.87, 848.2 DF, $t = 4.28$, $p < 0.0001$). A decrease in diurnal activity at the start of *Zugunruhe* was more pronounced for first year birds, regardless of the season (interaction effect = –3.51, 845.62 DF, $t = -2.19$, $p = 0.0289$). We found no significant interactions with population or sex. In the 15 d following *Zugunruhe* completion, diurnal activity in autumn increased relative to the preceding 15 d (effect = 3.13, 863.94 DF, $t = 2.7$, $p = 0.007$), and even more so in spring (interaction effect = 6.33, 862.58 DF, $t = 3.8$, $p = 0.0002$). There were no significant interactions with age, population, or sex.

Individual birds showed significant negative relationships between diurnal and nocturnal activity during periods of *Zugunruhe*: at the level of the individual day, birds were less active during days following high-activity nights (Supplementary material Appendix 2, Fig. A7; autumn: effect = –0.09, 202.5 DF, $t = -5.3$, $p < 0.0001$; spring: effect = –0.20,

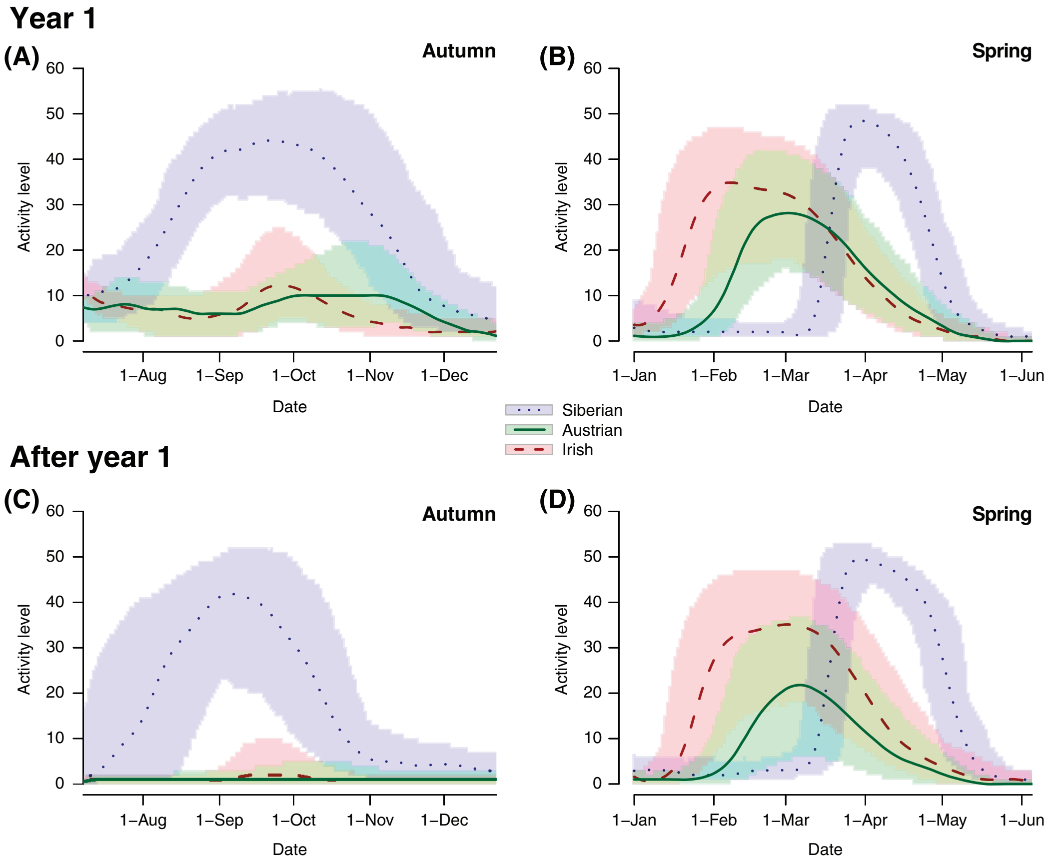

Figure 7. Population-level nocturnal activity in Siberian, Austrian and Irish stonechats, contrasting different age groups during the autumn and spring migration periods (first year (A) and (B) versus later years (C) and (D) for autumn and spring, respectively). Activity level is quantified as the number of active ten-minute periods during the night for an individual bird. Lines show medians and coloured bars show the interquartile range (middle 50%) of smoothed activity values corresponding to that day. Data shown are smoothed by fully overlapping 30-d windows, incremented by one day. For details, see Fig. 5C–F.

242.43 DF, $t = -10.36$, $p < 0.0001$). During summer and winter, diurnal and nocturnal activity did not covary significantly on a daily basis (effect for both periods = –0.02, 259.89 DF, $t = -0.11$, $p = 0.91$). During migration periods, neither sex nor population had a significant effect on diurnal activity, whereas during summer and winter, females were on average more active (effect = 5.81, 552.24 DF, $t = 3.99$, $p < 0.0001$).

Zugunruhe and activity outside a migration context

On a population level, when all individuals were included, nocturnal activity during migration periods was greatly elevated over summer and winter baseline levels for all populations studied (Fig. 8, top row). Within individuals, nocturnal activity levels during spring migratory periods were positively associated with those during summer and winter after accounting for age, sex, and population (winter: effect = 0.05, 358 DF, $t = 3.41$, $p = 0.0007$; summer: effect = 0.07, 181.66 DF, $t = 3.78$, $p = 0.0002$). This was also true for activity during autumn migratory periods (winter: effect = 0.06, 318.81 DF, $t = 4.19$, $p < 0.0001$; summer: effect = 0.02, 2.03 DF, $t = 1.32$, $p = 0.3167$); the non-significant effect of summer may have been due to a lack of data (none for first year birds) and thus very low power.

Nocturnal activity during migration periods also explained variation in diurnal activity during summer and winter, both for spring (winter: effect = 0.32, 290.41 DF, $t = 4.33$, $p < 0.0001$; summer: effect = 0.50, 146.51 DF, $t = 3.56$, $p = 0.0005$) and autumn (winter: effect = 0.29, 241.94 DF, $t = 3.66$, $p = 0.0003$; summer: effect = 0.13, 65.66 DF, $t = 0.63$, $p = 0.5341$). This indicates, for example, that a bird more active than another by an average of 100 min per night during the migration season also averaged 13–50 min more activity during the day at other times of the year.

Overall, therefore, more active individuals during the migration periods tended to also be more active during other times of the annual cycle, both during the day and at night.

Discussion

Population-specific patterns of *Zugunruhe*

Our analyses reveal clear population-specific differences in the migratory programmes of stonechats, akin to documented

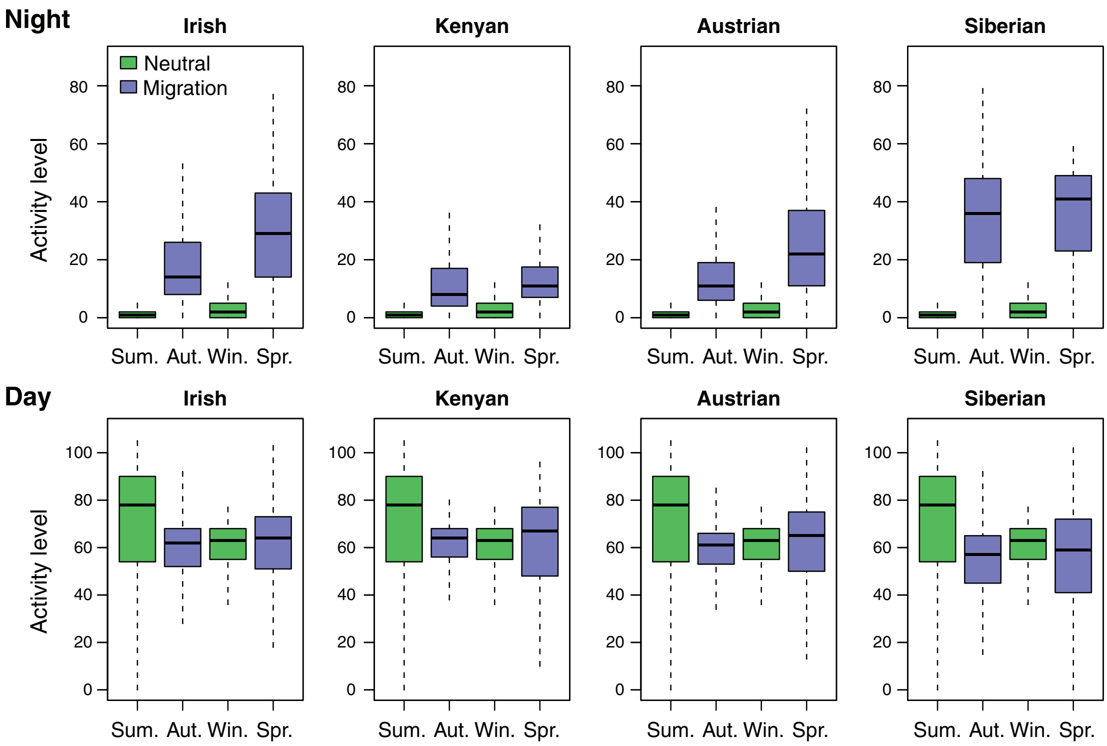

Figure 8. Comparison between overall nocturnal and diurnal activity levels by season for each population. Boxplots show activity levels for each migration season flanked by activity levels during summer and winter 'neutral' seasons (for definitions, see Fig. 6). The boxplots show daily activity levels as the number of 10-min active periods for night (top row) and day (bottom row); boxplots as in Fig. 2).

differences in many traits of life history, physiology, morphology, and biological time-keeping (Gwinner et al. 1983, 1995, Helm et al. 2005, 2009, Helm 2009, Tieleman et al. 2009, Baldwin et al. 2010, Fuchs et al. 2014, Versteegh et al. 2014). These population-level differences were largely consistent with our predictions: long-distance migratory Siberian stonechats showed by far the strongest migratory tendencies and most consistent behaviour. Siberian birds rarely failed to engage in *Zugunruhe* and consistently showed high *Zugunruhe* intensities in both spring and autumn. Among the migrant populations, Siberian stonechats were the first to initiate *Zugunruhe* in autumn and the last to do so in spring. Siberian birds had the longest *Zugunruhe* period in autumn and the shortest in spring. This extended autumn *Zugunruhe* period is likely related to the long distances travelled by this population, paired with a possibly slower pace of autumn migration (Yamaura et al. 2016, but see Raess 2008). Alternatively, the long fall *Zugunruhe* may reflect a necessity to facultatively remain in migratory condition because of unpredictable resource availability (Helms 1963). Although short, the spring *Zugunruhe* periods of Siberian stonechats were exceptionally intense (peak activities were near 100% of the night length). This may reflect the need for a rapid long-distance return journey to the breeding grounds within a tightly constrained time window (i.e. late enough that spring has arrived – but not too late for breeding in a short season, Alerstam 2006, 2011). This view is supported by spring field records from stonechats (Raess 2008).

On the other end of the migration spectrum, resident Kenyan stonechats clearly showed the weakest migratory tendencies, but they still regularly engaged in *Zugunruhe*, especially first-year birds (Helm 2006, Helm and Gwinner 2006). Most Kenyan birds showed *Zugunruhe* at least once, but also refrained from engaging in *Zugunruhe* at least once, including the overwhelming majority of older birds. Under temperate photoperiods in the laboratory, Kenyan birds showed well-defined population timing, starting at about the same time as Austrian birds in autumn, but significantly later in spring. In both seasons, *Zugunruhe* profiles of Kenyan birds had relatively short durations and low intensities. Although the present analysis finds relatively low levels, it corroborates the persistence of *Zugunruhe* and several of its features in African stonechats. The interpretation of this behaviour is still unclear and merits further investigation (Zink 2011).

The Irish and Austrian populations are currently classified as members of the same species (European stonechat), and are both medium distance migrants that reach Mediterranean winter quarters. However, in contrast to obligate Austrian migrants, British Isles stonechats are partial migrants, with roughly half of the birds remaining at or near the breeding sites in winter (Helm et al. 2006). Our study population originated from a coastal site in Ireland where birds overwinter, such that our sample could have been biased towards resident phenotypes (Helm 2003). Nonetheless, we found that *Zugunruhe* behaviours in these two populations were generally similar, showing intermediate phenotypes of timing and incidence compared to Kenyan and Siberian birds. Counter to predictions for partial migrants (Berthold 1988a, Pulido et al. 1996, Pulido and Berthold 2010), we could not detect a heightened proportion of Irish stonechats showing no *Zugunruhe*. Most unexpectedly, Irish birds exhibited significantly higher spring *Zugunruhe* intensity than Austrian birds. These patterns are difficult to explain if *Zugunruhe* is expected to correspond closely to actual migration, and if partial migrant populations are expected to show greater dimorphism of migratory phenotypes (Berthold 1988a). They are more easily reconciled with regulation of migration where *Zugunruhe* may mark a window of opportunity during which environmental factors act to repress or activate actual migration (Helms 1963, Gwinner and Czeschlik 1978, Chan 2005, Helm 2006).

Austrian and Irish stonechats clearly differed from Siberian long-distance migrants. Both European populations showed significantly longer *Zugunruhe* periods during spring compared to autumn; this pattern was opposite to the one observed in Siberian stonechats. The long spring period of nocturnal restlessness is likely to represent *Zugunruhe*, rather than summer restlessness (Gwinner and Czeschlik 1978) because it ceased when the birds' reproductive organs matured (Helm and Gwinner 2005), just like migration of free-living stonechats (Raess and Gwinner 2005). Instead, the early, and long, spring restless periods of both European populations may reflect the readiness of these short-distance migrants to react to variation in local conditions that may allow for an early return to the breeding grounds, or, contrarily, for maximising arrival condition by pausing migration at favourable stop-over sites (Alerstam 2006, 2011). We have no convincing explanation for the short *Zugunruhe* window in autumn relative to Siberian stonechats, but speculate that it may reflect the shorter migration distance of the European populations.

The primary difference we detected between the two European populations related to the onset of *Zugunruhe* and matched our predictions. Irish stonechats showed by far the earliest spring migratory tendencies of all populations, regularly starting by late January. This early endogenous spring window fits well with field data, including those from ringing recoveries (Helm et al. 2006). Early spring arrival is expected both because of the more temperate environment of the British Isles, allowing for suitable environmental conditions earlier in the year, and because returning partial migrants will compete with resident conspecifics for territories upon arrival (Lack 1943, 1944). However, Irish birds also started *Zugunruhe* significantly earlier in autumn compared to their continental counterparts. This finding is more challenging to interpret in ecological terms. In terms of biological timekeeping mechanisms, it confirms a shift of the entire annual cycle of Irish compared to Austrian stonechats: annual cycle organisation and photoperiodic responses of both populations were identical, but migrations, reproduction and moult were all advanced by approximately one month in Irish stonechats (Helm 2003, 2009, and unpubl.).

Hybrid phenotypes

Our data show that hybrid stonechats express behavioural traits that are generally intermediate with respect to their parental groups. This is most obvious for the timing measures of Austrian × Siberian hybrids compared to Austrian or Siberian groups, and it indicates a strong genetic basis for both timing and intensity of migratory restlessness. These findings of intermediate phenotypes parallel data from other traits in stonechats, including timing of reproduction and moult, immune traits, metabolic measures, and life history traits (Gwinner et al. 1995, Helm et al. 2009, Versteegh et al. 2014, but see Tieleman et al. 2009). They also align with findings from other crossbreeding studies of migratory birds, including silvereyes *Zosterops lateralis* (Chan 2005) and Blackcaps (Berthold 1988a, Helbig 1996), although inheritance patterns in quail *Coturnix coturnix* appeared to be biased towards resident types (Deregnaucourt et al. 2005).

Sexes

In contrast to the extensive differences between populations, the sexes of stonechats exhibited similar endogenous migratory programmes, in line with their unusual behaviour of wintering in heterosexual pairs (Gwinner et al. 1994). We found no effect of sex on the frequency with which birds abstained from *Zugunruhe* or on the intensity or autumnal timing of *Zugunruhe*. However, males started spring *Zugunruhe* on average 4.6 d earlier than females. Protandry in spring migratory timing has been documented in the wild in many species, and it is seen as advantageous that males arrive to defend territories as early as possible (Kokko et al. 2006, Coppack and Pulido 2009, Alerstam 2011). Our findings add to the increasing evidence that such differences between the sexes can be hard-wired. Maggini and Bairlein (2012) have recently shown that in wheatears *Oenanthe oenanthe*, protandry of *Zugunruhe* persisted even in the absence of environmental cues such as photoperiod, and is therefore part of the birds' circannual programme (Gwinner 1986, 1996).

Age, season and individual activity levels

Development and age

In our study, juvenile stonechats showed strong nocturnal restlessness even before the beginning of postjuvenile moult. Likewise, hand-raised first year birds of other species also showed periods of elevated nocturnal activity after fledging, but prior to finishing postjuvenile moult (Gwinner 1990, Mukhin 1999). Wild birds are unlikely to commence migration during intense moult (Jenni and Winkler 1994), but postfledging movements have been associated with movements to moulting areas or explorative behaviours (Mukhin et al. 2005, Brown and Taylor 2015). Prospecting and training flights of young birds during the summer may be relevant for the development of celestial compass systems and establishment of navigational targets for return migration (Mukhin et al. 2005). Stonechats have been reported to move locally in juvenile flocks, for example to suitable moulting sites (Urquhart 2002), and ringing recoveries confirm such early-life movements (Helm et al. 2006). Juvenile restlessness in captivity could therefore represent a true urge to move, but one that differs from actual migration.

Subsequently, the expression of the stonechat endogenous migratory programme changed profoundly with age in ways that depended on season and population. Generally, occurrence and intensity decreased with age, and these decreases were most conspicuous in the more weakly migratory populations (Kenyan, Austrian, Irish, compared to Siberian) and in the lower-intensity migratory season, autumn. Across all populations, older stonechats were approximately twice as likely to abstain from *Zugunruhe* compared to first year birds. Decreases in overall activity with age are well known from many animal species, including vertebrates and invertebrates (Ingram 2000) and could well be unrelated to migration. We therefore used our data on activity outside of a migration context to assess whether the reductions in *Zugunruhe* represented general age-related patterns. We identified a consistent, but slight, reduction of activity levels with age for nocturnal activity also during summer and winter, and for diurnal activity around the annual cycle. In contrast to *Zugunruhe*, this reduction was consistent for the populations and seasons. Our findings thus suggest that the pronounced decrease in *Zugunruhe* in older birds was predominantly associated with migratory programming, rather than a general ageing process.

The magnitude of the age-related reductions in *Zugunruhe* was astonishing. Age effects on *Zugunruhe* are rarely discussed in the literature, and where they have been reported, patterns were inconsistent, for example between the sexes of European blackbirds (Lundberg 1988, Schwabl and Silverin 1990). It is possible that the reductions derived from long periods spent in captivity (Schwabl and Silverin 1990), or from modifications of the migration programme by prior experience (Ketterson and Nolan 1983, 1988). For example, based on experiments with dunnocks *Prunella modularis*, Schwabl et al. (1991) speculated that birds may recognise previous wintering locations and accordingly reduce *Zugunruhe* when exposed to them. Whatever the interpretation, it is interesting to note that in stonechats, age effects were absent in the most migratory population (i.e. Siberian stonechats).

We also found effects of age on the timing of *Zugunruhe*. Autumn timing was consistently earlier in older birds by approximately 2–3 weeks across populations, but duration did not change. These findings are consistent with those from other annual cycle events in stonechats, including earlier reproductive cycles and earlier moult in second-year compared to first-year stonechats (Helm et al. 2009). In the field, adults of many bird species commence autumn migration before juveniles (Newton 2008), presumably because juveniles benefit from a longer stay on the breeding grounds for maturation and the completion of postjuvenile moult. In spring, older stonechats started *Zugunruhe* slightly later but ended it earlier, possibly primed by previous photoperiodic experience (Sockman et al. 2004).

Seasons

Overall, our analysis demonstrates stark differences between spring and autumn *Zugunruhe*. *Zugunruhe* was more difficult to measure in autumn than in spring because of its more drawn out time profile and lower, more variable intensity. Autumn *Zugunruhe* was also confounded by juvenile restlessness and is known to be affected by other early-life effects, in particular by variation in hatching date (Fig. 1B; Helm and Gwinner 2006). Intensity of *Zugunruhe* was much higher in spring than in autumn for Austrian and Irish stonechats. Siberian birds appeared to make greater use of the available night time in spring than in autumn, but their high activity levels in both seasons were statistically inseparable.

These seasonal differences correspond well with *Zugunruhe* data of other species and with observations of wild birds. Many species migrate more rapidly during spring than autumn (Alerstam 2006, Newton 2008, Nilsson et al. 2013, Bäckman et al. 2016, Horton et al. 2016), and several aspects of migratory physiology reflect this faster pace. For example, when being re-fed after a fasting period, blackcaps pause *Zugunruhe* in autumn, but not in spring (Fusani and Gwinner 2005). Such differences may result from higher selection pressure on the timing of spring migration because of its proximity to the breeding season, relative to the apparently more 'casual' pace of autumn migration (Lack 1943, 1944, Helms 1963, Both et al. 2004, Alerstam 2006, Newton 2008). In our data, this interpretation is further supported by findings from diurnal activity. During *Zugunruhe*, mean diurnal activity was lower than before or after *Zugunruhe*, in accordance with the idea that birds require more rest to compensate for the increase in nocturnal activity (Rattenborg et al. 2004, Fuchs et al. 2006, Bäckman et al. 2016). The drop in mean diurnal activity during *Zugunruhe* was less pronounced during spring, indicating that birds generally maintained high diurnal activity levels in spring. However, in both seasons, stonechats compensated for increased nocturnal activity on a day-to-day basis by reducing diurnal activity levels after highly active nights, and this effect was at least as clear in spring as in autumn.

Finally, unlike for intensity, differences in the duration of *Zugunruhe* between the seasons were not consistent between populations (e.g. spring migration was shorter than autumn migration for Siberian stonechats, but the opposite was true for Irish stonechats); this type of heterogeneity might be expected from bird migration theory (Alerstam 2006, 2011).

Individual activity levels

Within individuals, *Zugunruhe* occupied a unique position in the annual cycle, with no significant elevations of nocturnal activity detected outside the migration seasons. However, intensity of *Zugunruhe* also covaried with individual differences in overall activity and was positively correlated with activity levels outside of the migration season, both during daytime and night-time. This finding implies that *Zugunruhe* intensity is not solely a measure of migratory tendency but also contains some information about a bird's overall behavioural phenotype, including, for example, possible differences in 'personality' or physiology (Mettke-Hofmann et al. 2005, Reale et al. 2007, van Oers and Naguib 2013). Breeding programs for high levels of *Zugunruhe* (e.g. in blackcaps, Berthold 1988a) may have thus selected in part for generally high locomotor activity, although in our study within-individual correlations between activities were low relative to the blackcaps' large selection response. Locomotor activity levels are known to be highly heritable. For example, genetic studies of mice found a QTL (quantitative trait locus) for the amount of activity, indicating high potential for selection (Mayeda and Hofstetter 1999).

Because variation in *Zugunruhe* intensity can predict variation in activity in other behavioural contexts, *Zugunruhe* intensity may be less useful than previously believed as a measure of migratory tendency. However, this depends on whether heightened overall activity levels covary with migration in the wild. Consequently, there is a need for further research on the relationship between *Zugunruhe* and other behavioural traits (Marchetti and Baldaccini 2003, Nilsson et al. 2010). In future genetic experiments on *Zugunruhe*, data should be collected on traits that shed light on the migratory context of behaviour (Noordwijk et al. 2006).

Changepoint analysis as a quantitative tool for *Zugunruhe*

Our analytic approach allowed us both to classify presumed migrants and non-migrants and identify periods of *Zugunruhe* on the individual level for the vast majority of birds from all taxa and age groups. Overall, the algorithm performed equally well for classifying *Zugunruhe* regardless of a population's migratory phenotype. The parameters of the method can easily be adjusted to fit other phenotypes or answer different questions. In contrast to fixed exclusion criteria (Maggini and Bairlein 2010), changepoint analysis has the advantage of assessing changes in nocturnal activity in the context of a given bird's behavioural profile, thus accommodating individual differences by using an individual-specific baseline. Consequently, changepoint analysis is presumably less prone to bias from behavioural differences or recording methods. Some studies have applied individual-specific criteria, e.g. nocturnal activity relative to diurnal activity (Ramenofsky et al. 2008), or white-noise techniques (Helm and Gwinner 2006). However, unlike changepoint analysis, these measures were not specific to the seasonal features of *Zugunruhe*. In comparison to autocorrelation techniques (Helm and Gwinner 2006), changepoint analysis classified fewer birds as exhibiting *Zugunruhe,* presumably because of its focus on major changes in nocturnal activity profiles. Importantly, and in contrast to commonly used 'eyeballing' methods, changepoint analysis is objective and repeatable as long as its settings are documented. Strong contrasts and sharp delineation between *Zugunruhe* and neutral periods, especially during spring migration, were easiest to measure unambiguously (Supplementary material Appendix 2, Fig. A1A, C). However, even in cases with noisy data, the decisions made by the analytic approach were objective compared to methods of manual classification of raw data. Delineation of *Zugunruhe* by changepoint analysis was also more adaptable to the features of *Zugunruhe* than methods based on fixed thresholds (Pulido et al. 1996, Owen and Moore 2008), and general algorithms such as 'edge detectors' (Helm and Gwinner 2005).

Our findings on *Zugunruhe* intensity were robust to variation in analysis method: population-level comparisons of raw activity data largely mirrored results of *Zugunruhe* intensity. This suggests that more conventional analytic methods are sufficient for detecting coarse intensity patterns. Overall, we feel that the main advantage of our approach is its general applicability, and we hope to aid its implementation with our provided R script (Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.484m0>).

Conclusions: implications for avian migration studies

Our study shows that *Zugunruhe* is a robust component of the annual cycle in the stonechat complex: the behaviour was present in four populations with drastically different migratory phenotypes. Characteristic differences in *Zugunruhe* between the populations were apparent in our common-garden set-up, supporting the view that genetic variation underlies differences in the migration programme (see also Berthold 2001, Maggini and Bairlein 2010, Ketterson et al. 2015). A heritable basis of the main features of *Zugunruhe* was further indicated by intermediate patterns in hybrids, in line with findings from other crossbreeding studies of migratory birds, and matching evidence from wild species. For example, tracking data from wild Swainson's thrushes *Catharus ustulatus* revealed intermediate routes taken by hybrids from a migratory divide (Delmore and Irwin 2014). The largely consistent evidence for genetic migration programmes is encouraging for future studies of the evolutionary architecture of movement behaviour (e.g. identifying the specific genes that are responsible for such variation, their regulation, and their interactions), which could combine *Zugunruhe* with genomic tools (Peterson et al. 2013, Liedvogel and Lundberg 2014).

In our stonechat study, the differences between populations imply high evolutionary lability of migratory traits as well as some phenotypic plasticity of individuals, for example with increasing age. In agreement with findings from other species, *Zugunruhe* levels were higher and more robustly programmed in spring than in autumn (Helms 1963, Maggini and Bairlein 2010). Several comparisons between populations indicated that the timing of spring and autumn migration can be modified independently. Remarkably, however, we observed an apparent coupled change across seasons within European stonechats: Irish birds showed a consistent phase shift in timing compared to Austrian birds throughout the annual cycle, despite their overlapping wintering ranges (Helm et al. 2006, Helm 2009). Similarly consistent phase differences (often referred to as carry-over effects) within species have recently also been reported in field studies of migratory waders and songbirds (Conklin et al. 2010, Briedis et al. 2016) and may thus have an inherited basis.

We also found patterns that are not commonly reported, despite possibly being widespread. For example, stonechats of all groups showed juvenile nocturnal restlessness during their postfledging phase, sometimes even before the start of moult (Mukhin 1999). A better understanding of this behaviour could provide important cues for studies of avian navigation, prospecting and dispersal. In addition, the striking reductions of *Zugunruhe* with age could indicate plasticity and learning processes that are yet to be understood, requiring testing in wild birds over several years of their life. Furthermore, our comparisons of diurnal and nocturnal activity across the annual cycle suggest that individuals that showed higher levels of *Zugunruhe* were also generally more active birds. This calls for closer study of relationships between *Zugunruhe* and other behaviours, including personality traits (van Oers and Naguib 2013), and for cautious interpretation of findings from selective breeding experiments (Berthold et al. 1988a).

Clearly, many questions remain about the interpretation of *Zugunruhe*. Our findings of undiminished *Zugunruhe* in partially migrant Irish stonechats and confirmation of *Zugunruhe* in Kenyan residents underscore an urgent concern: the parts of this behaviour that align with actual migration need to be distinguished from those that indicate an environmentally sensitive preparedness to migrate (Merkel 1956, Helms 1963, Gwinner and Czeschlik 1978, Helm

2006). This view is supported by exciting new research from wild birds. Bäckman et al. (2016) have provided the first annual-cycle data of activity of a free-living migratory bird, a red-backed shrike *Lanius collurio*. Intriguingly, the same species had earlier been recorded in captivity (Gwinner and Biebach 1977). The overall timing of migration is well-matched in both studies. However, in agreement with observations from stop-over sites, the wild bird showed relatively few nights with migratory flights, whereas its captive conspecifics showed several months of continued *Zugunruhe*. Another recent study, on European blackbirds *Turdus merula* (Zúñiga et al. 2016), found that radio-tracked wild migrants showed no increase in nocturnal activity until the night of departure from the breeding grounds, whereas captive birds slowly built up *Zugunruhe* over several weeks. The physiological and ecological mechanisms that affect alternations between flight and stopover mode are now under intense investigation, using both *Zugunruhe* and tracks of free-flying birds (Fusani et al. 2009, 2013, Goymann et al. 2010, Eikenaar et al. 2014, Skrip et al. 2015). Dissection of the genetic and environmental regulators of migration will not only aid migration research, but also allow important advances for understanding how genes and environment interact to shape complex behaviour.

We believe that *Zugunruhe* will continue to be a powerful tool in the study of avian migration. If used with circumspection and in combination with new tools, from molecular methods to new tracking technologies (Alerstam 2011, Liedvogel and Lundberg 2014, Ketterson et al. 2015), *Zugunruhe* will reveal new answers to ancient questions about the migration of birds (Alerstam 1990).

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Supplementary material (Appendix JAV-01348 at <www.avianbiology.org/appendix/jav-01348>). Appendix 1–2.

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** Equal contributions.*

2

Evolutionary response to climate change in pied flycatchers

Evolutionary Response to Climate Change in Migratory Pied Flycatchers

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SUMMARY

Climate change is rapidly advancing spring phenology [1–3] but at different rates in different species [1, 4]. Whether these advances are solely driven by phenotypic plasticity [2, 5] or also involve evolution is hotly debated (e.g., [5–7]). In some species, including avian long-distance migrants, plastic responses to early springs may be constrained by inherited circannual timing programs [8, 9], making evolutionary adjustment the only viable mechanism for keeping pace with shifting phenology [5, 10]. This constraint may be contributing to population declines in migratory species [5, 10–12]. To test whether a migrant's timing program has evolved [10, 12], we replicated an experimental study of the annual cycle of long-distance migratory pied flycatchers (*Ficedula hypoleuca*) after 21 years of warming. Flycatchers are a model for studying constrained ecological responses to climate change [6, 10, 12, 13]. We show that the phase of the flycatcher circannual clock controlling spring moult, migration, and reproductive timing advanced by 9 days. A nearby wild population mirrored these changes, concurrently advancing egg-laying by 11 days. Furthermore, the time window during which wild flycatcher reproductive timing was most sensitive to ambient temperature advanced by 0.8 days year^{-1}. These results support a role of phenotypic evolution [14] in changing spring phenology [15, 16]. We suggest that the timing programs of long-distance migratory birds may have greater adaptive potential than previously thought, leaving some scope for evolutionary rescue in a changing climate.

RESULTS AND DISCUSSION

Replicated Experimental Study

Changing temperature regimes can impart strong selection pressures on annual cycle timing and migration traits [4, 16–19], which are often heritable [20–23]. However, the extent to which climate adjustment requires evolutionary change depends on an organism's timing strategy [3, 23]. For example, in songbirds, populations that can continuously access information about their reproductive environment (e.g., year-round residents [24]) often show high plasticity. Conversely, many migrants use rigid, inherited circannual programs to predict suitable conditions over long distances [2, 8–10, 16]. Although these species show some plasticity (e.g., sensitivity to local temperatures [16, 25]), they require evolutionary adjustment of timing and migration traits to keep pace. Currently, it is unclear whether phenotypic evolution, defined as the change in the mean phenotype of a population over successive generations, can match rapid climate change [5, 14, 17, 18, 26]. Evolutionary changes in timing programs are difficult to detect without experimentation, genetic time series, or longitudinal data from pedigreed populations [5, 17, 19, 22, 24, 26]. Hence, evidence for climate-induced evolution in timing traits is scarce, particularly in vertebrates.

Here we provide experimental evidence for climate-induced evolution in the annual cycle from two studies on the pied flycatcher (hereafter "flycatcher") designed by the late Eberhard Gwinner. We investigated the first full annual cycle of flycatchers in replicated studies of cohorts hatched in 1981 [27] and 2002. In this common garden experiment through time [21], nestlings were collected from the same German field site, on the same dates (Figures S1 and S2), and raised in identical captive settings [13, 27]; thus, we considered any systematic timing changes between cohorts as evidence of evolutionary change in the birds' inherited timing programs. We recorded the timing of annual cycle events and grouped them by season (autumn, winter, spring) [9, 13, 27, 28] (Figure 1).

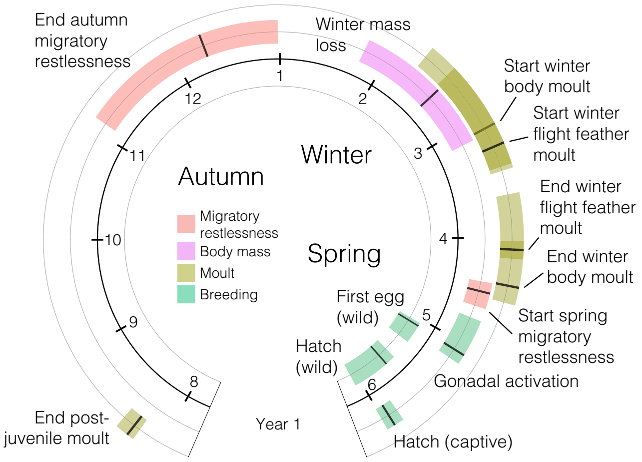

Figure 1. Annual Cycle Events in First-Year Captive and Wild Pied Flycatchers

Boxplots (central bars indicate median, boxes show interquartile range) show the timing of annual cycle events for 1981 and 2002 cohorts combined, as well as reproductive events in wild birds (inside circle).
See also Figures S1 and S2.

Based on extensive documentation of climate-induced advances in spring phenology [2, 5, 6, 10, 15, 25, 29], we expected earlier spring timing (end of winter moults, start of migratory restlessness, reproductive activation) in the 2002 cohort compared to 1981. Because flycatchers are protandric and there is a high fitness prime on early male [30] but not necessarily female phenology [18], we expected particularly evident advances in males. In contrast, for autumn, phenological trends and underlying selection pressures are inconsistent for migratory songbirds [31, 32]. We therefore considered advances and delays in autumn phenology (end of post-juvenile body moult and migratory restlessness) to be equally possible, and we did not expect consistent differences between the sexes. Likewise, we had no directional expectation for changes in winter timing (body mass drop, start of winter moults) in either sex. To test these hypotheses, we derived seasonal timing indices by averaging the times of events for each individual. We also examined timing traits individually.

Captive flycatchers showed some evidence of delayed autumn timing. The autumn index averaged later in 2002 by 10 days (95% CI −1.6 to 22; $\chi^2_1 = 2.9$; p = 0.087; Figures 2A and 3). This delay was more pronounced in males, although the cohort × sex interaction did not reach statistical significance ($\chi^2_1 = 2.1$; p = 0.15; males: 18 days, 95% CI 2.4 to 34; females: 1.2 days, 95% CI −16 to 18). The observed delay was associated with autumn migratory restlessness, which was variable but ended 17 days later in 2002 (95% CI −7.1 to 42; Figures 3 and S3). In contrast, the end of post-juvenile moult, which occurs before migration, was only slightly delayed in 2002 (2 days, 95% CI −1.3 to 5.4) and strongly depended on hatch date (0.89 d d^{-1}, 95% CI 0.54 to 1.3).

In winter, the sign of phenology changes reversed. The winter timing index averaged 7.7 days earlier in 2002, but the effect was not statistically significant (95% CI −23 to 7.8; $\chi^2_1 = 1.0$; p = 0.31; Figures 2B and 3). The observed difference was largely attributable to winter moults, which started 8–9 days earlier in 2002 (body moult: −9.1 days, 95% CI −23 to 5; flight feather moult: −8.1 days, 95% CI −24 to 7.7; Figures 3 and S3). In contrast, there was no advance in the timing of body mass drop (0.38 days, 95% CI −19 to 20), which occurs before moult. Winter and autumn timing indices were not correlated (r = 0.18).

Captive flycatchers significantly advanced spring phenology in 2002 relative to 1981 (Figures 2C and 3). The spring timing index averaged 9.3 days earlier in 2002 (95% CI −16 to −2.9; $\chi^2_1 = 7.3$; p = 0.007) and across cohorts males were protandric by 6.4 days (95% CI −13 to −0.18, $\chi^2_1 = 4$; p = 0.045). The spring advance was particularly evident in winter flight feather moult, which terminated 14 days earlier in 2002 (95% CI −26 to −1.8; Figures 3 and S3). End of winter body moult and start of spring migratory restlessness both occurred 4 days earlier in 2002 (body moult: −4.4 days, 95% CI −13 to 4.5; restlessness: −3.8 days, 95% CI −11 to 3.6). The timing of gonadal activation advanced clearly in males (−7.8 days, 95% CI −15 to −0.16) but not in females (0.34 days, 95% CI −7.3 to 8). There was a correlation between spring and winter timing indices (r = 0.87) but not between spring and autumn (r = 0.16).

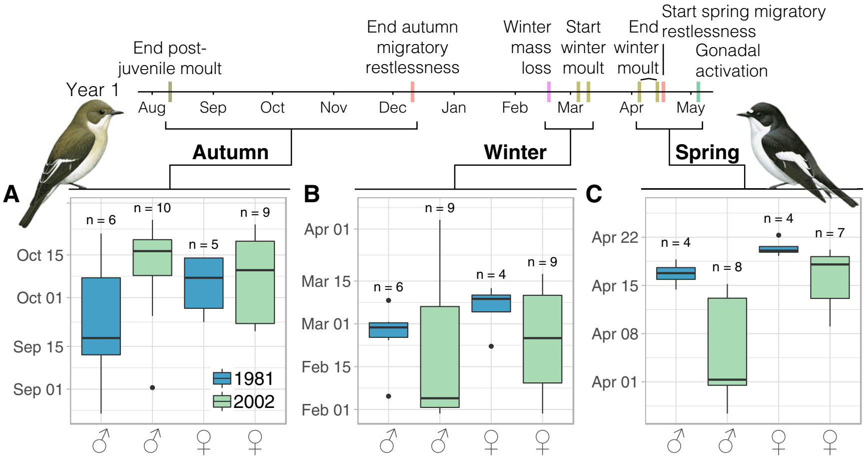

Figure 2. Changes in Captive Flycatchers

(A–C) Comparison between the 1981 (blue) and 2002 (green) cohorts in annual cycle timing (A, autumn; B, winter; C, spring). The top timeline shows the median time of each event during the year (pooled across study cohorts). Below are timing indices calculated by averaging across seasonal traits for each individual. Boxplots show the median as a line, the interquartile range as a box, and data within 1.5 times the interquartile range as whiskers; further points are shown as dots. The illustrations are reproduced with permission from *Handbook of Birds of the World* [33].
See also Figures S1–S3.

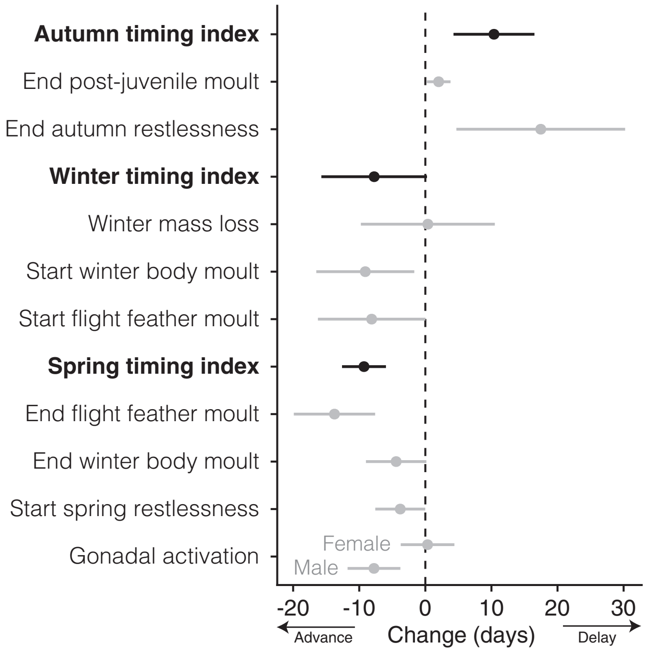

Figure 3. Differences in Timing Traits between 1981 and 2002
Shown are means and one SE of timing of captive flycatchers, estimated from linear mixed-effects models. Negative values indicate that the event occurred earlier in 2002.
See also Figures S1 and S2.

Field Data from Wild Flycatchers

To link the replicated laboratory experiment to responses in wild conspecifics, we analyzed data from a 46-year field study of nearby breeding flycatchers [34] (Figure S1), testing for changes in reproductive timing and sensitivity to local ambient temperature [35] (Figure 4). We expected the degree of advance in the spring phenology of captive birds to be comparable to that of wild conspecifics, although wild birds might show additional phenological plasticity of −1 to −2 days °C^{-1} [16].

Field data indicated that wild flycatchers also advanced spring phenology (Figure 4A). During the interval between captive studies (1981–2002), wild flycatchers commenced egg-laying progressively earlier (slope: −0.53 days year^{-1}, 95% CI −0.73 to −0.34), achieving an 11.2-day advance over those 21 years. Over the entire field time series (1973–2018), lay dates changed by −0.31 days year^{-1} (95% CI −0.39 to −0.24).

Advances of breeding phenology in wild flycatchers were partly explained by ambient temperature on the breeding grounds (Figure 4B). We identified the time window in which mean temperature was most closely associated with lay date using R package *climwin* [35, 36]. This temperature-sensitive window occurred from March 29 to May 13 (1973–2018; Figure S4; *climwin* randomization $p < 0.001$). Mean temperature during this window increased rapidly, by 0.080°C year^{-1} (95% CI 0.012 to 0.15) between the captive experiments, and by 0.063°C year^{-1} (95% CI 0.039 to 0.088) from 1973–2018 (Figure 4B).

In addition to temperature sensitivity (i.e., phenological plasticity), flycatcher lay dates also showed directional change over time. Between captive experiments (1981–2002), flycatcher lay dates covaried with temperature by −1.5 days °C^{-1} (95% CI −2.6 to −0.32) while advancing at a rate of 0.41 days year^{-1} (95% CI −0.6 to −0.21). From 1973 to 2018, plasticity was identical (−1.5 days °C^{-1}, 95% CI −2.3 to −0.72), but the rate of annual change was lower (−0.22 days year^{-1}, 95% CI −0.3 to −0.14). Hence, our study interval captured a particularly strong directional change during a period of rapid warming. These figures fit well with studies of flycatchers in regions with strongly increasing spring temperature [10, 12, 16] (Figure S4). Accounting for the effect of year was important; a model including temperature as the sole predictor overestimated plasticity (−2.7 days °C^{-1}, 95% CI −3.5 to −1.9).

Beyond advancing egg-laying, wild flycatchers advanced the timing of the temperature-sensitive window itself (Figure 4C). The mean date of the best window advanced by 0.83 days year^{-1} (bootstrapped 95% CI −1.1 to −0.45) over 24 years. Lay dates early in our time series (e.g., 1973–1995) were best explained by breeding-ground temperatures from mid-April to mid-May, while lay dates in the later years (e.g., 1996–2018) were best explained by temperatures from late March to early May.

In summary, our captive experiment revealed advances in the timing of spring events that were not likely attributable to plasticity, since flycatcher cohorts monitored in 1981 and 2002 were raised and studied under replicated laboratory conditions. Spring advances of 9 days in captive birds mirrored advances in the lay dates of wild birds of 11 days during the same period. We also detected a potential delay in autumn timing and a tendency of earlier timing in late winter in the captive birds.

Changes to the Timing Program

Our findings suggest that the circannual timing program of flycatchers has undergone phenotypic evolution. Circannual clocks are inherited [9] and track the time of year, even under constant experimental conditions. Importantly, they regulate organisms' timing responses to environmental factors, in particular, photoperiod and ambient temperature [9, 37]. Rapid microevolutionary change in the circannual program is feasible in songbirds and has been reported in Eurasian blackcaps (*Sylvia atricapilla*) [38, 39]. Timing changes may advance or delay the entire annual cycle [29], but in our captive flycatchers shifts were season specific.

In spring, the clear phenology advance of our flycatchers mirrored widely reported shifts in migratory birds [2, 5, 6, 10, 15, 25, 29], which may partly reflect high selection pressures linked to reproduction [4, 17, 18, 30]. Because early departure from African wintering quarters facilitates early arrival on the breeding grounds [40, 41], it is clear how selection for reproductive timing may translate into earlier preparation to depart Africa. Among the contributing traits, the strong advance of flight feather moult is expected because this moult is largely completed before birds migrate, whereas body moult may overlap with migration (Figure 1). A weaker signal for migratory restlessness timing may be due to the large sampling variance of that trait and our small sample size; migratory restlessness is a proxy for wild migratory behavior, and its timing is difficult to quantify with high precision [8, 42]. Our findings were robust when this trait was excluded to enable larger sample sizes (see STAR Methods). Last, as predicted for our protandric

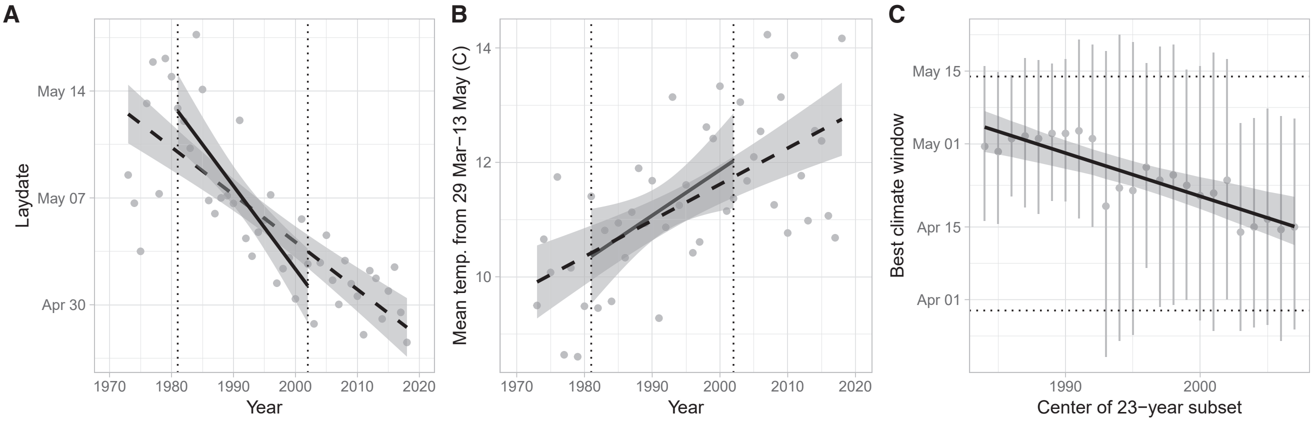

Figure 4. Changes in Wild Flycatchers

(A) Annual mean lay dates.

(B) Ambient temperature during the climate-sensitive window preceding flycatcher breeding.

(A and B) Solid lines show slopes for the time period between captive studies (delineated by vertical dotted lines); dashed slopes are over the entire study period. Error shading represents 95% confidence limits.

(C) Timing of the best model-averaged climate window for flycatcher lay dates, identified from 23-year subsets centered on the year indicated on the x axis. Gray circles show the median date of each window. The horizontal dotted lines indicate the start and end of the overall best climate window identified using the entire dataset. Shading represents 95% confidence limits from 1000 reruns of *climwin* after bootstrapping flycatcher lay dates [16].

See also Figures S1 and S4.

species, we found earlier timing in males during reproductive activation [30].

Climate-associated shifts in autumn migration timing have been reported for many avian species, with variable directionality [31, 32]. In Europe, autumn migration generally advanced in trans-Saharan migrants and single-brooded species, whereas shorter-distance and multi-brooded migrants tended to delay [31]. Flycatchers were among the slightly advancing migrants, but recent observations of increasing late, potentially second, broods (D.H., unpublished data) may indicate shifts to autumnal delays. For winter, data on changing phenology are scarce, but earlier spring departure dates have been reported, for example, for Barn swallows (*Hirundo rustica*) in South Africa [41].

Season-specific changes in phenology in our captive flycatchers imply selective modification of the underlying timing program [8]. One possible mechanism is a change to the photoperiodic response. In spring, increasing day lengths advance the annual cycle and prompt spring phenology in many bird species; in autumn, photoperiodic responses are reversed [9, 37, 43]. A spring advance could be achieved by heightened photoperiodic sensitivity [19, 22, 23], but individuals showed no correlated spring and autumn responses. Furthermore, pied flycatchers and other migrants are largely insensitive to photoperiod in winter, when the flycatchers' phenology advance began [8, 9, 43]. Instead, it is more likely that flycatchers experienced an evolutionary change to the circannual clock itself. By effectively speeding up the clock over winter, the flycatchers' spring phase and concurrent environmental sensitivity were reactivated earlier. Such a change could also explain the advance of the climate window in the wild population.

The selective advance of spring timing also argues against alternative interpretations of the differences between cohorts. Major influences of developmental factors, for example, hatching date and perinatal conditions, exclusively on spring phenology are unlikely [44, 45], in particular, because within cohorts we found no effect of hatching date on timing after the juvenile phase. Only delayed manifestation of highly specific developmental effects could explain our finding of season-specific timing shifts. Alternatively, cohort differences might have originated from sampling different subsets of the local population. By keeping collection date constant while lay dates advanced, chicks collected in 2002 originated from relatively later-laying parents than those in 1981 (Figure S2). However, this scenario predicts a timing delay in the 2002 cohort instead of the advance we observed [18].

An evolutionary response could have taken several routes seen in other taxa: first, the local population could have experienced selection on existing variation. Selection could have changed allele frequencies of genes involved in circannual rhythms and photoperiodic pathways [23, 46], or modified transgenerational epigenetic effects [45, 47]. Second, the population could have experienced introgression by earlier-timed immigrants [7]. A final possibility is random change due to genetic drift. However, spring timing is linked to fitness in flycatchers [12], and captive data paralleled the climate-linked changes in nearby wild flycatchers. This makes selection a more likely explanation [10, 12, 18, 25], potentially aided by assortative mating for timing [39].

There is growing evidence of evolutionary change in timing in response to warmer springs [2, 5, 6, 10, 15, 25, 29]. Several studies have also detected components of spring advancement that are not explained by plasticity [2, 15, 16, 25]. In a comparison of long-term breeding data of four UK songbird species [25], flycatchers were the least temperature sensitive, and the only species for which the temporal trend in lay date was significantly more extreme than could be explained by plasticity alone [25]. The authors' interpretation, that microevolution may have compensated for imperfect temperature sensitivity, accords with our findings [25]. Our full-annual cycle data from captive flycatchers identify the putative mechanism of these advancements as accelerated circannual timing during winter, before birds prepare for reproduction [3, 8, 9].

It is promising to observe season-specific change in a species whose ability to keep pace with a shifting climate may depend on its capacity for evolutionary change [8, 10, 39]. Long-distance migrants are in decline and face a myriad of anthropogenic threats. As the earth's climate continues to change, the consequences of failing to keep pace with the seasons have been well demonstrated; flycatchers are declining most strongly where they are the most mistimed relative to the spring peak in food abundance [12]. However, whether evolutionary change will suffice for flycatchers to keep pace with climate change remains to be determined. Further common garden studies over time could shed light on the evolutionary potential of phenology in a changing world.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE
- LEAD CONTACT AND MATERIALS AVAILABILITY
- EXPERIMENTAL MODEL AND SUBJECT DETAILS
  - Pied flycatchers
- METHOD DETAILS
  - Description of replication study in captivity
  - Description of field study
  - Breeding phenology
- QUANTIFICATION AND STATISTICAL ANALYSIS
  - Analysis of captivity data
  - Annual cycle timing traits
  - Model construction and evaluation
  - Analysis of field data
- DATA AND CODE AVAILABILITY

SUPPLEMENTAL INFORMATION

Supplemental Information can be found online at https://doi.org/10.1016/j.cub.2019.08.072.

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AUTHOR CONTRIBUTIONS

B.H. helped the late Ebo Gwinner with the design and execution of the captive study. U.H. and D.H. collected the field data. B.M.V.D. carried out all analyses, with help from B.H., and B.H. and B.M.V.D. wrote the paper.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Experimental Models: Organisms/Strains		
Pied flycatchers (*Ficedula hypoleuca*)	Wild-caught	N/A
Deposited Data		
Custom analysis scripts and associated data	This paper	https://doi.org/10.17632/6n38vwnwc7.1
Software and Algorithms		
R statistical computing environment	https://cran.r-project.org	N/A
Other		
Local hourly ambient temperature data from two weather stations in southwest Germany	German weather service	https://www.dwd.de/EN/climate_environment/cdc/cdc_node.html

LEAD CONTACT AND MATERIALS AVAILABILITY

Further information and requests for resources should be directed to and will be fulfilled by the Lead Contact, Barbara Helm (b.helm@rug.nl). This study did not generate new unique reagents.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Pied flycatchers

The experimental subjects were pied flycatchers (*Ficedula hypoleuca*). All experimental procedures conformed to the relevant regulatory standards under permit by the state of Upper Bavaria, Germany.

METHOD DETAILS

Description of replication study in captivity

Pied flycatchers from southwest Germany were studied in the Max Planck Institute for Ornithology by the late Eberhard Gwinner in research on circannual rhythms and photoperiodism [9, 13, 27]. The original studies in the 1980s established the annual cycle of hand-raised birds under different photoperiodic cycles [13, 27]. One experiment in 1981 [27] mimicked the natural daylengths experienced by the birds during breeding, on migration, and in their West African wintering area (10° N). Under these conditions, captive young flycatchers underwent post-juvenile moult soon after independence and started autumn migratory restlessness at very young ages (Main text, Figure 1). Autumn migratory restlessness was often biphasic and extended into early winter. The substantial fat reserves deposited in autumn were also maintained until late winter. Thereafter, the flycatchers lost these fat reserves and undertook prenuptial winter moult of body plumage, as well as tertials and some inner secondaries (collectively “flight feathers”). Moult was followed by the start of spring migratory restlessness and gonadal growth.

In 2002, Gwinner, with help from author BH, replicated this study under identically mimicked conditions [13, 27], although sadly he did not live to see the full results. The goal of the replication was to test for evolutionary change in flycatcher timing since 1981. Gwinner collected flycatchers in 2002 from the same area as in 1981 (Figure S1), hand-raised them in the same way, and tested them under identical conditions, using original lighting devices and both, original and new recording methods.

In 2002, birds were collected in Lahr in southern Germany (48.3° N / 7.3° E; elevation 160 m asl; Figure S1) as nestlings and hand-raised as described earlier [48]. For precise replication, nestlings were collected at similar dates and ages (Figure S2). Because the timing of a bird’s hatching may influence the timing of subsequent events in its annual cycle [44], we tested whether hatch date was significantly different between cohorts. There was no detectable difference between the 1981 and 2002 cohorts tested by linear model (effect = 1.61 days, $t_{30} = 0.97$, $p = 0.34$), nor between males and females (effect = -2.49 days, $t_{30} = -1.59$, $p = 0.12$), and the interaction term was likewise not significant (effect = 2.08 days, $t_{29} = 0.62$, $p = 0.54$). In 1981, mean hatch date was ordinal (julian) day 148.5; in 2002, it was day 150. Hatch date was also included in all our models and was not a significant predictor of any timing trait, with the exception of the end of postjuvenile moult. Age at collection also did not differ (8.4 days in 2002; 9.0 days in 1981; t test, $p = 0.52$).

Once independent, young birds were kept in individual cages (42x23x23cm) in climate-controlled chambers (ca. 20°C) with light provided by 40-W fluorescent bulbs in the daytime (400 lx at perch level) and by 10-W incandescent bulbs at night (ca. 0.01 lx). Birds were exposed to simulated local daylength until the approximate start of autumn migration. Thereafter, they were progressively shifted to the photoperiodic conditions they would naturally experience *en route* and at their West African wintering areas slightly north of the equator, based on information from ringing and field data [40, 49]. Because birds were thereafter kept at a simulated latitude of 10°N for further study, the end of migratory restlessness, gonadal regression, and post-nuptial moult were not analyzed.

Birds were weighed and checked for moult at least weekly, and every 2-3 days during the post-juvenile period, by the Institute team led by the authors of the original flycatcher study [13]. We checked body moult by inspecting the entire bird and scored presence of moult if we detected feather growth in any of 19 defined body areas. Wing moult was scored for each flight feather of the right wing following [50]. In addition, starting in their first winter, birds of both sexes were assessed for the state of their reproductive development (testis diameter in males, diameter of the largest follicle in females) by laparotomy approximately every three weeks [51].

To quantify the timing of migratory restlessness, we measured activity continuously to identify phases of nocturnal activity [42]. Activity was recorded throughout the study period via microswitches attached to the perches. We then derived the number of 30-min intervals showing any activity during the night (i.e., during the lights-off period, discounting immediate effects of switching on and off of the lights). We analyzed the resulting time series of nocturnal activity with a changepoint algorithm that defines the start and end of migratory restlessness [42].

Because the point of our experiment was to investigate whether flycatchers had changed their behavior compared to the original captivity experiment 21 years ago, we took particular care to ascertain that in 2002 we quantified the birds' behavior in the same ways as in 1981, and that no systematic measurement bias occurred between replicates. In 2002, microswitch data were collected electronically for all birds by computer-based event recorders. In 1981, the microswitches were attached to an inkwriter (Esterline Angus, Washington USA). The inkwriter recorded activity onto time-charted paper rolls, after which the ink marks were hand-counted by an observer. For each 30 min interval on the recording paper that showed an ink mark during night hours, a bird was scored as "active" for that interval.

In order to minimize differences between the 1981 and 2002 replicates, we carried out two calibration steps of recording methods. The first involved comparing activity recording by inkwriters to those of electronic event recorders. In 2002, in parallel to electronic event recorders, we recorded activity with two Esterline-Angus inkwriters from the original stock, which we moved between cages during the entire recording period. In each cage, birds were recorded simultaneously by both methods for one week, and then the inkwriters were moved to the next bird, so that 2-3 weeks of comparative data were available for all birds. We then hand-counted the ink recordings for comparison with the parallel electronic recordings. Using a linear mixed-effects model (n = 328 nights of paired recordings), we quantified the methods' repeatability and the mean difference between them: repeatability was high (0.951), and the mean difference was 0.75 (95% CI 0.56 to 0.95).

Additionally, we calibrated our hand-counting in 2002 against hand-counting in 1981 using the original ink paper rolls of 5 birds from the 1981 experiment. Our new counts were compared against those noted in the original scoring sheets from 1981 for the same birds. The repeatability (quantified as above) was 0.952 (n = 590 recounted nights). The recounting slightly overestimated activity compared to the original count (mean = 1.01, 95% CI 0.93 to 1.10).

Thus, the calibration data indicated close correspondence between the methods. The slight deviations in both steps are expected to partially offset each other. The original observer of ink counts had counted somewhat more conservatively, but the new electronic method, in turn, was slightly more conservative than the inkwriter. Remaining small mean differences between methods were not expected to affect outcomes because we generated bird-specific estimates for start and end of migratory restlessness by changepoint analysis, which uses relative differences in time series [42]. Thus, we are confident that we measured behavior equivalently in the two replicates.

Description of field study

We obtained field information from three sites, which, like the origin of the captive population, were all located in the Upper Rhine valley (Figure S1; see there for distances). One site is an active study location of free-living flycatchers [34]. The remaining two sites are weather stations, which framed the flycatcher sites to the north and south within the Rhine valley.

Breeding phenology

To assess changes in local pied flycatcher breeding phenology in the wild during the study period, we used a 46-year dataset from Harthausen near Speyer, Germany (49.3° N / 8.4° E; elevation 105 m asl; Figure S1). From 1973-2018, authors DH and UH collected information on the timing of clutch initiation (laydate), hatching, and breeding success of a population of flycatchers, monitoring 55 ± 14 nests per year, of which we obtained laydate information from 40 ± 15 per year. Data were gathered as part of a ringing study in a nest-box population situated in a mixed coniferous/deciduous woodland at 100 m asl [34]. First arrival of birds was in the first ten days of April (range: 1 to 9 April; data from 15 years). Mean clutch size was 6 eggs, mean incubation period 12 days (12.4 ± 1.73 days; n = 49 nests from 2 years; Hoffmann, unpubl.), and on rare occasions birds were double-brooded. To focus on changes at the start of the breeding season, we followed [16] by only including clutches initiated within 30 days of the mean laydate of the first five nests in a given year. In total, we analyzed laydates from 1,834 clutches over 46 years (998 of which occurred in the 21 years spanning the captive studies). In our phenology analyses, we used the mean laydate for each year.

Local ambient spring temperature

We obtained local hourly ambient temperature data from two weather stations in southwest Germany (German weather service, https://www.dwd.de/EN/climate_environment/cdc/cdc_node.html; Figure S1): Mannheim (station ID 5906; 49.47°N, 8.50°E) and Freiburg (station ID 1443; 48.02°N, 7.83°E) from 1973 to 2018. Ambient temperatures of the two stations were closely correlated during the study period (r = 0.96). We averaged the temperature data from these two stations to develop a single regional temperature measure relevant for our flycatcher studies. For missing hourly data points (0.03% of data), we used an exponentially weighted moving average to replace the missing temperature values.

QUANTIFICATION AND STATISTICAL ANALYSIS

Analysis of captivity data

Overall, we compared data from 11 birds from 6 families in 1981 (5 females and 6 males), and 22 birds from 8 families in 2002 (11 females and 11 males). In spring, data were missing for one 2002 bird, and for autumn migratory restlessness, data were missing for three 2002 birds.

Annual cycle timing traits

We compiled data on the timing of moults, migratory restlessness, body mass, and reproductive activation (Main text, Figure 1). The timing of migratory restlessness was quantified from nightly activity profiles as described above. The timing of body mass changes was also quantified using changepoint analysis [42] to determine the date at which a bird shifted from high (winter) to low (spring) body mass states. Moult timing traits were dates of start and end. For the body and flight feather moults, we defined start as the first date on which a given moult was recorded, and end as the last date of recording this moult. We quantified variation in reproductive timing with weighted averages, weighting each measuring date by gonad size on that date. Thus, birds that showed enlarged gonads earlier in the season were assigned an earlier date, and vice versa. We did not include the declining phase of the reproductive cycle.

Because we had season-specific predictions, we analyzed timing traits in seasonal blocks. In autumn, our measures included only the end date of post-juvenile body moult and the end date of autumn migratory restlessness. We did not use the start dates because on several occasions these events may have started before data collection began. In winter, we used the start dates of winter moult of body plumage and flight feathers, and the start date of the winter drop in mass. Finally, in spring, we examined the end dates of winter body plumage and flight feather moult, the start date of spring migratory restlessness, and the weighted mean date of gonadal activation as described above.

Model construction and evaluation

We used linear mixed-effects models (lme4 package in R [52]) to test for a difference between cohorts in timing traits during autumn, winter, and spring. Because our hypotheses were structured by season and all of our predictors (traits) were in the same units (days), we first derived seasonal timing indices by averaging across seasonal traits for each individual. We thus obtained autumn, winter, and spring mean timings for each bird. We could not compare seasonal means for individuals missing data in any trait in a season, so we excluded individuals with missing data. We retained 30 birds in autumn (11 from 1981, 19 from 2002) and 28 in winter (10 from 1981, 18 from 2002). In spring, we had 23 individuals with complete data (8 from 1981, 15 from 2002); an additional 5 did not show any spring migratory restlessness or were not monitored. Therefore, we calculated two versions of the spring index, one including migratory restlessness but fewer (23) birds, and another version that excluded migratory restlessness but included 28 birds (10 from 1981, 18 from 2002). Both versions produced highly similar results in our analysis. The spring index without migratory restlessness, including the five additional individuals that were missing data, averaged 8.5 days earlier in 2002 (95% CI -17 to -0.49), compared to 9.3 days earlier (95% CI -16 to -2.9, $\chi^2_1 = 7.3$, $p = 0.007$) based on the 23 individuals with complete data (see Main text).

The response variables were the seasonal timing indices. We included a random intercept of brood ID (sibgroup) to account for any similarities in timing due to genetic similarities among siblings. The fixed effects were cohort (1981 or 2002), sex, a cohort × sex interaction, and hatch date (to account for any effect of the timing of hatching on subsequent annual cycle timing). To maximize the precision of our estimates given a small sample size, we removed non-cohort fixed effects if they were weakly supported ($p > 0.15$). We report effect sizes, 95% confidence intervals, and likelihood ratio test P values for remaining fixed effects. If there was evidence for a cohort × sex interaction, we report separate effects for males and females.

After testing seasonal indices, we repeated the above procedure for each individual timing trait and present effect sizes and confidence intervals for the effect of cohort on these traits. Our goal here was to better understand the drivers of seasonal differences while fully utilizing all data.

Analysis of field data

We tested for change in laydate (d_{lay}) with linear models. For nests where hatchdate (d_{hatch}) but not laydate was recorded, we estimated laydate with the following formula:

$$d_{lay} = d_{hatch} - (N_{egg} - 1) - 12$$

where N_{egg} is the number of eggs in the complete clutch. The constant 12 reflects the local incubation period.

We used the R package *climwin* [36] to identify the absolute spring time window ("climate window") in which mean ambient temperature at the breeding site most closely predicted breeding phenology (Figure S4). We searched all climate windows of one week or longer in duration, up to 90 days before the last recorded laydate in our dataset (4 June). Searching a large number of climate windows increases the likelihood of a false positive result. Therefore, we used the *randwin* function to create 100 randomized datasets and used the *pvalue* function to determine the probability of discovering the relationship we observed by chance. We determined overall start and end dates by taking an average across models, weighted by the Akaike model weights provided by *climwin*.

We also calculated climate windows for direct comparison with another recent study of phenology in flycatchers [16]. Samplonius et al. [16] (see Figure S4) restricted the length of study years and set their reference date to the average of annual mean laydates (May 2 in our case), searching all possible climate windows at least 15 days in duration between 0-60 days before this date. This was in contrast to the wider search interval (90 days) and the later reference date (June 4) in our analysis, which yielded a larger number of possible windows.

Once we identified these biologically-relevant time windows, we calculated the mean temperature for each year during the window and regressed these values against year to determine the change in temperature during the study period (21 years) and over the entire time series (46 years). We then constructed linear models where the response variable was mean annual laydate. In one model, we included temperature as the sole predictor. In a second model, we included both temperature and year; this allowed us to test whether there was a significant effect of year while accounting for plasticity in response to temperature, and vice versa. In both models, we weighted each observation by the square root of the number of nests monitored in that year.

Because we expected an advance in the birds' spring phenology, we speculated that the birds' climate-sensitive window itself may have also advanced. We explored the possibility of a shifting window by searching for climate windows across different subsets of study years. Specifically, we used subsets that were 23 years in duration (50% of the years in the study), incremented by one year. For example, we started with the 23-year subset from 1973-1995, then 1974-1996, then 1975-1997, etc., until the final subset of 1996-2018. Therefore, in total we tested 24 different subsets. In this manner, we investigated robustness of the climate window approach to small changes in the choice of study years and searched for any longitudinal trends in identified climate windows. We calculated the slope of change in the median date of the window over time and performed 1000 bootstrapped reanalyses with *climwin* to assess the robustness of the slope to variation in sampled nests.

DATA AND CODE AVAILABILITY

All biological data used in the analysis are available within the article and on the Mendeley Data repository (https://doi.org/10.17632/6n38vwnwc7.1). The weather data are publicly available from the German weather service: https://www.dwd.de/EN/climate_environment/cdc/cdc_node.html).

Current Biology, Volume *29*

Supplemental Information

Evolutionary Response to Climate Change in Migratory Pied Flycatchers

Barbara Helm, Benjamin M. Van Doren, Dieter Hoffmann, and Ute Hoffmann

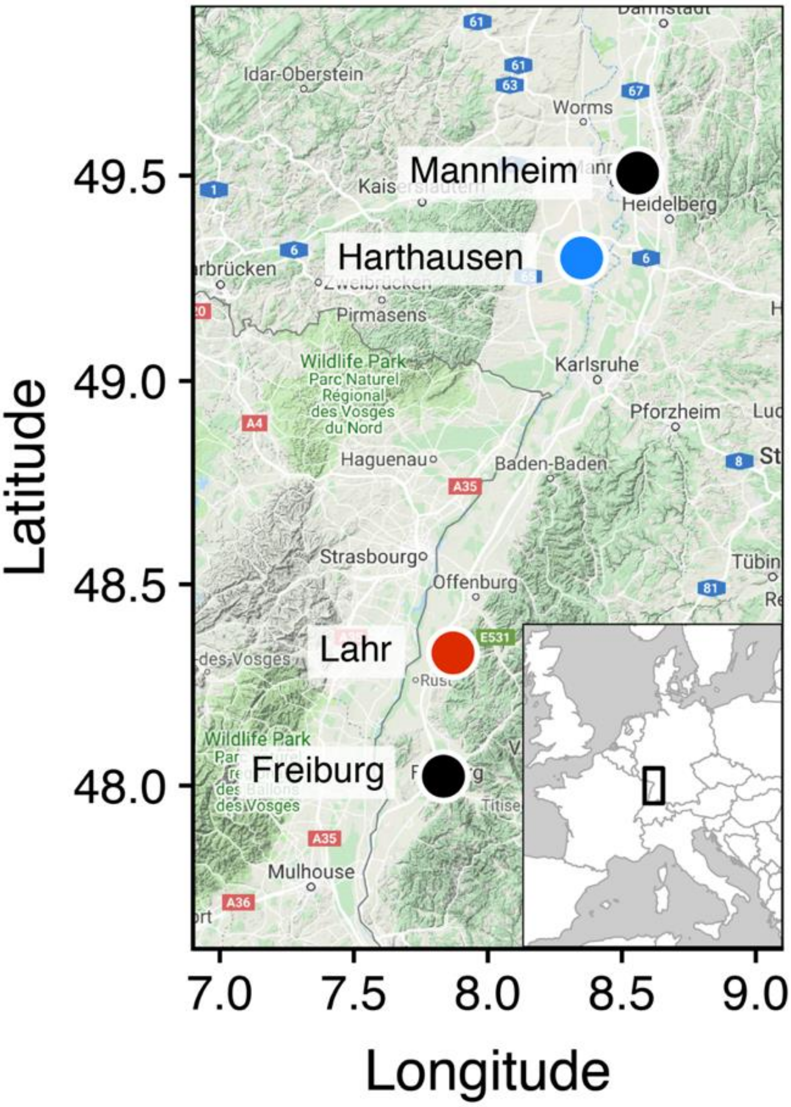

Figure S1. Field sites, located in the Upper Rhine Valley, Germany. Related to Figures 1-4. Black markers indicate the two weather stations (Freiburg and Mannheim, 173 km apart) whose data were averaged. Red marker (Lahr) shows field site of the captive flycatchers, 34 km from Freiburg. Blue marker (Harthausen) shows the wild population, 113 km from Lahr and 27 km from Mannheim. Inset: black rectangle shows the location within Central Europe; map sourced from Google Maps.

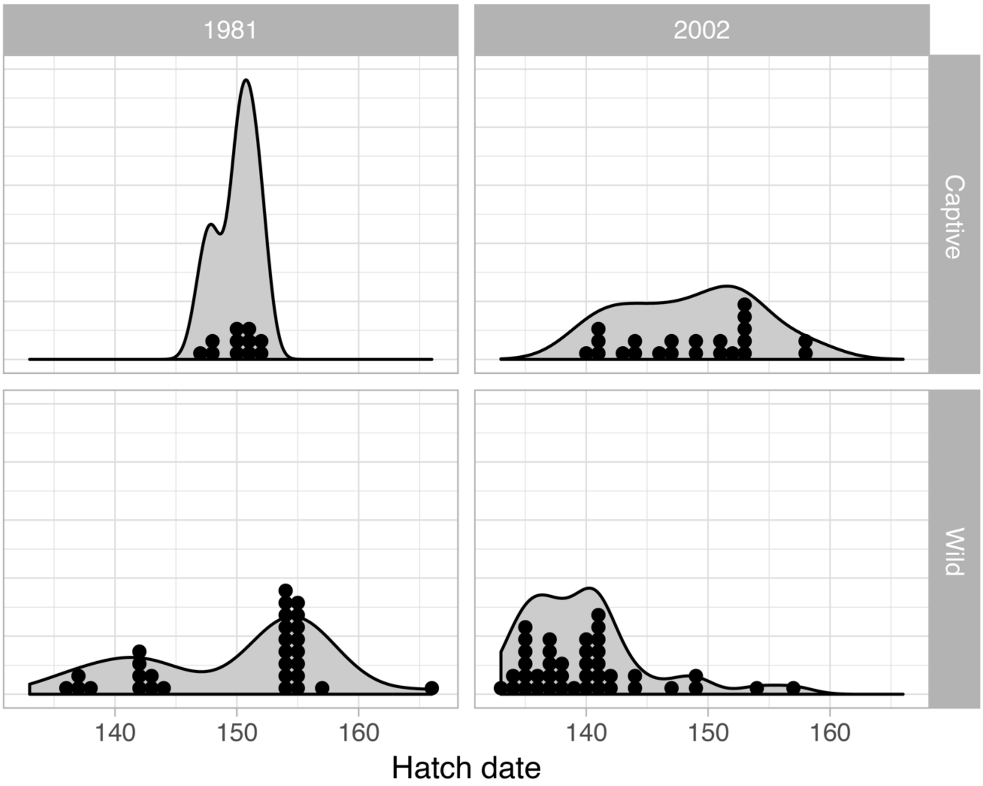

Figure S2. Hatch dates of captive (upper panels) and wild (lower panel) pied flycatchers in 1981 (left) and 2002 (right). Related to Figures 1-3. Each black circle represents one individual, shading indicates Kernel density estimates.

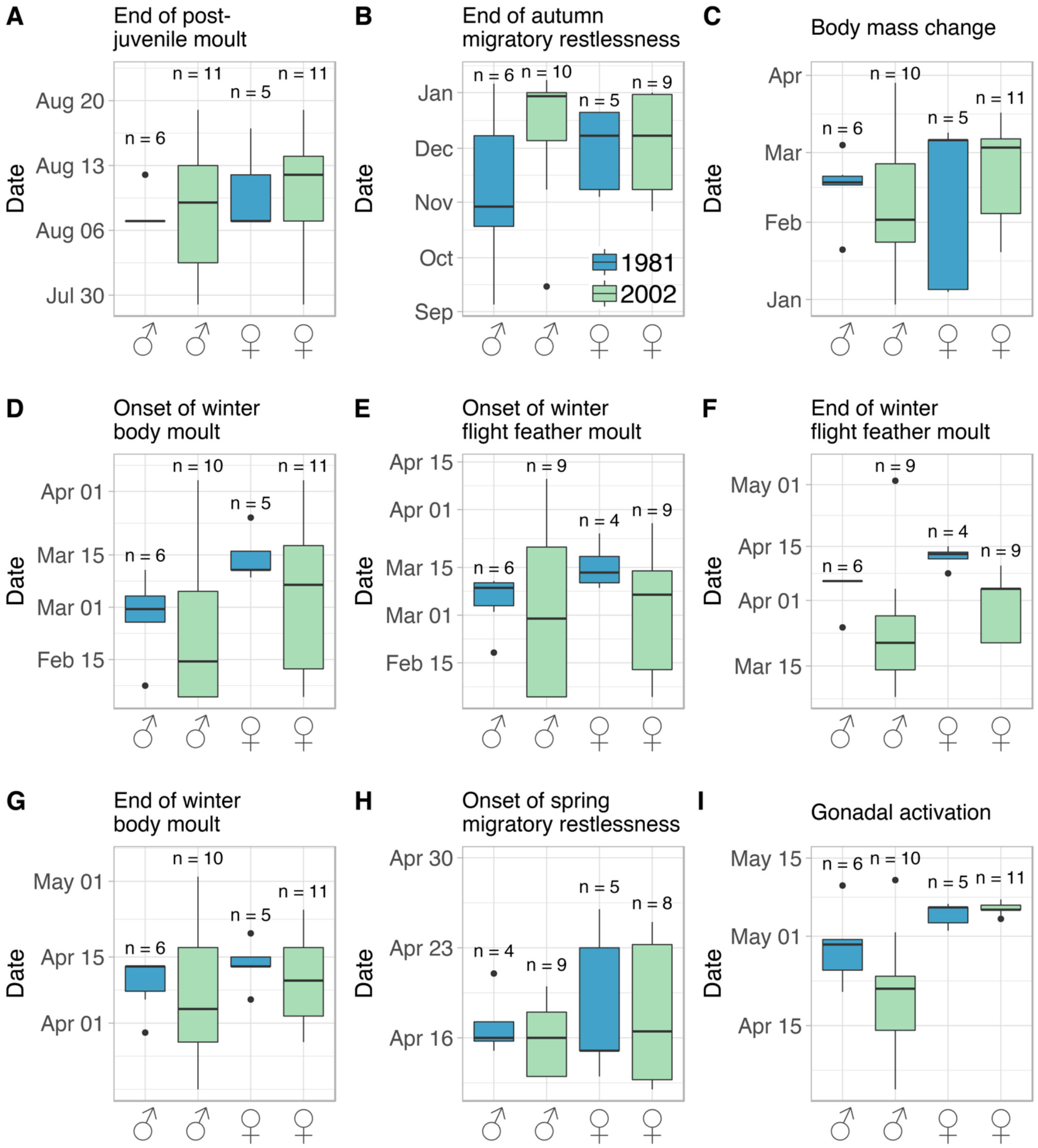

Figure S3. Timing traits by age and sex in 1981 and 2002. Related to Figure 2. Boxplots show the distribution of annual cycle events observed in captivity in 1981 (blue) and 2002 (green) for male and female flycatchers; for details, see Main text, Figure 2. **(A)-(I)** show individual timing traits as indicated by figure titles.

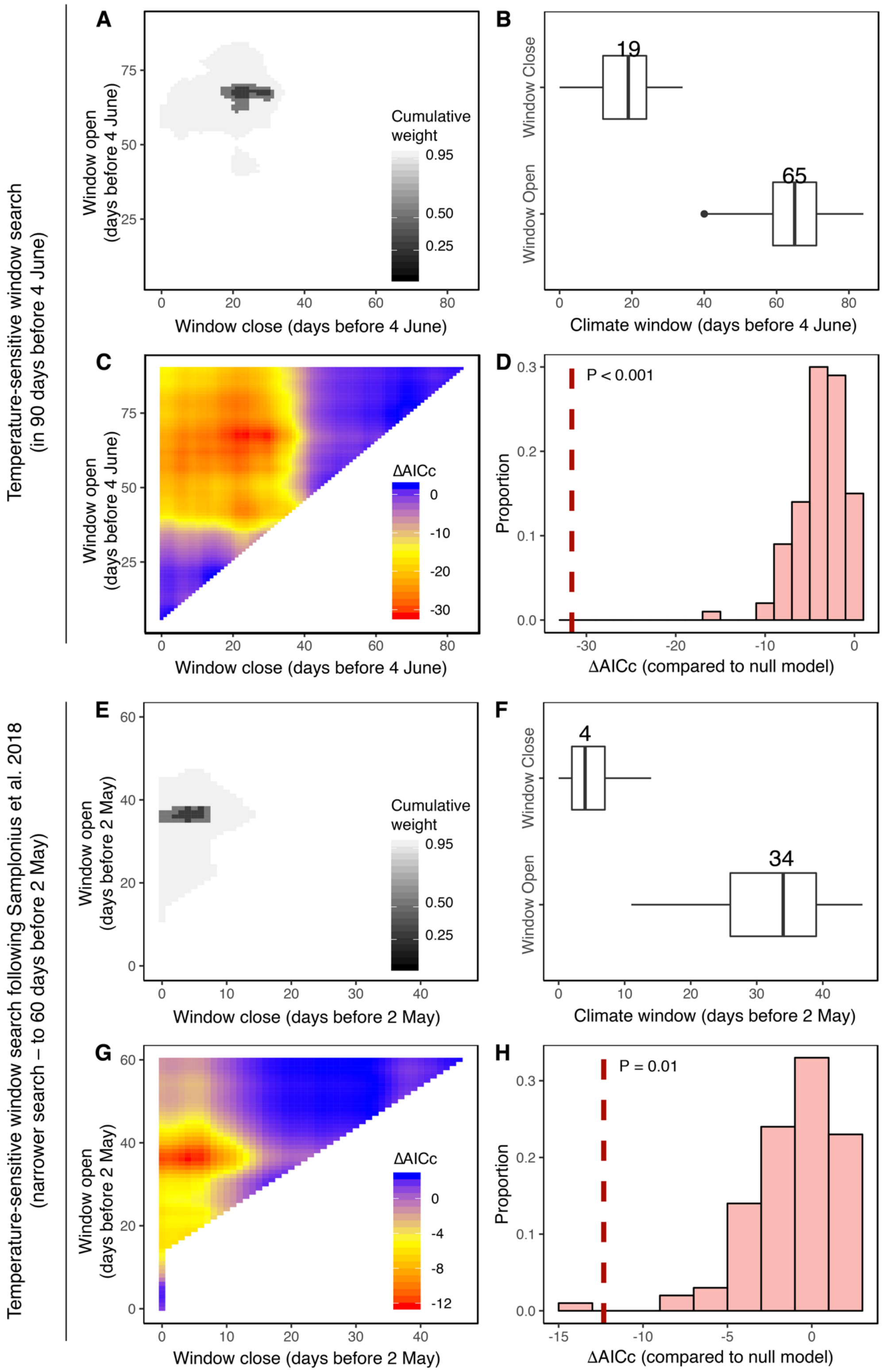
Temperature-sensitive window search
(in 90 days before 4 June)
A
Window open
(days before 4 June)
Window close (days before 4 June)
Cumulative
weight
0.95
0.50
0.25
B
Window Close
Window Open
19
65
Climate window (days before 4 June)
C
ΔAICc
0
-10
-20
-30
D
P < 0.001
Proportion
ΔAICc (compared to null model)
Temperature-sensitive window search following Samplonius et al. 2018
(narrower search – to 60 days before 2 May)
E
Window open
(days before 2 May)
Window close (days before 2 May)
F
4
34
Climate window (days before 2 May)
G
ΔAICc
0
-4
-8
-12
H
P = 0.01
Proportion
ΔAICc (compared to null model)

Figure S4. Identification of the time window in which mean ambient temperature best explains flycatcher laydate. Related to Figure 4. (A–D) Only in a small number of windows did mean breeding site temperature show a strong relationship with laydate. The model-averaged best climate window occurred between March 29 and May 13. **(A)** Cumulative model weight; models summing to 0.95 of cumulative weight occupied a small range of windows. **(B)** Boxplots indicating the starting and ending dates of models summing to 0.95 cumulative weight; boxplots show the median as a line, the interquartile range as a box, and the farthest outliers less than 1.5 times the interquartile range from the box as whiskers. **(C)** Heatmap showing ΔAICc values for all tested climate windows. **(D)** Results of a randomization procedure to determine the probability that the observed signal is a false positive; histogram shows the lowest ΔAICc value for each randomization, and the red dashed line indicates the observed lowest ΔAICc value. **(E-H)** Samplonius et al. [S1] compared several flycatcher populations. Compared to our study, they used different years (1991-2015) and examined a narrower temporal range for possible climate windows. If we apply these methods to our population, estimated slopes of temperature and flycatcher laydate against year for 1991-2015 are comparable with Figure 4 in [S1]: temperature: 0.074 ºC yr^{-1}, 95% CI [0.0055,0.14]; laydate: -0.26 d yr^{-1}, 95% CI [-0.39, -0.13]). The model-averaged best climate window occurred between March 26 and April 27. The relationship between laydate and temperature, accounting for longitudinal change over time, was -1.1 d $ºC^{-1}$ (95% CI [-1.8,-0.37]), and the rate of annual change was -0.18 d yr^{-1} (95% CI [-0.31,-0.056]). Not accounting for longitudinal trend, the relationship between laydate and temperature was -1.5 d $ºC^{-1}$ (95% CI [-2.2,-0.75]). Our detected rate of change in laydate (-0.26 d yr^{-1}) was consistent with the advance predicted by Samplonius et al. [S1], given a measured change in temperature of 0.074 ºC yr^{-1} (see Figure 4 in that study). Similarly, our measured degree of plasticity (-1.1 d $ºC^{-1}$, accounting for the effect of year) is comparable with other flycatcher populations in Figure 3 in [S1].

Supplemental Reference

S1. Samplonius, J.M., Bartosova, L., Burgess, M.D., Bushuev, A.V., Eeva, T., Ivankina, E.V., Kerimov, A.B., Krams, I., Laaksonen, T., Magi, M., et al. (2018). Phenological sensitivity to climate change is higher in resident than in migrant bird populations among European cavity breeders. Glob Change Biol *24*, 3780-3790.

Part II

A continental perspective

Delmore, K., **Van Doren, B.M.**,* Conway, G.J., Curk, T., Garrido-Garduño, T., Germain, R.R., Hasselmann, T., Hiemer, D., van der Jeugd, H.P., Justen, H., Lugo Ramos, J.S., Maggini, I., Phillips, R.J., Remisiewicz, M., Roberts, G.C.M., Sheldon, B.C., Vogl, W., and Liedvogel, M. Formatted for* Current Biology.

** Equal contributions.*

3

Versatile migratory strategies in blackcaps

3.1 Summary

Migration is ubiquitous in the animal kingdom and may play a key role in promoting reproductive isolation (Bearhop et al. 2005; Bensch et al. 1999; Helbig 1991b; D. E. Irwin and J. H. Irwin 2005) and underpinning responses to environmental change (Berthold et al. 1992; Plummer et al. 2015). Migratory divides are contact zones between populations with different migratory phenotypes and ideal natural laboratories for studying the evolution of migration (Delmore and D. E. Irwin 2014; Delmore et al. 2016). The Eurasian blackcap (*Sylvia atricapilla*) is a songbird that exhibits a migratory divide in central Europe between populations that migrate southwest (SW) and southeast (SE) in autumn (Helbig 1991a; Helbig 1991b; Helbig 1992) and has recently established a wintering population in Britain (Bearhop et al. 2005; Berthold et al. 1992; Berthold and Terrill 1988; Leach 1981). We tracked 108 annual migrations of 100 blackcaps captured across their range to characterize both the migratory divide and novel wintering strategy. Blackcaps to the west and east of the divide used predominantly SW and SE directions, respectively, but close to the contact zone many individuals took intermediate (S) routes. At 14.0ºE, we documented a sharp transition (22 km) in migratory direction from SW to SE, implying a strong selection gradient across the divide. Blackcaps wintering in Britain took northwesterly migration routes from continental European breeding grounds. They originated from a surprisingly extensive area, spanning 2000 km of the breeding range. British winterers bred in sympatry with SW-bound migrants but arrived 10 days earlier on the breeding grounds, suggesting some potential for assortative mating by timing. Overall, our data reveal complex variation in songbird migration and suggest that selection can maintain variation in migration direction across short distances while enabling the spread of a novel strategy across a wide range.

Keywords: migration, divide, timing, songbird, speciation, assortative mating

3.2 Results and Discussion

Pioneering studies of blackcaps revealed that songbird migration has a genetic basis and can rapidly evolve, and these findings underlie much of our current understanding of bird migration (Bearhop et al. 2005; Berthold et al. 1992; Berthold 1988; Berthold and Pulido 1994; Helbig 1991a; Helbig 1996; Mueller et al. 2011; Pulido et al. 2001; Pulido 2007; Pulido and Berthold 2010; Pulido et al. 1996; Rolshausen et al. 2009). Today, blackcaps may offer important insight into adaptation to environmental change, as recent population increases (EBCC/BirdLife/RSPB/CSO 2018) and new routes (Berthold et al. 1992) illustrate how this species has successfully kept pace with a changing world. A major limitation of past studies on blackcaps has been a reliance on indirect experiments in captivity (see Chapter 1; Zúñiga et al. 2016) and infrequent recaptures of ringed birds to infer phenotypes. We sought to bridge this gap by intensively tracking blackcaps in the wild across the species' range, examining the processes shaping migratory divides and contemporary migratory change, and placing our results in an evolutionary context.

3.2.1 Tracking blackcaps across a migratory divide

Ringing and orientation studies suggest that a migratory divide exists in central Europe between blackcaps that migrate SW and SE, running north-south at 14ºE (Helbig 1991b; Helbig 1992). We tracked 41 annual migrations of 36 adult male blackcaps from breeding territories across the divide in Austria. To contrast behavioral variation inside and outside the divide, we also tracked blackcaps (3 F, 39 M) from breeding sites in the Netherlands (N=21), west Austria (N=6), central Germany (N=4), northern Poland (N=8), and east Austria (N=3). We expected to find a mix of strategies in the divide versus pure SW and SE directions at sites west and east of the divide, respectively.

Our tracks from central Austria clearly demonstrate the existence of a migratory divide (Figures 3.1, 3.2 & 3.3). We estimated each blackcap's autumn migration direction by drawing a rhumb line between breeding and wintering areas. Migration directions varied between 130 and 288º. Intermediate (S) routes were more common (53.7%) than SE (26.8%) and SW (17.1%) strategies (Figure 3.1A). One individual from within the divide migrated NW to winter in Britain. Multi-year tracks revealed highly repeatable routes (Figure 3.4). Among-individual variation in migratory direction was considerably greater in the divide (Figure 3.5), suggesting that the contact between migratory phenotypes gives rise to increased diversity of behaviors.

A cline analysis using migration directions suggests that strong selection is maintaining the divide. Specifically, we examined the change in directions from western Austria (entirely SW), through the divide to eastern Austria (largely SE) (Figure 3.2; see Methods). We fit a cline through these directions to characterize its center and width. Clines maintained by selection should be narrow relative to dispersal distance, with a rapid transition between phenotypes (Barton and Gale 1993). Our data showed this pattern: the center of the cline occurred at 14.0ºE [interval within two log-likelihood units: 13.8–14.2º], and its width was only 22 km [2LL: 14–93 km]. This transition from SW to SE directions is very narrow compared to the average natal dispersal distance in blackcaps of 41.2 km (Paradis et al. 1998).

Our data do not allow direct identification of the source of selection, but possible processes include prezygotic selection for assortative mating and postzygotic selection reducing the fitness of hybrids. We discuss the potential for assortative mating in the next section. Helbig (1991a) selectively mated SW and SE blackcaps in captivity and observed intermediate orientations in their offspring. He argued that these

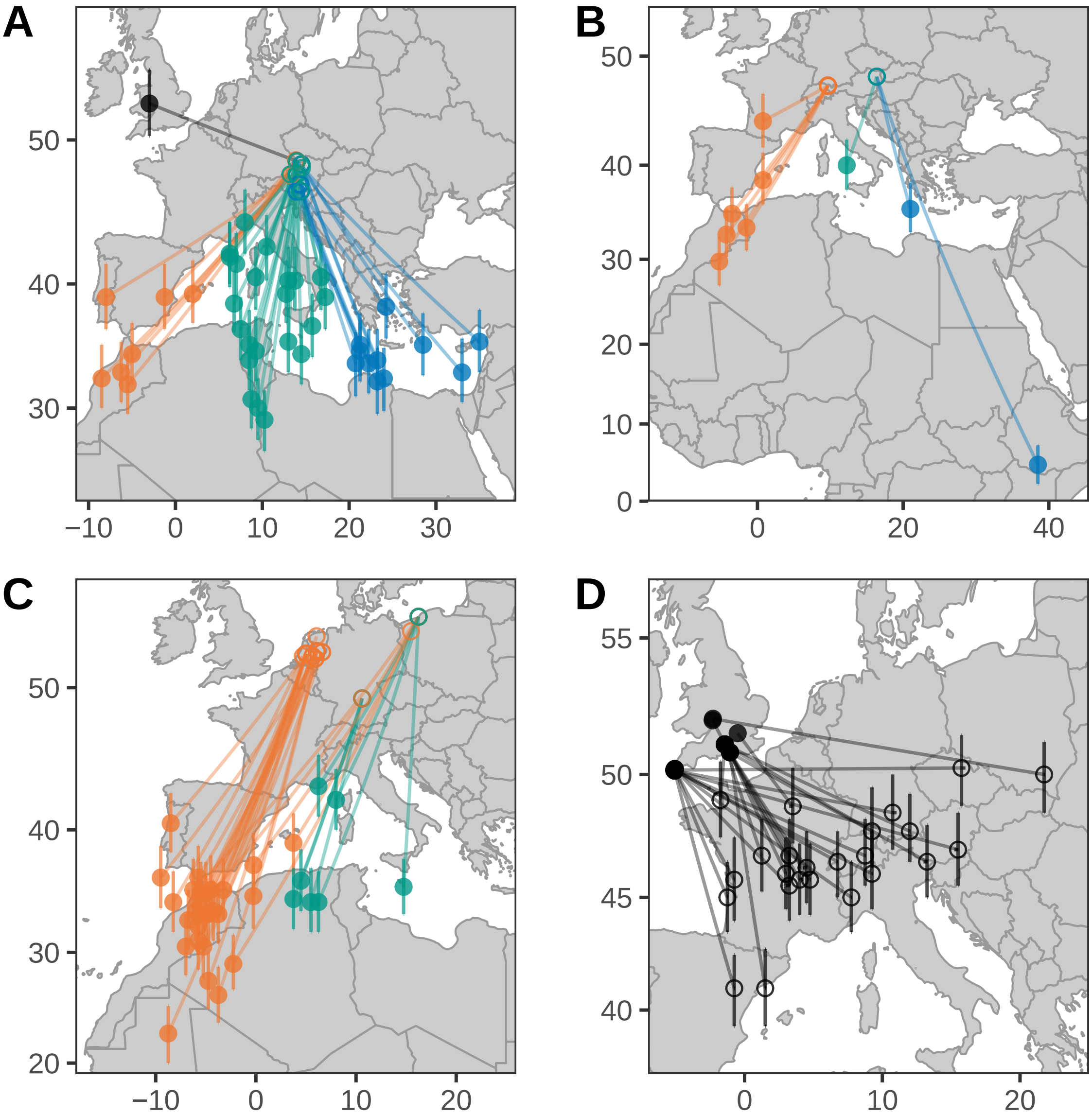

Figure 3.1: Wintering (i.e. non-breeding) and breeding locations of migratory blackcaps. Wintering and breeding location estimates made with `GeoLight` shown with closed and open circles, respectively. Uncertainty in latitude estimation is indicated with vertical bars, which show estimates for sun angles higher and lower than the calibrated sun angle by 1º (following Hiemer et al. 2018). Colors indicate SW (orange)/intermediate (green)/SE (blue)/NW (black) phenotypes, categorized by wintering location. **(A)** Blackcaps breeding within the central European migratory divide transect in Austria. **(B)** Blackcaps breeding in Austria east or west of the migratory divide. **(C)** Blackcaps breeding in the Netherlands, southern Germany, and northern Poland. **(D)** Blackcaps wintering in Britain.

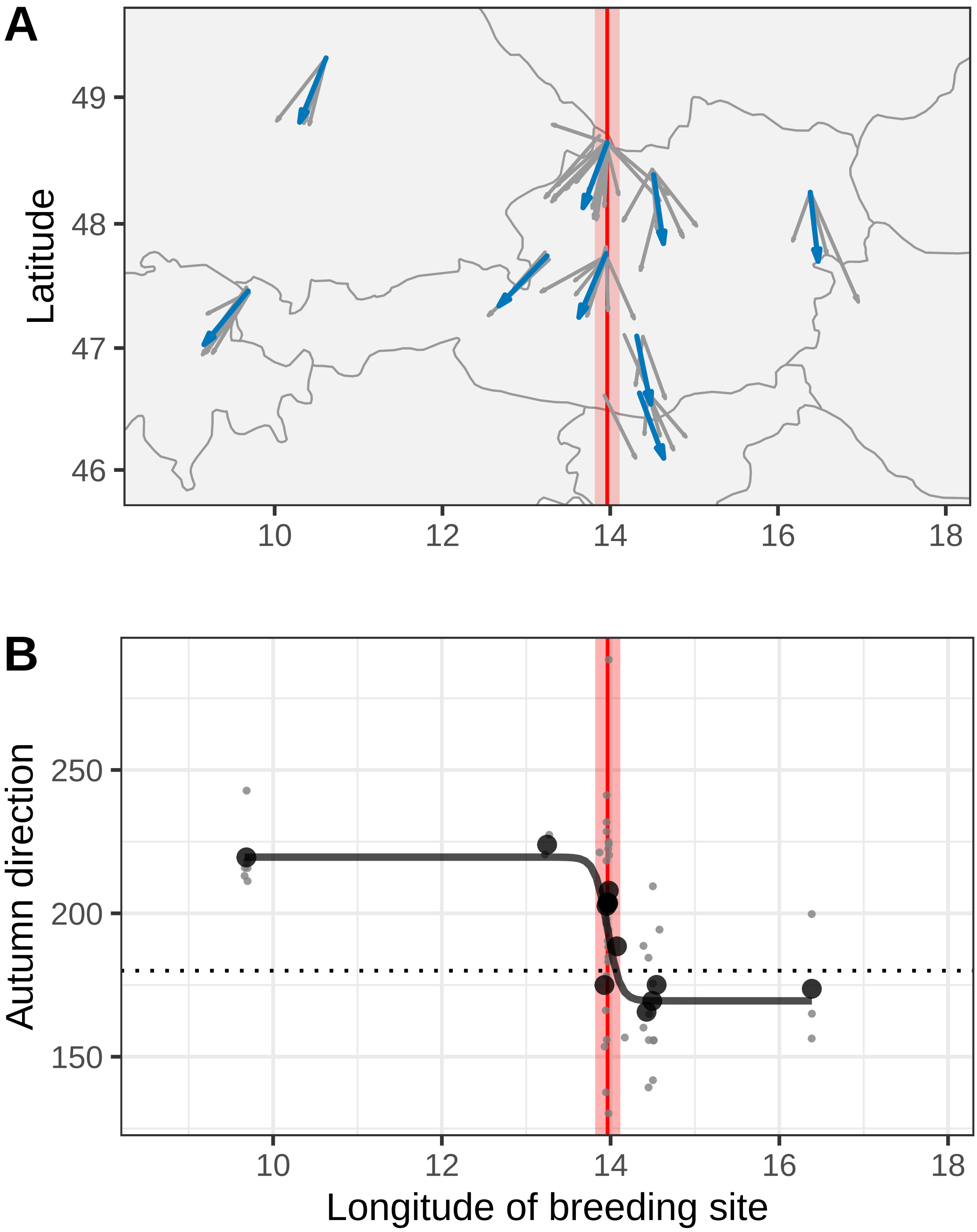

Figure 3.2: Autumn migration directions of blackcaps in central Europe. (A) Gray lines indicate migration directions of individual blackcaps, and blue lines indicate the mean direction at each capture site. In both panels, the solid vertical red line indicates the estimated cline center, and the red shading shows estimated cline width. **(B)** Autumn migration direction by breeding longitude for Austrian blackcaps, with the maximum likelihood cline plotted. Small gray dots show the directions of individual blackcaps, and large black dots represent groupings of birds treated as sites for the analysis with `hzar`, which requires grouped input data. The dotted horizontal line is 180º (due south).

hybrids would experience lower fitness through reduced survival, as they would have to cross the Alps, Mediterranean Sea, and Sahara Desert. This is a widely held hypothesis today (Bensch et al. 2009; Helbig 1991a; D. E. Irwin and J. H. Irwin 2005), but our data do not necessarily support it, as a considerable number of the birds we tracked successfully took intermediate routes, survived, and returned to be recaptured. Most of these birds encountered portions of the Alps, but many did not cross the Mediterranean, in which case they never encountered this barrier or the Sahara Desert. Many of the birds that wintered in Africa navigated around the Mediterranean, and others used Italy as a land bridge (Figure 3.1 and 3.3).

There is one important caveat: to maximize recapture success, we exclusively tracked adult birds, which had already completed at least one migration. It is possible that some blackcaps attempt to migrate over the Mediterranean and Sahara but do not survive to adulthood. Indeed, there is a striking deficit of birds wintering in Africa around 5ºE and 15ºE (Figure 3.1 and 3.3; note that birds from Dutch and Polish populations did winter in these areas). This deficit would not have been present in Helbig's work because he was not tracking free-flying birds. Alvarado et al. (2014) argued similarly after failing to recover hybrids in a divide between hermit thrushes (*Catharus guttatus*). At present, tracking of small songbirds is limited to archival tags not capable of transmitting daily location estimates, so we cannot address this idea further.

3.2.2 Migration timing in the divide

Migration timing is an important component of the annual cycle that affects reproductive success (Taylor and Friesen 2017; Winker 2010) and mate selection (Bearhop et al. 2005). Assortative mating based on migratory phenotype might occur if migration timing and breeding differ consistently among phenotypes (Bearhop et al. 2005). This could result in divergence between populations with different strategies and explain the rapid transition from SW to SE phenotypes (D. E. Irwin and J. H. Irwin 2005). However, we found no differences in spring arrival timing between birds using SW and SE autumn strategies (effect = -0.2 days, t_{23}=-0.046,

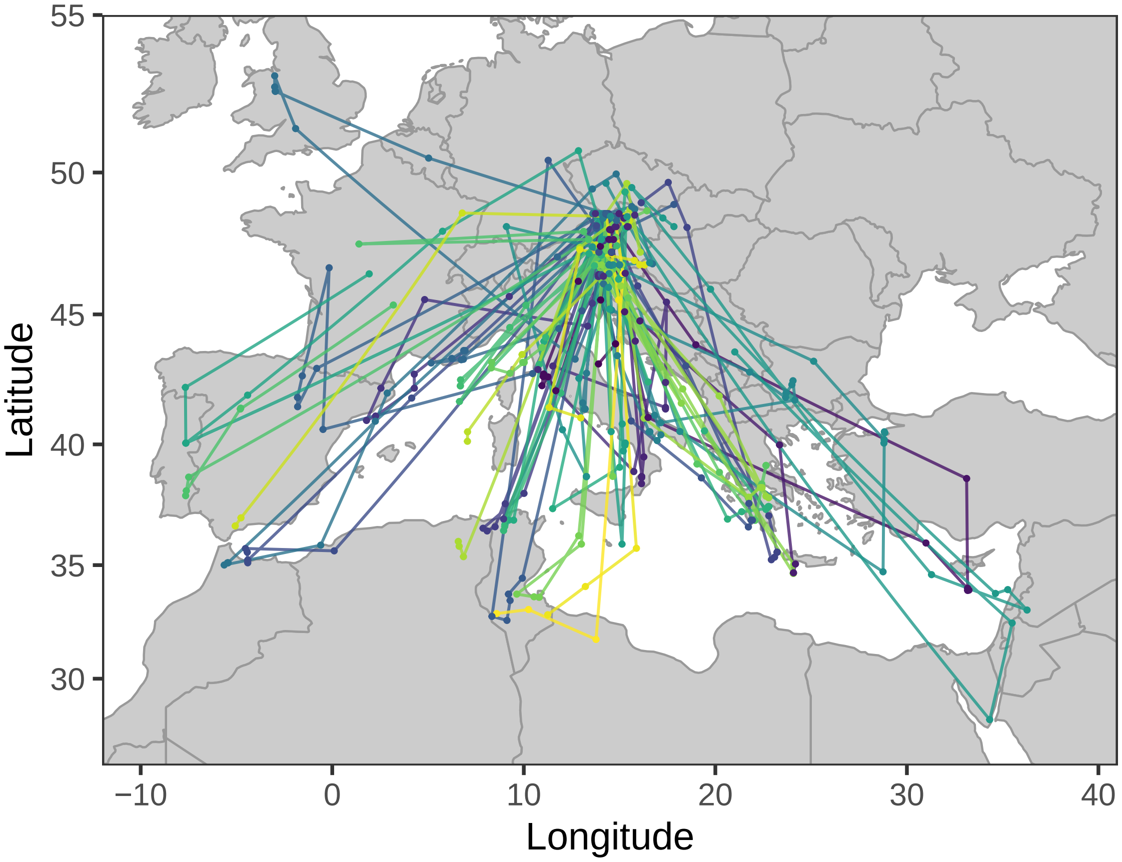

Figure 3.3: Full tracks of blackcaps from the migratory divide. Tracks estimated with `FLightR`, with each track in a different color. To reduce clutter, one point is shown for each month and error bars are omitted. `FLightR` estimated some wintering locations at slightly higher latitudes than the *siteEstimate* function in `GeoLight`; for example, some `FLightR` tracks that end in the southern Balkan Peninsula have `GeoLight` estimates on the northeast coast of Libya (Figure 3.1A). Note that headings over short distances are sensitive to the calibration used and may not be fully trustworthy.

P=0.96), nor in any other migration timing trait (Figure 3.6, Table 3.1). Data from eight individual blackcaps tracked over two years suggests repeatability in timing was higher on spring migration (spring migration start: R [95% CI]=0.85 [0.4,0.99], end: R [95% CI]=0.78 [0.36,0.96]; autumn migration start: R [95% CI]=0 [0,0.75], end: R [95% CI]=0 [0,0.75]), albeit with considerable uncertainty in all estimates. We therefore find no evidence that the migratory divide is maintained by temporal premating isolation. Variation across the divide in other traits, including body size (approximated by tarsus length or wing length) is also absent from our dataset.

So what is maintaining this migratory divide? One intriguing possibility is revealed by an analysis of timing that includes intermediate (S) migratory strategies.

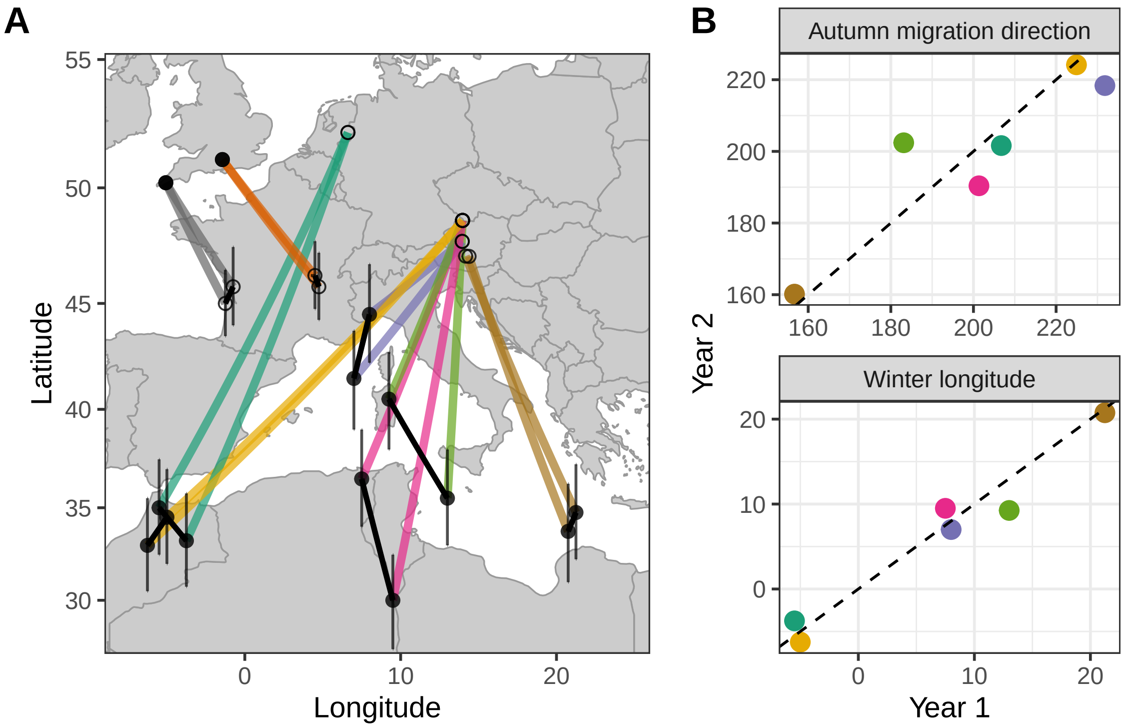

Figure 3.4: Repeatability of migratory phenotypes within individuals. (A) Each color represents one individual tracked over two subsequent years, with solid black lines connecting location estimates for the same individual. Breeding and non-breeding sites and error bars as in Figure 3.1. For the two British winterers, our repeated location estimates were very similar (59 and 92 km apart, respectively), strongly suggesting that they bred in the same area. **(B)** Migratory phenotype estimates for individuals tracked from continental Europe for two years (excluding those tagged in Britain). The dashed line is the identity line. We estimated repeatability in winter longitude as R [95% CI]=0.99 [0.96,1] and repeatability in migration direction as R [95% CI]=0.91 [0.78,1]. The winter location estimates for these individuals averaged 385±253 km apart in consecutive winters.

These blackcaps began spring migration on average 15 days earlier than SE and SW migrants (effect = -14.6 days, t_{23}=-2.7, P=0.014) and arrived 10 days earlier on the breeding grounds (effect = -9.6 days, t_{23}=-2.6, P=0.015) (Figure 3.6A, Table 3.1). This pattern is apparent even if we do not categorize individuals into discrete groups (Figure 3.6B). Early spring arrival may relate to the fact that blackcaps following intermediate strategies have the shortest distances to migrate (Figure 3.7D), so cues on the wintering site may predict conditions on the breeding grounds (Both et al. 2010; Butler 2003). Importantly, early arrival may lead to assortative mating among intermediates, allowing them to exist relatively independently of pure SW and SE migrating populations within the 22 km cline. Selection against

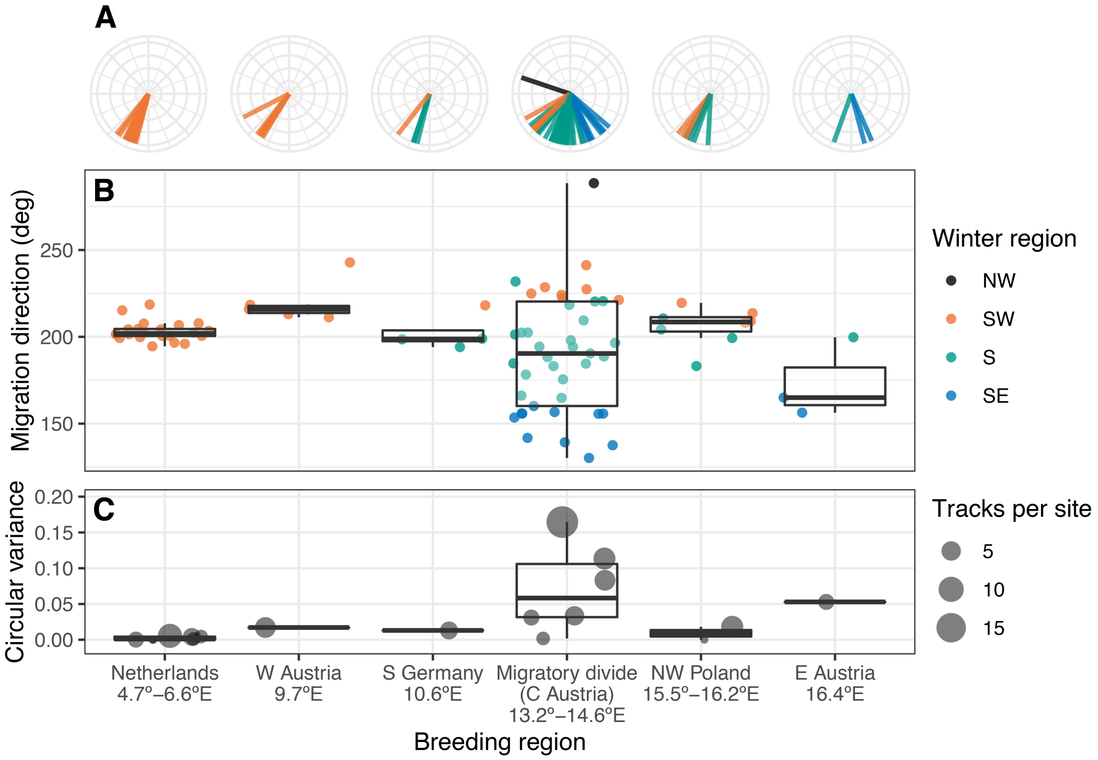

Figure 3.5: Variation in autumn migration direction by breeding area. (A) Migration direction of tracked blackcaps caught at breeding sites across continental Europe. Each line points in the direction of autumn migration and is colored by winter region (SW=orange, intermediate=green, SE=blue, and NW (Britain)=black). Levene's test among sites with 5 or more tracked birds showed significantly higher variation in the area of the migratory divide: divide vs. Netherlands $F_{1,61}=29.3$, $P<0.0001$; divide vs. west Austria $F_{1,45}=6.36$, $P=0.015$; divide vs. Poland $F_{1,47}=7.68$, $P=0.008$ (excluding the NW migrant does not appreciably change this result). **(B)** Each dot shows the migration direction of one tracked blackcap (colored as in A). **(C)** Circular variance of autumn migration directions at each capture site, categorized by breeding region. Dot size shows the sample size at each site.

birds deviating from an immediately intermediate route (discussed previously) could limit the area where intermediates are favored to the observed cline width.

We used simulations to test if our measured distribution of arrival times would generate assortative mating among intermediate birds, comparing simulations where mate choice is dependent or independent of arrival time. The proportion of matings between intermediates was substantial and increased when we added mate selection based on timing (from 28% with no timing to 41% with timing), suggesting early arrival on the breeding grounds may facilitate assortative mating

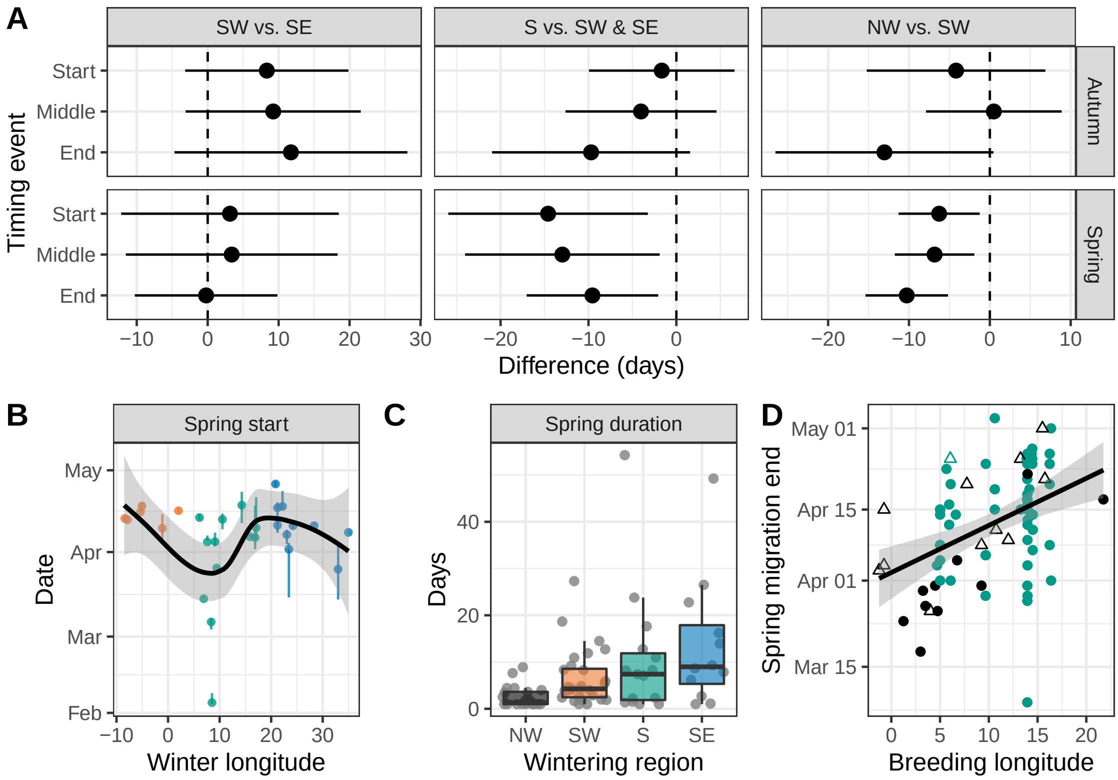

Figure 3.6: Blackcap migration timing. **(A)** Timing within the migratory divide, showing model results for three timing comparisons: SW vs. SE (left), intermediate (S) vs. SW/SE (center), and NW vs. SW (right). Dots give model estimate and bars 95% confidence interval. Negative values indicate that SW or intermediate (S) groups, respectively, had earlier timing or shorter migrations. **(B)** Timing of the start of spring migration for birds tracked within the migratory divide. Points colored by wintering area, and vertical lines indicate the interquartile range of timing estimates made with `FLightR`. Curve is a loess smooth. **(C)** Boxplots showing spring migration duration by wintering area. Gray points correspond to individual tracks. **(D)** Breeding longitude vs. spring migration timing, with NW migrants in black and other birds in green. Triangles show females and circles show males.

among intermediates, especially given their high relative abundance. Hybrid zones maintained by increased hybrid fitness are referred to as zones of bounded superiority (Moore 1977). Additional work is needed to support this idea, including direct observations of mated pairs and their offspring in the divide. We also note that genetic differentiation across this divide is low (Delmore et al. 2020; also see Pérez-Tris et al. 2004; Rolshausen et al. 2009). However, all of the genetic work on this system has focused on allopatric populations distant from the divide (Mueller et al. 2011; Pérez-Tris et al. 2004; Rolshausen et al. 2013; Rolshausen et al. 2009).

Table 3.1: Model results comparing migration timing in the migratory divide between SW and SE phenotypes and between intermediate (S) and SW/SE phenotypes. Log-transformed variables indicated by "(log)".

Contrast	Season (response)	Estimate	SE	df	t-ratio	P-value
SW vs. SE	Spring start	3.14	7.41	23	0.42	0.676
SW vs. SE	Spring middle	3.39	7.21	23	0.47	0.643
SW vs. SE	Spring end	-0.22	4.86	23	-0.05	0.964
SW vs. SE	Autumn start	8.33	5.61	27	1.49	0.149
SW vs. SE	Autumn middle	9.23	6.04	29	1.53	0.137
SW vs. SE	Autumn end	11.73	8.04	30	1.46	0.155
SW vs. SE	Autumn duration (log)	0.19	0.70	25	0.27	0.791
SW vs. SE	Spring duration (log)	-0.80	0.55	23	-1.44	0.162
SW vs. SE	Autumn speed (log)	-0.05	0.68	25	-0.08	0.938
SW vs. SE	Spring speed (log)	0.94	0.55	23	1.72	0.099
S vs. SW & SE	Spring start	-14.60	5.49	23	-2.66	0.014
S vs. SW & SE	Spring middle	-12.97	5.35	23	-2.42	0.024
S vs. SW & SE	Spring end	-9.55	3.62	23	-2.64	0.015
S vs. SW & SE	Autumn start	-1.67	4.04	27	-0.41	0.683
S vs. SW & SE	Autumn middle	-4.03	4.20	29	-0.96	0.345
S vs. SW & SE	Autumn end	-9.70	5.51	30	-1.76	0.089
S vs. SW & SE	Autumn duration (log)	-0.99	0.53	25	-1.89	0.070
S vs. SW & SE	Spring duration (log)	0.17	0.42	23	0.41	0.688
S vs. SW & SE	Autumn speed (log)	0.39	0.51	25	0.76	0.454
S vs. SW & SE	Spring speed (log)	-0.65	0.42	23	-1.56	0.133

3.2.3 Origins of blackcaps wintering in Britain

Blackcaps wintering in the UK in increasing numbers represent a rapid and recent change in migratory behavior, illustrating the speed at which movement strategies can evolve (Berthold and Terrill 1988; Leach 1981). Early experiments supported a genetic basis for this migratory phenotype (Berthold et al. 1992; Helbig et al. 1994), but its nature is still poorly understood. Foremost is a lack of knowledge of the breeding grounds of birds wintering in Britain. No studies have tracked the direct migrations of free-living blackcaps to understand how many adopt this novel phenotype and determine whether those breeding in Britain are also changing their behavior by adopting residency. We fitted geolocators to blackcaps wintering in the UK and obtained 24 tracks from 22 blackcaps (12 F, 10 M), in addition to the one NW migrant tracked from our central Austrian cohort.

Blackcaps wintering in Britain originated from breeding areas in an unexpectedly broad expanse covering much of western and central Europe, remarkably extending south to latitudes occupied by the species in winter (Figure 3.1D). Their autumn migrations ranged from northerly (e.g. from Spain) to westerly (e.g. from Poland). This strategy enabled them to use short migration routes, on average 940±360 km; in contrast, birds tracked from central Europe flew on average 1865±717 km when they chose a southerly direction (Figure 3.7A). Although British winterers had the shortest routes in our sample, most also bred relatively close to suitable southerly wintering areas. To determine how far a blackcap would need to fly if it selected an alternative southerly migration route instead of a northerly route to the UK, we calculated the distance from the breeding site of each British winterer to the 10 closest wintering locations of tracked continental breeders. In 19 out of 25 cases, the tracked route to the UK was longer than the average of the 10 possible southerly routes, often by 400-600 km (Figure 3.7C). This suggests that migration distance is of limited importance in explaining the British overwintering strategy. The availability of reliable supplemental food in British gardens may be a key driver (Plummer et al. 2015) by positively influencing body condition and survival.

Only one of 41 individuals tracked from within the central European divide spent the winter in Britain (2.4%, 95% CI [0.13, 14]), and neither did any of the remaining 43 individuals tracked from elsewhere in continental Europe. Previous studies estimated that northwest migrants comprise 6.8–25% of individuals breeding in central Europe, based on ringing data, cage experiments, and stable isotopes (Helbig 1991b; Helbig 1992; Rolshausen et al. 2010; Rolshausen et al. 2009). One cage-orientation study suggested that as many as 50% of birds breeding in the vicinity of Linz, Austria migrate northwest (Helbig 1991b). Our results from free flying birds suggest these may be overestimates. Blackcaps wintering in Britain appear to breed across most of Europe at low densities, instead of occurring locally at higher densities.

3.2.4 Timing of northwest migrants

We tested for timing differences between NW migrants (British winterers) and SW migrants that might lead to reproductive isolation. Such timing differences have long been anticipated: Terrill and Berthold (1990) predicted that differences in spring photoperiod should lead British winterers to depart and arrive c. 5 and 16

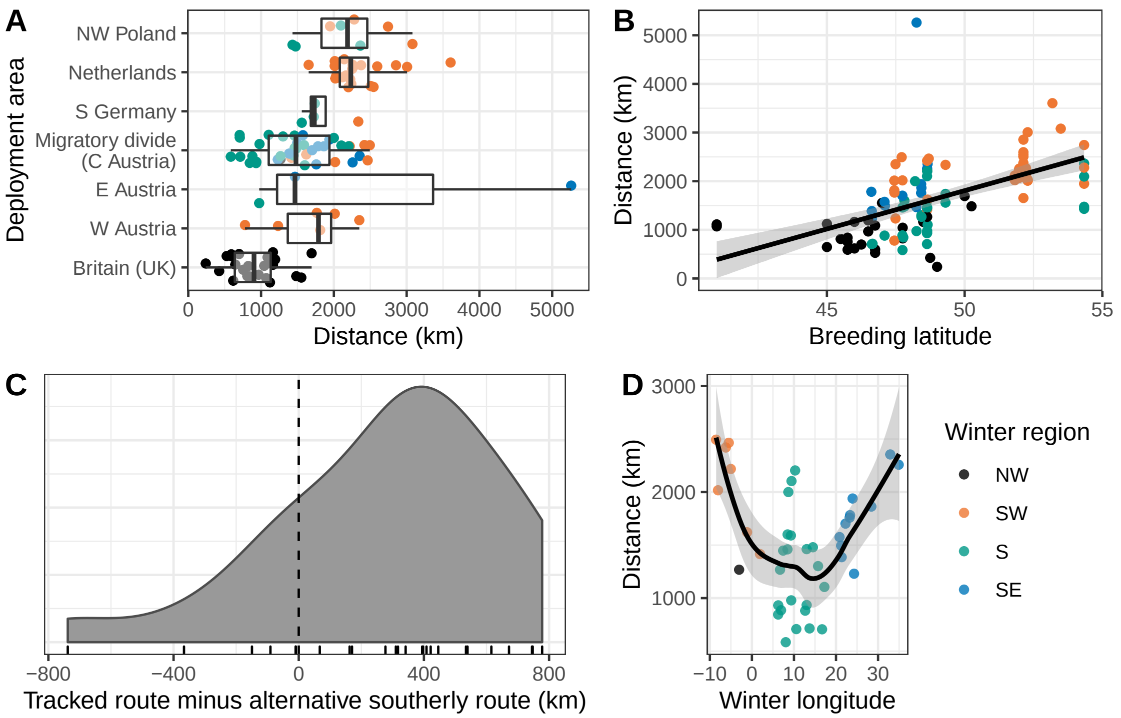

Figure 3.7: Migration distances. Colors indicate SW (orange)/intermediate (green)/SE (blue)/NW (black) phenotypes, categorized by wintering location. **(A)** Boxplots showing the distance between breeding and wintering sites for all blackcaps tracked, by deployment area. **(B)** Migration distance by breeding latitude, for all blackcaps tracked. **(C)** British winterers fly further than necessary. Values shown are the difference between the observed migration distance and the average of the distances to the 10 closest tracked individuals that wintered in traditional southerly areas, instead of in the UK. **(D)** Migration distance by wintering longitude for blackcaps tracked within the migratory divide only. Individuals with intermediate directions had the shortest migration distances.

days earlier, respectively, and Bearhop et al. (2005) reported evidence of assortative mating by wintering latitude based on stable isotopes from claw samples. Given that the NW phenotype appears to occur at low densities across Europe, assortative mating could be key to explaining how it is maintained in the population.

Other important factors may influence migration timing in blackcaps. For example, protandry is common among migratory songbirds and documented in blackcaps (Rainio et al. 2007). In our study, females were primarily sampled from among blackcaps wintering in Britain, where they showed later spring timing than their male counterparts (Table 3.2). In addition, different parts of continental Europe experience different spring phenology. In our dataset, blackcaps breeding further west in Europe underwent earlier spring migrations (Table 3.2, Figure 3.6D).

Table 3.2: Model results comparing migration timing of British winterers (NW migrants) to SW migrants. All models tested for timing differences between NW and SW phenotypes; other predictor variables were removed if P>0.1 and are therefore omitted from the table. Log-transformed variables indicated by "(log)". NW and SW phenotypes differed more consistently in spring timing measures than in autumn. Likewise, protandry was evident only in spring, and breeding longitude was most strongly associated with the timing of spring migration. Breeding latitude did not show strong associations with any timing trait. Year effects were evident only in autumn, implying higher inter-annual consistency in spring.

Predictor	Season (response)	Estimate	SE	df	t-ratio	F-value	P-value
NW vs. SW	Spring start	-6.27	2.49	43	-2.52	-	0.016
NW vs. SW	Spring middle	-6.83	2.44	44	-2.80	-	0.008
NW vs. SW	Spring end	-10.28	2.53	44	-4.06	-	<0.001
NW vs. SW	Autumn start	-4.18	5.50	50	-0.76	-	0.451
NW vs. SW	Autumn middle	0.49	4.18	51	0.12	-	0.906
NW vs. SW	Autumn end	-13.04	6.71	49	-1.94	-	0.058
NW vs. SW	Autumn duration (log)	-1.10	0.38	48	-2.89	-	0.006
NW vs. SW	Spring duration (log)	-0.80	0.24	44	-3.29	-	0.002
NW vs. SW	Autumn speed (log)	0.43	0.44	48	0.98	-	0.334
NW vs. SW	Spring speed (log)	-0.08	0.23	44	-0.34	-	0.737
Male vs. Female	Spring start	-9.50	2.88	43	-3.30	-	0.002
Male vs. Female	Spring middle	-9.36	2.83	44	-3.30	-	0.002
Male vs. Female	Spring end	-11.13	2.94	44	-3.79	-	<0.001
Male vs. Female	Autumn duration (log)	-1.00	0.47	48	-2.10	-	0.041
Breeding longitude	Spring start	1.22	0.20	43	6.02	-	<0.001
Breeding longitude	Spring middle	1.20	0.20	44	6.02	-	<0.001
Breeding longitude	Spring end	1.16	0.21	44	5.59	-	<0.001
Breeding longitude	Autumn end	0.86	0.39	49	2.17	-	0.035
Breeding longitude	Autumn duration (log)	0.10	0.03	48	3.32	-	0.002
Breeding longitude	Autumn speed (log)	-0.07	0.03	48	-2.79	-	0.007
Breeding latitude	Autumn end	-1.62	0.91	49	-1.79	-	0.08
Breeding latitude	Autumn speed (log)	0.13	0.07	48	1.93	-	0.06
Year (F-test)	Autumn start	-	-	-	-	6.44	0.001
Year (F-test)	Autumn middle	-	-	-	-	6.94	0.001
Year (F-test)	Autumn end	-	-	-	-	2.25	0.094
Year (F-test)	Autumn duration (log)	-	-	-	-	2.85	0.047
Year (F-test)	Autumn speed (log)	-	-	-	-	3.13	0.034

After including breeding latitude, longitude, sex, and year as predictors to account for their effects on timing, we found that NW migrants spending the winter in Britain reached their breeding grounds earlier than SW migrants that wintered in Iberia and northwest Africa (effect = -10.3 days, t_{44}=-4.1, P=0.0002; Table 3.2, Figure 3.6). They accomplished this by leaving the wintering grounds earlier (effect = -6.3 days, t_{43}=-2.5, P=0.016; compare Terrill and Berthold 1990) and having shorter migration durations (ratio = 0.4x, t_{44}=-3.3, P=0.002). In autumn, there were no timing differences between NW and SW migrants (Figure 3.6, Table 3.2).

Our data support the hypothesis that differences in arrival timing may contribute to reproductive isolation among blackcaps wintering in Britain, likely due to a combination of differing photoperiodic cues and shorter migrations (Terrill and Berthold 1990). Early-arriving individuals from Britain may experience fewer hazards during faster journeys, they may be in better condition due to supplemental food in British gardens (Bearhop et al. 2005; Plummer et al. 2015), and they may be able to use local weather cues to judge the suitability of their continental breeding areas. In turn, these individuals may be able to secure higher quality territories. However, it is unclear whether the magnitude of the timing difference (10 days) could result in effective reproductive isolation. Rolshausen et al. (2010) modeled assortative mating based on a timing difference of 10 days and a relative abundance of NW migrants of 1 out of 13 breeding individuals, concluding that NW migrants had a 28% chance of mating assortatively. Although we only tracked one NW migrant from within the migratory divide and therefore cannot capture the distribution of arrival dates in this particular breeding population, our similar average timing difference and lower relative abundance of NW migrants corroborate their conclusion of weak evidence for effective isolation solely based on timing. However, differences in body condition or microhabitat selection by migratory phenotype (Rolshausen et al. 2010) could still contribute to reproductive isolation.

3.2.5 Conclusion

We find considerable variation in blackcap migratory behavior across the central European migratory divide and diverse breeding origins for blackcaps exhibiting the novel British overwintering strategy. A narrow cline in migration direction across the divide suggests that selection on migratory strategy is strong. Assortative mating among birds orienting immediately south and selection against those deviating from this direction may help maintain this narrow cline. British winterers arrived on continental breeding grounds earlier than migrants from Mediterranean wintering areas, but the difference in timing may be insufficient to drive assortative mating. Accurately characterizing the migrations of individual blackcaps reveals fascinating variability in the migratory behavior of this species, paving the way for targeted studies of the genetic basis of migration and adaptation to global change.

3.3 Methods

3.3.1 Geolocator application and retrieval

From 2016–2019, we deployed 806 archival light-level geolocators on breeding blackcaps in Austria (N=376, May–June), Germany (N=57, May–August), the Netherlands (N=189, May–July), and Poland (N=53, April–May and August), and on wintering Blackcaps in the United Kingdom (N=131, January–March) (Table 3.3). In Austria, we focused our sampling on the anticipated location of the migratory divide, where blackcaps with eastern and western migratory routes meet, and including populations that prior studies suggested contained NW migrants (Helbig 1991b; Helbig 1992).

We captured birds using mist nets and tape luring with audio recordings of the male blackcap territorial song. In the UK, we captured birds attending feeding stations in suburban gardens with mist nets and potter traps. We used leg-loop harnesses (Rappole and Tipton 1991) made from elastic, viton, or nylon to attach geolocators. Tags were various models manufactured by Migrate Technology Ltd (see Table 3.3). Overall, we retrieved 117 devices, of which 108 contained data from at least one complete migration. We concurrently marked control cohorts in the United Kingdom and the Netherlands (see Table 3.3). Return rates did not significantly differ between control and tagged birds (Fisher's exact test, UK: P=0.25; Netherlands: P=1).

3.3.2 Analysis of light data

We first used the *preprocessLight* function in the `TwGeos` (Wotherspoon et al. 2016) R package to define twilight events. We used a light threshold of 1.5 lux because blackcaps often occupy darker understory and mid-story habitats (Rakhimberdiev et al. 2016). To maximize repeatability, we minimized manual processing. We

Table 3.3: Geolocator deployment summary. All devices manufactured by Migrate Technology Ltd. Nylon material refers to 1 mm nylon braid for harnesses, viton refers to 0.6 mm viton rubber cord, and elastic refers to 0.7-0.8 mm stretch elastic. "Deploy", "Return", and "Recover" respectively refer to the number of devices deployed, the number of birds that were observed to have returned with devices, and the number of devices ultimately recovered from returning birds.

Region	Year	Deploy	Return	Recover	Material	Device
Austria	2016	202	24 (5 viton)	24	nylon, viton	P65Z1top2end-11
Austria	2017	159	28	27	nylon	P50Z11-11
Austria	2018	15	4	3	nylon	P65Z1top1-11
Netherlands	2016	61	5	5	nylon	P50B1-11
Netherlands	2017	61	8	7	nylon	P50B1-11
Netherlands	2018	67	14	13	elastic	P30Z11-7-DIP-NOT; P65B1-7-NOT
Poland	2015	12	1	1	nylon	W30Z11-DIP-NOT; W65B1-DIP NOT
Poland	2016	9	1	1	nylon	W30Z11-DIP-NOT; W65B1-DIP NOT
Poland	2017	12	4	4	nylon	W65B1-DIP NOT; W30Z11-DIP-NOT
Poland	2018	20	4	3	nylon	W65B1-DIP NOT; W30Z11-DIP-NOT
S Germany	2018	57	7	5	elastic	P30Z11-7-DIP-NOT; P65B1-7-NOT
UK	2016-17	36	8	6	elastic	P50Z11-11-NOT
UK	2017-18	48	11	7	elastic	P50Z11-7-DIP-NOT
UK	2018-19	47	15	11	elastic	P50Z11-11-NOT

manually removed only obviously erroneous twilights, focusing on calibration periods. After manual processing, we used the *twilightEdit* function in `TwGeos` to perform additional automated editing and deletion of erroneous twilights. We used the following settings in *twilightEdit*: window = 4, outlier.mins = 30, and stationary.mins = 15. In the case of two devices with substantial shading of the light sensor, *twilightEdit* removed too many twilights to use in downstream analysis; in this case, we used only manually processed twilight times.

We used `FLightR` (Rakhimberdiev et al. 2017; Rakhimberdiev et al. 2015) to determine migration timing. `FLightR` uses the slope of the light curve around twilight to estimate locations and is therefore sensitive to data quality. In our dataset, several devices experienced substantial shading due to mantle feathers covering the light sensor, especially after the summer molt of body feathers. Geolocators with shorter “light pipes” (“-7” models, see Table 3.3) or with the light sensor on the body of the device itself (deployed in Poland, see Table 3.3) were prone to this issue, whereas devices with a light sensor at the end of a 11-mm “light stalk” (“-11” models) rarely experienced shading. We performed an automated step to remove highly shaded light curves. For each twilight event, we took the mean of all “log.light” values returned by `FLightR` and removed twilights with values less than 1. We removed no more than 10% of twilights with this method; if more than 10% of twilights were heavily shaded, we removed the worst 10%. This approach improved performance for most individuals with light to moderate shading of the light sensor, but we were unable to obtain `FLightR` tracks for 6 heavily shaded devices. These were excluded from the `FLightR` timing analysis.

To identify birds’ migration destinations (i.e. breeding or wintering sites, depending on the season of deployment), we used the R package `GeoLight` (Lisovski and Hahn 2012). `GeoLight` contains a function *siteEstimate* for estimating a bird’s location during a given time period, specifically designed for blackcaps and other birds for which shading of the light sensor can be a problem (Hiemer et al. 2018). We succeeded in using *siteEstimate* to obtain location estimates for all birds, including those for which `FLightR` had failed. For devices deployed in summer, we used twilights from 15 December to 15 January to estimate wintering locations. For devices deployed in winter, we used twilights from 1 June to 1 August to estimate summer breeding locations. In both cases, we set these time periods in mid-winter and mid-summer, when they are least likely to overlap with spring and autumn movements. We used the same time window for all birds to obtain comparable locations across individuals.

Both `GeoLight` and `FLightR` require that users define calibration periods during which the bird was stationary in a known location. We set calibration periods by visually inspecting plots of the log of observed versus expected light slopes for the deployment site over time (*plot_slopes_by_location* function in `FLightR`). When a bird moves away from the deployment site, the observed and expected slopes visually diverge (Lisovski et al. 2020). For some individuals, visual resighting data were available after deployment and before recapture to aid calibration. After running `FLightR`, we refined calibration periods if the analysis suggested that movement had occurred during calibration periods. Some devices had insufficient calibration periods, if, for example, the bird departed shortly after tagging and the device stopped recording before the return migration. In these cases, and cases where the resulting track showed clear signatures of poor calibration (e.g. latitudinal drift during stationary periods or widely varying location estimates), we used a global calibration made from the combined data of all devices. For this global calibration, we used a linear model to estimate the overall mean calibration slope, accounting for the magnitude of shading to the light sensor. We did not include devices that lacked light pipes or light stalks, which made the light data qualitatively different from those collected by the other devices.

In `GeoLight`, we used the same calibration periods as for `FlightR`, with one additional refining step: we used *siteEstimate* to estimate the location of deployment and compared the result to the actual deployment location; if a lower or higher sun angle (±0.25º increments) resulted in a more accurate estimate of the deployment site, we used the adjusted sun angle instead.

We defined the `FLightR` model search grid between 10ºS and 65ºN latitude and 20ºW and 52ºE longitude. We chose these settings after visually inspecting light data with the *thresholdPath* function in the R package `SGAT` (Lisovski and Hahn 2012; Sumner et al. 2009) to confirm that no tracks were likely to occur outside of this area. `FLightR` contains a prior for the decision to move, which has a default of 0.05. We adjusted this setting outside of the migration season (i.e. from Dec 15–Mar 1 and May 15–Aug 15) to a value of 0.001. For the final run of each individual, we ran the particle filter with the recommended 1 million particles.

3.3.3 Migratory phenotypes

For comparative analyses of migratory phenotypes, we used both (1) winter longitude and (2) autumn migration direction. We estimated the bird's direction on autumn migration as the rhumb line connecting breeding and wintering sites (*bearingRhumb* in R package `geosphere`, Hijmans 2017). We used this simplified representation of the route for calculating migration direction because geolocator tracks over short distances are sensitive to bias caused by imperfect calibration, especially close to an equinox.

In geolocation analyses of bird migration, longitude can generally be estimated with greater precision than latitude (Ekstrom 2004; Fudickar et al. 2012; Lisovski et al. 2012). Latitude estimates are derived from daylengths, which can be affected by shading and are unreliable around the spring and autumn equinoxes. We compared destination longitudes estimated with `GeoLight` (*siteEstimate*) to estimates derived from `FLightR`. The two methods were highly correlated (ρ=0.99), affirming destination longitude as a reliable measure of migratory phenotype that is insensitive to the choice of analysis method. Destination latitude showed a slightly lower correlation between the two methods (ρ=0.82).

On 8 occasions, we were able to track the same individual for two subsequent years (5 from the migratory divide, 1 from the Netherlands, and 2 from Britain). From these data, we estimated individual repeatability using the R package `rptR` (Stoffel et al. 2017) as the proportion of total variation explained by bird identity, where the total includes both variation from bird identity and among-year variation among birds.

We assigned individuals to four categories based on wintering location. For birds wintering north of 37.5ºN, we considered those west of 5ºE to be southwest (SW) migrants, those east of 20ºE to be southeast (SE) migrants, and those between 5-20ºE to have intermediate southerly (S) routes. For birds wintering south of 37.5ºN, we used a cutoff of 0º to distinguish SW from S because these longer routes require less of a westerly component to reach the same longitude.

We used Levene's test to compare variances (*leveneTest* R function in the `car` package) to determine whether the distribution of autumn migration directions differed among breeding sites. We controlled for multiple testing by applying a false discovery rate correction using the *p.adjust* R function.

3.3.4 Timing

We calculated migration timing using the *find.times.distribution* function in `FLightR`. To use this function, the user defines a spatial area, and the function reports the time at which the bird was likely to have crossed into and out of that area. For each individual, we used the shortest-distance route (i.e. a great circle route) between summer and winter areas to aid in defining migration progress. Specifically, we calculated paths perpendicular to the shortest-distance route at 30%, 50%, and 70% of the way between summer and winter locations, and we used *find.times.distribution* to determine when on migration the bird crossed these thresholds. We chose values of 30 and 70% because we found using values closer to the endpoints of the journey (e.g. 15%/85%) caused a higher proportion of calculations to fail, which typically occurs when the bird does not transit cleanly across the threshold. Close to summer and winter sites, local movements and geolocation uncertainty over time may lead to the modeled bird's path approaching the threshold more than twice per year. We treated these thresholds (30%, 50%, 70%) as representing early, middle, and late stages of the migratory journey, and we considered a bird to have reached each point at the 0.50 quantile time returned by *find.times.distribution.* As a measure of migration duration, we calculated the number of days it took each bird to travel from early (30%) to late (70%) migration stages, setting the value to one if it was estimated as less than one day. We calculated the speed of migration by dividing migration distance by duration. Because timing estimates of north-south movements can be inaccurate near the equinox, we did not retain timing estimates of movements taking place within 7 days of an equinox along a route within 15º of due north or south.

We validated `FLightR` timing estimates using simple longitude coordinate output from `GeoLight` (*crds* function), which we used to derive alternative measures of migration timing across an east-west axis. With this method, we considered a bird to be halfway through its migration when its estimated longitude was closer to the longitude of its destination than its origin. We defined the start of migration as the time when a bird crossed a threshold from its starting longitude and did not return. Our threshold was defined as 10% of the difference between origin longitude and destination longitude. We defined the end of migration as the point when a bird crossed to within 10% of its destination longitude. We expected migration timing estimated from longitude data to be most comparable to `FLightR` estimates for birds that primarily used east-west routes. For birds that primarily moved along a north-south axis, the component of movement across longitudes is small relative to the component across latitudes. Therefore, we excluded birds with strongly southerly migration directions (150º–210º) from this validation. The timing of spring migration was consistent across methods (all Spearman $\rho>0.78$). In autumn, ρ ranged from 0.61 to 0.76.

We constructed linear models to compare the timing of migration for three different comparisons. For individuals tracked within the Austrian migratory divide, we tested for differences (1) between SW and SE parental phenotypes, and (2) between intermediate (S) and parental (SW/SE) phenotypes. Finally, we (3) tested for differences between NW (i.e. UK) and SW phenotypes. In all cases, we tested fixed effects of wintering area (NW/SW/S/SE) and year. We attempted to fit a random effect of bird identity, but our sample size of repeat tracks (N=8) was insufficient to estimate a variance component of bird identity, resulting in singular fits. Therefore, for birds with repeat tracks we randomly chose one track to include in the timing analysis, so that only one data point per individual was included for each timing measure. For comparison 3 (NW vs. SW), we also included effects of sex and breeding latitude and longitude. These effects were not relevant for comparisons 1 and 2 because all birds were tracked from a single breeding area (the divide zone), and all tracked birds were males. We used the R package `emmeans` (Lenth 2019) to construct the proper contrasts for comparisons 1 and 2. To maximize the precision of our estimates given a limited sample size, we removed terms with P-values greater than 0.10. For migration speed and duration, which had right-skewed distributions, we log-transformed the response variable before fitting the model.

We used simulations to investigate whether our measured arrival timing differences in the migratory divide among SW, SE, and S (intermediate) phenotypes could lead to substantial assortative mating. In each simulation, we used the observed relative abundances of S, SW, and S phenotypes in the divide to draw a random sample of birds of equal number, following a multinomial distribution. Then, we used density curves fit to the original data to draw a sample of arrival dates for each phenotype group. Finally, for each individual, we selected a random mate based on the proportions of individuals present five days after its simulated arrival date. We used this delay because pair formation occurs within days of arrival (Bairlein 1978) and females tend to arrive later than males. We repeated this simulation 1000 times and extracted the proportion of pairings that occurred between individuals that had taken intermediate routes.

3.3.5 Routes

We used route output from `FLightR`. For tags that stopped in late winter or close to the spring equinox, track estimates could be unreliable. In these cases (n=16), we ignored location estimates for dates after 1 January if the tag stopped operation within three weeks of the spring equinox.

3.3.6 Cline analysis

We used the R package `hzar` (Derryberry et al. 2014) to estimate the location and width of the cline marking the transition from westerly to easterly migratory directions in the migratory divide. We used code from the supplementary material of Derryberry et al. (2014) as the basis for the analysis. Because `hzar` assumes that data come from a one-dimensional transect (in our case, an east-west transect), we limited the sites we included to the narrow range of latitudes within Austria. The analysis requires input data in the form of sites (not individuals), so we grouped individuals in the following way: we treated individuals as belonging to the same site group if their breeding territories were within 0.2 degrees of longitude, setting a maximum group size of 5 unless doing so would create an individual without a group. In this way, we assigned individuals to similarly-sized groups based on the longitude of their breeding site in Austria.

3.3.7 Author contributions

Conceptualization: KD, BMVD, BCS, ML; Methodology: KD, BMVD; Formal Analysis: KD, BMVD; Fieldwork: KD, BMVD, TC, TGG, RRG, TH, DH, HJ, IM, JSLR, BSM, RJP, MR, GCMR, HPJ, WV, ML; Writing –Original Draft: BMVD with input from KD and ML; Writing –Review & Editing: KD, BMVD, GJC, TC, TGG, RRG, JSLR, IM, BSM, MR, BCS, HPJ, WV, ML; Visualization: BMVD; Supervision: GJC, MR, HPJ, BCS, ML; Project Administration: WV, IM, HPJ, GJC, MR, ML; Funding Acquisition: BMVD, MR, HPJ, ML.

3.3.8 Declaration of Interests

The authors declare no competing interests.

3.3.9 Acknowledgements

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In Austria, fieldwork was approved by the institutional ethics and animal welfare committee and the national authority (GZ 68.205/0048-WF/V/3b/2016) according to §§ 26ff. of Animal Experiments Act, Tierversuchsgesetz 2012 – TVG 2012. Permit numbers: GZ BMWFW-68.205/0048-WF/V/3b/2016 and BMWFW-68.205/0139-WF/V/3b/2016 (AT), UID: ATU36801500, MA22-24411/2016 (Wien): BHBR-I-7100.00-69/2016-13 (VA), ABT13-53V-10/1998-42 (Steiermark), 205-05RI/549/58/7-2016 (Salzburg), N-2016-197947/8-Pin (Oberösterreich), VL3-NS-3068/2016 /005/2016) (Kärnten, Villach), SV19-ALL-938/2016 (004/2016) (Kärnten, St Veit), SP3-NS-2823/2016 (007/2016) (Kärnten, Spittal), HE3-NS-1280/2016 (005/2016) (Kärnten, Hermagor), FE3-NS-2127/2016 (006/2016) (Kärnten, Feldkirchen), 5/N.AB-10120-8-2016 (Burgenland), RU5-BE-286/011-2016 (Niederösterreich). In the UK, geolocator deployments were approved by the University of Oxford Animal Welfare Ethical Review Body. Work was conducted under licenses from the British Trust for Ornithology, approved by the Special Methods Technical Panel. In Poland, work was approved by the General Directorate for Environmental Protection within the permit to capture and ring wild birds (DZP-WG.6401.03.36.2015.km, DZP-WG.6401.03.98.2016.km, DZP-WG.6401.03.97.2017.jro, DZP-WG.6401.03.2.2018.jro). In Germany, the permit was issued by the Regierung von Mittelfranken, Bavaria. Permit number: 54-2532.1-13/14. In the Netherlands, the permit was issued by the Centrale Commissie Dierproeven. Permit number: AVD801002016519 valid 27-6-2016 through 31-5-2021.

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4

A continental system for forecasting bird migration

MIGRATION

A continental system for forecasting bird migration

Benjamin M. Van Doren[1]* and Kyle G. Horton[2]

Billions of animals cross the globe each year during seasonal migrations, but efforts to monitor them are hampered by the unpredictability of their movements. We developed a bird migration forecast system at a continental scale by leveraging 23 years of spring observations to identify associations between atmospheric conditions and bird migration intensity. Our models explained up to 81% of variation in migration intensity across the United States at altitudes of 0 to 3000 meters, and performance remained high in forecasting events 1 to 7 days in advance (62 to 76% of variation was explained). Avian migratory movements across the United States likely exceed 500 million individuals per night during peak passage. Bird migration forecasts will reduce collisions with buildings, airplanes, and wind turbines; inform a variety of monitoring efforts; and engage the public.

Billions of birds migrate between distant breeding and wintering sites each year, through landscapes and airspaces increasingly transformed by humans. Hundreds of millions die annually from collisions with buildings, automobiles, and energy installations (*1*), and light pollution exacerbates these effects (*2*). Pulses of intense migration interspersed with periods of low activity characterize birds' movements aloft (*3*, *4*), and efforts to reduce negative effects on migrants (e.g., turning off lights and wind turbines at strategic times) (*5*) would be most effective if they targeted the few nights with intense migratory pulses. However, bird movements are challenging to predict days or even hours in advance.

For decades, scientists have studied the drivers of avian migration. Winds, temperature, barometric pressure, and precipitation play key roles (*6*–*8*). However, such general relationships have not produced migration forecasts accurate at both broad continental extents and fine spatial and temporal resolutions (*9*, *10*). Local topography, regional geography, and time of season modify relationships between conditions and migration intensity, and hundreds of species with diverse behaviors frequently pass over a single location during migration. The complex interactions between environmental conditions and animal behavior make predicting bird migration at the assemblage level a challenge.

One major difficulty has been amassing behavioral data that appropriately characterize bird migration at a continental scale. Radar, used globally as a tool to study animal migration (*3*, *11*–*14*), offers a realistic solution to monitor hundreds of species (*15*). In the continental United States, the Next Generation Weather Radar (NEXRAD) network comprises 143 weather surveillance radars (*16*) and an archive with more than two decades of data. Although designed for meteorological applications, these radars measure energy reflected by a diversity of aerial targets, including birds. Only recently have advances in computational methods [e.g., (*17*)] facilitated the use of the entire radar archive for longitudinal studies of bird migration at continental scales.

Using the NEXRAD archive, we quantified 23 years (1995 to 2017) of spring nocturnal bird migration across the United States (Fig. 1). We developed a classifier to eliminate radar scans contaminated with precipitation. We then trained gradient-boosted trees (*18*) to predict bird migration intensity from atmospheric conditions reported by the North American Regional Reanalysis (*19*). Our model used 12 predictors, including winds, air temperature, barometric pressure, and relative humidity (fig. S1), which we used to predict a cube-root-transformed index of migration intensity (expressed in square centimeters per cubic kilometer). The cube-root transform reduces skewness but is less extreme than a log transformation, which would have given considerable weight to biologically unimportant differences between small values. We measured migration intensity in 100-m altitude bins up to 3 km to model the three-dimensional distribution of migrating birds over the continent. To express migration intensities in numbers of birds, we assumed a radar cross section per bird of 11 cm^2. The radar cross section is a measure of reflected energy; this value is typical of medium-sized songbirds and representative of migratory species (*12*).

Our migration forecast model explained 78.9% of variation in migration intensity over the United States (Figs. 2 and 3A). Performance was consistent across years (mean yearly coefficient of determination $R^2 = 0.781 \pm 0.010$ SD). We quantified the importance of each predictor by calculating gain, a measure of how much predictions improve by adding a given variable. Air temperature was most important, with an average gain more than three times that of the second-ranked predictor, date (fig. S2). High temperatures coincided with large migration pulses (Fig. 4 and figs. S3 and S4). As a predictor of bird migration, temperature likely plays a dual role as an index of spring phenology and a short-term signal for movement, as favorable

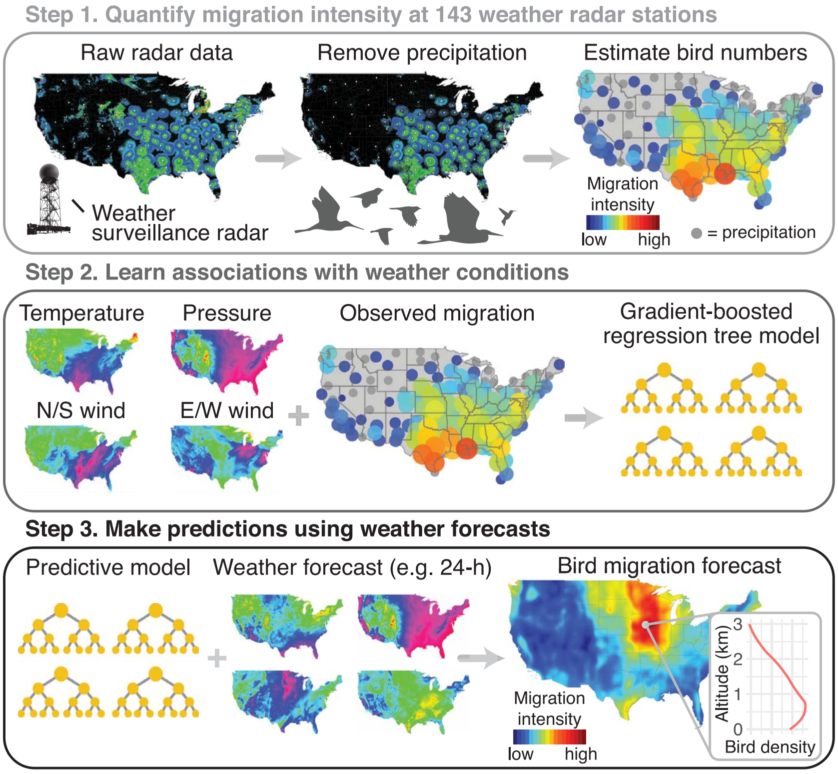

Fig. 1. Methodology for generating migration forecasts. We used weather surveillance radars to quantify 23 years of spring bird migration, modeled migration intensity as a function of observed atmospheric conditions, and used this model to forecast future migration events under predicted weather conditions.

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southerly winds usually accompany warmer air masses. Other important predictors included altitude, longitude, surface pressure, latitude, and wind (fig. S2).

The model provides informative predictions several days in advance. We evaluated its utility as a true forecast system with archived weather forecasts from the North American Mesoscale Forecast System (NAM) and Global Forecast System (GFS). NAM has higher spatial resolution but is a shorter-range forecast (12-km grid, 3-day range) than GFS (0.5° grid, >7-day range). We made predictions up to 3 days in advance with NAM and up to 7 days in advance with GFS, expecting performance to degrade with time because of the decreasing accuracy of longer-range weather forecasts. Predictions on the basis of 24-hour NAM forecasts explained 75% of variation in migration intensity, 3-day NAM forecasts explained 71%, and 7-day GFS forecasts explained 62% (fig. S5).

The model captures patterns of bird migration across the United States with high spatial accuracy, particularly in the central and eastern regions (fig. S6). We evaluated spatial accuracy over areas without radar coverage by iteratively removing the data from each radar station, retraining the model on the remaining data, and testing performance on the withheld station. Median R^2 for withheld stations was 0.72, and R^2 was 0.60 or higher for 75% of stations (fig. S7). Spatial variation in performance likely stems from local influences on migratory behavior (e.g., topography), which our model did not explicitly incorporate.

Previous research suggests that migration behavior and weather conditions in the days immediately preceding a migration event can predict its intensity [e.g., (*10*)]. We found that including atmospheric data from the preceding night and 24-hour changes in conditions did improve performance, but not markedly. A model that included atmospheric conditions 24 hours before an event explained 80.1% of variation in migration intensity, and further including observed migration intensity from the previous night increased R^2 to 81.3%.

Finally, we used model predictions to estimate the total number of birds actively migrating each night across the United States. Summing predictions countrywide, we infer that nightly movements frequently exceed 200 million birds (Fig. 3B). Peak passage occurred in the first half of May, when the median predicted movement size was 422 million birds per night. Although our model tended to underpredict the largest observed movements (Fig. 3A), a conservative forecast system

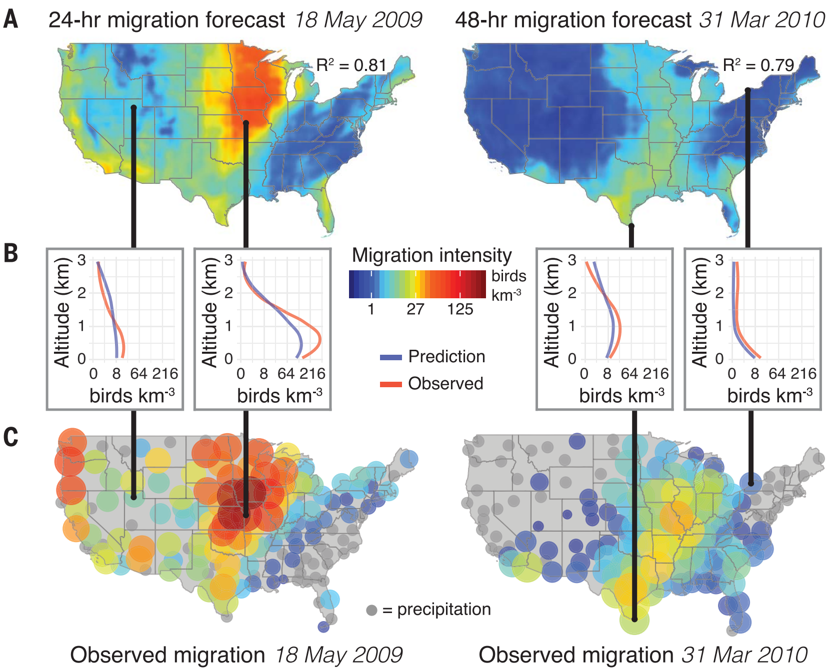

Fig. 2. Migration forecasts and corresponding observed migration. (**A**) Countrywide migration forecast surfaces showing predicted mean migration intensity across altitudes. (**B**) Altitudinal profiles at four stations, showing predicted and observed intensity values. (**C**) Mean migration intensity observed at all radar stations. Gray circles indicate stations where migration intensity could not be measured because of precipitation.

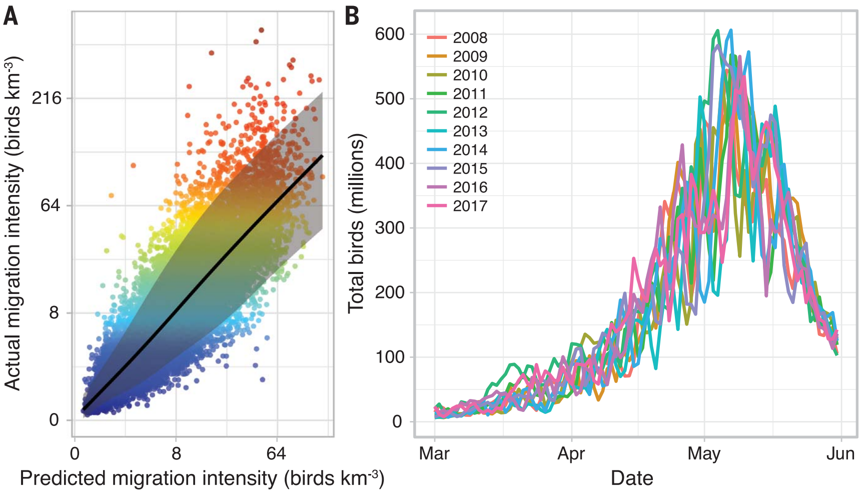

Fig. 3. Accuracy of forecasts and nightly continental predictions. (**A**) Mean predicted and observed migration intensities for test data, with points colored by observed migration intensity (*y* axis). The scatterplot shows values after averaging across altitudes. Shading shows empirical 90% prediction intervals, which covered 90.5% of observed values. (**B**) Nightly peak migration magnitude estimated across the continental United States for 2008 to 2017. The size of migratory movements varied markedly from night to night during the peak of the migration season.

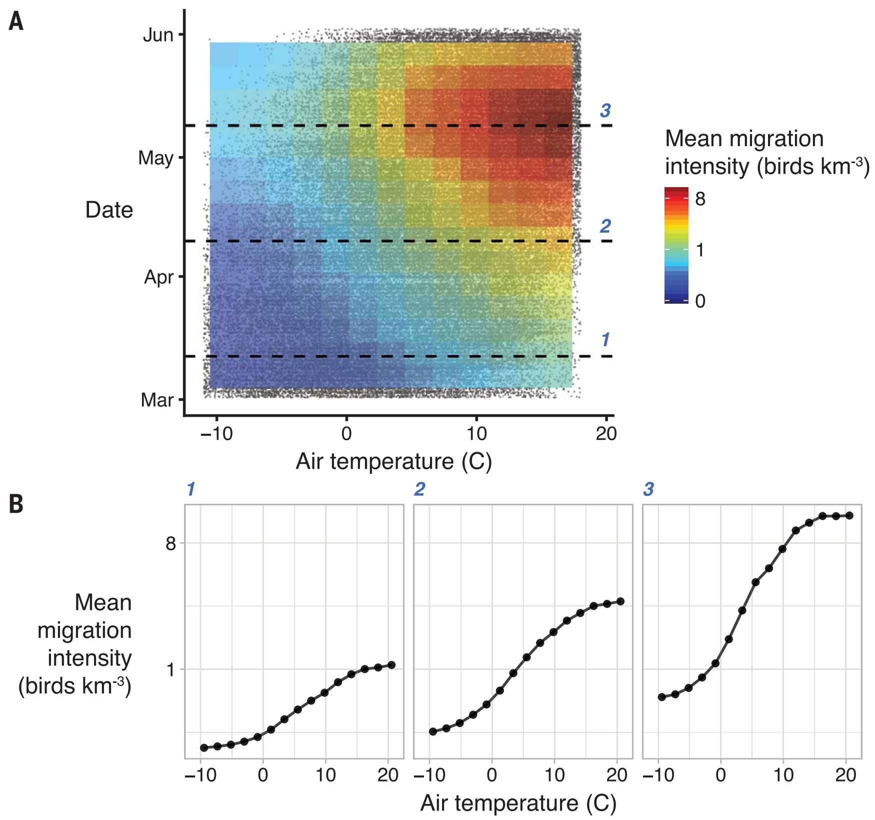

Fig. 4. Migration intensity predictions by air temperature and date. (**A**) Heat map colors show migration intensity predictions for dates and air temperature values. Each data point on the scatterplot behind the heat map represents data for one night from one radar. Only well-supported predictions and corresponding data points are shown (the outer 10% of temperature and date values are excluded). Temperature values correspond to air temperatures at altitudes up to 3000 m. (**B**) Cross sections of model predictions for three spring dates. For a given date, the model predicts migration intensity to vary closely with temperature. Fewer observations correspond to cold temperatures later in the season.

decreases the risk of taking unneeded mitigation action. More accurately predicting the largest migration events may require explicit modeling of migrant flow across the continent, including responses to topographical features (*20*).

Migration forecasts will further ecological research while aiding monitoring and mortality mitigation efforts. Accurate predictions can inform decisions to temporarily shut down lights and wind turbines, halt gas flares, choose airplane flight paths, and take other actions to prevent human and avian mortality (*10*, *21*). Global health workers monitoring avian-borne diseases can use migration forecasts to anticipate bird movements. Further integration of large citizen science datasets with radar observations will provide the means to study species-specific patterns of behavior at a large scale (*22*), and studying local variation in migratory behavior will lead to more accurate models of atmospheric bird distributions (*23*). Migration forecast systems have great potential to aid environmental monitoring and conservation efforts; fully realizing this potential will require the cooperation not just of scientists but also of governments and agencies that produce and disseminate radar products (*21*).

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SUPPLEMENTARY MATERIALS

www.sciencemag.org/content/361/6407/1115/suppl/DC1
Materials and Methods
Figs. S1 to S10
References (*25–37*)

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Supplementary Materials for

A continental system for forecasting bird migration

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This PDF file includes:

Materials and Methods
Figs. S1 to S10
References

Materials and Methods

Doppler radar

We used the NEXRAD network operated by the National Oceanic and Atmospheric Administration to characterize spring migratory movements (March 1st to May 31st) from 1995 to 2017. These radars scan 360° at multiple elevation angles (e.g. 0.5°, 1.5°… 4.5°), fully sampling the airspace every 5 to 10 minutes. We downloaded radar scans from Amazon Web Services (https://s3.amazonaws.com/noaa-nexrad-level2/index.html), selecting those in a 30-minute window centered on three hours after local sunset. We chose this time window because it approximates the time of peak nocturnal migration across the United States (e.g., *3*, *25*). However, there is spatial variation in the time of peak nocturnal migration (e.g., stations along the Gulf of Mexico experience peak migration earlier in the night, *26*), so in some areas our predicted totals will be conservative. We processed scans using the WSRLIB weather surveillance radar package for MATLAB (*27*). To characterize migration intensity, we used radar reflectivity factor, a measure of reflectance to the radar. To sample the airspace from 0-3 km above ground level, we extracted radar reflectivity factor values 5-37.5km from each radar (*28*) and cast them into vertical profiles with 100-m altitudinal resolution. We converted radar reflectivity factor (dBZ) to radar reflectivity (dBη) using the equation $\eta[dB] = Z[dBZ] + \beta$, where $\beta = 10\log_{10}(10^3\pi^5|K_m|^2/\lambda^4)$. We set the radar wavelength (λ) to 10.71 cm, the average for NEXRAD radars (*16*) and set the refractive index ($|K_m|^2$) to 0.93 for liquid water. This yielded $\beta = 13.35$. We converted dBη to η using the equation $\eta= 10^{dB\eta/10}$, yielding units of cm^2km^{-3}. To estimate numbers of birds from η, we divided η by a radar cross-section of 11 cm^2. This resulted in units of birds km^{-3}.

To mitigate the influence of time-invariant clutter (e.g., buildings, terrain, wind turbines), we applied binary clutter masks to each low elevation scan prior to the construction of the vertical profile of migration intensity. Masks were generated by summing a minimum of 100 low elevation scans (0.5° elevation), starting on January 1st (16:00 UTC to 18:00 UTC) and continuing to January 15th. This time window falls well outside typical migration periods. If 100 samples were not tallied by January 15th, the window of selection was expanded until the threshold was met. We classified any pixel above the 85th percentile of the summed reflectivity as clutter and masked it from our calculation of migration intensity.

To discriminate radar scans contaminated with precipitation from those containing only clear air or bird-dominated signal (hereafter termed "clear"), we created a random forest classifier using the package "randomForest" (*29*). We trained the classifier on 157,279 manually classified nocturnal scans (generated every 5-10 minutes) selected from a 3-hour period on March 15th, April 15th, and May 15th for every radar and every year in the training set (fig. S8). We designed this sampling to capture any geographic, seasonal, or longitudinal patterns in the data. We extracted derived predictor variables from profiles of radar reflectivity, groundspeed, and summaries of the number of density values above 35 dBZ (extreme densities characteristic of intense precipitation). We generated 1,000 trees and set the minimum terminal node size to 50. Overall, the model showed a 5.6% classification error. We used the algorithm to classify a total of 979,326 scans. As an additional step to reduce the inclusion of precipitation incorrectly classified as clear, we used only scans with a probability of being clear >70% (rather than a majority rule, i.e. >50%).

Identifying and removing flying insects from weather surveillance radar data has been a long-standing challenge for ornithologists. The standard method of ameliorating insect contamination is to filter data by airspeed values, because samples with large average airspeeds must be dominated by strong flyers (*30*, *31*). One downside to this approach is that it may also remove samples containing slow-flying birds or a mix of birds and insects. Here, we filter vertical profiles by removing altitude bins with mean airspeeds of 5 m s^{-1} or less (*3*, *22*, *32*), a cutoff value chosen to remove the majority of insects (*30*, *33*). Slow-flying samples represented 16% of total summed reflectivity. We examined the sensitivity of our analysis to this step by comparing model predictions with and without insect filtering (fig. S9).

Weather reanalysis

The North American Regional Reanalysis, or NARR (*19*), compiles data from numerous observational data sources to produce a best estimate of weather conditions that occurred in North America. The reanalysis is published in 3-hour intervals across a 32-km grid. We downloaded NARR data for 1995-2017 and extracted the following parameters: air temperature (°C), geopotential height (m), zonal and meridional wind components (m s^{-1}), surface pressure (Pa), relative humidity (%), visibility (m), vertical velocity (Pa s^{-1}), mean sea level pressure (Pa), total cloud cover (%), albedo (%), total precipitation (kg m^{-2}), convective available potential energy (J kg^{-1}), and snow cover (%). For variables available at multiple pressure levels, we extracted data from the surface to 300 mb. To match weather data to radar stations, we averaged data within 37.5 km of each radar station. We then calculated altitude above ground level by subtracting surface geopotential height from the geopotential height at each pressure level, and we used linear interpolation to calculate vertical profiles of weather data at 100-m altitude bins from 0-3000 m. Finally, we matched radar profiles to weather profiles by taking the observation closest in time for each radar station. Pairwise correlations among predictor variables were generally low (fig. S1).

Weather forecasts

The North American Mesoscale Forecast System, or NAM (https://www.ncdc.noaa.gov/data-access/model-data/model-datasets/north-american-mesoscale-forecast-system-nam), generates weather forecasts out to 84 hours; forecasts are hourly from 1-36 hours and subsequently every 3 hours until hour 84. Forecast models are run every 6 hours. NAM predictions are made on a 12-km grid. We downloaded 0Z NAM forecast data for 2008-2017, extracted the same parameters as for NARR, and matched NAM data to radar stations in the same manner as for NARR.

In addition to NAM, we used the Global Forecast System, or GFS (https://www.ncdc.noaa.gov/data-access/model-data/model-datasets/global-forcast-system-gfs) to generate longer-range migration forecasts. GFS forecasts with 0.5° spatial resolution currently extend out to 384 hours at 3-hour increments, but this range has improved with time; in 2010, the range was 180 hours. We downloaded 0Z GFS forecast data for 2010-2017 and extracted weather predictions up to 7 days (168 h) in advance.

Supervised learning

We used gradient boosted trees to predict bird migration from weather data (Fig. 1). We used the R implementation of XGBoost (*18*, *34*), a highly efficient and scalable gradient boosting framework. The algorithm automatically detects nonlinear effects and complex interactions among predictors, and it is not hindered by predictor collinearity. We trained an XGBoost model on NARR weather data, with the cube root of bird density as our response variable.

We divided our dataset into three groups: a training set, for learning; a validation set, for hyperparameter tuning; and a test set, to evaluate performance. We split the dataset by whole days instead of individual data points to prevent any spatial autocorrelation from inflating performance metrics. From 2,115 total days (comprising 3,434,703 altitude bins across 143 radar stations after filtering steps), we randomly selected 75% of days for training, 10% for validation, and 15% for testing.

We tuned model hyperparameters with grid searches across hyperparameter space (fig. S10). For our first search, we set the learning rate *eta* to 0.05 while varying maximum tree depth *max_depth* between 8-16. Trees of these depths are complex, but predicting bird migration across the entire United States from March to May at 30 different altitude bins is a complex problem. We used the *early_stopping_rounds* argument to stop the algorithm after 10 boosting iterations in which performance on the validation set failed to improve. Larger trees perform better on training data, but trees that are too large lower performance due to overfitting. We therefore used the validation dataset to select the best-performing value of maximum tree depth. We then tested the following modifications to additional parameters that can prevent overfitting: decreasing *subsample* from 1.0 to 0.70, increasing *min_child_weight* from 1 to 5, and increasing *gamma* from 0 to 1 or 10. We tried all 12 combinations of these modifications. The best combination of parameters was the following: *max_depth* = 12, *min_child_weight* = 5, *gamma* = 1, *colsample_bytree* = 1, and *subsample* = 0.7, Using the best combination of hyperparameters, we further lowered the learning rate to 0.01 and set *early_stopping_rounds* to 100 to determine the optimal number of boosting iterations for that learning rate. Lower learning rates decrease the contribution of each tree to the model, making the boosting algorithm more conservative and further preventing overfitting, but lower learning rates require more iterations. With this information, we fit a final model with learning rate = 0.01 on the combined training and validation sets. We then evaluated its performance on the test dataset (15% of data), which had been withheld from all training and validation. To assess performance, we calculated two metrics: root mean square error and the coefficient of determination (or R^2). We calculated R^2 by dividing the sum of squared errors by the total sum of squares, and then subtracting this value from 1. An R^2 value of 0 indicates that the model does not explain the data any better than a simple null model that predicts the mean for each observation, while a negative R^2 value indicates that the model explains the data worse than this null model.

In an XGBoost model, correlated or uninformative predictors generally have little negative effect; they will generally not be incorporated during tree construction. However, extraneous predictors increase computational time and data storage requirements, making the forecast system more unwieldy to operationalize. For this reason, we sought to remove uninformative predictors. Using the *xgboost* package, we calculated the gain, a predictor importance metric that quantifies how much a tree improves by adding a split on a given variable. Gain values are scaled to sum to 1. After the first grid search step, we identified and eliminated predictors with gain values less than 0.01 and restarted the tuning procedure. In this manner, we eliminated albedo, vertical velocity, convective available potential energy, total precipitation, and snow cover. This left 12 variables in the final model: ordinal date, height above ground level, latitude, longitude, air temperature, relative humidity, zonal wind, meridional wind, surface pressure, mean sea level pressure, visibility, and total cloud cover.

We trained and tested two further modifications to the final model: one which also included additional conditions variables from the previous night (winds, temperature, and surface pressure) and their 24-hour changes, and another which included these lagged weather variables plus migration intensity measured during the previous night. Our aim here was to determine how much additional explanatory power we could achieve with a model that took into account recently observed conditions and behavior.

Performance and importance

To assess performance of the final model using weather forecasts instead of reanalysis (i.e. NARR) data, we tested the model using archived NAM forecasts made 1-3 days in advance. We did the same for GFS forecasts made 1-7 days in advance. Because GFS does not contain a visibility variable, we first retrained the model without visibility included in order to conduct this evaluation.

To assess model performance at unobserved spatial locations, we performed a cross-validation where we randomly removed one station (out of 143 total) from the dataset, retrained the model on the remaining data, and tested its performance on the withheld station.

We identified the predictor variables that were most important for model predictions using gain, a measure of the variable's importance in making accurate predictions. We also generated partial dependence plots using the R package *mlr* (*35*) to explore how these variables influence predictions. Here, we used a learning rate *eta* of 0.05 instead of 0.01 to make computation tractable.

Prediction intervals

We constructed empirical prediction intervals using residuals from XGBoost predictions for the validation dataset. We fitted a generalized additive model (*36*) on squared XGBoost residuals against the XGBoost-predicted value to account for an error variance that increased with the magnitude of the predicted value. The generalized additive model produced an estimated error variance for each predicted value, which we used to construct 90% prediction intervals using 0.05/0.95 Gaussian quantiles. We constructed separate models for upper and lower limits to allow for asymmetry in the width of the interval, and we used the Gamma distribution family in the generalized additive model to constrain the predicted variances to be non-negative.

Forecast output and estimation of nightly migration magnitude

Using our validated migration forecast model, we made predictions across the entire 12-km NAM grid. For smooth presentation, we averaged predictions across 9×9 cell blocks. We also used our model to estimate the total number of birds migrating over the continental United States each night. For this we used the NARR dataset because it is the best retrospective estimate of occurred conditions. For each 32-km NARR grid cell covering the continental United States, we multiplied the bird density estimate by the area of the cell and summed totals across all grid cells for each night.

NEXRAD radars operate at slightly different carrier frequencies (and hence different wavelengths) to reduce interference from neighboring radars, and this variation may introduce noise into estimates of total bird numbers if radars differ substantially in wavelength (*37*). However, such noise is likely to be minor because (1) most radars operate at more similar wavelengths than the example presented in (*37*), (2) variation in carrier frequency is not correlated with geography (i.e. no consistent spatial bias would be introduced), and (3) including wavelength as a model predictor to account for any systematic difference in detected bird densities did not appreciably change model performance.

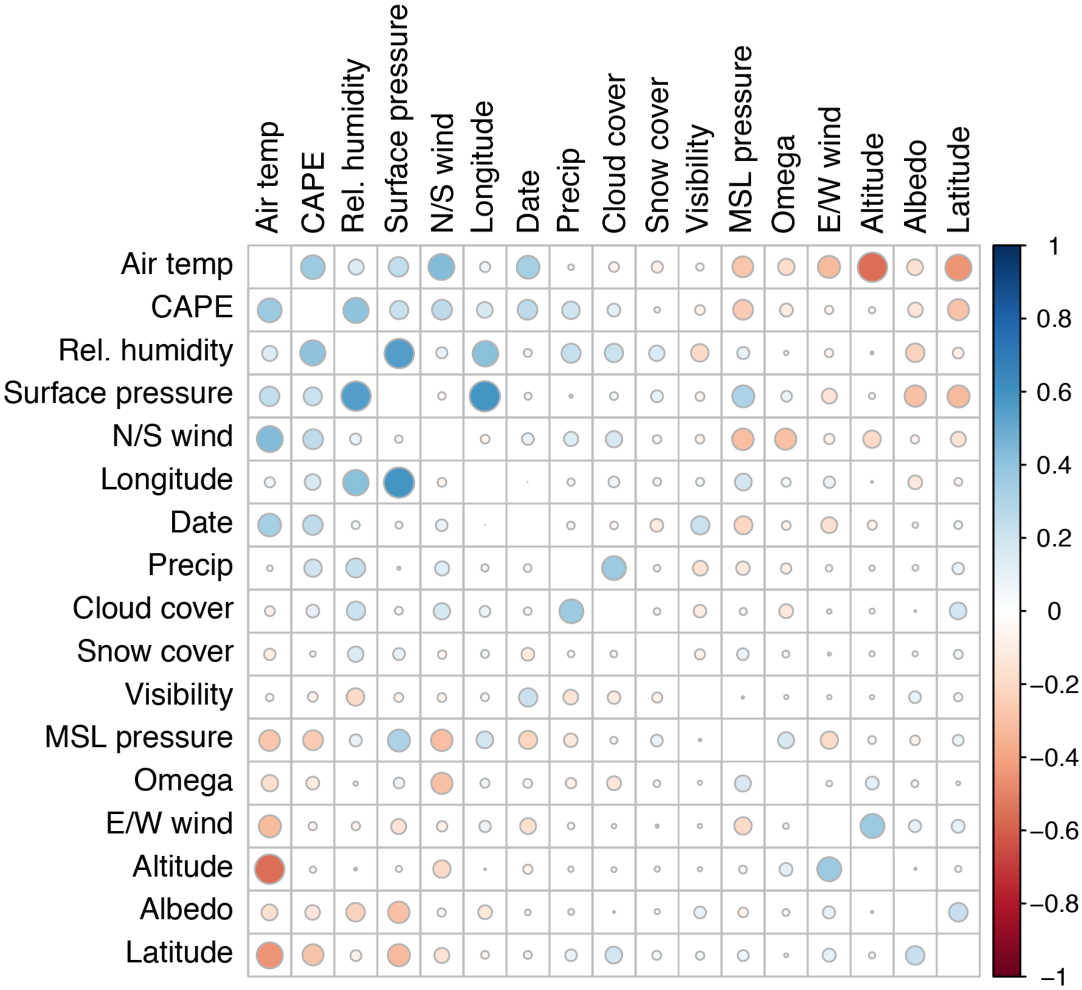

Fig. S1. Spearman rank correlations among all pairs of predictor variables. No pair of predictors had absolute Spearman or Pearson correlation coefficients greater than 0.60.

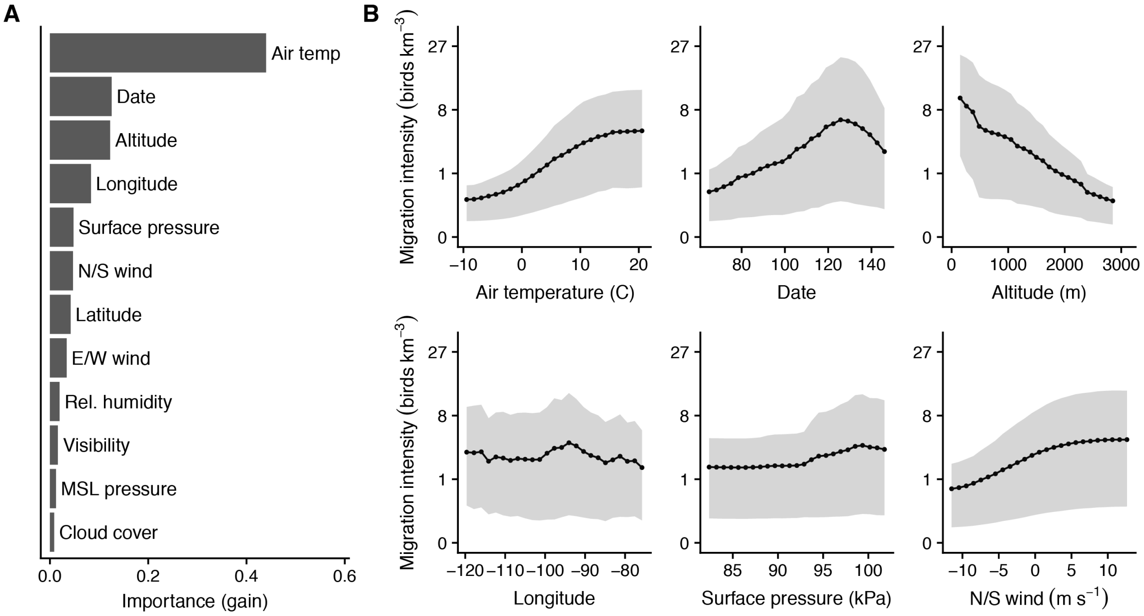

Fig. S2. Predictor importance and partial dependence. (A) Predictor importance measured by gain. Gain is a measure of each variable's importance in making accurate predictions. (B) One-dimensional partial dependence plots for the six most important predictor variables. Solid lines show the mean and shading shows the middle 50% of predicted y-values. Note that this is not a confidence interval; it shows the marginal distribution of y-values over the values of all other predictors and should be expected to be wider than confidence limits. Narrower shading indicates that the predictor explains a greater proportion of variance in the predicted values.

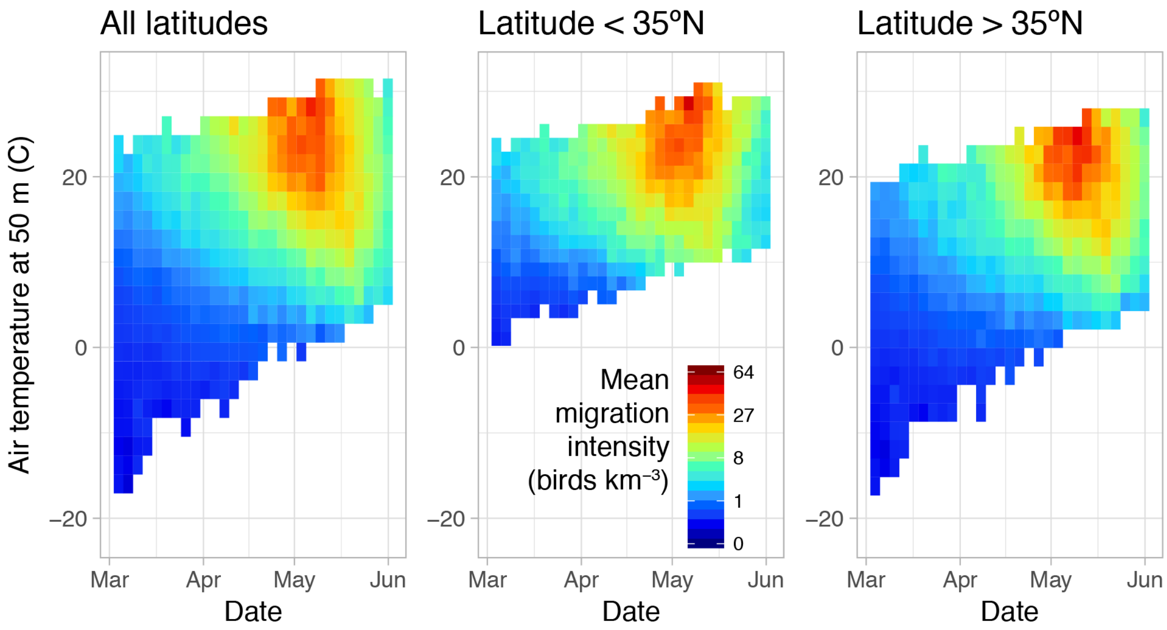

Fig. S3. Mean observed migration intensity by date and temperature close to surface. For a given date, the highest migration intensities occurred where temperatures close to the surface were warmest, especially at higher latitudes. This figure summarizes raw data and does not show model output.

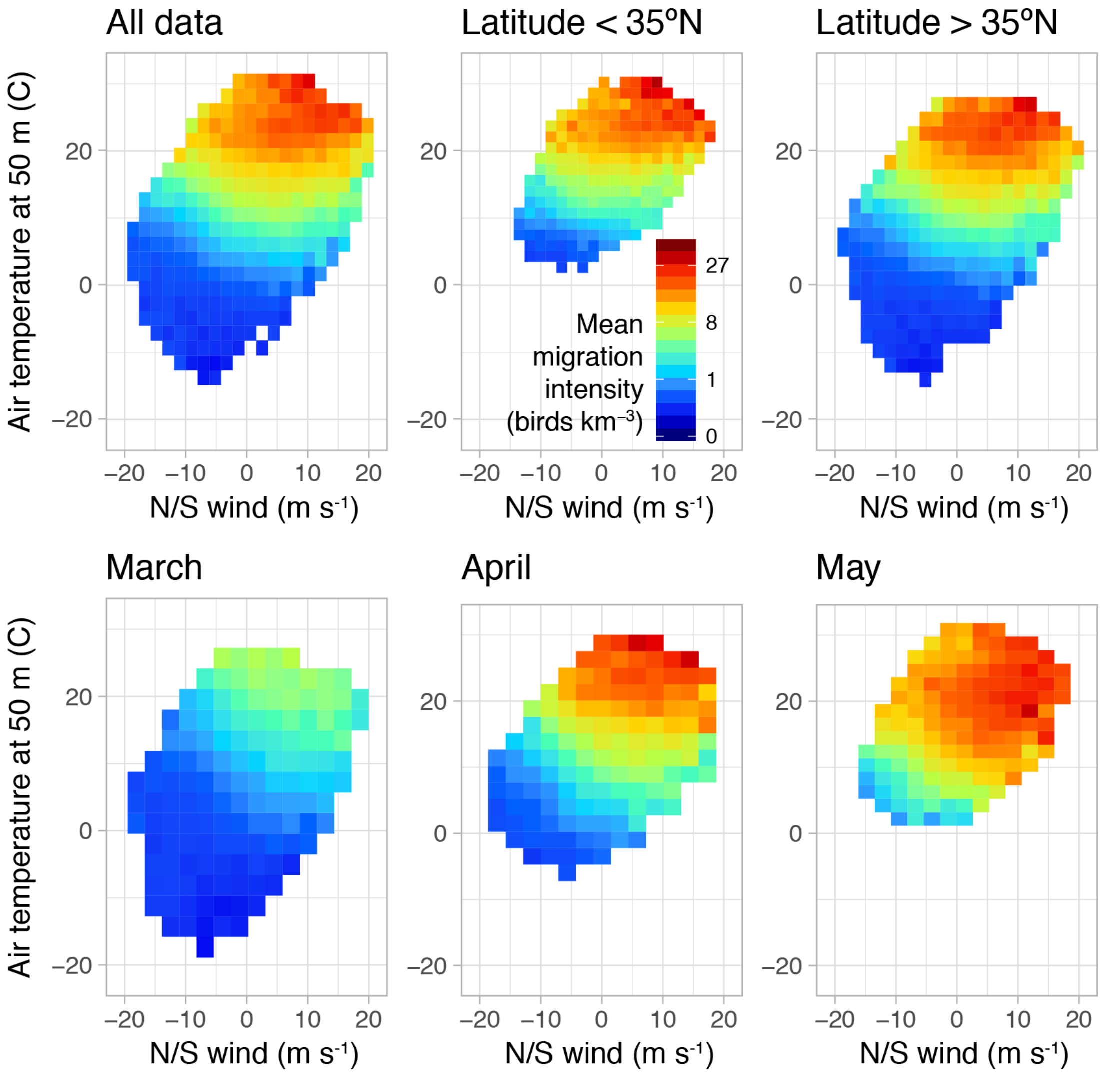

Fig. S4. Mean observed migration intensity by temperature close to the surface and wind direction. For given wind conditions, the highest migration intensities occurred where temperatures close to the surface were warmest, especially at higher latitudes. This figure summarizes raw data and does not show model output.

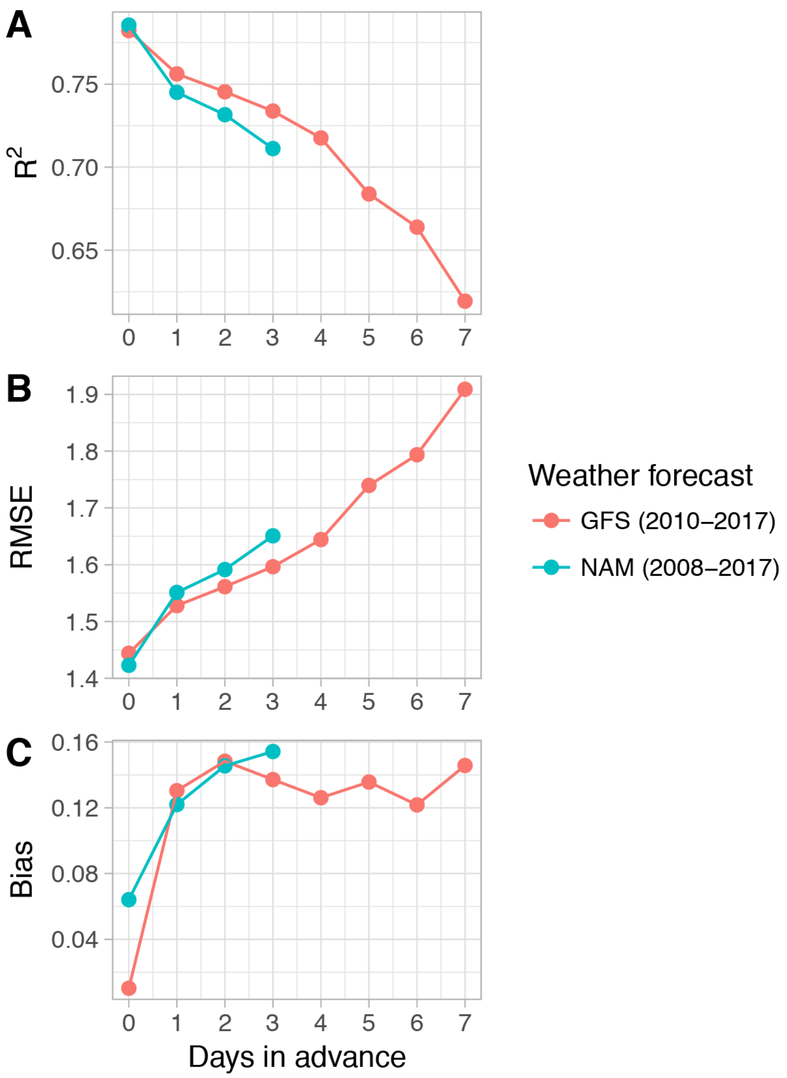

Fig. S5. Model performance using weather forecast data. We evaluated performance on the test dataset using the Global Forecast System (GFS) and North American Mesoscale (NAM) forecast system.

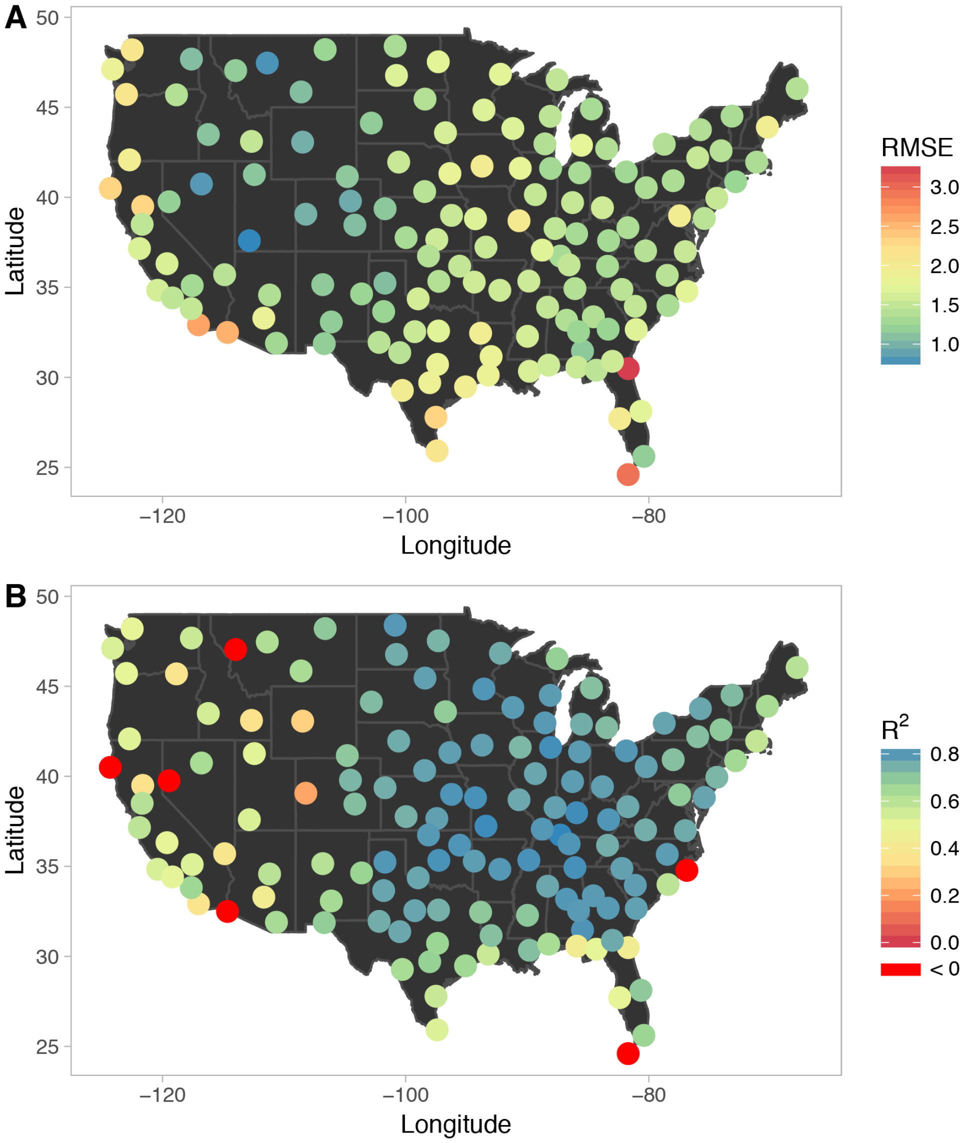

Fig. S6. Relative and absolute performance at radar stations withheld from the training dataset. Performance was best at interior sites, especially in the central and eastern United States. At a small minority (4%) of withheld sites, relative performance was poor ($R^2 < 0$, indicating performance was worse than a naive model that predicts the mean response for each observation), which may be due to local influences such as topography (e.g. see Florida Keys).

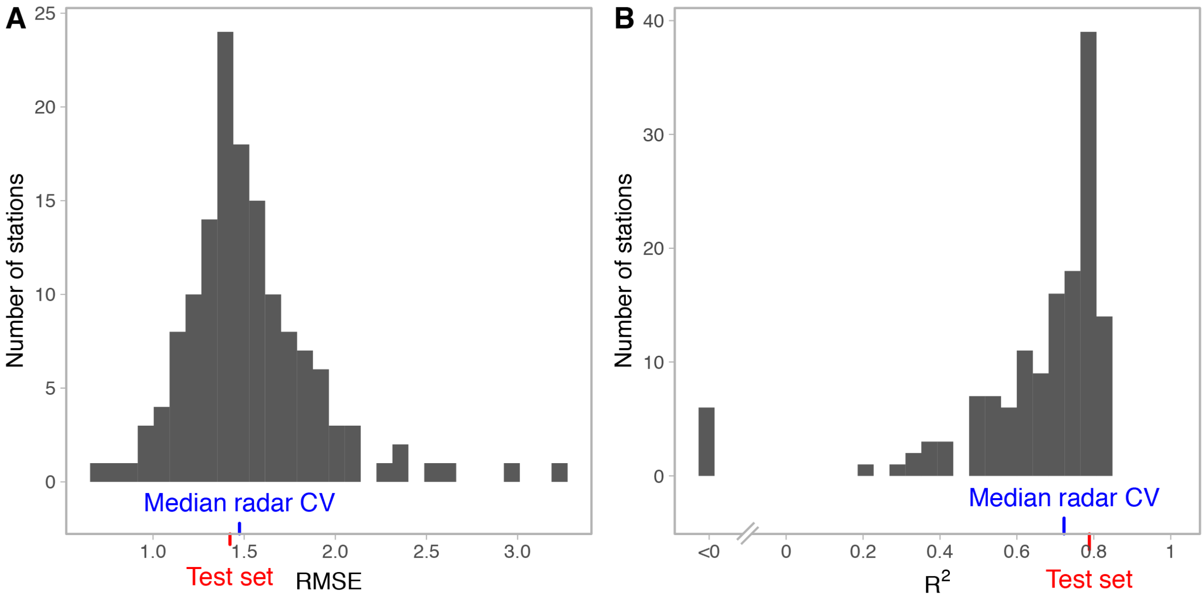

Fig. S7. Model performance at unobserved locations. Histograms show the distribution of (A) absolute and (B) relative performance metrics for radar stations that were withheld from the training dataset. The blue tick marks show the median value across sites, and the red tick marks show the corresponding value for the randomly-selected test set (all locations included).

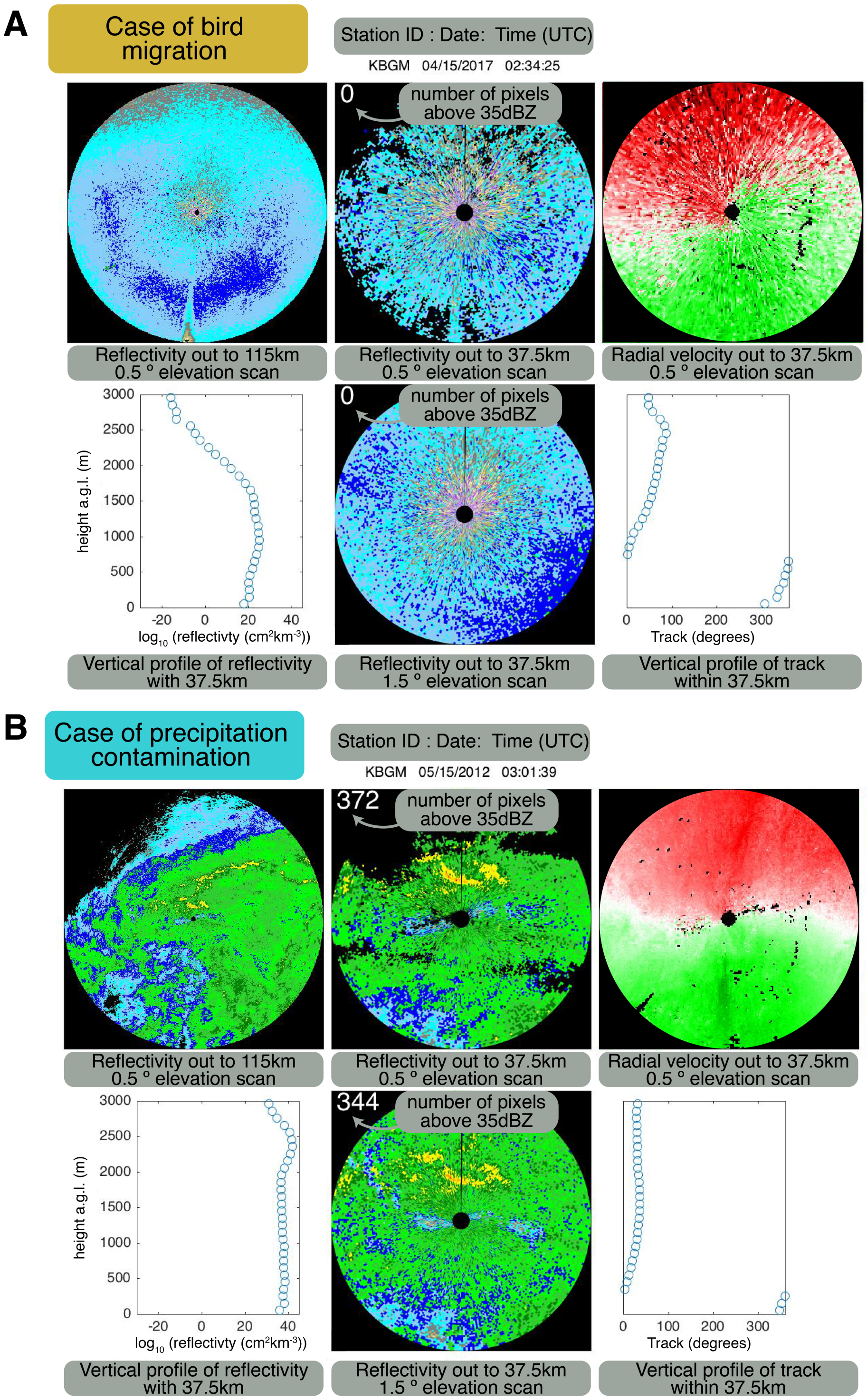

Fig. S8. Composite images used for classifying radar scans containing precipitation. Panels show example cases of (A) bird migration and (B) precipitation contamination.

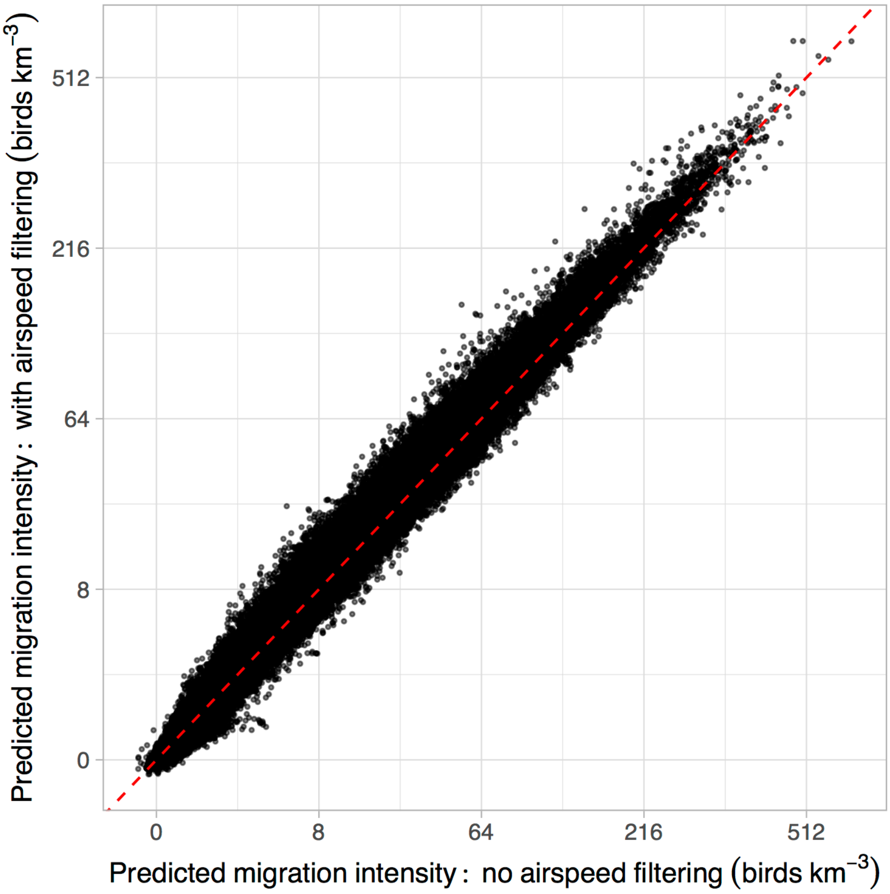

Fig. S9. Model results are robust to possible insect contamination. We removed altitude bins with mean airspeed ≤ 5 m s^{-1} to limit the inclusion of flying insects in our dataset. Predictions made by a model trained without airspeed filtering corresponded closely to those made by the final model with airspeed filtering (Pearson's $r = 0.995$). Prediction error for these two models was comparable (RMSE = 1.422 with filtering; RMSE = 1.442 without filtering). The dashed red line is the identity line.

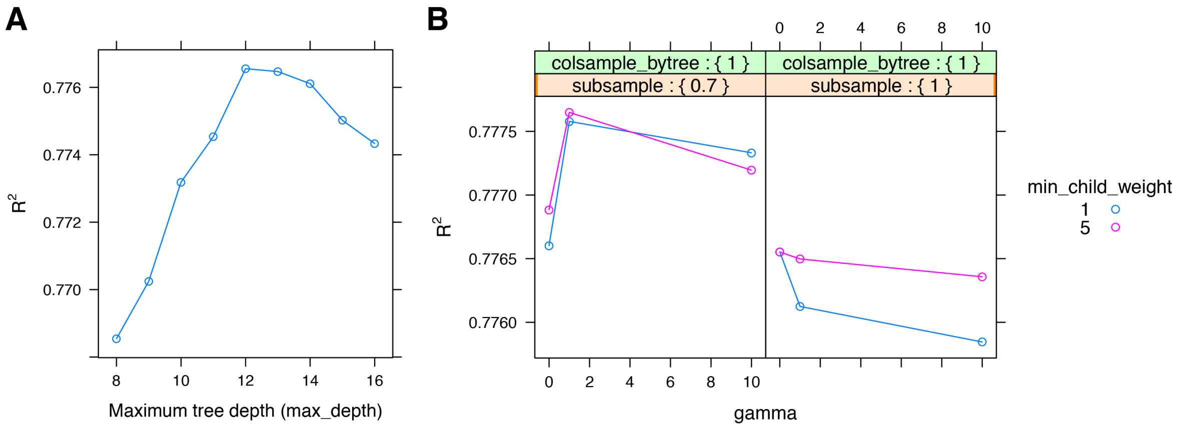

Fig. S10. Hyperparameter tuning using validation dataset. (A) We first varied maximum tree depth, and second (B) varied three parameters that may aid in limiting overfitting. Note that hyperparameter tuning affected performance only to a small degree (~1% in A and ~0.3% in B).

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Part III

Migration in the Anthropocene

Van Doren, B.M.,* *Horton, K.G.,* Dokter, A.M., Klinck, H., Elbin, S.B., and Farnsworth, A. (2017). High-intensity urban light installation dramatically alters nocturnal bird migration.* PNAS *114, 11175–11180.*

* *Equal contributions.*

5

High-intensity artificial light alters bird migration

High-intensity urban light installation dramatically alters nocturnal bird migration

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Billions of nocturnally migrating birds move through increasingly photopolluted skies, relying on cues for navigation and orientation that artificial light at night (ALAN) can impair. However, no studies have quantified avian responses to powerful ground-based light sources in urban areas. We studied effects of ALAN on migrating birds by monitoring the beams of the National September 11 Memorial & Museum's "Tribute in Light" in New York, quantifying behavioral responses with radar and acoustic sensors and modeling disorientation and attraction with simulations. This single light source induced significant behavioral alterations in birds, even in good visibility conditions, in this heavily photopolluted environment, and to altitudes up to 4 km. We estimate that the installation influenced ≈1.1 million birds during our study period of 7 d over 7 y. When the installation was illuminated, birds aggregated in high densities, decreased flight speeds, followed circular flight paths, and vocalized frequently. Simulations revealed a high probability of disorientation and subsequent attraction for nearby birds, and bird densities near the installation exceeded magnitudes 20 times greater than surrounding baseline densities during each year's observations. However, behavioral disruptions disappeared when lights were extinguished, suggesting that selective removal of light during nights with substantial bird migration is a viable strategy for minimizing potentially fatal interactions among ALAN, structures, and birds. Our results also highlight the value of additional studies describing behavioral patterns of nocturnally migrating birds in powerful lights in urban areas as well as conservation implications for such lighting installations.

artificial light | nocturnal migration | remote sensing | radar ornithology | flight calls

The extent of artificial light at night (ALAN) at regional and global scales has increased 5–10% annually in portions of North America and Europe and exponentially in some other regions (1), resulting in sky glow that is often significantly brighter than luminance of the natural sky. ALAN may affect a diverse array of nocturnally active animals, and recent studies have highlighted the need for primary research into these potential impacts (2, 3). The biological effects of anthropogenic light pollution may be especially significant for nocturnally migrating birds (2–6).

Birds engage in seasonal migrations that are often global in distribution and span a broad range of spatial and temporal scales (7, 8). Avian migratory movements are often thought of as feats of endurance; some species undertake days-long, nonstop, transhemispheric flights, while others embark on complex, months-long journeys (9). Failed migration may have detrimental effects at individual and population scales (10, 11). Despite birds' primarily diurnal activity for the majority of the annual cycle, most migratory movements are nocturnal (7, 8), and the numbers of birds that migrate at night are enormous (12, 13). Numerous studies have offered perspectives on factors that govern nocturnal movements (14–18) and insights into adaptations necessary to orient and navigate at night (19, 20).

Visual cues are essential for navigation during migration (21), and ALAN may alter birds' abilities to orient and navigate (22, 23). The avian geomagnetic sense, which provides songbirds with a compass to inform their spatial maps (19, 20, 24), may function with a dependency on frequencies of light, and ALAN may interfere with this dependency (25–28). Impediments to orientation and navigation senses may prove costly for avian migrants, creating new hazards during an already challenging and dynamic period of the annual cycle (29). Additionally, ALAN can alter the ways birds communicate (30) and avoid predation (31).

Accounts of birds' responses to light are numerous in literary and historical anecdotes, peer-reviewed journal articles, and popular media. Mortality at lighted structures has been documented across a wide geographic area and a broad range of species (4, 6, 32–44). It is likely that hundreds of millions of birds die annually from nocturnal collisions with buildings (29), representing a diverse array of migrant species (32, 33). Understanding the causes of these events is paramount; proposed explanations include that birds exhibit phototaxis and experience light-induced disorientation.

Generally, negative impacts of ALAN for birds in flight have been associated with conditions that are already poor for navigation and orientation, such as low cloud ceiling, fog, and stalled or weak frontal boundaries between air masses (34–39, 43, 45–48). Experimental field studies are generally rare (22, 26, 49–51) and offer limited evidence of the extent and intensity of ALAN's effects on nocturnally migrating birds, particularly with respect to

Significance

Artificial light at night is a novel stimulus in the evolutionary history of nocturnal animals. Light pollution can significantly alter these organisms' behaviors, from migration to foraging to vocal communication. Nocturnally migrating birds are particularly susceptible to artificial light because of adaptations and requirements for navigating and orienting in darkness. However, light's effects on in-flight behaviors have not been well quantified, especially in urbanized environments. Here we report that an iconic urban light installation dramatically altered multiple behaviors of nocturnally migrating birds—but these effects disappeared when lights were extinguished. We recommend selective removal of light pollution during nights with substantial bird migration to mitigate negative effects on birds, in particular collisions with lighted structures.

Author contributions: A.F. developed the study, collected visual observations and weather data, and wrote the paper; B.M.V.D. shaped the study, performed statistical analyses, and contributed to writing the paper; K.G.H. analyzed radar data and contributed to writing the paper; B.M.V.D. and K.G.H. generated figures and animations; A.M.D. developed simulations and produced associated figures and text; H.K. performed acoustic energy analysis; H.K. and A.F. analyzed acoustic data; S.B.E. provided bird mortality data, provided coordination, support, and access to the study site.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

Data deposition: All visual counts made at Tribute in Light are archived in the eBird database at ebird.org/ebird/hotspot/L1744278.

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behaviors in clear sky conditions (but see ref. 48) and urbanized (e.g., heavily photopolluted) environments. Understanding the disruptive effects of short-term ALAN (e.g., lighting installations, sporting events) on nocturnal bird migration in urbanized and photopolluted areas and identifying the extents of these effects in clear sky conditions are important conservation priorities.

We took advantage of a unique opportunity to quantify birds' responses to ALAN by monitoring numbers, flight patterns, and vocalizations of birds aloft during alternating periods of illumination and darkness in the powerful light beams of the National September 11 Memorial & Museum's (NSMM's) "Tribute in Light" (TiL) in New York, NY (Fig. 1*A*). First, we quantified densities and flight speeds of aerial migrants near the light installation using data from the KOKX Brookhaven, NY WSR-88D radar station, revealing how numbers of birds and their rates of passage changed in the presence or absence of illumination. Second, we measured birds' vocal activity by recording their in-flight vocalizations, or flight calls, from the base of the installation. Increased flight calling activity in nocturnally migrating birds may indicate disorienting or confusing conditions (30, 52). If nocturnally migrating birds were attracted to and disoriented by the lights, we expected to observe higher densities of birds flying at slower flight speeds and vocalizing more frequently during periods of illumination. Finally, we used a flow model to simulate bird behaviors in ALAN conditions for comparison with observed radar data. These spatiotemporal distribution simulations investigated three important behavioral parameters to explain bird concentrations at the installation: the probability that the lights affected nearby birds, the distance over which the lights affected birds, and whether disoriented birds showed preferred flight directions toward the display. Together, these parameters determined how long birds remained in the illuminated area.

Results

We detected large aggregations of circling birds above the installation under clear sky conditions during periods of illumination (Figs. 1 *B* and *C* and 2*A*, Movies S1–S3, and *SI Appendix*, Fig. S1). By summing the differences between bird numbers within 5 km of the installation and the number expected in that area given baseline densities, we estimate that ≈1.1 million birds (95% CI: 0.6–1.6 million) were affected by this single light source during our study period of seven nights over 7 y (*SI Appendix*, Fig. S2). The numbers of birds affected varied by year, in part due to variation in the magnitude of migratory passage through the surrounding area on the study night (*SI Appendix*, Fig. S3), but all years showed strong increases in bird density with decreasing distance to the light source (Fig. 3 and *SI Appendix*, Fig. S4*A*). Under illumination, peak bird densities near the installation reached magnitudes 20 times greater than the surrounding baseline during all 7 y (*SI Appendix*, Fig. S5*A*), where we defined baseline as the mean density in the area 2–20 km from the site. Peak bird densities exceeded 60 times baseline in 5 of the 7 y and 150 times baseline in 3 y (2008, 2012, and 2013), but peak densities never exceeded 13 times baseline in the absence of illumination (*SI Appendix*, Fig. S5*A*). Vocal activity beneath the lights was intense during periods of aggregation (Fig. 2*C* and *SI Appendix*, Fig. S6). Bird densities, flight speeds, and vocal activities all varied closely with illumination (Fig. 2). Removal of illumination resulted in rapid changes in nocturnal migration behaviors, with birds dispersing, increasing flight speeds, decreasing calling activity, and moving away from the site in a matter of minutes (Fig. 3 *C* and *D*).

We found a strong effect of illumination on the maximum standardized peak bird density and the maximum number of birds detected within 500 m of the installation during each period of darkness and adjacent periods of illumination. Considering the 0.5° radar elevation angle, maximum standardized bird densities were 14 times greater when the light display was illuminated ($t = 5.70$, $P < 0.0001$). Maximum bird numbers averaged 3.4 times greater during lit periods ($t = 3.89$, $P = 0.0003$). Remarkably, these effects were also present at high altitudes (1.5° radar elevation angle, sampling altitudes of 2.4–4.1 km): maximum standardized densities increased on average by 3.9 times ($t = 3.25$, $P = 0.002$) and maximum bird numbers by 3.3 times ($t = 2.34$, $P = 0.023$) during lit periods at high altitudes. We note that we did not detect many birds congregating in the beams during 2014; this year was not included in the above analyses because the lights were not shut down. We observed a strong effect of light on bird behavior during all other years (*SI Appendix*, Fig. S7).

Considering all radar observations, total numbers of birds within 500 m of the installation averaged 3.4 times higher during illuminated periods ($t = 9.34$, $P < 0.0001$). Standardized peak densities showed a similar pattern (factor = 6.4 times, $t = 3.72$, $P = 0.0003$), with the effect strengthened to 46 times higher during illuminated periods in 2015 ($t = 2.91$, $P = 0.004$). Again,

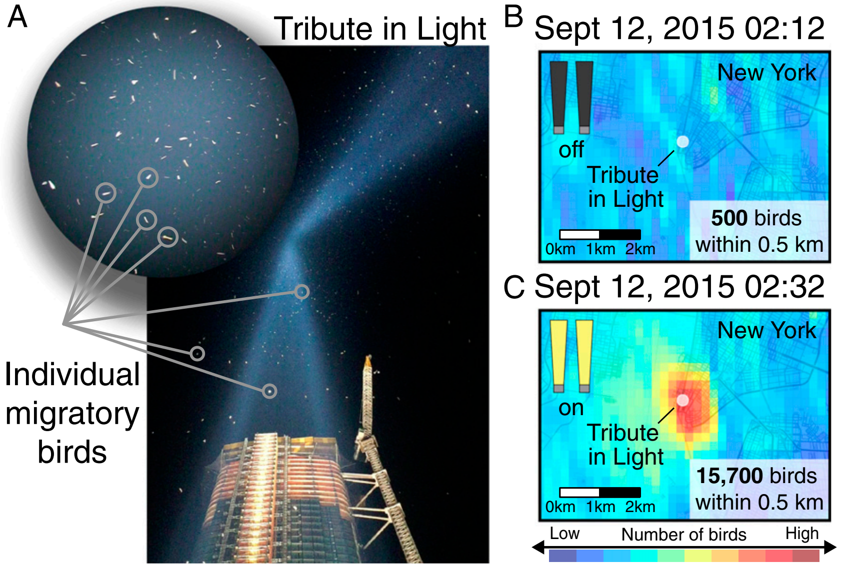

Fig. 1. Tribute in Light site. Observations (in Coordinated Universal Time) from the September 11–12 2015 Tribute in Light depicting altered behaviors of nocturnally migrating birds. (*A*) Direct visual observation. (*B*) Radar observation without TiL illumination and (*C*) with TiL illumination.

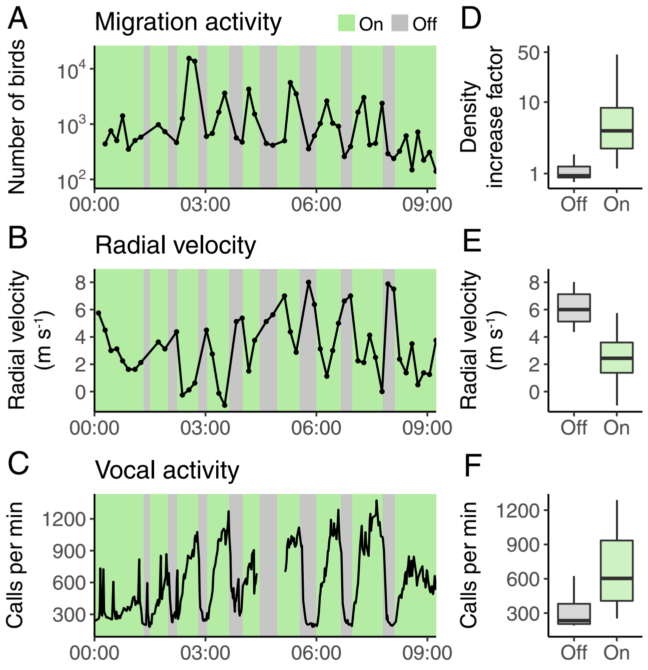

Fig. 2. Time series of radar and acoustic measures of Tribute in Light impact on migratory birds. Observations (in Coordinated Universal Time) from September 11–12, 2015 of (*A*) migration activity within 500 m of the installation, (*B*) radial velocity within 500 m of the installation, and (*C*) vocal activity during periods of TiL illumination. *D*–*F* show corresponding data with and without illumination. Density increase factor (*D*) is defined as the peak bird density near the installation divided by the mean density 2–20 km away.

these effects were also significant in the high altitude 1.5° radar data (total numbers: factor = 1.9 times, t = 3.49, P = 0.0006; standardized peak density: factor = 4 times, t = 4.00, $P < 0.0001$). Radial velocities were significantly lower during illuminated periods (main effect = -1.7 ms^{-1}, $t = -2.10$, P = 0.037), especially during 2012 (effect with interaction = -5.4 m/s, $t = -2.38$, P = 0.02) and 2015 (effect with interaction = -4.3 m/s, $t = -2.52$, P = 0.01). Flight call rates recorded beneath the installation were significantly higher during illuminated periods (main effect = 1.4 times, t = 4.53, $P < 0.0001$), especially in 2015 (factor with interaction = 2.9 times, t = 6.88, $P < 0.0001$); the effect was reduced in 2013 (factor with interaction = 1.1 times, $t = -2.30$, P = 0.02). Because our model of vocal activity included bird density as a predictor to account for variation in calling explained by the sheer quantity of birds, the significant increases in calling with illumination can be attributed primarily to behavioral differences.

Simulation results showed that birds were highly likely to become disoriented as they approached the installation (*SI Appendix*, Fig. S8). The model matching radar observations most closely (model 1; Fig. 4 and *SI Appendix*, Tables S1 and S2) had disorientation probability a = 0.95, indicating a very high likelihood of disorientation near ALAN, and the characteristic disorientation distance (σ) was 1,500 m. The concentrations of birds observed at the installation could only be explained by including directed flight toward ALAN for disoriented birds (concentration parameter $\kappa > 0$; best model $\kappa = 0.1$). In contrast, simulated birds diffused easily away from ALAN when assuming a nondirectional random walk ($\kappa = 0$; model 3 in *SI Appendix*, Table S1). These results support our visual observations of birds circling around the installation and are indicative of light attraction.

The stabilization time to a steady-state increased with disorientation probability (a) and flight directionality toward ALAN (κ) (Fig. 4, Movies S4–S8, and *SI Appendix*, Table S1). The stabilization time provides information on the residence time of birds in the beam, as a steady state is only reached over time periods longer than the average residence time. Our model 1, which is conservative in this regard, predicts a stabilization time of 34 min. We note that this is the result of average behavior for all birds contributing to the density pattern, and individual residence times may be considerably longer or shorter. Our simulation provides a theoretical framework for explaining our visual and remotely sensed observations, underscoring that the light installation attracted and entrained passage migrants.

Finally, direct visual observations showed that birds frequently circled the installation during periods of illumination and decreased speed on approach to the installation (*SI Appendix*). Such observations also highlighted a particular hazard that nocturnally migrating birds face in urbanized areas with ALAN: collisions with structures. Observers noted in 2015 and 2016 that many birds collided with the glass windows of a building under construction just north of the lights (50 West Street; Fig. 1*A*). The full extent of mortality was not clear, primarily because of challenges surveying nearby sites, scaffolding preventing birds from falling to ground level, and removal of carcasses by scavengers and building staff. We therefore do not have sufficient data to analyze mortality with respect to illumination and migration intensity. However, existing data are archived in the New York City Audubon D-Bird database (https://d-bird.org/).

Discussion

This study quantifies ALAN-induced changes in multiple behaviors of nocturnally migrating birds. Our data show that the light installation strongly concentrates and disorients migrants flying over a heavily urbanized area, influencing ≈1.1 million birds during seven nights over 7 y.

Existing published accounts report attraction to lights almost exclusively under poor-visibility conditions (45, 53), but our results show alterations to migrants' behaviors in clear and mostly clear

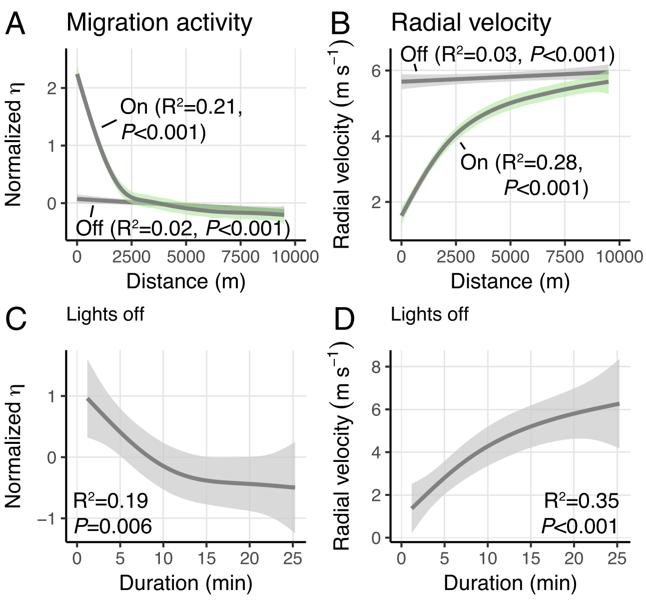

Fig. 3. Spatial and temporal influence of Tribute in Light on migratory birds. Migration activity (*Left* column) and radial velocity (*Right* column) at the installation pooled across years by distance from the study site (*A* and *B*) and activity as a function of time since TiL shutdown (*C* and *D*). To account for year-to-year variation, migration activity was normalized across years using a z-score standardization (values minus the nightly mean, divided by the nightly SD). Illumination represented by green and periods without illumination by gray. *C* and *D* include only measures ≤500 m from the installation. Data fit with generalized additive models (*A* and *B*: bs = "cs," m = 2, k = 10; *C* and *D*: bs = "ds," m = 2, k = 5) and weighted by migration activity for radial velocity models. Shading represents 95% confidence intervals.

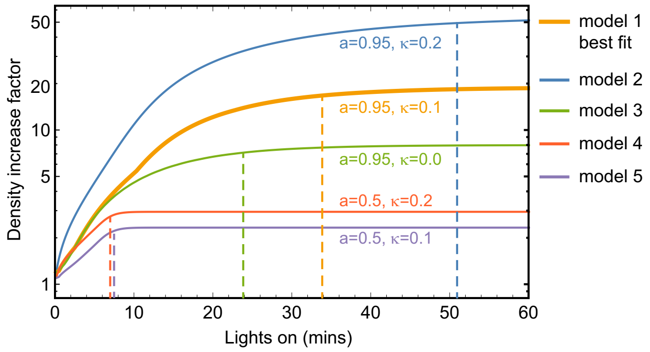

Fig. 4. Simulated bird concentrations over time at an ALAN source (solid lines). Vertical dashed lines indicate time to steady-state stabilization. Model parameters a and κ are described in *SI Appendix*, Eqs. **S1** and **S2**, with parameter σ fixed at 1,500 m (*SI Appendix*, Table S1). Model 1 represents the best fit to the observed patterns at the installation, but this model is still conservative in that higher-than-predicted concentrations of birds occurred in certain periods. In general, bird concentrations at the installation could only be explained by including directed flight toward ALAN for disoriented birds ($\kappa > 0$). These results support our observations that birds were disoriented by and attracted to the installation.

sky conditions (e.g., after ref. 48). Furthermore, to the best of our knowledge, no previous studies have reported attractive effects of ground-based lights to extend far above the ground, although nocturnally migrating birds will attempt to escape from direct illumination by a searchlight (54). In our study, we found behavioral responses to the installation up to ≈4 km above the ground. The vertical orientation of the light beams may be partly responsible for their high-altitude effects, as illuminated atmospheric moisture, dust, insects, or potentially other birds may attract migrants. We also demonstrated that short-term removal of ALAN eliminated its disruptive effects almost instantaneously. Our ground-truthed, direct visual observations of decreases in flight speed and increases in circling behaviors corroborate previous findings that birds shift direction and fly more slowly and erratically in the presence of ALAN (22, 23, 32, 33, 39, 44, 48, 49, 55). Furthermore, the increase in vocal activity that we describe agrees with other studies' findings, highlighting disorientation due to artificial lighting (23, 30). Finally, although each year exhibited a unique array of atmospheric conditions, we documented a strong concentrating effect of light in all but one of the 7 study years (*SI Appendix*, Fig. S7). We conclude that high intensity lights have the ability to greatly impact avian migratory behavior under a wide range of conditions. The fact that we did not document a strong effect during 1 y (2014) highlights a need for further research on how differing ambient conditions influence birds' attraction to light sources at night.

Light-induced alterations to nocturnal migration behaviors may represent significant energetic expenditures for migrating birds, but the effects of such alterations have not been quantified (56). Our visual observations indicate that bright lights alone can induce unnecessary ascent and descent, long periods of circling, and other types of complex and irregular maneuvering in birds close to the ground (22); these flight patterns are undoubtedly more energetically expensive than typical straight-path migratory flights. Specific hazards resulting from altered flight behavior may include susceptibility to predation (31), collisions with man-made structures (29), and changes to stopover ecology (57). Importantly, birds entrained for hours (39, 41, 42, 55, 58) by artificial lighting expend energy to remain airborne but do not make forward progress. Those that do not die from complications of exhaustion (59) may be delayed for days, as it takes time for lean migrants to regain fat stores during migratory stopover (60). Although our best model's stabilization time of 34 min suggests that most birds do not remain at the installation for hours, this model could not explain the largest concentrations we observed; other methods will be necessary to better understand variation in individual birds' behavior over time in the lights.

Further controlled experiments in field and laboratory settings would help determine the causes of attraction and disorientation at local and landscape scales. Studies that varied light intensity locally found that birds respond more strongly with more intense light (61–63). Sampling bird migration at and near light installations of varying intensities may provide additional opportunities to study attraction and disorientation. There are few vertically pointing light installations of comparable intensity in the United States (e.g., Luxor, Las Vegas, NV), but many structures use similarly powerful horizontal lights (e.g., sports stadia, construction sites, offshore oil rigs). Studies at such locations have not used multimodal remote sensing to quantify disruptions but have noted behavioral changes similar to those that we observed (e.g., aggregation, circling, and increased vocal activity) (57, 64).

Studies of ALAN are revealing large-scale effects on bird behavior that range from flight alterations to changes in stopover habitat use. There is mounting evidence that migratory bird populations are more likely to occur in urban areas during migration, especially in the autumn (65). Light pollution may explain this relationship, as recent research suggests that birds associate with higher levels of ALAN during migration (66). Given alarming declines in migratory bird populations (67, 68), these studies highlight a need to understand ALAN's implications for migratory bird populations.

Finally, our study highlights a model relationship for collaboration among diverse stakeholders. A hallmark of this project was frequent and public cooperation among the NSMM, the Municipal Arts Society, New York City Audubon, the Cornell Lab of Ornithology, and stakeholders with direct interest and responsibility for this event, all of whom acknowledged its potential to negatively impact birds. All parties agreed to keep the display illuminated unless potentially hazardous conditions for birds necessitated a short-term shutdown of the lights. Whereas discontinuing the display would be best for nocturnally migrating birds, such a scenario may not be possible at this time. TiL is arguably one of the world's most iconic and emotional displays of light. The fact that the event's organizers and participants were willing to periodically shut down the lights for the benefit of migratory birds is an encouraging acknowledgment of the importance of bird conservation. Moreover, despite occasional confusion and frustration among the tribute's viewers, media coverage often highlighted a unified message from stakeholders about balancing potential hazards to migrating birds with the intent and spirit of the display.

Methods

During our 7-y study period, the tribute lights were shut down a total of 22 times, for ≈20 min each. This allowed us to directly contrast birds' behaviors during adjacent dark and illuminated periods. We note that this study was opportunistic and not a controlled experiment. Furthermore, we note that such an opportunistic approach results in some inevitable challenges in interpretation, for example because we were unable to control for additional factors that could influence the degree to which birds congregate at light sources. Such factors likely include wind speed, wind direction, temperature, cloud cover, and ground-based sources of light and sound. However, because ambient conditions were generally similar within each night, we can still readily measure the additive effect of illumination on bird behavior, given each year's suite of conditions.

Study Site and Scope. TiL is an event held annually since 2002 on September 11th to memorialize lives lost during the terrorist attacks of September 11th, 2001 (www.911memorial.org/tribute-light). NSMM currently operates the light installation atop a parking garage near the site of the former World Trade Center in New York City (NYC), NY at the southern end of Manhattan Island (40.707°, −74.015°).

Massive nocturnal migratory movements of birds regularly occur over our study area during mid-September (12, 13, 69, 70). However, since the timing of these movements depends on local and regional weather and wind conditions (71–74), the magnitude of migratory passage on the single night of September 11th varies greatly among years. An agreement between New

York City Audubon (NYCA) and NSMM governs when to initiate the shutdown procedures: when numbers of birds circling in the beams exceed 1,000 individuals, based on visual observations, NYCA requests that lights be extinguished for ≈20 min. These requests originate from observers on site that are directly monitoring birds and their behaviors in the beams.

We examined September 11th nights from 2008 to 2016. High-resolution radar imagery did not exist before 2008, which limited our temporal scope. We excluded 2009 and 2011 because of the presence of precipitation, which interferes with analysis of radar data containing bird migration information. Of the remaining 7 y, migration conditions varied from marginal to favorable, assessed based on prevailing atmospheric conditions. Of these 7 y, the lights were shut down at least once during 5 of them; as a result, many of our analyses are restricted to these 5 y (2010, 2012, 2013, 2015, and 2016). Of the remaining 2 y, the first (2008) occurred before stakeholders could reach a consensus on a protocol for shutting down the light installation when birds were present and in danger. Organizers did not shut down the installation in 2014 because few birds were present in the lights.

Local Weather Conditions. We downloaded hourly local climatic data (LCD) for September 11 and 12, 2008–2016 (excluding 2009 and 2011 as described above) from the closest official National Weather Service station to the installation between evening and morning civil twilight (sun angle 6° below the horizon): WBAN 94728, Central Park, New York, NY at 40.789°, −73.967°; and meteorological terminal aviation routine weather reports (METARs) from Newark Liberty International Airport, the closest such station at 40.690°, −74.174°. Based on a review and summary of these data, we classified all nights during our study as clear (*SI Appendix*, Tables S3 and S4).

Weather Surveillance Radar Data. We gathered radar data from the Brookhaven, NY WSR-88D radar (KOKX; 40.866°, −72.864°) to quantify migrants' flight behaviors and extracted georeferenced measures of reflectivity (η; $cm^2\ km^{-3}$) and radial velocity (ms^{-1}) from the ≈0.5° and ≈1.5° elevation scales (12, 13, 70, 75, 76). We measured between civil twilight periods within a 20-km radius surrounding the installation (98.5 km from the radar, azimuth 260°) and consolidated analyses into 500-m height annuli bins. We dealiased velocities when necessary following refs. 76 and 77. We restricted our analyses to data points within 90 min of a shutdown period except when described.

We studied the effect of light stimuli on migratory birds using several metrics. First, we used the radar sweep with the lowest elevation angle (≈0.5°) to estimate the number of birds present in a cylinder centered on the installation with a radius along the ground of 500 m and a height of 1.7 km, the approximate width of the radar beam above the site (78). We calculated total effective scattering area per unit volume ($cm^2\ km^{-3}$) of birds in this cylinder using bird density measures from the 0–500-m bin. Then, we converted to numbers of birds using an estimated value of one bird = 8.1 cm^2, which is the measured cross-sectional area on S-band radar of a small passerine songbird (common chiffchaff, *Phylloscopus collybita*) (79). We chose a relatively small cross-section value because visual observations indicated that birds in the lights were predominantly small songbirds. The radar beam set to the 0.5° elevation angle passes above the installation at an altitude of ≈1.5 km (50% power range, 0.7–2.4 km), which is higher than the altitudes at which the greatest migratory activity during this season in this region generally occurs (80). Therefore, we used an analysis of the entire radar scan to estimate the proportion of migration occurring beneath (or above) the radar beam at the installation, out of sight of the radar. We then adjusted our estimates to account for these undetected birds by multiplying by the necessary correction factor (*SI Appendix*, Fig. S10). This approach assumes that the light beams did not greatly alter the altitudinal distribution of birds near the installation. The validity of this assumption is supported by direct visual observations at the site, where observers noted descent only by the lowest-flying individuals, which would not be detected by radar. Furthermore, any unaccounted-for descent at higher altitudes would render our estimates conservative, because a greater proportion of birds flying below the radar beam than expected would yield a lower estimate of total bird numbers.

To complement estimates of the total number of birds in proximity to the installation, we also calculated the extent to which birds were concentrated at high densities in the airspace near the installation, relative to the baseline value in the surrounding airspace. To produce this baseline, we calculated the mean and SD of density values between 2 and 20 km from the installation. We then found the peak bird density value within 500 m of the installation, and we subtracted the baseline mean density from this peak density and divided the difference by the baseline SD (again, 2–20 km from the installation). The resulting value, referred to as "standardized peak density," represents the number of SDs the peak density falls above the baseline density.

Acoustic Data. We collected continuous acoustic data at 32-kHz sampling rates and 16-bit sample sizes during each year's event with a pressure zone microphone (Old Bird 21c; Old Bird, Inc.) specifically designed for monitoring avian flight calls, connected to (*i*) a Nagra ARES-BB+ (2010 and 2013) or (*ii*) a custom-built passive acoustic recording system (2015 and 2016), comprising a Raspberry Pi 2 Model B (Raspberry Pi Foundation) with a Cirrus Logic Raspberry Pi audio card (Cirrus Logic). We focused analysis on the 6- to 9-kHz frequency band to minimize interference from anthropogenic, geophonic, and nonavian biophonic noise and because many of the migrating birds in the New York City area emit flight calls in this frequency band (81). The microphone sensitivity in the relevant frequency band for this study (6–9 kHz) was −33 dB re 1 V Pa^{-1} (±2 dB).

Visual Observations. We complemented remote sensing data that characterized behaviors of nocturnally migrating birds above the installation with visual observations. Numerous observers, including one of us (A.F.) and volunteers from NYCA and the local birdwatching community, made visual counts of nocturnally migrating birds at the installation during the period between civil twilight dusk and dawn. All visual counts are archived in the eBird reference database (ref. 82; ebird.org/ebird/hotspot/L1744278).

Statistics. We used generalized additive models (R package mgcv) (83) to quantify the effects of TiL illumination on birds' behaviors (*SI Appendix*). We tested the categorical factors of light (on/off) and year on four metrics: standardized peak density, the total number of birds present within 500 m of the installation, the radial velocities of birds above the installation, and the number of flight calls recorded beneath the site. For models of time series, we also included smooth terms that accounted for overall variation in densities and behavior through the night. We confirmed that there was negligible temporal autocorrelation of residuals using the acf function in R for all analyses involving time series (*SI Appendix*). We log-transformed response variables when necessary to reduce residual skewness; for models with log-transformed response variables, we express effect size as a multiplicative factor, found by exponentiating the coefficient. Finally, to determine whether the light effects we present in the study are representative of those observed across years, we compared standardized peak densities across the lighted periods of all 7 y, including the 2 during which no light shutdowns occurred.

Simulations. To understand the dynamic patterns of bird density at the installation, we formulated a spatiotemporal flow model to simulate behavioral changes resulting from exposure to light. In our simulation, birds could transition between two behavioral states: an undisturbed migratory state and a disoriented state induced by ALAN. Detailed methodology of our simulations is in *SI Appendix*.

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Supporting Information

High-intensity urban light installation dramatically alters nocturnal bird migration

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SI Methods

Study Site. Tribute in Light consists of two ground-based installations of lights, each comprising 44 7,000-8,000-watt xenon bulbs pointing skyward, giving the appearance of two tall towers of light. The bulbs have a dichroic treatment as well as nickel rhodium reflectors that significantly reduce infrared and ultraviolet spectra and create an effect similar to daylight. Beam projection and visibility is highly dependent on weather conditions, but the columns of light can project vertically from thousands of meters to tens of kilometers and are visible from distances up to 100 km.

At the time that the agreement for shutting down the installation in the presence of birds was developed, there was no information available about the dynamics of how birds arrive and depart the tribute site, nor was there information about how the installation affected behaviors. The shutdown process takes several minutes to complete because each bulb of the two 44-bulb installations must be turned off individually. Once dark, lights remained off for 22 ± 6 SD minutes. A dark period of approximately 20 minutes represented the best consensus among all stakeholders to balance potentially conflicting interests to maintain the integrity and intent of the event and to remove the attractive stimulus to birds, allowing them to depart from the area of potential hazard.

Weather Data. Weather data included details of temperature, visibility, wind direction and speed, and general conditions (Table S3) as well as more detailed cloud ceiling and cover aloft (Table S4). Clear skies prevailed among the 77 hourly LCD observations, with 66 of 77 hours (85.7%) exhibiting conditions described as clear or mostly clear skies. Local visibility never dropped below 11 km on any of our monitoring nights, and visibility of 16 km or greater occurred in 66 of 77 samples (87.5%). Visibility was at maximum (18.5 km) for 71 of 77 hours, with the remaining six hours never dropping below 13.0 km. Additionally, cloud cover was less than 50% for all but eight hours, generally 12.5% or less, and never below 0.5 km above the ground, mostly 0.5-1.5 km above the ground (Table S4). Thus, we did not classify any of these nights as poor visibility conditions.

Weather Surveillance Radar. In addition to the methods presented in the main text, a number of methodologies were important for our calculations of metrics describing the influence of the installation. To quantify the total number of birds affected by the installation, we estimated the number of birds within 5 km of the installation up to a height of 4.5 km using data from the 0.5° elevation angle and applying the correction factors described in the main text (Fig. S10). We did this for all radar scans across all years. The correction factors allowed us to estimate the total number of birds present from altitudes of 0-4.5 km given the number of birds detected in the 0.5° sweep. For comparison, we calculated the average bird density between 10-20 km from the installation and found the expected number of birds within 5 km of the installation, assuming densities were the same as those 10-20 km away. The difference between the expected number and the directly measured number was our estimate of the number of birds influenced by the installation in that radar scan. When the density of birds near the installation was lower than baseline, we set the number of birds affected to zero for that scan. Because our simulations (see below) provide information on the actual turnover time, we arrived at a total estimate that avoids double-counting birds by subsampling our dataset by a factor equal to the median time between radar scans (9.5 minutes) divided by the stabilization time estimate. For example, if the average turnover time is 20 minutes and the median time between radar scans is 10 minutes, we would subsample by a factor of 10/20 = 0.5, summing on average every other radar scan. To quantify uncertainty in our estimate, we calculated 95% confidence intervals by subsampling 10,000 times and finding the 0.025 and 0.975 quantiles of the resulting values.

We also analyzed data from the radar sweep with an elevation angle of ≈1.5°. This sweep intersects the airspace above the installation at an altitude of approximately 3.2 km (50% power range 2.4-4.1 km), twice as high as the 0.5° sweep. These altitudes are at the upper limit of bird migration, particularly passerines, in this region (e.g. 1, 2). Using the approach described in the main text, we calculated the number of birds in a cylinder of radius 0.5 km along the ground and height 1.7 km. We did not apply an additional multiplier.

To construct standardized visuals (e.g. Fig. 1*B,C*; Movies S2, S3) of the area of influence during periods of illumination, we cast radar resolution cells of the 0.5° elevation sweep to a regular spatial grid (i.e. raster image, ≈0.002° x 0.002°) using an equidistant cylindrical projection. We used maximum values of reflectivity and those nearest the radar for radial velocity when two or more resolution cells occupied a cell. We used the mean value in each cell for periods with and without illumination for aggregate plotting.

Acoustic Analysis. Because of the high intensity of calling activity at the site, in which many calls overlapped in time and frequency, and to minimize effects of different microphones, we used the amplitude in the 6-9 kHz frequency band to derive an index of calling activity. We applied a 10th-order Butterworth band-pass filter with corner frequencies 6 kHz and 9 kHz to the dataset (see Fig. S6). We then calculated mean amplitude values for the 6-9 kHz frequency band for consecutive one-minute non-overlapping windows. Finally, we normalized the resulting time series to obtain a relative calling activity index, hereafter "normalized amplitude." A normalized amplitude of 1 represents the maximum observed calling activity.

To estimate numbers of calls from normalized amplitude, we manually counted flight calls from spectrograms (Hann Window, FFT size 512, overlap 87.5%, 375 Hz grid spacing; (3)) in 40 one-minute periods during the night of 11 September 2015. We randomly selected these periods during the night, while ensuring that there was equal representation from each quartile of the normalized amplitude distribution. Normalized amplitude was an excellent predictor of vocal activity ($R^2 = 0.90$, $P < 0.0001$; Fig. S11), demonstrating that it is an appropriate measure of vocal activity from flight calls. In this linear model, we forced the regression through the origin to avoid the impossible scenario of negative flight calls (i.e. there should be zero normalized amplitude when there are zero calls, but this assumes no interfering noises, which was not always the case).

In order to directly compare acoustic and radar observations with linear models, we downsampled acoustic observations to the frequency with which radar observations were gathered. We achieved this by simply selecting the nearest one-minute calling sample for each radar observation, provided that it occurred within three minutes of the radar observation.

Visual Observations. Visual observations represented, to the best of observers' abilities, estimates of numbers, species, and flight behaviors of birds. AF used Zeiss and Kowa optics (10 x 50 binoculars and 20-60 zoom x 85 spotting scope, respectively, in 2008, 2010, and 2012-2015) and Swarovski optics (12 x 50 binoculars and 30-70 x 95 spotting scope in 2016). These observations are archived as specified in the Methods. See Movie S1.

Hypothetically, decreases in average radial velocities observed by radar for nocturnally migrating birds during periods of illumination could mean either that birds' mean flight speeds slowed as they passed the installation, or that individual birds maintained flight speeds but, because many birds started circling, appeared to decrease in average speed relative to the radar station. We used visual observations to determine which of these scenarios was occurring.

Statistical Analyses. We used generalized additive models (R package mgcv (4)) to quantify the effects of illumination on birds' behaviors. We tested the categorical factors of light (on/off) and year on four metrics: standardized peak density; the total number of birds present within 0.5 km of the installation; the radial velocities of birds above the installation; and the number of flight calls recorded beneath the site. We looked separately at 0.5° and 1.5° radar sweeps. Because the light shutdown procedures took several minutes to complete, and to allow birds time to respond to the change of treatment, we excluded data points within 5 minutes of an on/off transition. In addition to the categorical factors listed above, we included two smooth terms (thin plate regression splines with basis dimension chosen automatically): 1) time of night and 2) mean bird density between 2-20 km away, fitted separately for each year. These terms accounted for any overall variation in densities and behavior through each night unrelated to local light pollution (e.g. due to weather factors and regular circadian patterns; see (5-7)) and additionally served to account for autocorrelation. Importantly, in our model of vocal activity, we also included the peak bird density above the installation (as measured by radar) as a continuous predictor to account for variation in calling explained simply by the number of birds present. For each metric, we compared models with three possible combinations of categorical factors: light alone; light and year; and light and year with an interaction. We evaluated these models with the Akaike Information Criterion (AIC) and selected the model with the lowest AIC score. However, if the model with the lowest AIC score was within 1 AIC unit of a model with fewer parameters, we used the more parsimonious model. We checked the distribution of model residuals and applied data transformations when necessary. Initially, the residuals for the models of standardized peak density, total number of birds, and number of flights calls were highly skewed, and it was necessary to apply a log transformation to these response variables. We used the *logst* transformation in the R package *regr0* (8), which is equivalent to a $\log_{10}$ transformation for all but the smallest values, which are scaled such that the transformation yields all finite values. We chose this option because, unlike adding an arbitrary constant value to all observations, this method of scaling small values is determined by the distribution of the data. It only modifies the smallest observations, leaving all others unchanged. For models with log-transformed response variables, we express effect size as a multiplicative factor, found by exponentiating the coefficient.

In addition to testing for average differences in bird numbers between light and dark periods over the entire night, we looked at changes in peak concentrations between periods. We compared measurements made during periods of darkness (up to 30 minutes in duration) to those made during adjacent 30-minute illuminated periods. In each period, we found the maximum values of standardized peak density and total number of birds for both 0.5° and 1.5° sweeps. We constructed linear models as above, but without smooth terms because autocorrelation was not an issue. Again, we tested for the best of three possible models using AIC. We log-transformed response variables to satisfy model assumptions.

Figures were produced using the R packages *lattice* (9), *Hmisc* (10), *ggplot2* (11), and *cowplot* (12).

Simulations. We defined our simulations with the following assumptions. A bird in the migratory state could fly undisturbed in an average preferred migratory direction. Birds enter the disoriented state following a normal probability distribution f (see Fig. S8*A*) that decreases with distance (d) from the light.

$$f(d \mid a, \sigma) = a e^{-\frac{d^2}{2\sigma^2}} \qquad (1)$$

Here, a is the model parameter specifying the maximum probability to disorient when a bird is within (or very near) the lights. The standard deviation (σ) specifies the characteristic distance from the light at which birds become disoriented. In the disoriented state, birds depart from their preferred migratory direction and draw their flight direction from circular normal distribution g (von Mises distribution, see Fig. S8*B*):

$$g(\alpha \mid \alpha_{\text{light}}, \kappa) = \frac{e^{\kappa \cos(\alpha - \alpha_{\text{light}})}}{2\pi I_0(\kappa)} \qquad (2)$$

with α_{light} the angular direction of the lights at the position of the bird, I_0 the modified Bessel function of order 0, and κ the concentration parameter. When $\kappa = 0$ the function g is uniform, and birds' flight paths follow a random walk. When $\kappa > 0$ there is a preferential flight direction towards the lights, with larger κ implying a more directed flight towards the light source.

The simulation model thus has three main parameters

- a, the probability of disorientation
- κ, the concentration parameter for disoriented flight, determining the extent to which birds fly towards ALAN when disoriented
- σ, the characteristic distance from the lights within which ALAN affects bird behaviors

The simulation grid had a 5 x 5 km extent, with grid cells of 50 x 50 m. The simulation time step $\Delta t = 10$ s. In each simulation step, we determined the proportion of birds in that cell affected by ALAN using Equation (1). We propagated these disoriented birds over a distance $\Delta t\ v_{bird}$ into directions given by the angular distribution of Equation (2). We propagated the remaining birds in the migratory state over an equal distance into the preferred migratory direction.

Model parameters were fit to the radar observations in years 2010, 2012, 2013, 2015 and 2016, when lights were manipulated. Simulations were performed on the basis of lights-on periods, in which we assumed the baseline migration density and speed to be constant. The baseline migration ground speed v_{bird} was calculated at the location of KOKX, using a vertical profile extraction following the methods of (13). The baseline migration density was calculated as the average bird density in the area 2-20 km distance from the installation, assuming a cross-section per bird of 8.1 cm^2. The peak density at the installation for each radar scan was calculated as the maximum density observed within 500 m of the installation. The frame of reference is rotated such that the birds' migratory directions were upward towards the lights, located in the center of the simulation grid. We excluded the first lights-on period after sunset, as bird densities change rapidly in this time window, and to not be affected by potentially different behavior during takeoff or when it is not fully dark. This gave 20 lights-on periods in total for the 5 years.

The model was fit by an exhaustive search in the model parameter space, considering a=0.25-0.98 (steps of 0.1), κ=0-0.8 (steps of 0.1), and σ=250-2000 m (steps of 250 m). All possible combinations of parameter values were tested in separate model runs coded in Wolfram Mathematica 11, requiring ≈12 days of CPU time on a

2.3 GHz Intel Core i5 processor. Goodness-of-fit of the simulation was quantified by the explained variance in peak density at the ALAN source, defined as $1-S_{err}/S_{tot}$, with S_{err} the sum of squared residuals between simulated and measured peak density, and S_{tot} the sum of squares of measured peak density. Explained variance for all parameterizations is reported in Table S2.

We visualized simulation runs for a high (a =0.95) and a low (a =0.5) disorientation probability, as well as for moderately strong (κ=0.2) and weak (κ=0.1) attraction to light (see Fig. 4). Parameterizations are illustrated in Fig. S8. We extracted from the runs the bird density increase factor at the ALAN source and a stabilization time, defined as the time required to reach 95% of the steady state peak density at the ALAN source.

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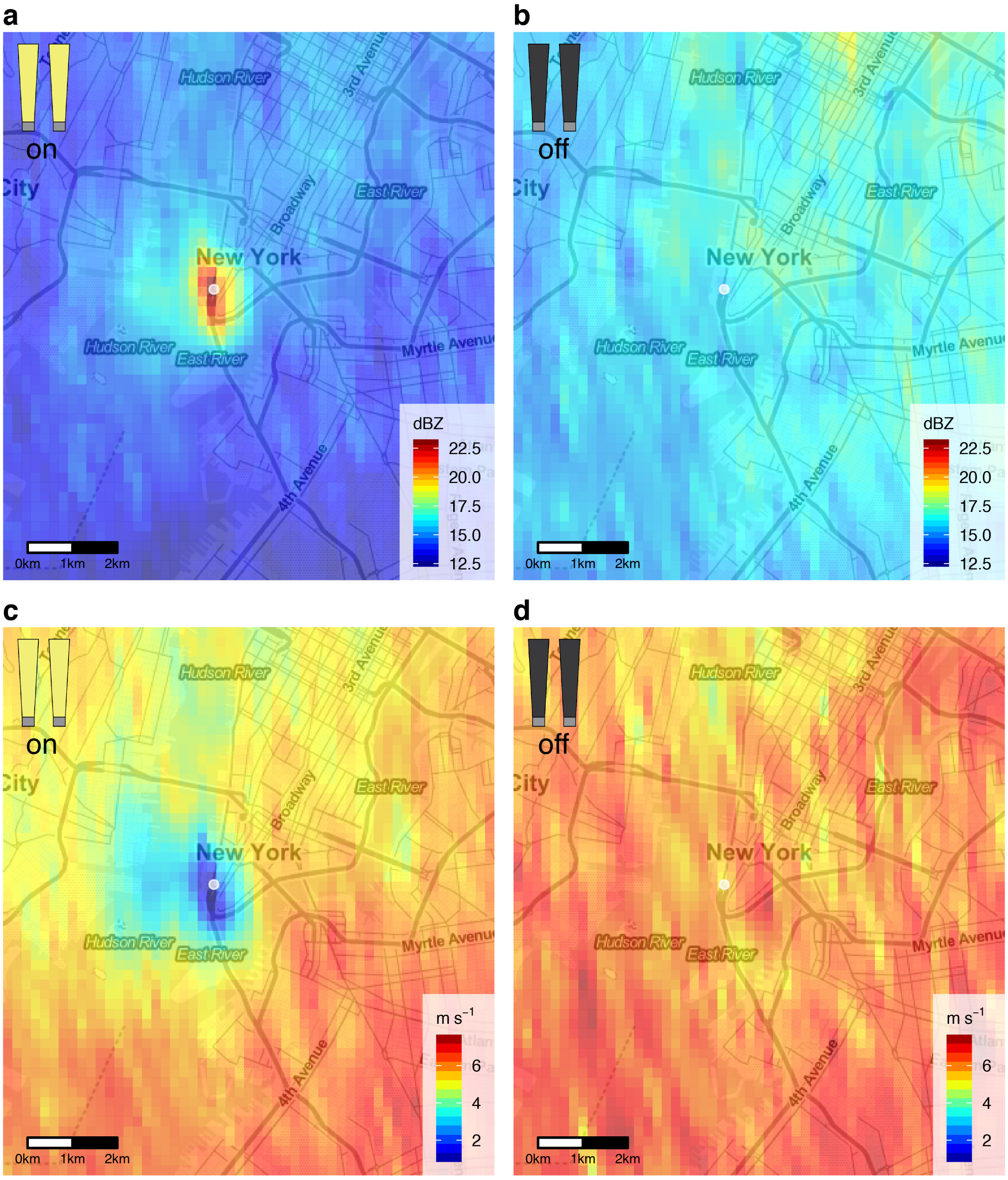


Fig. S1. Area of ALAN influence on nocturnally migrating birds at Tribute in Light, 11-12 September 2015. Bird density close to the installation (white dot) with illumination **a** was noticeably higher than in the surrounding area and without illumination **b**; radial velocity with illumination **c** was noticeably lower than in the surrounding area and without illumination **d**. Each cell shows the mean value for illuminated **(a, c)** and dark periods **(b, d).**

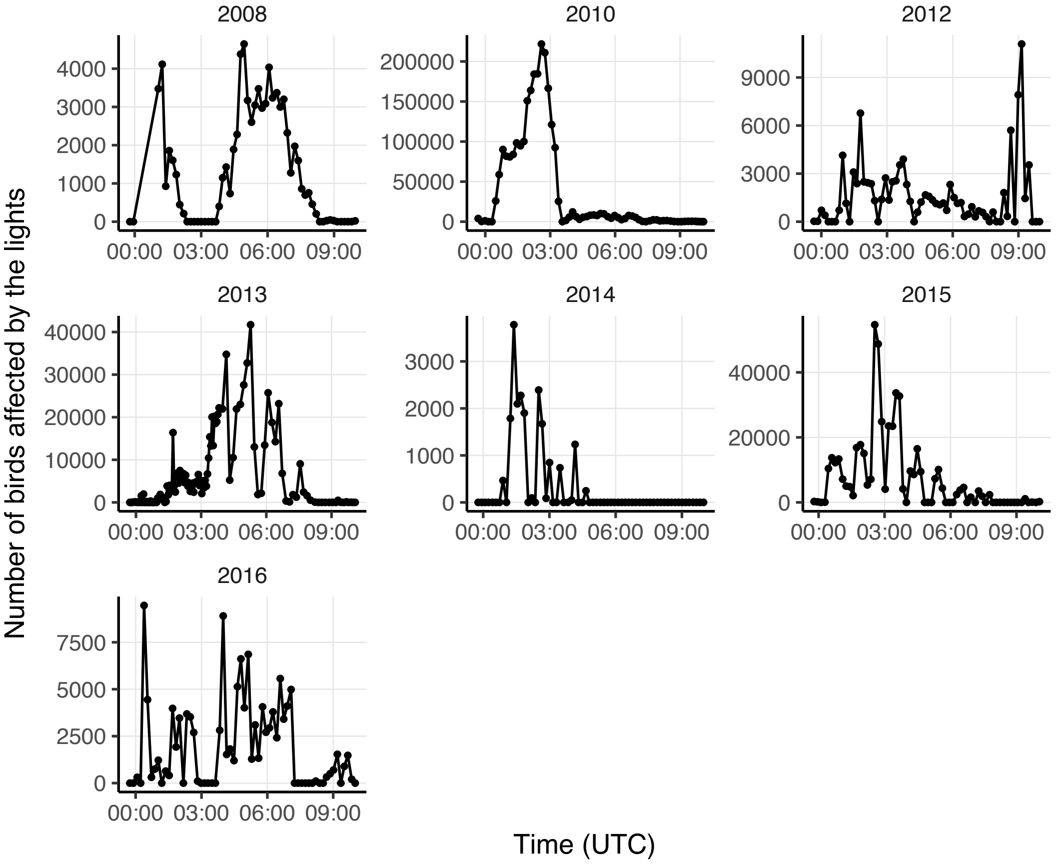


Fig. S2. Numbers of birds affected by Tribute in Light by year. Presented are differences between bird numbers within 5 km of the installation and the number expected in that area given baseline densities from 10-20 km away (Fig. S3). To arrive at an estimate of a total of 1.1 million birds (95% CI: 0.6-1.6 million) affected during the study, we divided the median time between radar scans of 9.5 minutes by the simulated stabilization time of 34 minutes (Fig. 4) and summed this proportion (≈0.28) of the dataset.

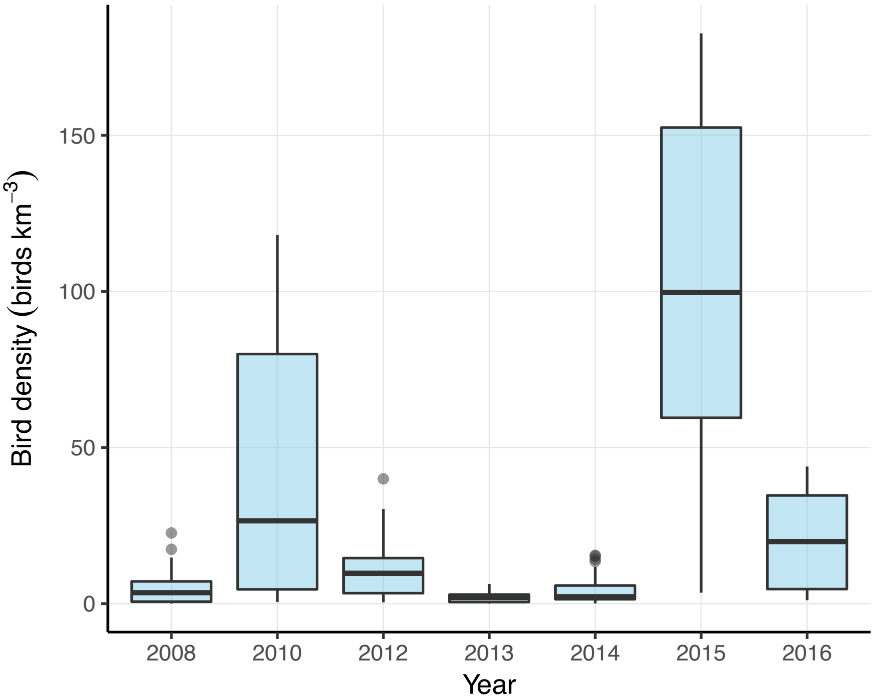
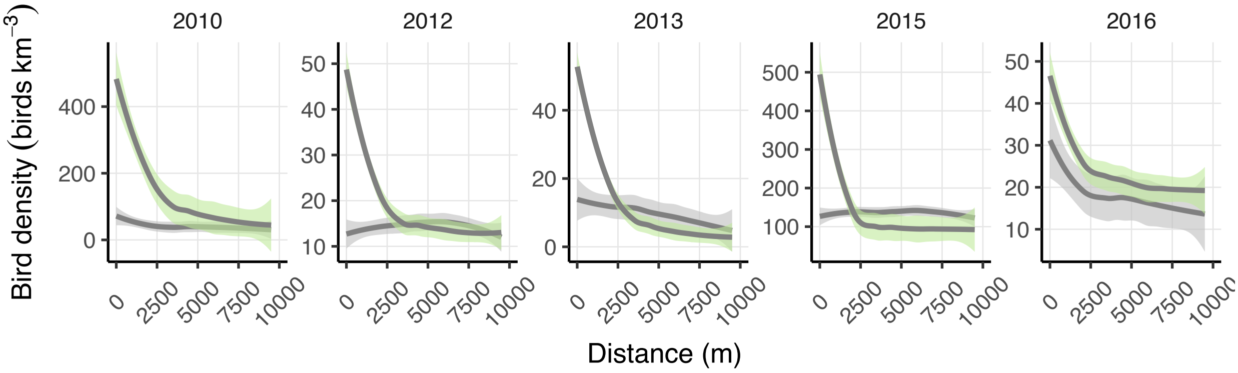


Fig. S3. Baseline bird density around Tribute in Light by year. Bird densities between 10-20 km from the installation as detected by the 0.5° elevation angle radar beam.

a Migration activity



b Radial velocity

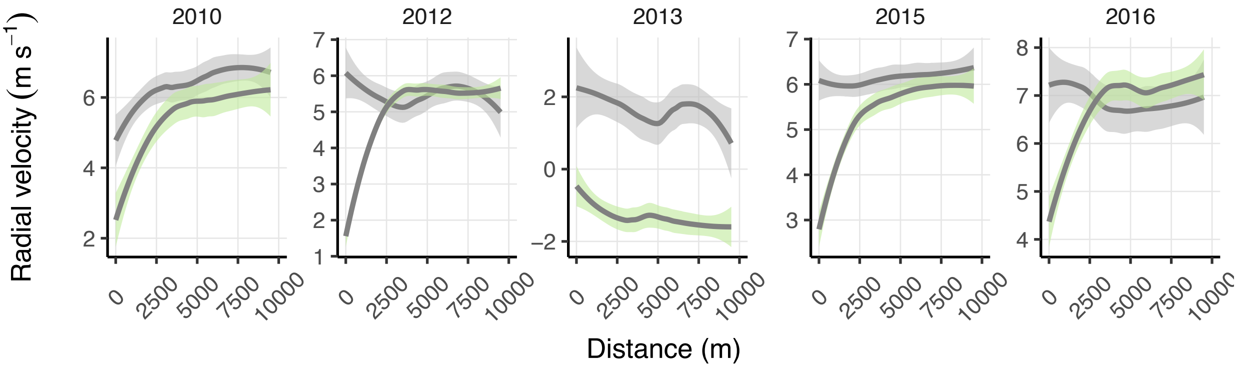


Fig. S4. Bird migration behavior by distance from Tribute in Light by year. Radar-measured bird density and radial velocity with increasing distance from the installation, with (green shading) and without (gray shading) illumination. Curves are local polynomial regression surfaces (*loess* function). Included are the five years during which light shutdowns occurred.

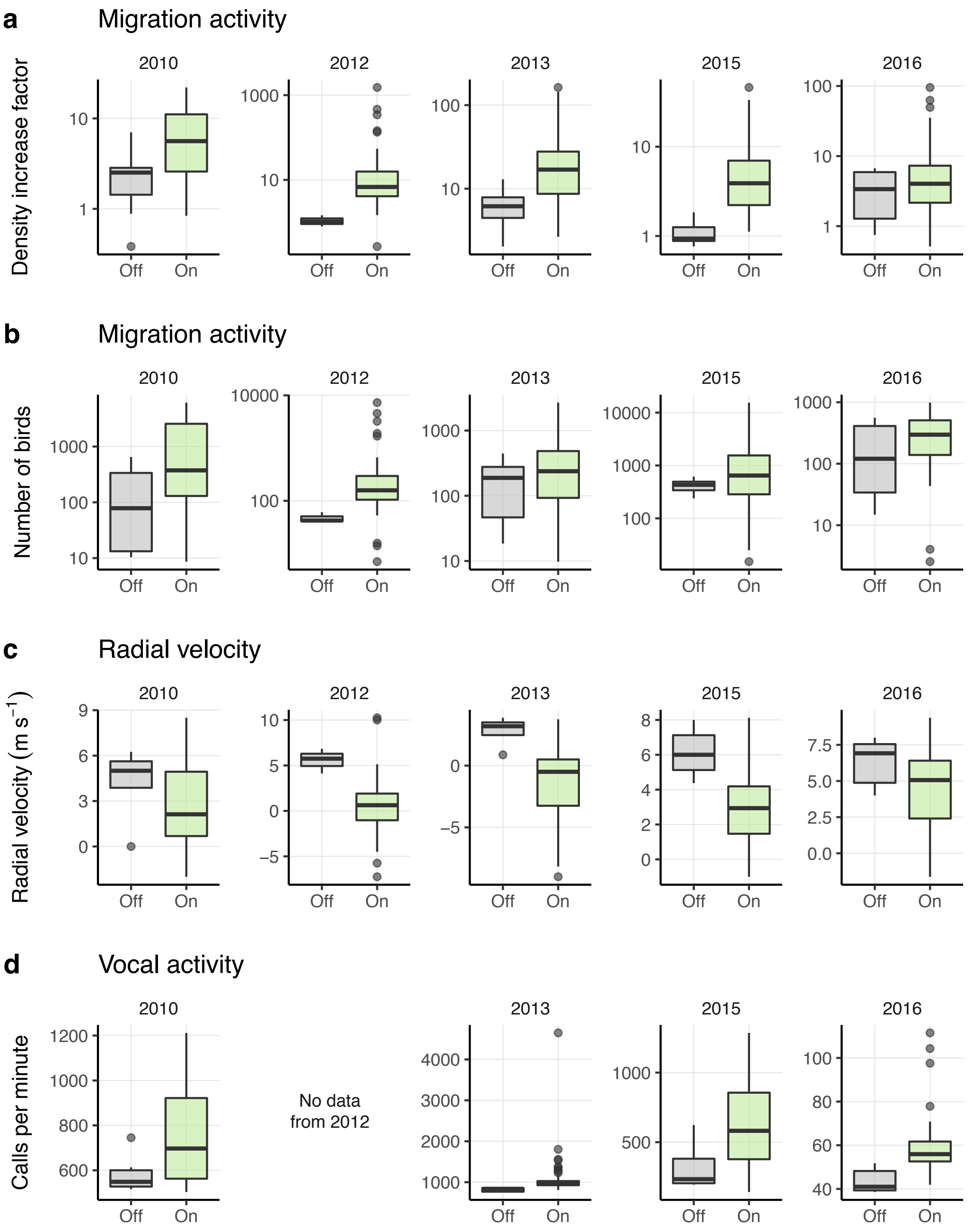


Fig. S5. Boxplots showing four behavioral metrics with and without illumination by year. (a) Density increase factor, defined as peak bird density within 500 m of the installation divided by mean bird density between 2-20 km from the site. Data points calculated from very low bird densities (baseline less than 0.1 birds km^{-3}) are not shown. (b) Estimated number of birds in the cylinder with radius 500 m and height 4.5 km, directly above the site. (c) Radial velocity 0-500 m from the site. (d) Number of flight calls per minute detected beneath the installation. Included are the five years during which light shutdowns occurred.

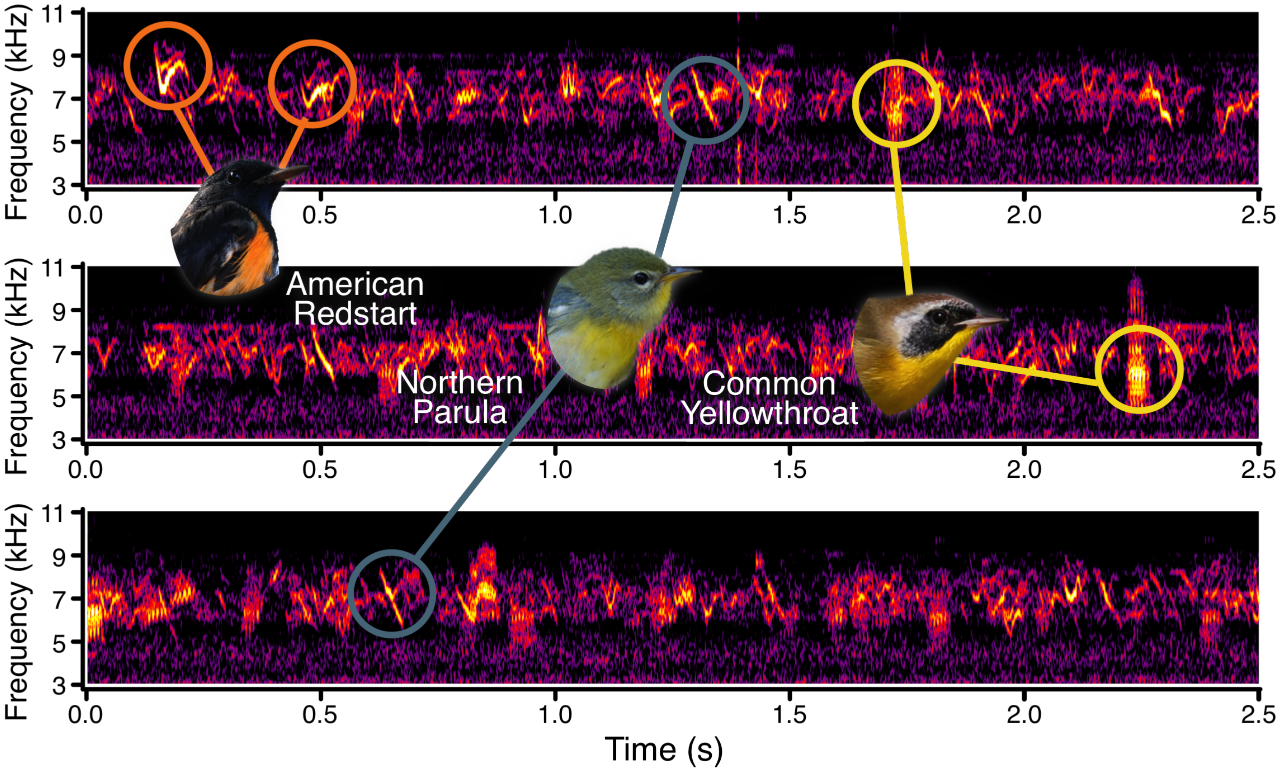


Fig. S6. Vocal activity of nocturnally migrating birds above Tribute in Light. Spectrographic representation of vocal activity in a 7.5-second audio sample from 12 September 2015, 0549 UTC (Coordinated Universal Time). Areas of brighter colors, such as reds, oranges, and yellows, have higher amplitude (i.e. are louder) than areas of purple or black. Note the large numbers of flight calls in the 6-9 kHz frequency range of this recording from an illuminated period at the installation, including many calls that overlap in frequency and time; we applied a band-pass filter to quantify acoustic energy within this frequency range. Among the diversity of species represented in this sample, circles highlight the calls of three species of American wood-warblers (family Parulidae) that were numerous at the study site: American Redstart, *Setophaga ruticilla* (orange), Northern Parula, *Setophaga americana* (blue), and Common Yellowthroat, *Geothlypis trichas* (yellow). Photos: American Redstart, Kyle Horton; Northern Parula, Ian Davies/Macaulay Library, eBird S24916843; Common Yellowthroat, William Keim/Macaulay Library, eBird S31689615.

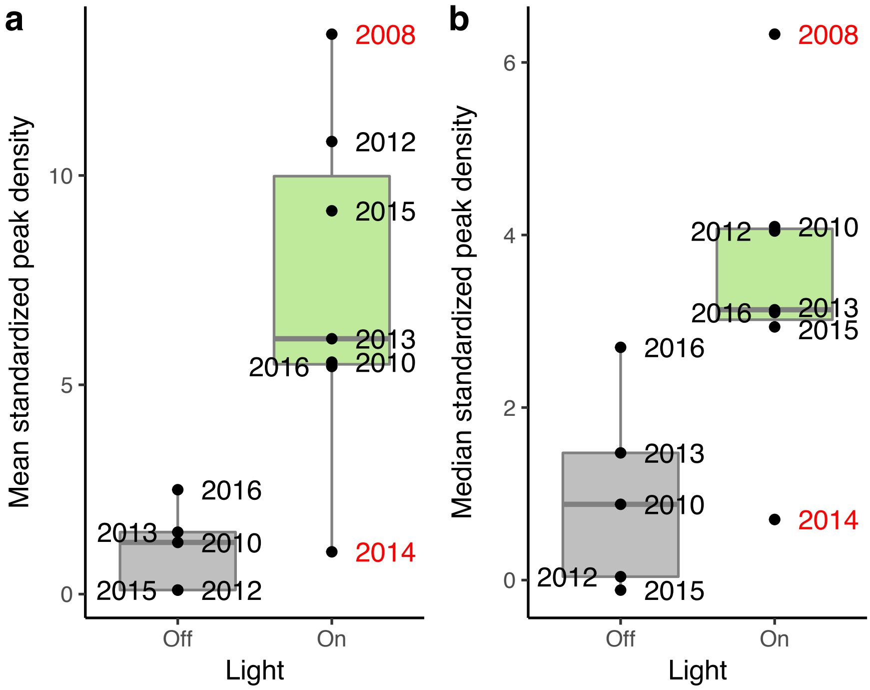


Fig. S7. (a) Mean and (b) median values of standardized peak density at Tribute in Light for 2008-2016 by illumination, excluding 2009 and 2011 due to the presence of precipitation. Lights were not turned off in 2008 or 2014 (shown in red), and therefore these years were excluded from core analyses. Note that 2008 showed an above-average concentration effect, while 2014 showed a below-average concentration effect. In other words, the five years included in the core analyses fell comfortably between the two years that were not included because no shutdowns occurred. Therefore, based on the available data, we conclude that the five primary study years are representative of typical light effects at the installation.

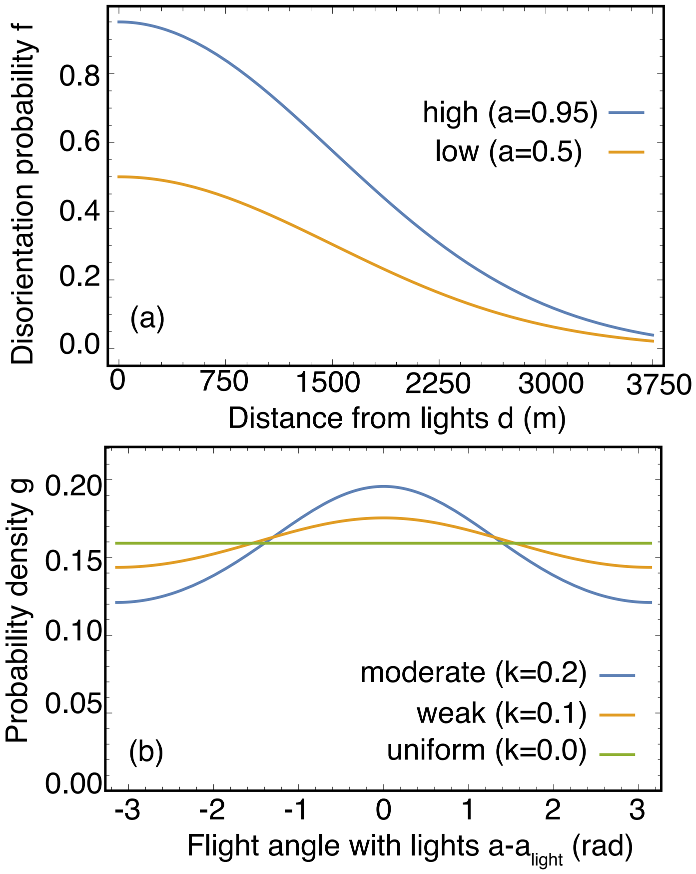


Fig. S8. Model simulation of disorientation. In the simulation, birds could transition between an undisturbed migratory state and a disoriented state. (a) Parameterizations of the distance-dependent disorientation probability *f* (Equation 1). *a* is the probability of disorientation. (b) Parameterizations of the angular Von Mises distribution *g* (Equation 2) for the case of uniform ($\kappa = 0$), moderate ($\kappa = 0.2$) and weak ($\kappa = 0.1$) directed flight towards ALAN for birds in the disoriented state. κ is the concentration parameter for disoriented flight, determining the extent to which birds fly towards ALAN when disoriented. When $\kappa = 0$, birds' flight paths follow a random walk; when $\kappa > 0$, birds fly toward the lights, with larger κ implying a more directed flight towards the light source.

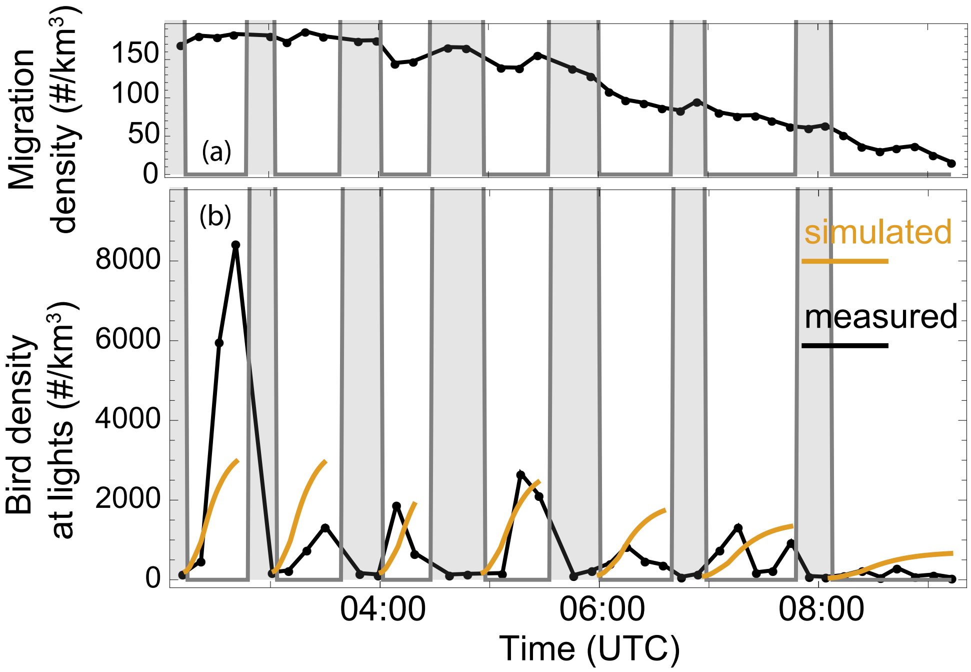


Fig. S9. Simulated and measured regional and local migration on 11-12 September 2015. (a) Background migration density (birds km^{-3}) in regions not affected by ALAN. This density is the mean migration density between 2-20 km from Tribute in Light. (b) Bird density at the installation as recorded with the KOKX radar in 2015. Shaded areas indicate periods when lights were off. This density is peak density observed within 500 m of the installation. Simulated densities during light-on periods are given in orange, using the parameterization of the best model fit (model 1).

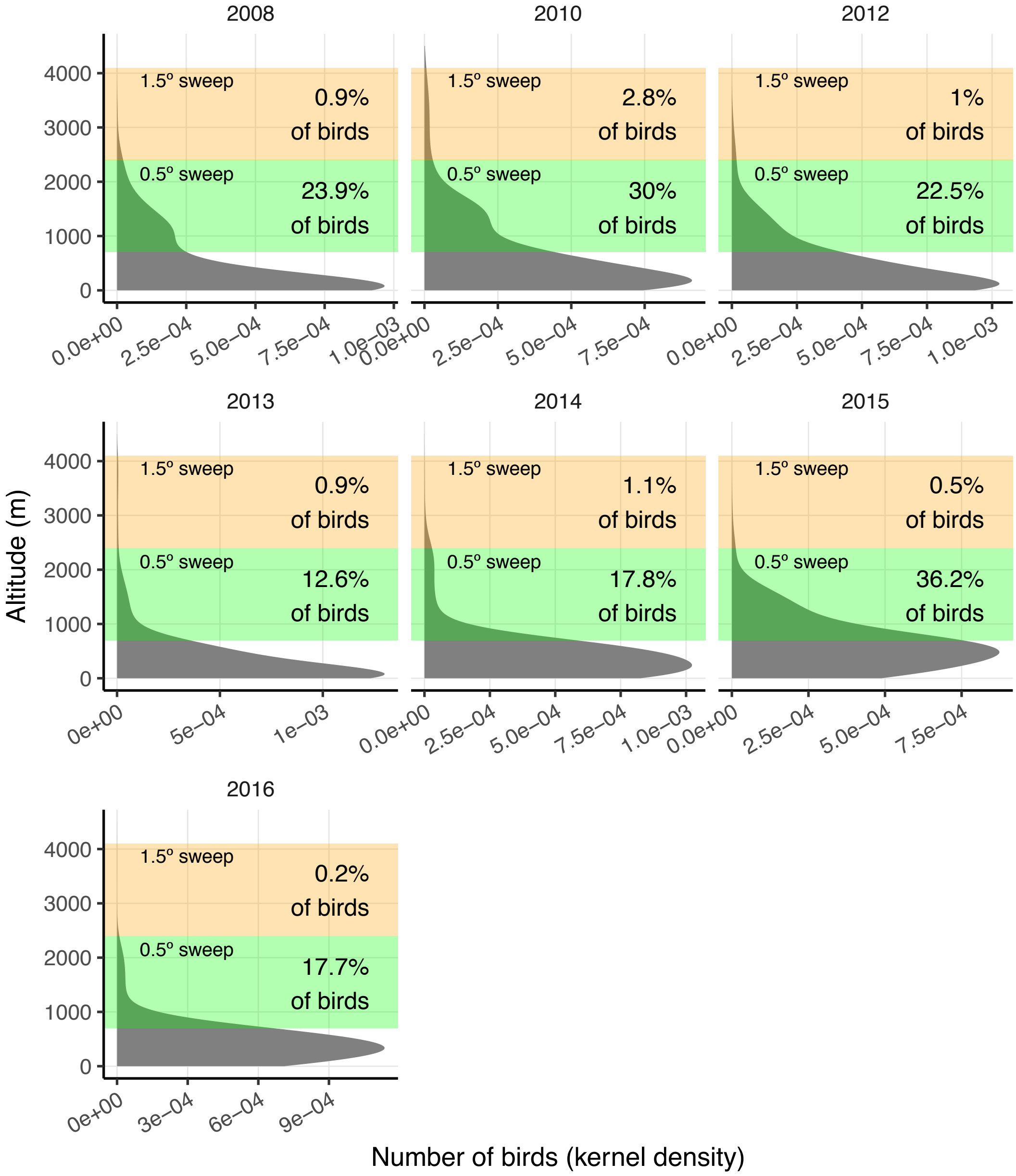


Fig. S10. Proportion of nocturnal bird migration by altitude and radar sweep coverage by year at Tribute in Light. Vertical profiles of bird density constructed from radar data between 5-60 km from the KOKX radar in New York. Each panel represents a different year. We calculated the proportion of migration occurring beneath (or above) the radar beam at the light installation, out of sight of the radar. Labels describe the percentage of birds detected in the altitude (y-axis) sampled by each radar antenna elevation angle (0.5° in green, 1.5° in orange). From the 0.5° sweep proportions, we calculated the correction factor needed to estimate the total number of birds at all altitudes up to 4.5 km by finding the inverse. For example, the correction factor for 2015 was 1/0.362 = 2.76.

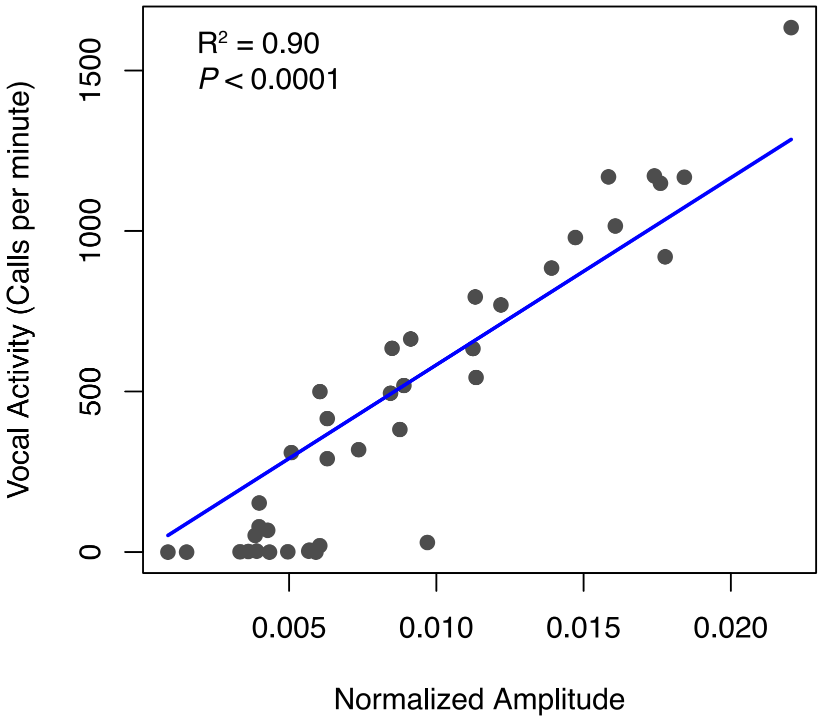


Fig. S11. Relationship of flight call count and normalized amplitude, a calling activity index. Regression of vocal activity on normalized amplitude for flight calls of nocturnally migrating birds in the 6-9 kHz range for 11-12 September 2015. Vocal activity is the number of flight calls counted in each one-minute audio recording. Normalized amplitude is the mean amplitude for the 6-9 kHz frequency band in each one-minute audio recording, normalized to unit.

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6

Human activity shapes the winter ecology of blackcaps

6.1 Abstract

Human behavior profoundly affects the natural world. Migratory birds are particularly susceptible to adverse effects because the global networks of ecosystems on which they rely are undergoing rapid transformation. The blackcap (*Sylvia atricapilla*) is one of few migratory species thriving in this changing, human-dominated world. Its recent establishment of a high-latitude wintering population in the British Isles has been linked to climate change and supplementary garden bird feeding. We studied this wintering population to understand the landscape-scale drivers of its new distribution, interactions with supplementary food resources, and anthropogenic influences on its movement behavior and ecology. We found that blackcaps wintering in Britain were strongly associated with suburban areas and preferred warmer climates, suggesting an important role of human-modified landscapes and recent climatic shifts in facilitating the species' winter range expansion. High reliability of supplemental food may select for winter movement behavior different from the itinerancy characteristic of traditional wintering areas; in Britain, we detected relatively high site fidelity and low transience among wintering

locations. Individuals tracked with geolocators generally stayed at garden sites until immediately before spring departure, suggesting that experiences in gardens may have direct carry-over effects to the breeding season. Nonetheless, blackcaps did not exclusively feed in gardens, and visits were mainly associated with periods of harsh weather. Supplemental food hence may benefit survival, but it does not define their diet. Most striking was a high degree of individual variation in movement behavior and interactions. It may be this variability, and the flexibility it imparts, that has allowed the blackcap to flourish despite global environmental change.

6.2 Introduction

Humans are increasingly influencing the natural world. Organisms of all kinds are affected by a range of pressures, including effects of development and agriculture on natural habitats; changing temperature and precipitation regimes wrought by climate change; hunting and exploitation; and light and noise pollution (Benítez-López et al. 2017; Gaston et al. 2013; Hanski 2011; Kunc et al. 2016; Mantyka-pringle et al. 2012; Urban 2015). Organisms differ in their ability to adjust to environmental change, and the extent to which ecological communities will be able to keep pace is unclear (Feeley and Rehm 2012; Liang et al. 2018; Poloczanska et al. 2013; Urban et al. 2016). Migratory birds are key to ecosystem health (Bauer and Hoye 2014), but they are particularly susceptible to environmental change because successful migration requires the integration of a number of disparate components, each one sensitive to ongoing changes that may be poorly correlated. Migrants must time their journeys precisely, navigate accurately through a dynamic atmosphere, locate resources safely, reliably and efficiently, and thrive in ecological contexts that differ across seasons and hemispheres. As climate change shifts optimal timing windows, wind regimes, and storm patterns, and as humans modify both the landscapes through which birds pass and the areas where they breed and winter, a migratory strategy may become increasingly untenable (Runge et al. 2015; Wilcove and Wikelski 2008). Migrant birds are in decline in multiple regions, in part because many lack the flexibility to rapidly respond and adapt to these large scale environmental changes (Beresford et al. 2019; Both et al. 2010; Fraser et al. 2019; Sanderson et al. 2006).

Whether migratory species have the capacity to adjust to rapid change is a focal question of current research. Although plasticity in response to climate change is well documented (Gienapp et al. 2007; Usui et al. 2017), many migratory birds, especially long-distance travelers, rely on innate timing and navigational programs with limited flexibility (Åkesson et al. 2017; Gwinner 1996). These programs must undergo evolution for adjustments to be realized. There is some evidence that microevolutionary change—not just plasticity—may be occurring, but it is unclear whether this can match the pace of warming (Chapter 2: Helm et al. 2019; Van Buskirk et al. 2012; Charmantier and Gienapp 2014; Merilä and Hendry 2014). As changes continue, species will not only need to shift timing but also undergo large-scale distributional changes to track suitable conditions. Climate-induced range shifts have been documented in birds (Ambrosini et al. 2011; La Sorte and Thompson III 2007; Lehikoinen and Virkkala 2016; Tingley et al. 2012), but we lack an understanding of the ecological and behavioral processes that facilitate these shifts. This poses a challenge for predicting how species will respond in the future.

The Eurasian blackcap (*Sylvia atricapilla*) is one of few migratory songbirds thriving in the face of environmental change (EBCC/BirdLife/RSPB/CSO 2018). This widespread species shows a spectrum of migratory strategies from sedentary to fully migratory (Cramp and D. J. Brooks 1992), and it has experienced substantial and continuing population increases across Europe (+155% since 1980; EBCC/BirdLife/RSPB/CSO 2018). In addition, the blackcap has expanded its European wintering range northward in the last half century, most notably in the British Isles, where its status has changed from a rare visitor to an established component of the winter avifauna in some regions (Bearhop et al. 2005; Berthold et al. 1992; Berthold and Terrill 1988; Fouarge 1980; Fransson and Stolt 1994; Johansen 2002; Leach 1981). This transformation has been hypothesized to be linked to human activity in two ways (Berthold and Terrill 1988; Plummer et al. 2015): first, climate change has resulted in milder winters, and second, abundant garden feeding stations now provide a reliable food source through the winter. Surprisingly, available evidence (Chapter 3; Berthold et al. 1992; Plummer et al. 2015; Wernham et al. 2002) indicates that virtually all British overwinterers are *not* residents that originate from British breeding populations, but rather are visitors from continental Europe that undertake highly atypical northwesterly migrations in autumn. These individuals differ from those that use traditional Mediterranean winter areas in a number of important ways: they use a novel migratory direction, winter at higher latitudes, utilize human-dominated habitats, and are closely associated with supplementary food provided by humans. Blackcaps wintering in the British Isles have adapted to many of the characteristic features of the Anthropocene, and understanding the processes linked to their success will help us understand what it takes for a migratory bird to succeed in the face of global change.

Here, we study the ecology and behavior of blackcaps wintering in the British Isles across scales. We start with a landscape analysis of the species' distribution in this newly established wintering region and use these insights to inform individual-based analyses of movement and behavior. We use two nationwide winter bird atlases conducted from 1981–1984 (Bland 1986) and 2007–2011 (Balmer et al. 2013) to examine the associations between blackcap distribution and weather, climate, land use, and fruit-producing plants over time. Previous research using a 12-year dataset from observers in British gardens showed that blackcap presence is increasingly associated with garden bird feeding and warmer climates (Plummer et al. 2015). We build on this work by taking a landscape-scale perspective not exclusive to garden sites, examining associations with a range of climate and land cover variables, and testing for biotic interactions with potentially important food plants (holly, ivy, mistletoe, and traditional orchards).

Because a landscape-scale study contains limited information on the behavior of individual birds, we conduct a complementary analysis using ringing recoveries and a detailed dataset of individual captures and resightings. We study how individually-marked birds utilize garden habitats and food resources and how their behavior is influenced by local environmental conditions. We hypothesize that blackcaps are not wholly reliant on supplementary food throughout the winter, but that it may be a lifeline during challenging conditions. We also examine the site fidelity of individuals between winters. Studies in Mediterranean and African wintering areas report winter blackcap recapture rates of only 0–5% in subsequent years (Cuadrado 1992; Cuadrado et al. 1995; King and Hutchinson 2001; Lövei et al. 1985); we investigate whether British overwinterers have adopted greater site fidelity to take advantage of more reliable garden feeding sites. We use ringing data to study movements within and across winters, and we combine ringing with individual tracking to examine the breeding origins of wintering blackcaps. Finally, we compare sighting records and geolocator tracks to examine the hypothesis that the high-quality food available in gardens plays an important role in migratory fueling.

6.3 Methods

6.3.1 Winter Bird Atlases

We used two international bird atlases to study the drivers of blackcap winter distribution in the UK. The UK and Ireland undertook combined avian winter atlases from 1981–1984 and 2007–2011. The 1981–84 atlas sampled across a 10x10 km grid, and the 2007–2011 atlas primarily used finer 2x2 km resolution. In order to make direct comparisons between atlases, we aggregated records from 2007–2011 to 10x10 km (Figure 6.1AB). We focused on Britain for this analysis because it matched the geographic extent of our land cover and climate data.

In both 1981–84 and 2007–11 atlases, observers recorded birds detected within grid cells, but the survey methodology differed. In 1981–84, surveyors visited 10x10 km grid cells and recorded the duration of their survey. In addition, they recorded casual observations without associated effort data. In 2007–11, surveyors also used a combination of standardized timed counts and opportunistic visits with unrecorded effort. In addition, the 2007–11 atlas included data from BirdTrack, a citizen science repository. For both atlases, we only retained records with associated effort data, thereby excluding casual and opportunistic records.

Due to the methodological differences between atlases, we were unable to estimate and directly compare relative abundance. Instead, we converted atlas data into a binary variable for each 10x10 km grid cell, set to one if at least one blackcap was detected during the atlas, and zero if effort was put in but no blackcaps were detected. For 1981–84, we used the recorded survey duration per 10x10 km cell visit as our measure of effort in that cell. For 2007–11, we used a similar measure: the sum of the duration of timed counts that took place with the 10x10 km cell. In this way, we assigned zeros to cells where no blackcaps were detected despite survey effort. We excluded cells with no survey effort from our analysis.

6.3.2 Climate data

We compiled environmental data from a number of sources for comparison with winter bird atlas data. First, we used the 10 m vector land map from Natural Earth [`http://naturalearthdata.com`] for land and water boundaries and to determine the land area of each grid cell. We downloaded historical climate data from the *HadUK-Grid* dataset available from the UK Met Office [`https://www.metoffice.gov.uk/research/climate/maps-and-data/data/haduk-grid/overview`].

To capture variation in climate across the British Isles, we used the 30-year monthly averages from 1981–2010 provided in the HadUK dataset. This temporal scope aligned closely with our study period. We downloaded the following variables: average of daily maximum, minimum, and mean air temperature; total precipitation; surface wind; number of days with ground frost; and number of days with snow on the ground. The data are provided at a 1x1 km resolution, which we aggregated to the necessary spatial resolution and averaged from November to March.

To capture annual variation in weather conditions across each winter, we downloaded yearly HadUK datasets summarized by month for the same variables as above. In our yearly measures, we were primarily interested in capturing annual deviations from the long term average (e.g. a colder-than-average winter). Therefore, we modified yearly measures by subtracting the 30-year average from the yearly data. Our final weather dataset thus includes 30-year climatic data, as well as yearly deviations from those 30-year averages.

6.3.3 Plant distributions

We investigated whether the distributions of certain key plant species are associated with blackcaps' winter distribution in the British Isles. We downloaded observational data from the New Atlas of the British and Irish Flora recording scheme, courtesy of the Botanical Society of Britain & Ireland, for three plant species: ivy (*Hedera helix*), holly (*Ilex aquifolium*), and mistletoe (*Viscum album*). We selected these species because their fruits are well-documented blackcap winter food sources (Hardy 1978; Leach 1981; B. Snow and D. Snow 2010). We downloaded observations at the 10x10 km grid level, requesting the number of 2x2 km cells for which observations had been submitted since 1970. We then summed the number of occupied 2x2 cells for each 10x10 cell as a relative measure of pseudo-abundance for that species. We elected to use this approach due to its simplicity and because the dataset provides high quality coverage across the British Isles.

We downloaded spatial data on the distribution of traditional orchards, given blackcaps' preference for apples provided in gardens (Hardy 1978; Leach 1981). Data for England was provided by Natural England [`https://naturalengland-defra.opendata.arcgis.com/datasets/traditional-orchards-hap-provisional-england`] and data for Wales from Lle [`http://lle.gov.wales/catalogue/item/TraditionalOrchards`]. We could not obtain data for Scotland, however traditional orchards in Scotland represent less than 1% of total traditional orchard area in Britain (BRIG 2008). We quantified traditional orchard coverage by summing the total area occupied by orchards in each 10x10 km cell and calculating the proportion of land area occupied by traditional orchards. We set all cells in Scotland to have a value of zero.

6.3.4 Land cover

We used land cover data from the UK Centre for Ecology & Hydrology [`https://www.ceh.ac.uk/services/land-cover-map-2015#data`]. We downloaded the

1 km raster version of the latest release, *LCM2015*. This dataset classifies each 1 km square in Britain to one of a number of land cover classes. We used the 10 broad “aggregate” classes, with three exceptions. In place of the aggregate class “built-up areas and gardens,” we used the more specific “suburban” and “urban” target classes. We removed “freshwater” and “saltwater” classes because these are not directly relevant to this species. This left the following nine classes: broadleaf woodland, coniferous woodland, arable land, improved grassland, semi-natural grassland, mountain/heath/bog, coastal, urban, and suburban. We created predictor variables describing the percent land cover occupied by these land cover classes in each 10x10 km cell.

6.3.5 Refining spatial predictors

We examined predictors to remove highly correlated variables, defined as correlation coefficient > 0.75. For correlated predictors, we retained the predictor that was likely to be most informative or most biologically relevant for understanding relationships with blackcap distributions. We removed holly (correlated with ivy) and 30-year averages of ground frost, snow cover, and minimum temperature (all correlated with mean temperature). This left the following predictors: land cover variables of broadleaf woodland, coniferous woodland, arable land, improved grassland, semi-natural grassland, mountain/heath/bog, coastal, urban, and suburban; plant cover variables of ivy, mistletoe, and traditional orchards; 30-year climate variables of mean air temperature and rainfall; and annual deviations from the 30-year climate averages for mean air temperature, rainfall, and ground frost.

6.3.6 Occupancy analysis

We conducted an occupancy analysis using the R package `unmarked` (Fiske and Chandler 2011) to investigate the drivers of blackcap distribution across Britain. We summarized atlas and BirdTrack data by 10x10 grid cell for each winter, assigning a value of 1 if blackcaps were detected in that cell in the given winter and 0 if not. We fit a dynamic occupancy model (MacKenzie et al. 2003) using the *colext* function. This model models four probabilities: the initial probability of occupancy at a site (ψ), yearly local colonization (γ) and local extinction (ϵ) probabilities, and the probability of detecting the species when present (p).

We divided our predictor variables into groups based on *a priori* hypotheses of their effects on blackcap distributions. We split our land cover variables into two groups: those related directly to human development (specifically, urban and suburban categories), and all others ("natural"). We also defined groups of the three plant cover variables (ivy, mistletoe, and traditional orchards), two climate variables (rainfall and temperature), and three annual weather deviation variables (ground frost, rainfall, and temperature).

We used the Akaike Information Criterion (AIC) to determine which predictor variable groups were most important in predicting blackcap distributions. We assembled a candidate model set with the following specifications. We modeled the initial probability of occupancy at a site with all possible combinations of the following variable groups: (1) natural land cover (seven variables), (2) developed land cover (two variables), (3) plant cover (three variables), and (4) climate (two variables). Our candidate models included either all variables in a group, or none. In addition, all initial occupancy models contained a variable describing the proportion of area in each 10x10 cell occupied by land. We modeled colonization and extinction probabilities with all possible combinations of the same four groups of predictors, with the addition of a categorical variable of atlas (1981–84 vs. 2007–11) for all models to allow for different average rates of turnover between atlases. We modeled detection probability with the following variables, which were the same for all models: atlas (to account for average differences in detection stemming from survey methodology or other factors), survey duration (no. hours surveyed within the cell), and our three annual weather variables (because detection is more likely during harsher winters as blackcaps utilize garden feeding stations) (Plummer et al. 2015).

6.3.7 Individual marking and resighting

At 55 sites in Britain (Figure 6.1C), we color-ringed wintering blackcaps between November and April. We considered blackcaps to be confidently categorized as individuals wintering in Britain (as opposed to early or late migrants passing through) if they were encountered between December 1 and March 15, defining these boundaries using ringing recovery data (Figure 6.2). We retained all records of these individuals. Wintering blackcaps were ringed between 19 November and 19 March and observed or recaptured between 31 October and 22 April. Capture sites were primarily suburban gardens and occasionally local parks. We gave each blackcap a unique combination of colored leg rings to enable individuals to be identifiable in the field. Most sites were active between the winters of 2016–2017 and 2019–2020, with the exception of the site run by GCMR and collaborators since 1992. The authors and volunteer observers made regular observations of individuals attending garden feeding stations throughout the winter.

Our compiled records consisted of captures (mist net or potter trap), visual resightings, and camera trap records. In total, we compiled a dataset of 8825 records of 608 color-ringed blackcaps.

6.3.8 Daily weather

We obtained local weather station data from the Met Office Integrated Data Archive System (MIDAS) (Met Office 2012) (`http://catalogue.ceda.ac.uk/uuid/220a65615218d5c9cc9e4785a3234bd0`). We selected MIDAS weather stations as close as possible to blackcap observation sites (between 9–30 km). We extracted (1) daily maximum air temperature (across 24 hours starting at 9 am), (2) total precipitation across the 12 hours from 6 am to 6 pm, and (3) mean wind speed and direction across the 12 hours from 6 am to 6 pm.

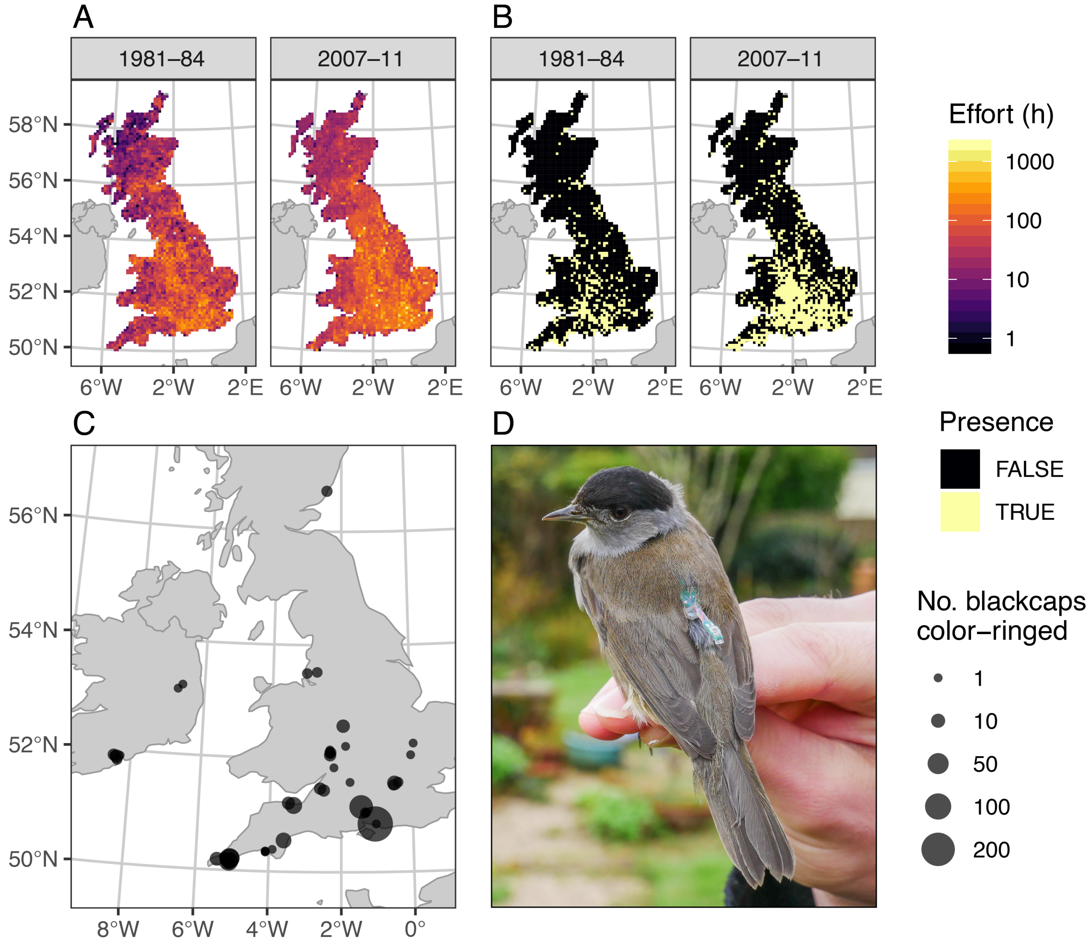

Figure 6.1: Blackcap records and capture sites. **(A)** Survey effort by 10 km grid cell in 1981–84 and 2007–2011 winter atlases, the latter also including citizen science contributions. **(B)** Grid cells in which blackcaps were detected during both periods. **(C)** Locations where wintering blackcaps were individually color-ringed for this study, with number of individuals marked. **(D)** A male blackcap in a British garden carrying a light-level geolocator. Photo by Ben Porter.

6.3.9 Daily counts

To understand the environmental factors influencing blackcap attendance at supplemental feeding stations, we counted the number of color-ringed individuals encountered daily at garden sites. For analysis, we retained data from a given site in a given winter if there were blackcap observations from at least 30 days in that winter. Thus we retained blackcap counts from 2266 days at 5 sites across 21 years. The majority of observation days came from the gardens of GCMR (72.2%) and GCE (17.1%).

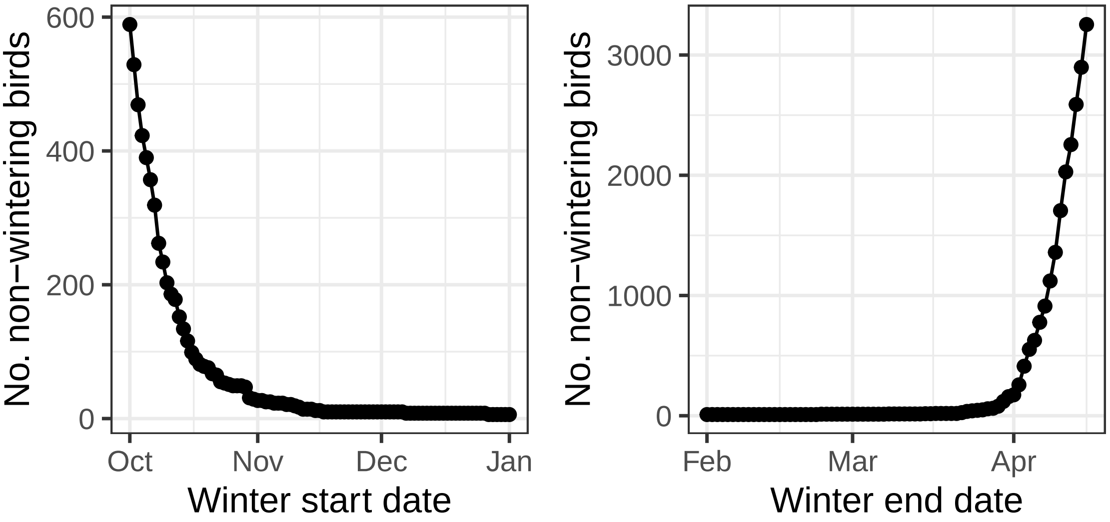

Figure 6.2: Defining the wintering period with ringing recovery data. Plots show the number of blackcaps recovered either in the British Isles in summer (1 June to 1 August, suggesting they are actually British breeders) or encountered outside of the British Isles in winter (1 December to 15 March, suggesting they are not British winterers). We defined a British winterer as an individual encountered in the British Isles between 1 December and 15 March to minimize the chance of erroneously including non-winterers in our dataset.

We modeled daily counts of color-ringed blackcaps with a generalized linear mixed-effects model. We specified fixed effects of daily maximum air temperature, precipitation, wind speed, and day of year (from 1 November). Because we expected that the effect of seasonal timing might not be linear, we specified date as a smoothed predictor and fit our model using the *gam* function in the R package `mgcv` (Wood 2017) with Poisson distribution family. We hypothesized that blackcaps would be more likely to feed in gardens on cold and wet days with high winds, because of increased energy demands and increased difficulty finding and using natural food sources. We specified interactions of temperature × precipitation, temperature × wind speed, and precipitation × wind speed because we hypothesized that the effects of precipitation and winds could be exacerbated at low temperatures and that winds could influence the effect of precipitation. We specified random effects of year and location to account for differences in the average number of blackcaps detected across years and across sites. We used the R package `standardize` to standardize predictor variables so that we could directly compare effect sizes across predictors and interpret intercepts at the average value of predictors. We simplified the model by removing non-significant interactions (P>0.05).

Our count dataset lacked zero counts, which are expected with a Poisson distribution family. To ensure that our Poisson model was not strongly affected by this violation, we also fit a model with the R package `glmmTMB` (M. E. Brooks et al. 2017), which supports a truncated Poisson distribution family. This package does not support smoothed predictors, so we could could only fit a linear term of date in this model. Nonetheless, we compared it with the above *gam* to verify that the choice of distribution family did not impact our conclusions.

6.3.10 Individual visitation

Our observations at gardens suggested large individual variation in blackcap behavior at garden sites. We leveraged our extensive dataset of individual observations to model the probability of individual blackcaps visiting garden feeding sites through the winter. We restricted our analysis to the well-covered sites in the previous "daily count" analysis. We used a binary response variable indicating whether each individual was observed on each day, restricting our analysis to the period during which the individual was observed at the site in a particular winter. We excluded individuals only encountered once in a winter. In total, we used observations of 308 individuals encountered a median of 12.5 times (range: 2–205).

We used a generalized mixed-effects model with a binomial distribution and logit link function to model the probability of an individual being detected in a garden on a particular day. We again fit the model with *gam*. It included all fixed effects specified in the "daily counts" model, with the addition of sex, and including the smoothed term of date. We simplified the model by removing non-significant interactions (P>0.05). We specified random effects of year, location, and individual to account for differences in the average probability of blackcap detection across years, sites, and individuals.

We calculated the proportion of variation in visitation explained by the random effects of location, year, and bird identity. We used the `rptR` package (Stoffel et al.

2017) to quantify these variance proportions on the original variable scale and used bootstrapping (N=100) to generate 95% confidence intervals for these estimates. We specified all fixed and random effects as described above.

6.3.11 Site fidelity

We examined the probability of a blackcap returning to the same garden in subsequent years. For each individual in our dataset, we determined whether or not it was seen in each of the three years following initial ringing. We only retained data points for sites where we had visual observation data for subsequent years. We modeled side fidelity with a binary response variable for whether the bird returned to the ringing site at least once in the three years after the winter of ringing. We included fixed effects of sex, the day of the season when the bird was first ringed, and the day the bird was last encountered during that first winter. We included random effects of ringing year and location to account for variation in the average probability of return among years and locations. We fit the generalized linear mixed-effects model with the *bglmer* function in the R package `blme` (Chung et al. 2013), which extends the *glmer* function in the R package `lme4` (Bates et al. 2015). This function fits mixed models in a Bayesian setting, with priors on model components that help prevent singular fits and aid convergence. We used this approach because the model did not converge when specified with *glmer*.

6.3.12 Transience

Our dataset included a large number of blackcaps that were encountered only briefly. Blackcaps are known to show transience during the winter, in which a proportion of the population stays in a given area while other individuals only pass through (Belda et al. 2007; Cuadrado 1992). We modeled the likelihood of transience in our dataset with a binary variable of whether each individual bird was encountered for more than one day during the winter it was first captured. We also repeated the analysis after defining the presence window for transients to be one week long instead of one day. We considered observations from sites where we had at least

10 visual records of any individual blackcaps in a given winter to ensure sufficient sighting effort. We constructed a generalized linear mixed-effects model with a binomial distribution family and logit link (*glmer* function in R package `lme4`). We used two fixed effects: (1) sex and (2) the day the bird was first encountered. We included random intercepts of year and location to account for variation in the average probability of transience among years and locations.

6.3.13 Movements

We examined blackcaps' movements within winters, among winters, and between winter and summer using ringing recoveries and individual tracking. Ringing data were from the British Trust for Ornithology (BTO) Ringing Scheme. We considered a bird to be present in the British Isles if the country of ringing or recovery was listed as one of the following: England, Scotland, Wales, Northern Ireland, Isle of Man, or Eire (Ireland). For resight data, we categorized blackcaps as British winterers if they were encountered between December 1 and March 15 (Figure 6.2).

Given the evidence for transient individuals among wintering blackcaps visiting gardens, we used ringing data to study movements undertaken by individuals within the same winter. We filtered ringing data to individuals we were confident were wintering in the British Isles (see above), but we considered all recoveries between 1 November and 1 April to understand how these individuals moved both early and late in the season. We also used ringing data to examine movements between winters, filtering the dataset to encounters that occurred between December 1 and March 15.

We combined ringing data with tracks from light-level geolocators to identify where blackcaps wintering in the British Isles spend the summer. We filtered ringing recoveries to those of British wintering blackcaps between 15 May and 15 August. Geolocator data were from Chapter 3. In addition to identifying breeding locations, we compared the timing of migration as determined from geolocators to observations in gardens. Specifically, we asked how soon after disappearing from gardens in spring do blackcaps leave Britain. A short delay would suggest that gardens are an important resource for migratory fueling.

6.4 Results

6.4.1 Occupancy analysis

Winter bird atlases held in the British Isles from 1981–84 and 2007–11 revealed strong evidence that blackcaps' winter distribution is influenced by anthropogenic factors. All dynamic occupancy models in the 95% confidence set (determined by AIC) included developed land cover and climate variables to model local colonization and extinction probabilities, and the best AIC model also included these variables for initial occupancy (Table 6.1). The best model, with an AIC weight of 0.55, was favored over the next-best model by an evidence ratio of 3.2. It included climate, developed land cover and natural land cover variables for both initial occupancy and colonization/extinction dynamics. In addition, it included plant cover variables in the colonization/extinction model. See Table 6.2 and Figure 6.3 for full model results.

In the best AIC model (Table 6.2), blackcaps showed strong positive associations with areas with warmer climates; an increase in average temperature by one standard deviation corresponded to an increase in the odds of initial occupancy by 2.2x and of colonization by 1.5x, and a strong decrease in the odds of extinction, by 0.4x. Blackcaps also showed positive associations with suburban areas, which were associated with greater odds of initial occupancy (1.8x) and colonization (1.1x) and smaller odds of extinction (0.7x). Plant cover strongly influenced colonization and extinction probabilities, with blackcaps more likely to appear in areas with more ivy, mistletoe, and orchard cover (1.5x, 1.3x and 1.2x, respectively) and less likely to disappear from those areas (0.7x, 0.8x and 0.9x, respectively).

Table 6.1: Occupancy models for blackcaps wintering in Britain. Shown is the 95 percent confidence set of models determined by AIC, plus the best model that does not contain developed land cover variables. The dynamic occupancy model incorporates four probabilities: initial occupancy, colonization, extinction, and detection. The first three columns show the predictors incorporated into these components. Some of these predictors refer to groupings of variables (e.g. developed land cover included both suburban and urban land cover); details in Methods. The best model evidence ratio is the ratio of the AIC weights, which can be interpreted as an evidence ratio in favor of the better model.

Initial occupancy	Colonization and extinction	Detection	Par	delta AIC	AIC Wgt	cumltv Wgt	Best Model Evidence Ratio
land_natural + land_develop + climate + land_area	atlas + land_natural + land_develop + plant_cover + climate	annual_weather + atlas + survey_hr	51	0.00	0.55	0.55	1.00
land_natural + climate + land_area	atlas + land_natural + land_develop + plant_cover + climate	annual_weather + atlas + survey_hr	49	2.30	0.17	0.72	3.15
land_natural + plant_cover + climate + land_area	atlas + land_natural + land_develop + plant_cover + climate	annual_weather + atlas + survey_hr	52	3.79	0.08	0.80	6.67
land_natural + land_develop + plant_cover + land_area	atlas + land_natural + land_develop + plant_cover + climate	annual_weather + atlas + survey_hr	52	4.84	0.05	0.85	11.22
plant_cover + climate + land_area	atlas + land_natural + land_develop + plant_cover + climate	annual_weather + atlas + survey_hr	45	5.23	0.04	0.89	13.68
land_natural + plant_cover + land_area	atlas + land_natural + land_develop + plant_cover + climate	annual_weather + atlas + survey_hr	50	6.86	0.02	0.91	30.82
climate + land_area	atlas + land_natural + land_develop + plant_cover + climate	annual_weather + atlas + survey_hr	42	6.94	0.02	0.93	32.14
land_natural + land_develop + plant_cover + climate + land_area	atlas + land_natural + land_develop + plant_cover + climate	annual_weather + atlas + survey_hr	54	7.12	0.02	0.94	35.08
land_natural + climate + land_area	atlas + land_natural + plant_cover + climate	annual_weather + atlas + survey_hr	45	17.03	0.00	-	4999.68

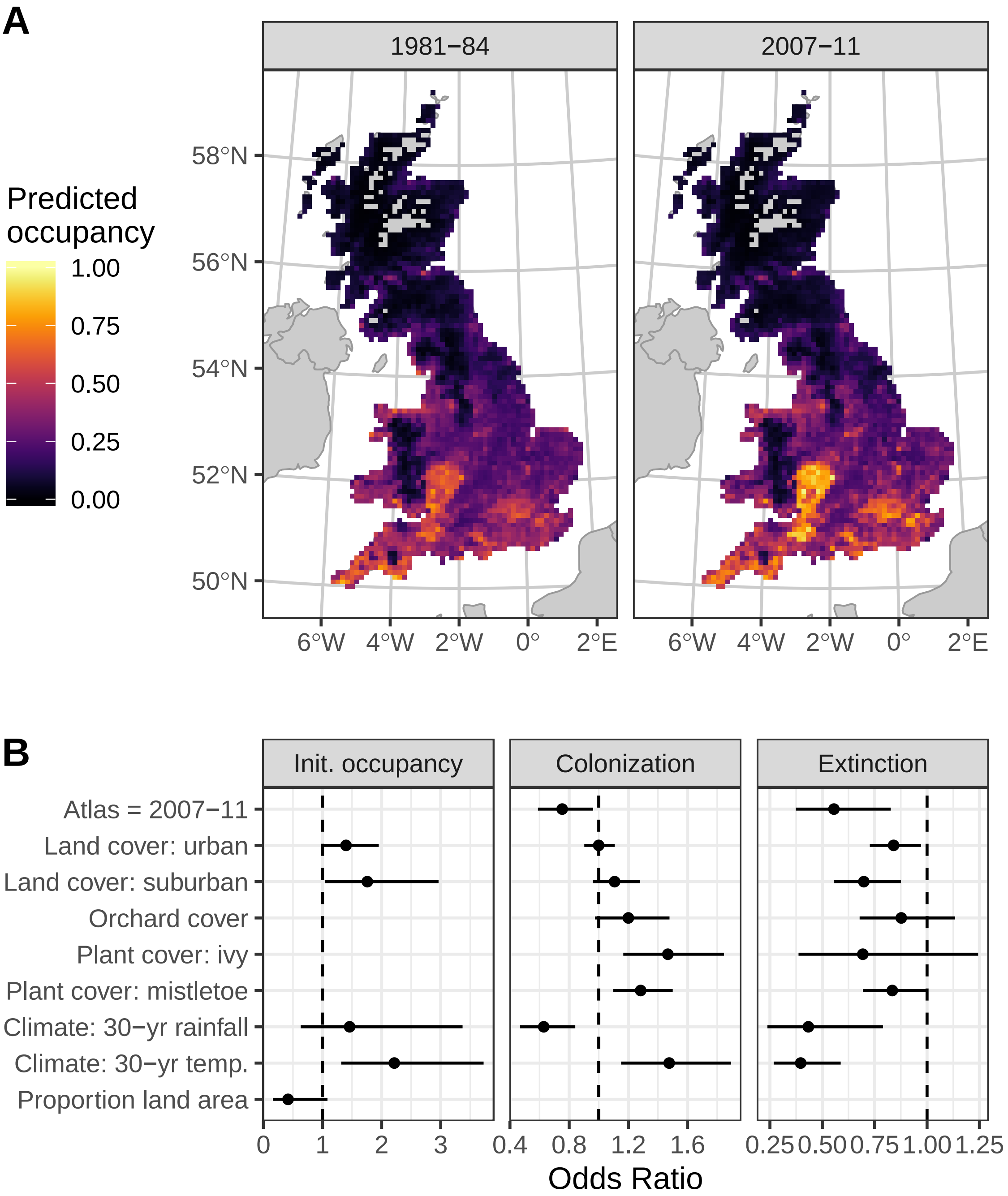

Figure 6.3: Dynamic occupancy model predicting blackcap occupancy in Britain. (A) Shows model predictions for the best AIC model averaged across years of the 1981–84 winter bird atlas and 2007–2011 winter bird atlas. **(B)** Shows coefficient estimates for initial occupancy, colonization, and extinction components of the model, excluding coefficients for natural land cover variables. Not shown are coefficients for detection probability. All coefficients can be found in Table 6.2.

Table 6.2: Output from occupancy model on winter bird atlases in 1981–84 and 2007–2011. This model comprises separate components modeling four probabilities: initial occupancy, colonization, extinction, and detection. Shown are odds ratios (exponentiated coefficients) and 95 percent confidence intervals. All continuous variables have been standardized to have a mean of zero and a variance of one so that coefficient estimates can be compared. The model intercept is not shown because the exponentiated intercept does not represent an odds ratio.

Component	Term	Ratio	CI
Init. occupancy	Land cover: broadleaf woodland	1.530	[1.061,2.205]
Init. occupancy	Land cover: coniferous woodland	2.424	[0.946,6.211]
Init. occupancy	Land cover: arable land	4.722	[1.053,21.172]
Init. occupancy	Land cover: improved grassland	3.674	[1.039,12.998]
Init. occupancy	Land cover: semi-natural grassland	1.454	[0.408,5.185]
Init. occupancy	Land cover: mountain/heath/bog	0.413	[0.041,4.143]
Init. occupancy	Land cover: coastal	1.263	[0.951,1.678]
Init. occupancy	Land cover: suburban	1.758	[1.043,2.964]
Init. occupancy	Land cover: urban	1.398	[1.001,1.952]
Init. occupancy	Climate: 30-yr rainfall	1.459	[0.631,3.370]
Init. occupancy	Climate: 30-yr temp.	2.215	[1.317,3.726]
Init. occupancy	Proportion land area	0.417	[0.160,1.084]
Colonization	Atlas = 2007-11	0.753	[0.589,0.962]
Colonization	Land cover: broadleaf woodland	1.011	[0.908,1.126]
Colonization	Land cover: coniferous woodland	1.137	[0.926,1.395]
Colonization	Land cover: arable land	0.898	[0.666,1.210]
Colonization	Land cover: improved grassland	1.122	[0.874,1.441]
Colonization	Land cover: semi-natural grassland	1.186	[0.911,1.543]
Colonization	Land cover: mountain/heath/bog	1.198	[0.848,1.692]
Colonization	Land cover: coastal	1.056	[0.921,1.210]
Colonization	Land cover: suburban	1.107	[0.960,1.277]
Colonization	Land cover: urban	1.000	[0.902,1.107]
Colonization	Plant cover: ivy	1.467	[1.166,1.846]
Colonization	Plant cover: mistletoe	1.283	[1.098,1.500]
Colonization	Orchard cover	1.200	[0.974,1.478]
Colonization	Climate: 30-yr rainfall	0.628	[0.469,0.841]
Colonization	Climate: 30-yr temp.	1.476	[1.151,1.893]
Extinction	Atlas = 2007-11	0.556	[0.373,0.827]
Extinction	Land cover: broadleaf woodland	0.812	[0.678,0.972]
Extinction	Land cover: coniferous woodland	2.108	[1.066,4.168]
Extinction	Land cover: arable land	0.400	[0.229,0.699]
Extinction	Land cover: improved grassland	0.521	[0.326,0.833]
Extinction	Land cover: semi-natural grassland	0.785	[0.432,1.428]
Extinction	Land cover: mountain/heath/bog	0.985	[0.375,2.583]
Extinction	Land cover: coastal	0.876	[0.712,1.076]
Extinction	Land cover: suburban	0.698	[0.557,0.875]
Extinction	Land cover: urban	0.840	[0.727,0.972]
Extinction	Plant cover: ivy	0.693	[0.387,1.244]
Extinction	Plant cover: mistletoe	0.834	[0.694,1.002]
Extinction	Orchard cover	0.877	[0.678,1.134]
Extinction	Climate: 30-yr rainfall	0.434	[0.238,0.790]
Extinction	Climate: 30-yr temp.	0.397	[0.268,0.588]
Detection	Weather: ground frost	0.932	[0.820,1.061]
Detection	Weather: rainfall	1.115	[0.975,1.275]
Detection	Weather: temperature	1.175	[1.008,1.369]

Table 6.2: *(continued)*

Component	Term	Ratio	CI
Detection	Atlas = 2007-11	3.023	[2.343,3.900]
Detection	Survey duration	1.065	[1.051,1.078]

6.4.2 Daily counts

Weather conditions and time of season strongly influenced garden blackcap counts (Table 6.3). More blackcaps were observed in colder temperatures, greater precipitation, and higher winds. In line with our predictions, the effect of temperature increased with precipitation. The effect of wind was dependent on precipitation, showing a positive relationship when there was little precipitation and a negative relationship at higher precipitation amounts; the combination of high winds and precipitation may simply discourage blackcaps from feeding altogether. Overall blackcap counts increased through the winter and began decreasing in mid-March (Figure 6.4). The significance and directionality of these effects were generally consistent in a truncated Poisson model that included a linear instead of smooth term of date (not shown); however, in that model the interaction between wind speed and precipitation was replaced by an interaction of wind speed and temperature.

Table 6.3: Predictors from Poisson generalized mixed-effects model of daily blackcap counts in British gardens. For fixed effects, shown are relative risk ratios (exponentiated coefficients), 95 percent confidence intervals, and P-values. Non-significant interactions have been removed. All continuous variables have been standardized to have a mean of zero and a variance of one so that coefficient estimates can be compared. The model intercept is not shown because the exponentiated intercept does not represent a relative risk ratio. For the smooth term, shown are the estimated degrees of freedom and P-value. For random terms, the standard deviation of the variance component is given.

Type	Term	Ratio	CI	P-value	EDF	SD
Fixed	Max air temp.	0.908	[0.884,0.934]	<0.001	-	-
Fixed	Precip. amount	1.049	[1.022,1.077]	<0.001	-	-
Fixed	Mean wind speed	1.032	[1.004,1.061]	0.025	-	-
Fixed	Precip. amount × Mean wind speed	0.962	[0.935,0.990]	0.009	-	-
Fixed	Max air temp. × Precip. amount	0.962	[0.931,0.994]	0.019	-	-
Smooth	Days after 1 Nov	-	-	<0.001	8.653	-
Random	Year	-	-	-	-	0.434
Random	Location	-	-	-	-	0.790

Table 6.4: Predictors from binomial generalized mixed-effects model of daily blackcap presence in British gardens. For fixed effects, shown are odds ratios (exponentiated coefficients), 95 percent confidence intervals, and P-values. Non-significant interactions have been removed. All continuous variables have been standardized to have a mean of zero and a variance of one so that coefficient estimates can be compared. The model intercept is not shown because the exponentiated intercept does not represent an odds ratio. For the smooth term, shown are the estimated degrees of freedom and P-value. For random terms, the standard deviation of the variance component is given.

Type	Term	Ratio	CI	P-value	EDF	SD
Fixed	Sex = Female	0.843	[0.666,1.066]	0.154	-	-
Fixed	Max air temp.	0.774	[0.745,0.803]	<0.001	-	-
Fixed	Precip. amount	1.094	[1.056,1.134]	<0.001	-	-
Fixed	Mean wind speed	1.023	[0.986,1.060]	0.226	-	-
Fixed	Precip. amount × Mean wind speed	0.921	[0.886,0.958]	<0.001	-	-
Fixed	Max air temp. × Precip. amount	0.929	[0.887,0.972]	0.002	-	-
Smooth	Days after 1 Nov	-	-	<0.001	6.567	-
Random	Year	-	-	-	-	0.533
Random	Location	-	-	-	-	0.754
Random	Bird ID	-	-	-	-	0.904

6.4.3 Individual visitation

Individual blackcaps were observed in gardens with an average daily probability of 0.16 (95% CI [0.056,0.26]), averaged across all fixed and random predictors (Table 6.4). Females attended gardens slightly less frequently than males. However, there was a great deal of individual variation in behavior. Of 154 individuals observed over total spans of at least 50 days, 30 were observed on less than 15% of those days, while 48 were observed on at least 50%. Unsurprisingly, individual identity explained the greatest variation in the dataset, representing 0.18 (95% CI [0.14,0.23]) of variation in behavior. This was substantially more than location (0.05 [0,0.1]) and year (0.05 [0.02,0.08]). Blackcaps responded strongly to air temperature and precipitation, visiting more frequently in colder and wetter weather; an interaction indicated that the effect of temperature was stronger in the presence of precipitation, and the effect of wind was again dependent on precipitation (Table 6.4 and Figure 6.4).

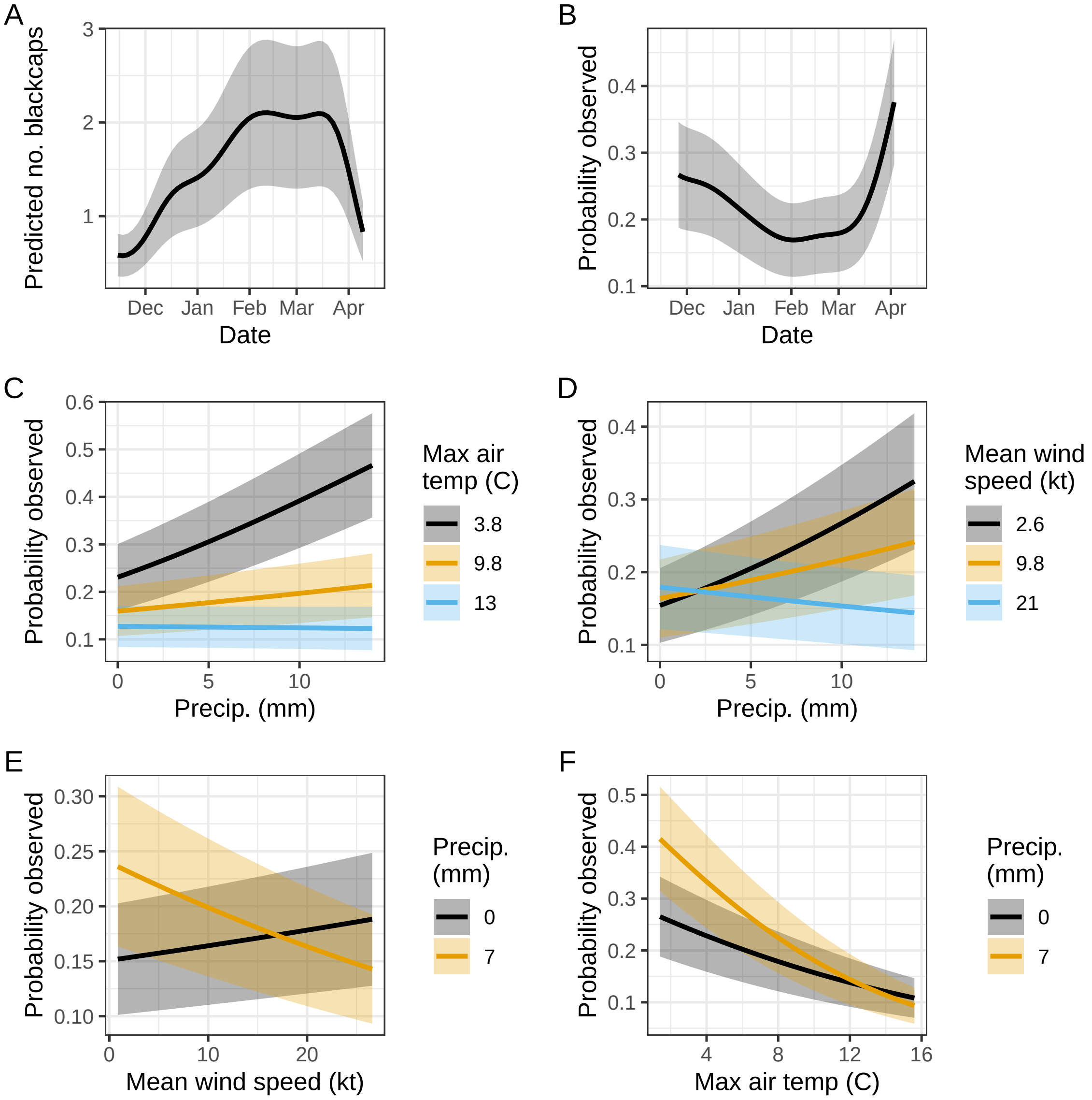

Figure 6.4: Patterns of blackcap behavior in British gardens, showing predictions from two models. The first model (shown in **(A)**) predicts the number of color-ringed blackcaps observed in gardens through the winter. The second model, shown in **(B–F)**, predicts the probability of a given blackcap being sighted in a garden between its first and last sightings in a winter. **(A)** Effect of date on predicted blackcap counts in British gardens, accounting for responses to weather. **(B)** Effect of date on the predicted probability of blackcap observation in British gardens, accounting for responses to weather. **(C)** Effect of precipitation (x-axis) on the probability of blackcap observation, at different air temperatures (colors). **(D)** Effect of precipitation (x-axis) on the probability of blackcap observation, at different wind speeds (colors). **(E)** Effect of wind speed (x-axis) on the probability of blackcap observation, under different precipitation conditions (colors). **(F)** Effect of temperature (x-axis) on the probability of blackcap observation, under different precipitation conditions (colors).

Table 6.5: Predictors from binomial generalized mixed-effects model of blackcap site fidelity to British gardens. For fixed effects, shown are odds ratios (exponentiated coefficients), 95 percent confidence intervals, and P-values. All continuous variables have been standardized to have a mean of zero and a variance of one so that coefficient estimates can be compared. The model intercept is not shown because the exponentiated intercept does not represent an odds ratio. For random effects, the standard deviation of the variance component is given.

Type	Term	Ratio	CI	P-value	SD
Fixed	Sex = Female	0.687	[0.382,1.235]	0.210	-
Fixed	Duration of presence (days)	0.896	[0.609,1.319]	0.579	-
Fixed	Last date encountered	2.492	[1.483,4.189]	0.001	-
Random	Year of ringing	-	-	-	1.107
Random	Location	-	-	-	0.547

6.4.4 Site fidelity

The overall probability of a blackcap returning to the same garden in subsequent years was 0.19 (95% CI [0.086,0.37]). This estimate applies for birds with average first capture dates and average last encounter dates. There was no difference between males and females in return rate, and the date at which the bird was first ringed did not predict whether it would return (Table 6.5). However, birds last seen in gardens later in the winter were much more likely to return the following year. This may be due in part to early-winter movements (see below).

6.4.5 Transience

The overall probability of residence (i.e. being encountered for more than one day) for a ringed blackcap was 0.61 (95% CI [0.32,0.83]). There was a lower probability of being encountered for more than one week: 0.48 (95% CI [0.24,0.72]). The effects of sex and ringing date were not statistically significant (Table 6.6).

6.4.6 Movements

Ringing data revealed that blackcaps wintering in the British Isles engage in within-winter movements, but movements of more than 10 km are largely restricted to November and December (Figure 6.5AB). Movements in November averaged 139 km ± 203SD, in December averaged 34.5 km ± 152SD, and in January and February averaged only 0.706 km ± 1.16SD.

Table 6.6: Predictors from binomial generalized mixed-effects model of blackcap transience in British gardens. For fixed effects, shown are odds ratios (exponentiated coefficients), 95 percent confidence intervals, and P-values. All continuous variables have been standardized to have a mean of zero and a variance of one so that coefficient estimates can be compared. The model intercept is not shown because the exponentiated intercept does not represent an odds ratio. For random effects, the standard deviation of the variance component is given.

Type	Term	Ratio	CI	P-value	SD
Fixed	Sex = Female	0.810	[0.492,1.335]	0.409	-
Fixed	Date first encountered	1.011	[0.772,1.324]	0.934	-
Random	Year	-	-	-	0.463
Random	Location	-	-	-	1.372

Above we show that many blackcaps return to the same garden in successive winters. Interestingly, individuals that do not show site fidelity may have moved substantial distances between winters. Ringing data showed that between-winter movements averaged 152 km ± 301SD (Figure 6.5C). Our detailed garden sighting data showed that even individuals established in a garden in one winter may spend the following winter far from the initial site. One individual [N676642] was sighted by GCE on 63% of days between 16 December 2017 and 4 April 2018. The following winter, it did not return to this site, but was present (and photographed) at a garden 53 km away between 7 January and 12 February 2019.

6.4.7 Breeding areas and migration timing

Combining ringing recoveries and geolocator data, we observe that blackcaps wintering in the British Isles occupy a wide breeding area, spanning 2000 km across Europe (Figure 6.5D). Estimates from geolocator data (from Chapter 3) suggest that the core source area for the wintering population is in western Europe (e.g. France), whereas almost all ringing recoveries come from further east.

Geolocator data indicate that British winterers depart on spring migration between 15 March and 26 April, with a median date of 3 April (Figure 6.6A). They return in autumn between 4 September and 22 October, with a median date of 13 October (Figure 6.6B). We focused on observations of birds carrying geolocators at three sites with good observer coverage to determine how departure from gardens

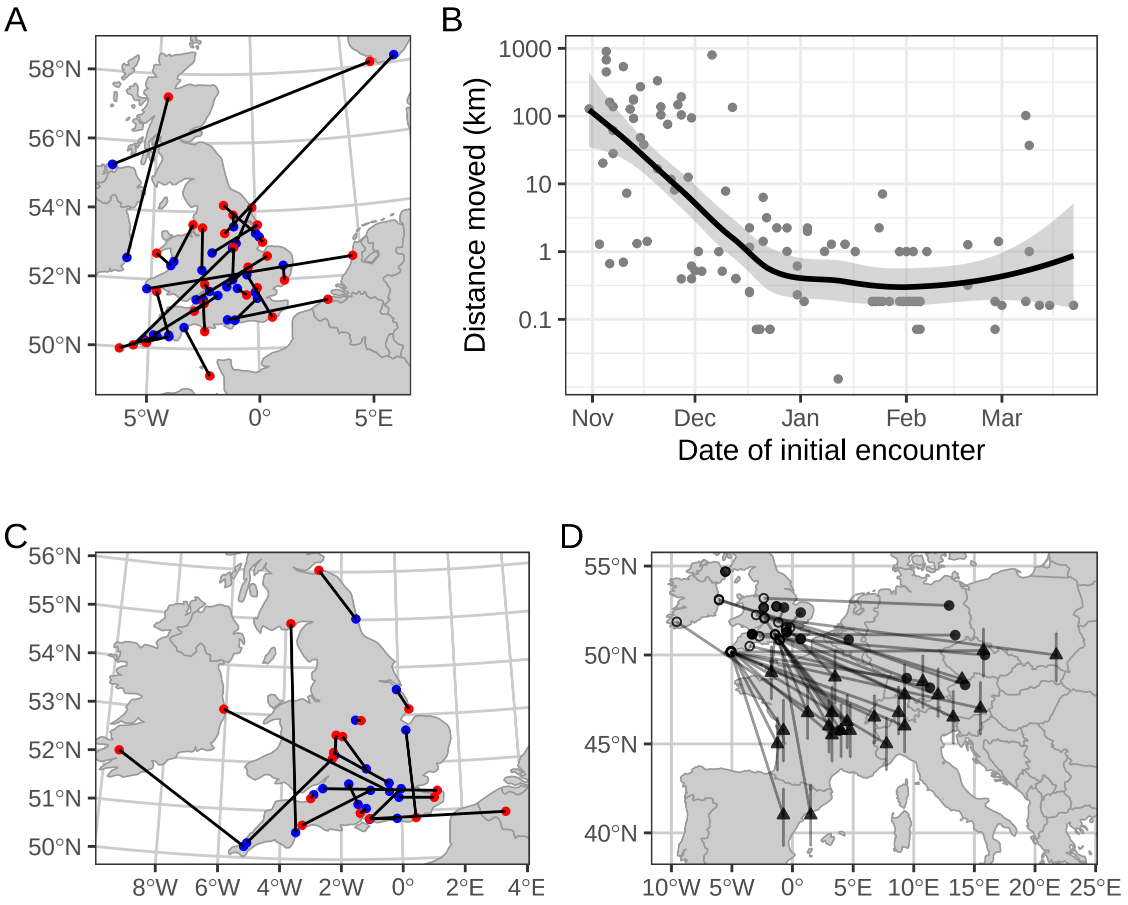

Figure 6.5: Movements of blackcaps wintering in the British Isles from ringing recovery data and light-level geolocators. **(A)** Ringing (red) and recovery (blue) locations of within-winter movements. **(B)** Distance of within-winter movements by ringing date. **(C)** Ringing (red) and recovery (blue) locations of between-winter movements. One recovery from Algeria and one from central France are not shown. **(D)** Wintering (open) and breeding (filled) locations of blackcaps wintering in the British Isles. Circles show capture sites and ringing recoveries, and triangles show breeding site estimates derived from geolocator data (from Chapter 3). For geolocation estimates, error bars indicate latitude estimates for sun angles ±1º.

compared to migratory departure from the British Isles. After excluding individuals that left the garden shortly after being fitted with a geolocator (N=3), we found that the remaining 9 individuals departed on migration on average 4.22 ± 4.49SD days after last being seen (Figure 6.6C). Due to short migration distances, these blackcaps typically arrived within a couple of days of departure; therefore, these birds arrived on or near the breeding grounds only 5.44 ± 5.48SD days after last being seen in their winter garden. This close correspondence between departure from the garden and departure on migration stands in contrast to the situation

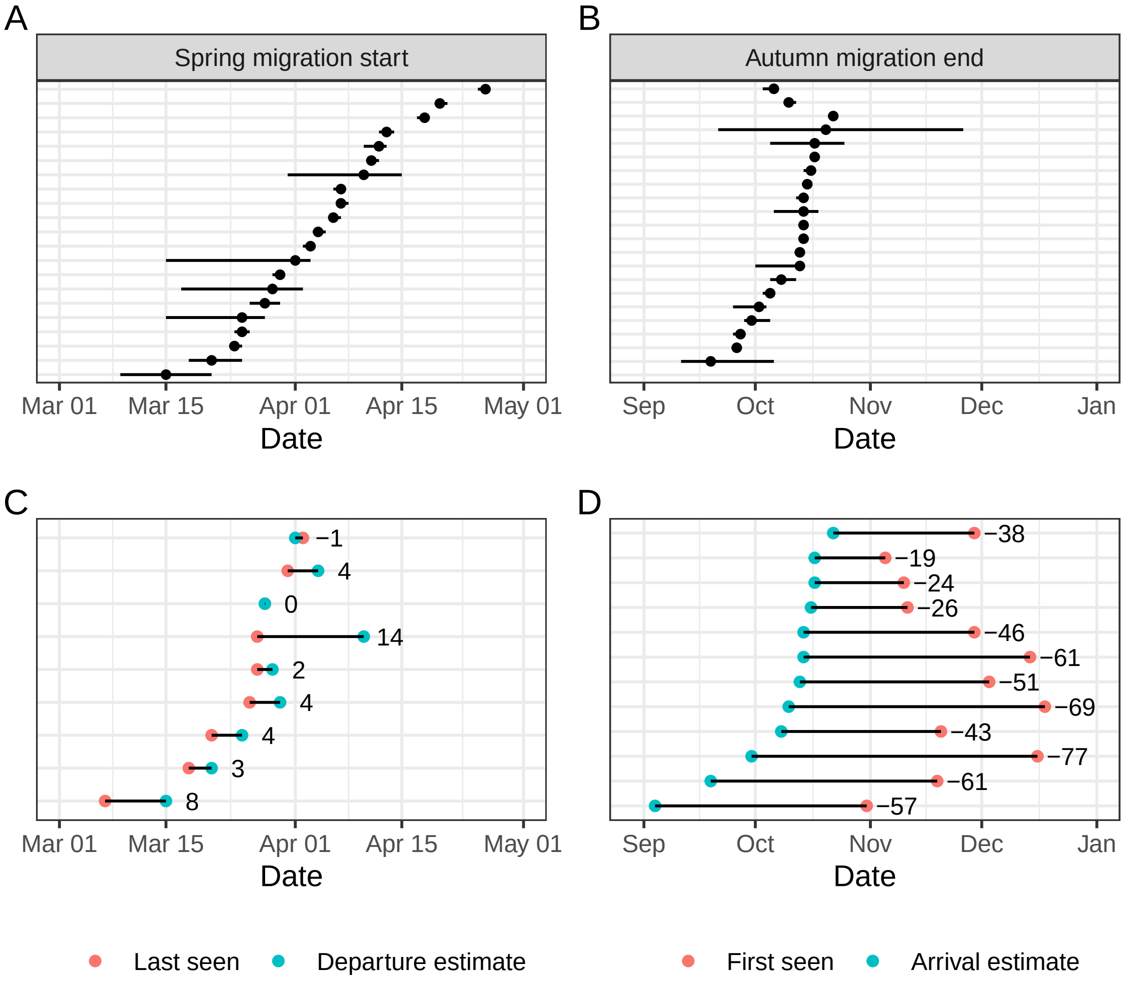

Figure 6.6: Migration timing of British wintering blackcaps. (**A**) and (**B**) show the distribution of departure and arrival dates; lines show uncertainty as the interquartile range of model estimates from Chapter 3. Spring and autumn timings are matched horizontally to the same individual. (**C**) and (**D**) compare geolocator timing estimates (blue) to the date the bird was first or last observed in the garden in which it wintered (red), in autumn and spring, respectively. Numbers give differences in days. Individuals are *not* matched horizontally.

in autumn. In autumn, blackcaps arrived in the British Isles on average 47.7 ± 18.4SD days before being first detected by garden observers (N=12; Figure 6.6D).

6.5 Discussion

6.5.1 Human influence on blackcap behavior

The distribution and behavior of blackcaps wintering in the British Isles is strongly shaped by human activity and mediated by environmental conditions. Our analysis shows that wintering blackcaps prefer suburban habitats, where many visit garden sites throughout the winter. Supplemental bird feeding is certainly an important driver of this pattern. Garden sites may be particularly important during periods of difficult weather, and our analysis showed increasing use of garden feeding stations in cold and wet conditions. In these conditions, foraging for berries and other fruit may be energy intensive. Access to reliable and high-energy, fatty foods, which are frequently provided in gardens, may be particularly important when birds have increased thermoregulatory requirements.

A stationary and reliable food source is unusual for a species that is primarily frugivorous during winter. Blackcaps in traditional Mediterranean wintering areas track ephemeral fruit resources or are forced to move once they are depleted (Belda et al. 2007; Cuadrado 1992; Rey 1995; Tellería et al. 2008). Studies in Africa and Iberia report inter-annual recapture rates of 0–5% for wintering blackcaps (Cuadrado 1992; Cuadrado et al. 1995; King and Hutchinson 2001; Lövei et al. 1985). A capture-recapture analysis in Spain estimated that 26% of individuals are likely to be resident at a given site during the winter, defining residency as presence for more than one week at that site (Belda et al. 2007). Our estimates of return rates and residency are substantially higher: we observed an average inter-annual re-encounter probability of 0.19 (95% CI [0.086,0.37]), and we estimated the probability of residency (>1 week) as 0.48 (95% CI [0.24,0.72]). (However, note that we did not use capture-recapture methods to estimate this value.) We suggest that blackcaps wintering in the British Isles show lower within-winter transience and higher between-winter site fidelity due to the higher reliability of supplemental garden food sources over fruiting plants.

Wintering in the British Isles might confer a number of advantages compared to traditional southwest migratory strategies (Berthold and Terrill 1988). Abundant supplemental food may allow blackcaps to attain better body condition and quickly amass the fat stores that will fuel their migratory flights. In turn, these factors may facilitate earlier and more successful breeding attempts. We find that blackcaps tracked with geolocators arrived at the breeding grounds on average only 5.4

days after last being seen in their gardens, suggesting that conditions at British gardens will strongly influence body condition on arrival. It is therefore plausible that the availability of reliable supplemental food puts British winterers at an advantage on the breeding grounds. The advantages of garden feeding may explain recorded differences in bill morphology between British and Iberian overwinterers (Rolshausen et al. 2009). Rolshausen et al. (2009) posited that the narrower and longer bills of the British winterers in their sample may result from a more generalist diet, compared to the largely frugivorous diet of Mediterranean winterers. This difference parallels observations from Great Tits (*Parus major*) in Britain, where selection for longer bills among British birds have been linked to supplementary feeding (Bosse et al. 2017).

6.5.2 Potential future changes in behavior

There is clear evidence that human activity has shaped the behavior of blackcaps wintering in the British Isles, both directly and indirectly. We found that blackcaps were more likely to occur in warmer parts of Britain, but that blackcaps were most likely to use garden sites in periods of cold and wet weather. In the coming decades, Britain is expected to continue to move towards a warmer climate (Lowe et al. 2018). This is likely to improve the suitability of the region for blackcaps, but it is also likely to affect their associations with gardens. In the future, milder weather may decrease blackcaps' use of gardens, even while the wintering population increases overall.

6.5.3 How reliant are blackcaps on supplemental food?

Although supplemental bird food is likely important when winter conditions become difficult, our analysis indicates that blackcaps are far from reliant on garden feeders. In reality, we estimated that the average blackcap visits gardens with a probability of 0.16 (95% CI [0.056,0.26]), suggesting that natural food may be sufficient much of the time. This estimate does not include transient individuals that do not frequent gardens, which represent approximately half of all blackcaps captured. Of course, it is possible that transient individuals simply move to other gardens; future radio-tracking would be a useful approach to better understand how wintering blackcaps interact with natural and artificial food sources through the winter. However, this is also consistent with the possibility that garden feeding stations may play a less pronounced role in the survival of most blackcaps wintering in the British Isles. Indeed, we found that even the most site faithful blackcaps do not appear in gardens until well after they arrive in the autumn—sometimes more than two months after arrival. The most plausible explanation is that blackcaps do not need to use garden feeding stations until natural food sources dwindle in late autumn and early winter. Consistent with this explanation, our analysis found positive associations between blackcap distributions and the distributions of ivy, mistletoe, and traditional orchards. Ivy, which ripens in late winter, may be a particularly important food source for blackcaps once other natural food has been depleted (B. Snow and D. Snow 2010).

6.5.4 Individual variation and flexibility

Large individual variation was a defining feature of our dataset. In our model of individual behavior in gardens, individual identity explained the greatest proportion of variation. Blackcaps existed on a continuum from frequent visitors to single-visit transients. Our results show that blackcaps exhibit a great deal of variation and flexibility in their strategies, which may be key to their success as environments rapidly change.

6.5.5 Breeding origins of British winterers and evidence for residency

We combined ringing recoveries and individual tracking data to show that blackcaps wintering in Britain originate from a 2000 km-wide swath of Europe (see Chapter 3). Ringing recoveries alone supported central European origins of the wintering population, but tracking data show that the breeding range extends well into southwest Europe, even to the Iberian Peninsula, and farther east than suggested from ringing recoveries. There were 9 recoveries of individuals encountered in the British Isles during both summer and winter, suggesting limited year-round residency. However, biases in ringing recoveries make local recaptures far more likely than external recaptures, and our tracking results indicate that at least the vast majority of wintering individuals come from outside the British Isles. None of the 25 geolocator tracks showed clear evidence for year-round residency in Britain, although one individual that wintered at Chilbolton, Hampshire, UK, spent the summer in extreme northern France or possibly the southern coast of England.

6.5.6 Conclusion

Most migratory birds facing the pressures of environmental change are in decline, but the blackcap is one of few exceptions: this species is thriving in a changing world. The recently-established wintering population of blackcaps in the British Isles provides an opportunity to understand how this species has managed to keep pace. Our results support the hypotheses that climate change combined with supplemental bird feeding has facilitated the rapid establishment of this population (Plummer et al. 2015). Moreover, our individual-level data reveal the tremendous individual flexibility that blackcaps exhibit in their movement patterns and responses to conditions. Among migratory species, those with large variation and flexibility in movement and foraging behaviors will likely be best equipped to respond to the coming decades of environmental change.

6.5.7 Author contributions

BMVD conceived of the study and organized data collection with GJC, ML, and BCS, who oversaw the project. BMVD, GJC, RJP, GCE, and GCMR collected data for the study. BMVD analyzed the data and wrote the paper with input from all authors.

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General Discussion

The power of perspectives across scales

Understanding natural phenomena as complex as bird migration requires a multilevel approach, as individual-level programs and reaction norms interact with population processes and broad biotic and abiotic factors. In this thesis, I have explored several perspectives on change and flexibility in avian migration, focusing on the contributions of the innate migratory program, birds' responses to environmental cues and conditions, and the influence of human activity on migratory behavior. In **Chapter 1**, I demonstrated that stonechats (genus *Saxicola*) possess inherited migratory programs that vary predictably among taxa according to their migratory behavior. However, these programs are not the sole determinant of migratory phenotype, especially among partial migrants, implying that environmental factors can readily interact with the inherited program. In **Chapter 2**, I combined field and laboratory studies to present evidence of changes in the innate migratory program of a long-distance migrant, the pied flycatcher (*Ficedula hypoleuca*), showing that ongoing responses of migratory birds to climate change can involve not only phenotypic plasticity, but microevolutionary change as well. In **Chapter 3**, I examined variation in the migratory behavior of the Eurasian blackcap (*Sylvia atricapilla*) across its European range, illustrating two different ways that natural selection can act on songbird migration: (1) to maintain opposing migratory strategies over short distances, in the case of a migratory divide, and (2) to enable the spread of a novel strategy across a wide range, in the case of individuals wintering in the British Isles. In **Chapter 4**, I showed that migratory flexibility is important not only on evolutionary timescales, but also to enable short-term responses to variable environmental conditions during active migratory flights. These responses are predictable enough to reliably forecast avian movements across continental extents. In **Chapter 5**, I examined how artificial light at night can drastically affect migratory journeys, an important example of anthropogenic impacts on bird migration. Finally, in **Chapter 6**, I returned to the blackcap to show how human activity can impact not only migrants' in-flight behaviors, but also shape their broader ecology. Overall, this body of work shows that migratory birds' flexibility stems from a range of sources, innate and external, and that the presence of variation in migratory phenotype may be key to enabling responses to environmental change.

The interplay of variation and flexibility

Variation is the engine of evolutionary change, providing populations with the raw material on which natural selection can act. Taxa with greater natural variation will be the most flexible—and best able to adapt to changing conditions. Among migratory birds, variation and flexibility are linked: long-distance migrants with rigid timing programs show the most consistency in phenotype (Gwinner 1996a). Shorter distance migrants show greater variation in behavior and less rigidly programmed migrations (Berthold et al. 1972; Gwinner 1991). These insights lead to the expectation that short-distance migrants will more quickly respond to climate change, a hypothesis supported by current evidence (Butler 2003; Usui et al. 2017).

In this thesis, the contrast between short- and long-distance migrants is evident in **Chapter 1**, where stonechat taxa with longer migrations showed less variation in behavior. Siberian stonechats nearly always showed migratory restlessness, whereas individuals from Irish and Kenyan populations frequently did not. Siberian stonechats are obligate long-distance migrants, Irish stonechats are partial migrants, and Kenyan stonechats are residents.

In **Chapter 2**, I observed a stark contrast between the phenotypic variation observed in the 2002 cohort of pied flycatchers and the older 1981 cohort, despite both groups having been raised under identical conditions. Although the experimental sample sizes were small, individual variation in winter and spring timing traits was greater in the 2002 cohort among both males and females. This pattern could suggest that climate change—itself variable and volatile—may be selecting for increased variation in phenotypes.

Blackcaps show broad variation in migratory traits at both individual and population levels. Populations of blackcaps range from entirely sedentary to fully migratory (Cramp and Brooks 1992), and the results from **Chapters 3 and 6** highlight the variability in blackcaps' individual strategies along many axes, from migratory direction to responses to winter weather. Blackcaps breeding near the central European migratory divide showed a large spread in migratory direction as well as in timing. In British gardens, blackcaps also showed large individual variation in behavior, with some individuals reliably using garden feeding stations in a range of weather conditions and others doing so primarily during harsher weather. Blackcaps have substantial diet flexibility, which may contribute to their ability to use gardens (Hardy 1978; Rey and Valera 1999).

Taking insights from the lab to the field—and back

Laboratory studies of migratory behavior have led to foundational insights into bird migration, including how migratory birds use the sun, stars, magnetic field, and polarized light to orient (Åkesson and Hedenström 2007; Alerstam and Högstedt 1983; Emlen 1967; Wiltschko and Gwinner 1974). Laboratory studies have also shown that songbirds' migratory behavior is innate and inherited (Berthold 1991; Helbig 1991) and even how birds respond to wind drift (Able 1977; Moore 1990). At the same time, laboratory studies of migration can be limiting simply because they examine the behavior of caged birds, not free-flying individuals. Exactly how closely lab-derived assays correlate with wild phenotypes is still an open question, but recent research has shown that the migratory restlessness behavior of birds held in captivity may not always be directly comparable to migration in the wild. For example, resident populations may show migratory restlessness (Helm and Gwinner 2006), and migrants that show restlessness every night in captivity may only undertake infrequent flights in the wild (Bäckman et al. 2017; Zúñiga et al. 2016).

This thesis affirms the value of laboratory experiments for studying migration while also illustrating why scientists should be cautious in the extent of inference drawn from lab-derived proxies of wild behavior. In **Chapter 2**, I showed that the spring timing advances of captive-raised pied flycatchers taken from the wild were of a similar magnitude to those observed in a nearby wild population. In this case, the wild and laboratory-derived data were highly complementary: by excluding plasticity as a source of timing differences, the captive study provided key insight into change in the wild population, while at the same time affirming the relevance of laboratory data for understanding wild processes. Similarly, blackcap migration has been extensively studied in a laboratory setting, and **Chapter 3** provides an opportunity to compare previous lab-derived insights to new migration tracks of wild birds. Captive experiments that interbred blackcaps from populations with southwest and southeast migratory directions found that their offspring showed a spread of intermediate migratory directions (Helbig 1991). The distribution of directions of wild birds tracked from the contact zone (**Chapter 3**) was highly similar to the distribution of directions from the experiment. However, it is important to note that these tracks were from adult blackcaps originating in the migratory divide, while Helbig measured the offspring of parental populations captured away from the contact zone. In another instance, orientation experiments with British winterers found a broadly west-northwesterly autumn orientation, in contrast to the southwesterly orientation of German blackcaps (Berthold et al. 1992; Helbig et al. 1994). Geolocator results showed that British winterers indeed migrate west and northwest to Britain from continental breeding areas (**Chapter 3**). Finally, a captive timing experiment found that blackcaps exposed to British photoperiods initiated migration on average five days earlier than those exposed to Mediterranean photoperiods, estimating that birds wintering in these two areas would arrive on the breeding grounds 16 days apart due to the shorter migration durations of British winterers (Terrill and Berthold 1990). Results from wild-tracked blackcaps were broadly consistent with this result, yielding estimates of a six-day difference in departure and ten-day difference in arrival. Taken together, these results generally affirm the utility of laboratory experiments in the study of avian migratory behavior.

Despite clear consistencies between laboratory results and the behavior of wild-tracked migrants, this thesis also highlights the caution needed when drawing inferences from laboratory proxies of migration. In **Chapter 1**, I showed that the migratory phenotypes of wild populations do not necessarily align with activity measures derived from migratory restlessness data. In that chapter, Irish stonechats, which are partial migrants (migratory individuals from Britain travel a median distance of 1139 km, Helm et al. 2006), showed intensities of spring migratory restlessness that were indistinguishable from those of Siberian stonechats, which are obligate long-distance migrants and travel upwards of 2600 km (Raess 2008). In addition, I detected migratory restlessness in resident Kenyan stonechats and striking changes in restlessness with age, which might be related to plasticity or poorly understood learning processes. I also found that individuals with higher nocturnal migratory restlessness tended to be more active birds overall (measured from diurnal data), which necessitates further work on how restlessness relates to other traits and caution on its exclusive interpretation as a measure of migratory tendency (e.g. Berthold 1988). In blackcaps, although tracking results in **Chapter 3** were consistent with many insights derived from experiments in captivity (see previous paragraph), these experiments provided an incomplete picture. Orientation studies could not have determined that many blackcaps migrating south from the migratory divide would winter north of the Sahara. The experiments had concluded that a southerly migration direction would likely result in low survival (Helbig 1991), when in reality this direction is used by a large fraction of birds in the divide (**Chapter 3**). As a last example, Terrill and Berthold (1990) used an average migration rate of 45 km per day to estimate that British winterers would take 24 days to travel from Britain to Germany on spring migration. However, data from **Chapter 3** indicated that the spring migrations of British winterers were often only a few days long. Overall, care is necessary when interpreting results from laboratory proxies of migratory behavior.

Impacts of human activities on bird migration

This thesis examines two examples of anthropogenic impacts on bird migration systems. The first is the behavioral alterations caused by the proliferation of artificial light at night. It is not known why migratory birds are attracted or disorientated by light pollution, but its negative influence on birds has been known for some time (Allen 1880). Impacts of light pollution on birds can be severe and acute, as in cases of mass attraction and potentially mass mortality (e.g. **Chapter 5**; Rich and Longcore 2013). However, this is not the only way light pollution can impact avian migrants. Recent research suggests that light at night may influence the behavior of migrating birds across a landscape scale, drawing them towards urbanized areas where suitable terrestrial habitats can be scarce (McLaren et al. 2018). Fortunately, action to reduce light pollution can have immediate positive impacts and allow migrants to continue their flights unhindered (**Chapter 5**).

Human activity has transformed much of the world and profoundly influenced the course of evolution of wild organisms (Boivin et al. 2016; Johnson and Munshi-South 2017; Palumbi 2001; A. P. Sullivan et al. 2017). Urbanization in particular has driven major phenotypic changes (Alberti et al. 2017) as organisms adapt to a human-dominated environment. As these changes reflect, one consequence of human activity is the creation of new and modified opportunities that wildlife can exploit. An obvious example of this phenomenon is the proliferation of supplemental feeding, which can have a range of impacts on the populations and behavior of wildlife (Cox and Gaston 2018; Galbraith et al. 2015; Plummer et al. 2019). This is especially true for birds, which are frequent beneficiaries of food provisioning. At least 45% percent of households feed birds in a number of countries, with higher provisioning rates in the United Kingdom (Davies et al. 2012; Galbraith et al. 2014; Orros and Fellowes 2015). In the UK, this behavior is an important determinant of wintering blackcap presence and a driver of their behavior (**Chapter 6**; Plummer et al. 2015; Plummer et al. 2019). Garden bird feeding has likely facilitated the growth of the winter blackcap population by increasing winter survival, especially when harsh conditions increase energy demands (**Chapter 6**; Plummer et al. 2015). This example demonstrates how a bird species with sufficient flexibility in migratory behavior can take advantage of novel resources. Blackcaps are not the only species adjusting migration in response to human-mediated changes in resource availability; species as diverse as white storks (*Ciconia ciconia*) and hummingbirds (Trochilidae) have adopted modified, shorter migrations (Satterfield et al. 2018). These highly flexible species are notable because of the speed of their response, and these examples may foreshadow similar ecological shifts in the future.

Future directions and applications

Natural systems are complex, reflecting the interplay among individual traits and behavior, external cues and stimuli, evolutionary processes, and other contributing factors. In this thesis, I have surveyed the drivers of bird migration across scales, seeking insights from individuals, species, and systems.

Dynamic approaches to conservation

This work has direct implications for conservation initiatives striving to mitigate the impacts of human society on migrating birds. **Chapter 5** highlights the effects that artificial light can have on migrating birds, but it also shows that timely removal of light pollution can eliminate these acute impacts. Mitigation should focus on urban areas, which generate a disproportionate amount of light pollution—especially those along key migratory corridors (**Appendix E**). Through migration forecasts (**Chapter 4**), alerts could be established that warn of upcoming large migration events in time for people to turn off non-essential lighting.

The genetic basis of migration

For decades, we have known that key aspects of songbird migration are innately programmed and have a genetic basis (e.g. Berthold and Querner 1981; Berthold and Pulido 1994; Gwinner 1996b; Helbig 1996; Pulido et al. 1996). Yet even today, we lack a meaningful understanding of the genetic architecture underlying migratory behavior. A large part of current knowledge stems from candidate genes associated with migration (e.g. Mueller et al. 2011; Saino et al. 2015; Johnston et al. 2016; Lugo Ramos et al. 2017). However, detected effects of candidate genes are generally limited and taxon- or sex-specific (Bazzi, Galimberti, et al. 2016; Bazzi et al. 2017; Mettler et al. 2015; Mueller et al. 2011; Parody-Merino et al. 2019; Ralston et al. 2019; Saino et al. 2015), with little evidence for general patterns (Lugo Ramos et al. 2017; but see e.g. Bazzi, Cecere, et al. 2016). Recent genomic work affirms a genetic basis of avian migratory behavior (Delmore et al. 2016; Toews et al. 2019), but we still lack any mechanistic or unified understanding of the processes involved. Epigenetic modifications could be important (Saino et al. 2017). Fortunately, future work with blackcaps is promising: blackcap migration clearly has a genetic basis (Berthold et al. 1992; Helbig et al. 1994; Helbig 1996) and the species shows minimal genetic structure across its migratory populations (Delmore et al. 2020; but also see Rolshausen et al. 2009). This scenario is encouraging for identifying genetic variants that influence migratory phenotypes. Furthermore, in **Chapter 3**, I illustrate that the species shows widely varying migratory strategies, as well as a narrow cline in migratory direction across the central European migratory divide. The narrow cline suggests strong selection on migratory direction (or a related trait), which may be detectable via whole genome sequencing and analysis.

"Big Data" Ecology

Ecology has entered an era of "big data," and **Chapter 4** provides one example of the many possible uses of large datasets in understanding the natural world. Integrating multiple datasets and modeling natural processes will lead to an even greater understanding of the intricacies of complex natural systems. For scientists studying migratory birds, large Doppler radar networks are but one source of big data. Citizen science initiatives now collect millions of observations from volunteer observers, and these data repositories are invaluable resources for understanding species behavior, distributions, and responses to change (e.g. B. L. Sullivan et al. 2014). Already, combining radar data and citizen science observations has led to new insights into bird migration (**Appendix C**). As repositories of many types of data grow, it will become feasible to combine radar and citizen science data with individual tracks, acoustic monitoring, landscape genomics, and technologies that have yet to be developed. It is an exciting time to study avian migration across scales.

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Appendices

A

Supplementary material for chapter 1

Journal of Avian Biology

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Van Doren, B. M., Liedvogel, M. and Helm, B. 2016. Programmed and flexible: long-term *Zugunruhe* data highlight the many axes of variation in avian migratory behaviour. – J. Avian Biol. doi: 10.1111/jav.01348

Supplementary material

Programmed and flexible: long-term *Zugunruhe* data highlight the many axes of variation in avian migratory behaviour

Benjamin M. Van Doren, Miriam Liedvogel and Barbara Helm

SUPPLEMENTARY MATERIAL

APPENDIX 1

SUPPLEMENTARY METHODS

Origin and Maintenance of Birds: Birds originated from the following locations: Austrian stonechats: Lower Austria (48°14’N, 16°22’E; n = 157); Irish stonechats: Iveragh Peninsula near Killarney, in the County of Kerry, Ireland (c. 52°N, 10°W; n = 83); African stonechats (data partly published in Helm and Gwinner 2006): Lake Nakuru region, Kenya (0°14’S, 36°0’E; n = 20), and Mount Meru region, Tanzania (3°50’S, 36°5’E; n = 4), and 1 F1, Kenya x Tanzania; Siberian stonechats: vicinity of Naursum National Park (c. 51.5°N, 63°E; n = 53), Kazakhstan.

Detailed descriptions of breeding and raising conditions have been published elsewhere (Gwinner et al. 1987, Helm 2003, 2009). Briefly, juveniles were taken from their nests while still depending on their parents, either from breeding aviaries or from the wild, and were then hand-raised in Andechs, Germany (48° N, 11° E). These birds had hatched at various times of the breeding period in this multiple-brooded species (Helm 2009). All birds received daily fresh water and a custom-made food mixture including mealworms (Gwinner et al. 1995). They were generally weighed and checked for moult once per week. To obtain detailed information on postjuvenile moult (in US terminology, the first prebasic moult, Humphrey and Parkes 1959), birds were temporarily checked more frequently (Helm and Gwinner 1999).

Photoperiodic Conditions: The vast majority was kept under conditions that simulated day length experienced by Austrian stonechats around the annual cycle, switching on and off daylight at the beginning and end of civil twilight, respectively. Day length was changed at weekly intervals, and between late September and mid March it was adjusted to simulate migration from a summer latitude of 47.5°N to a winter latitude of 40°N. For the subset of birds exposed to simulated day length experienced by Siberian stonechats, we accommodated for an alternative migration route by simulating wintering areas at 25°N and adjusting day length from early September until early May (for details on these conditions, see Helm et al. 2009).

Activity Recording and Initial Processing: Birds were kept in registration cages that recorded their locomotor activity around the clock via passive infrared detectors (Intellisense XJ-413T; CK Systems; 12m/40°range). In contrast to microswitches, infrared detectors record not only perch hopping, but all spatio-temporal changes of a bird's moving body. Custom-made recorders stored the number of movements per two-minute interval, and we then pooled the data of five consecutive two-minute intervals. Because infrared detectors are highly sensitive, we introduced a threshold to filter out noise. Screening of the data showed that noise patterns were suppressed if values below 20 activity counts per ten minutes were omitted (I. Schwabl-Benzinger, pers. comm.). Therefore, we scored each ten-minute interval as "active" if a total of 20 or more activity counts were registered in the five two-minute intervals. We then extracted the total number of ten-minute intervals with activity during the dark and light fractions of the day, discounting one transitional ten-minute interval in the morning and in the evening, respectively.

Treatment of Moult and Missing Data: Earlier observations (Helm 2003) indicated that juvenile stonechats show nocturnal restlessness at early ages, even before postjuvenile moult, when they are unlikely to commence actual migration. However, young birds can initiate migration during late stages of body moult (Jenni and Winkler 1994). Accordingly, we attributed early post-fledging nocturnal activity to behavioural development and excluded all data prior to the start of postjuvenile moult from our analysis (affecting 176 birds). We did allow for overlap of *Zugunruhe* with advanced moult stages, shown by approximately half of measured birds (Figure 2). In 22 cases, no information on moult was available, and we left these data unmodified. Our dataset contained a small amount of missing activity data for some birds, generally consisting of periods of a few days, but occasionally several weeks. Because our changepoint-based time series analysis could not handle missing data, we addressed this either by splitting up time series at large gaps (> 7 days missing) or by filling in small gaps with the average value of the two weeks flanking the gap (≤ 7 days missing).

Defining Spring and Autumn Migration Periods: To be maximally inclusive, we used data from all birds throughout the full annual cycle to identify elevated activity periods (i.e. those representing *Zugunruhe*). As migration occurs twice per year, we subdivided the annual cycle into two halves to quantify spring and autumn migration periods separately for each year. We defined spring/autumn cut-off dates separately for each population because of inherent population-level differences in migration timing. For each group, we first calculated the daily mean nocturnal activity level throughout the year. Then, we identified the two 60-day periods between the vernal and autumnal equinoxes with the lowest mean nocturnal activity, corresponding to summer and winter, respectively. The midpoints of these 60-day periods—

when nocturnal activity was at its minimum—delimited the start and end of spring and autumn seasons (see supplementary R script). We calculated the mean activity level in the 30 days surrounding these winter and summer boundary dates as a measure of baseline (i.e. non-migratory) activity. For a given bird, we only analysed migration periods with at least 90 days of activity data.

Changepoint Analysis for Identifying and Characterising Periods of Zugunruhe: For changepoint analysis, we applied the pruned exact linear time (PELT, Killick et al. 2012) algorithm implemented in the "cpt.meanvar" function, with a Poisson test statistic. A changepoint is identified if its addition to the model sufficiently improves the log-likelihood enough to overcome a penalty value used to prevent overfitting (i.e. to prevent too many changepoints from being identified). The Bayesian Information Criterion (BIC) is often used as such a penalty value, and it is proportional to the natural logarithm of the number of data points (= 2*ln(n), where n is the number of data points). Because bird activity usually varied considerably, this default penalty value (BIC) often resulted in over 10 changepoints identified per half-year period. Although these corresponded to clear changes in bird activity, we adjusted the default settings and used a more conservative penalty value to select the ~2-3 greatest points of change in activity level during a period, corresponding to the onset and end of *Zugunruhe* and any substantive within-period changes. By trial and error, we determined that multiplying BIC by 18 was appropriate and generally identified the expected number of changes (supplementary Figure 1). Finally, because we expected bouts of *Zugunruhe* to be weeks in duration, we used the "minseglen" argument to prevent successive changepoints from being identified within 15 days of one another. Such settings are flexible and can be adjusted in our script to fit patterns of any focal study species (for details, see supplementary script). For further details, see supplementary R script. In about 1% of migration periods, the analysis identified non-contiguous elevated segments; these cases were not consistent with our assumption of a single *Zugunruhe* period in a given season. We excluded five of these bimodal cases and retained a subset of data derived from the others when they matched expected patterns. Sometimes, the analysis detected no change in nocturnal activity during a given period; in these cases activity was typically quite low overall, in line with birds that did not engage in *Zugunruhe* at all (supplementary Figure 1D). Rarely, no changepoints were identified but the level of activity was consistently high. These cases generally corresponded to periods for which our data only covered a subset of a migration season, or potentially to aberrant individuals. Because we could not accurately determine these birds' *Zugunruhe* status, we excluded them from the analysis if mean activity was above a threshold, defined as the 95th percentile of mean nocturnal activity from summer and winter neutral periods. In this way, we assigned non-*Zugunruhe* status only to periods for which nocturnal activity levels were consistent with those during summer and winter non-migration periods; the < 2% of analysed migration periods that did not pass this criterion were excluded.

Factors Affecting Occurrence of Zugunruhe: We combined all years after the first because sample size declined greatly after the first year, and because we expected any transition to be most pronounced from the first, naïve year to subsequent migratory seasons with at least one completed migratory journey. We then combined automated stepwise removal of non-important terms by AIC ("stepAIC" function in the MASS package, Venables and Ripley 2002) and manual elimination of non-significant terms not removed in the preceding step. We tested pairwise inter-population differences in the proportion of periods with *Zugunruhe* during spring and autumn, and we corrected for multiple comparisons using the joint distribution of the *z* statistics ("single-step" option in "adjusted" function, package *multcomp*, Hothorn et al. 2008).

Variation in Zugunruhe Timing and Intensity: To achieve a larger and more representative dataset, we included data from all three photoperiods. We separately analysed data from spring and autumn periods. For each timing or intensity metric (e.g., onset, mean, and end dates, duration, mean and peak intensity), we constructed an initial model with population, sex, age, photoperiod, and age × population interaction as categorical fixed effects and individual bird as a random intercept effect. From this initial model, we manually removed terms that were non-significant. Once a model was solely composed of significant terms, we applied the Tukey method to conduct pairwise tests of significant difference among populations (package multcomp; Hothorn, 2008). When the age × population interaction was significant (rarely), the multiple comparisons presented in figures use a version of the model without the interaction for clarity and in order to show the overall effect of population. We do describe the interactions in the text when affecting one of the non-hybrid groups (only one case). Similarly, for comparing intensity and duration of *Zugunruhe* between spring and autumn migration periods, we used linear mixed models, beginning with the same fixed and random effects just described and dropping non-significant fixed terms. We manually defined contrasts to test for significance of the effect of season for each population and adjusted for multiple comparisons using the “single-step” option, as above.

Population-wide Nocturnal and Diurnal Activity During the Migration Periods: For each population, we identified the two 60-day periods in the first and second halves of the year with the highest mean nocturnal activity (similar to our procedure for identifying neutral periods) and calculated mean nocturnal and diurnal activity levels for each bird during this period. For each bird, we also used the mean nocturnal activity level for its most active 15-day period in the 60-day window as a measure of peak activity.

We first visually inspected activity profiles during the annual cycle at a population level, comparing the activity profiles between (i) hybrids and their parental populations, (ii) the three migratory populations, and (iii) age groups. We then used linear mixed models to analyse these data in a manner similar to that described for changepoint-derived *Zugunruhe* periods. We compared mean and peak activity levels across all individuals of the stonechat populations regardless of their assigned *Zugunruhe* status.

Covariation of Diurnal and Nocturnal Activity Levels: We analysed the association between nocturnal and diurnal activity levels within individuals, including data from all photoperiods to achieve a larger and more representative dataset. For each migration period, we conducted two tests: we compared mean diurnal activity levels in the 15 days immediately preceding Zugunruhe onset to mean diurnal activity in the first 15 days after onset. We then did the same for the end of Zugunruhe. In this way, we minimised the possibility that activity differences could be explained by differences in day length at the time when birds showed Zugunruhe. We used two linear mixed models, beginning with the fixed effects of time (during Zugunruhe or not), sex, population, age, and all interactions; and a random intercept term of individual bird. We then eliminated non-significant terms with the “step” function in the lmerTest package (Kuznetsova et al. 2015) and by manual elimination.

We also studied the association between nocturnal and diurnal activity levels within individuals during both migration seasons and the 30-day neutral summer and winter periods. We used linear mixed models, with activity during each day as the response variable and corresponding nocturnal activity as a fixed continuous predictor. Sex, population, and photoperiod were added as additional fixed effects and iteratively removed if not significant. We included a random intercept term of individual bird (to account for average variation in nocturnal activity level among individuals) and a random slope term (to prevent pseudoreplication when testing the significance of the fixed predictor). We constructed separate models for each season (autumn and spring *Zugunruhe* periods, and summer and winter neutral periods). Data were centred before modelling to aid convergence; this does not affect fixed effect estimates.

Covariation of Activity Between Migratory and Non-migratory Contexts: Finally, we studied whether variation in mean *Zugunruhe* intensity could explain variation in activity during other times of the year, among individuals. We constructed linear mixed models with a migration period's mean *Zugunruhe* intensity as a fixed predictor and mean diurnal activity level during the adjacent summer or winter as the response variable. We included population, age, and sex as additional fixed effects and individual bird as a random intercept. We ran separate models for spring and autumn migration periods and their respective adjacent summer and winter periods (8 models total).

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APPENDIX 2

SUPPLEMENTARY FIGURE CAPTIONS

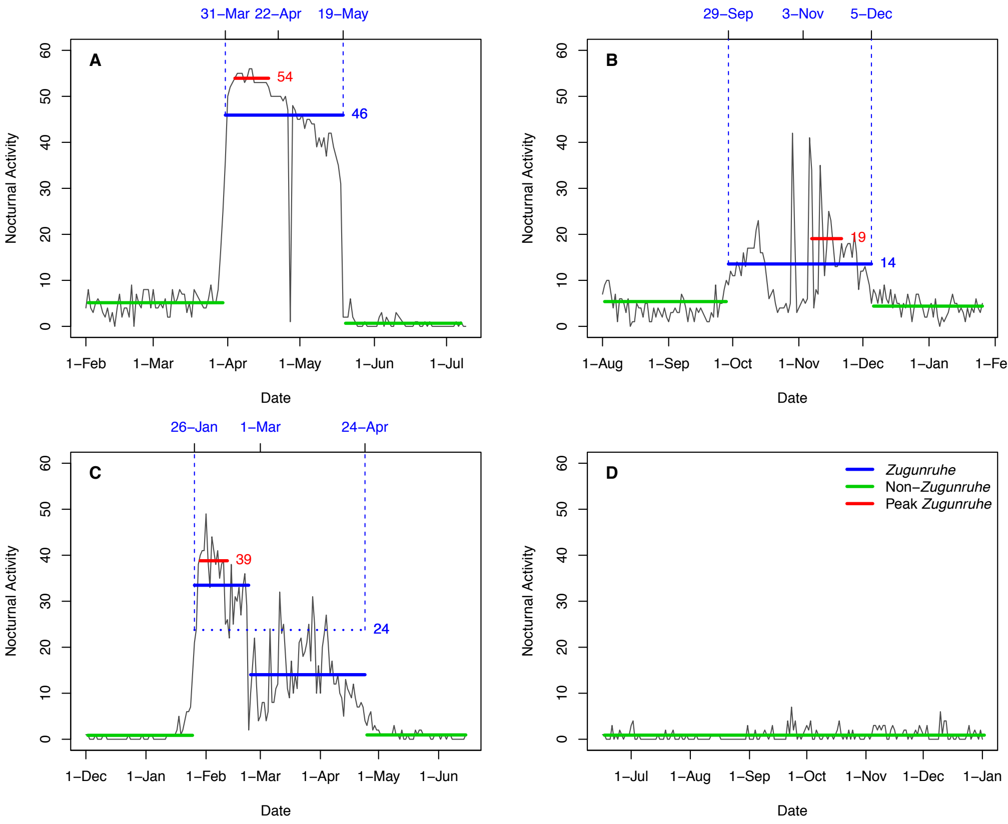


Figure A1. Example data analysed with changepoint analysis. The solid black line shows an individual bird’s pattern of nocturnal activity, quantified as the number of active ten-minute periods in a night. The coloured lines show the result of the analysis: solid blue lines show elevated time segments classified as *Zugunruhe*, and solid green lines are those not classified as *Zugunruhe.* Blue dates on top of each figure show the onset, mean, and end of the *Zugunruhe* time segments. The solid red line shows the 15-day period with the highest level of activity. When changepoint analysis identified more than one elevated *Zugunruhe* segment but the segments were adjacent (see **C**), mean *Zugunruhe* intensity was the mean activity level across all elevated segments (blue dotted line). (**A**) Spring data from a Siberian stonechat. (**B**) Autumn data from an Austrian stonechat. (**C**)

Spring data from an Irish stonechat. (**D**) Autumn data from an Irish stonechat, an individual that did not exhibit *Zugunruhe* for that season.

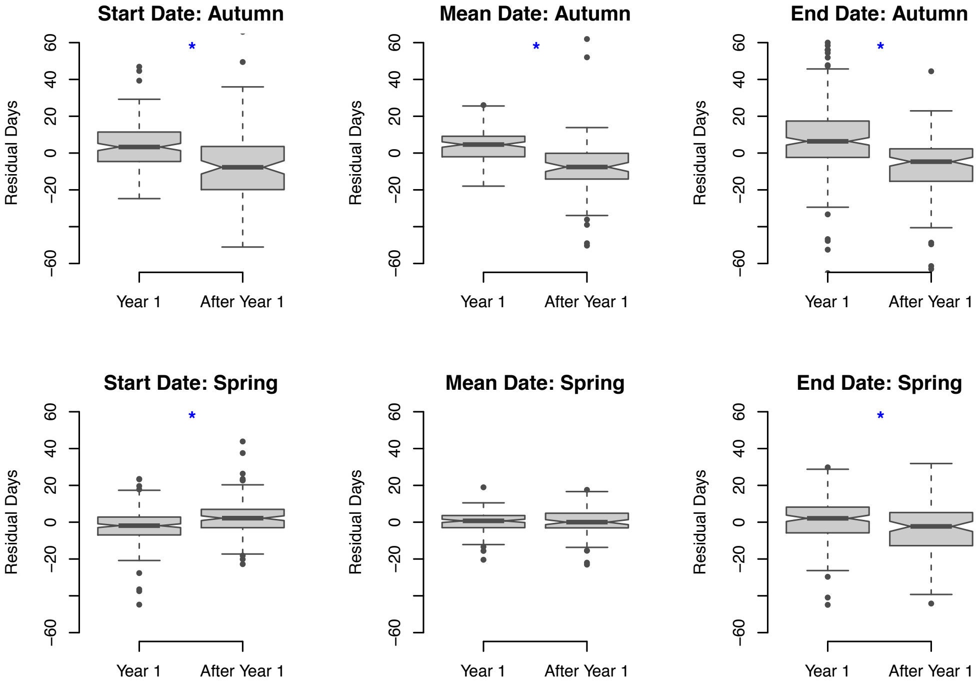


Figure A2. Age effects on timing of *Zugunruhe*. Boxplots show residuals from models on the timing of onset, mean, and end of *Zugunruhe* plotted against bird age group (first year or older) for all populations combined. Top row: autumn migration period; bottom row: spring migration period. A blue asterisk indicates significant differences of first year compared to older birds. Y-axes are standardized and some outliers are cut off in order to better visualize differences.

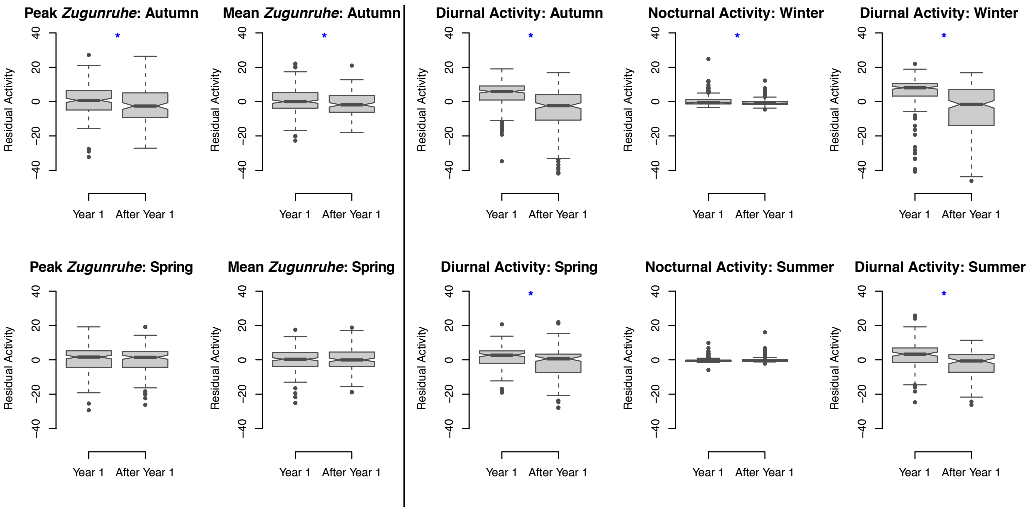


Figure A3. Age effects on diurnal and nocturnal activity levels. Boxplots show residuals from models on activity levels plotted against age group (first year or older). Diurnal activity is shown for all four seasons. Nocturnal activity is shown for all birds in summer and winter, but during migration seasons, only for birds that are identified as migrants using changepoint analysis. Left panel: data on two measures of *Zugunruhe* level (peak and mean) for autumn (top) and spring (bottom). Right panel: activity data for all birds during autumn and spring (diurnal only), and during winter and summer (diurnal and nocturnal). A blue asterisk indicates significant differences between the age groups.

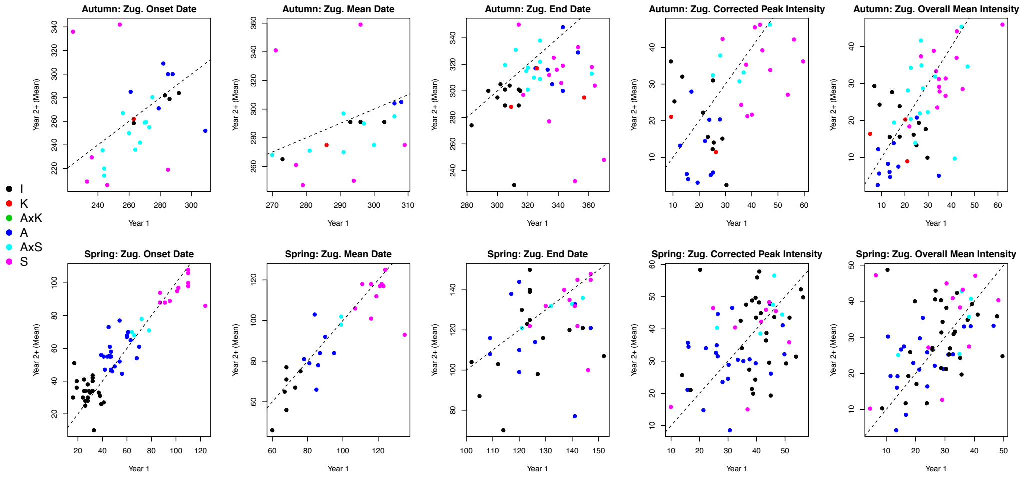


Figure A4. Relationship of *Zugunruhe* metrics during a bird's first year with those of later years, stratified by population. The figure shows the value of a given *Zugunruhe* metric in year 1 of a bird's life (x-axis) and the mean of all subsequent values of this metric in later years of its life (y-axis). Top panel: autumn, bottom panel: spring. Colour coding indicates the different populations. The dotted line is the identity line. Spring onset and mean date show the strongest relationship, but one that is driven entirely by inter-population differences (see Figure A5). However, sample sizes are small and some populations are not represented because many birds were not tested for successive years, or did not engage in *Zugunruhe* in one or more years.

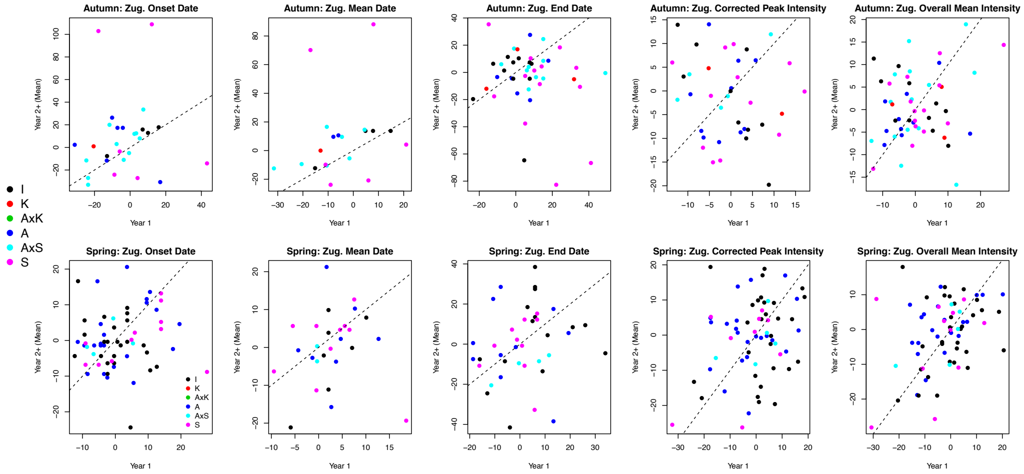


Figure A5. Relationship of *Zugunruhe* metrics during a bird's first year to those of later years (see Figure A4), but standardized to respective population means. After accounting for variation explained by population means, formerly strong relationships (see Figure A4) became non-significant. Here, only three comparisons show significant relationships (not corrected for multiple comparisons): spring corrected peak ($P = 0.028$), spring overall mean ($P = 0.003$), and fall overall mean ($P = 0.049$). Data plotted as in Figure A4.

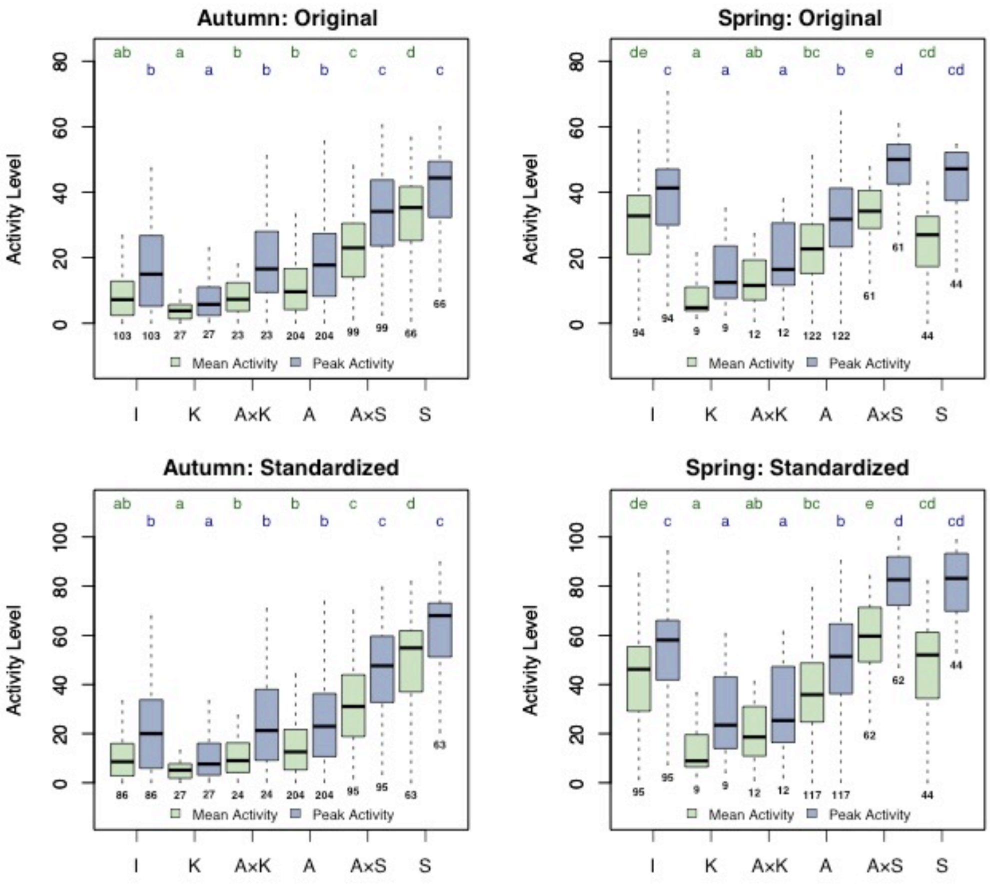


Figure A6. Nocturnal activity levels during the autumn and spring migration seasons, comparing mean and peak activity, and visualising the effects of accounting for night length. “Mean activity” is the average nocturnal activity level of a bird during the most active 60-day period for its population. “Peak activity” is the average nocturnal activity level of a bird during its most active 15-day window of the 60-day period. Top row shows boxplots of the raw (original) data; bottom row shows the result after representing activity as a proportion of night length. In the bottom row, a value of 100 indicates a bird was active for the entire night. Letters shown at the top of plots indicate significant pairwise differences: groups that do not share a letter are significantly different. Most results are similar between the top and bottom rows; the notable exception is that Siberian stonechats, and to a lesser extent Austrian × Siberian stonechats, show a higher peak activity level when expressed as a proportion of night length. This is because Siberian stonechats begin *Zugunruhe* relatively late in spring when nights are shorter than during their autumn migration. Hence, as a proportion of night length, Siberian birds are almost continuously active during spring.

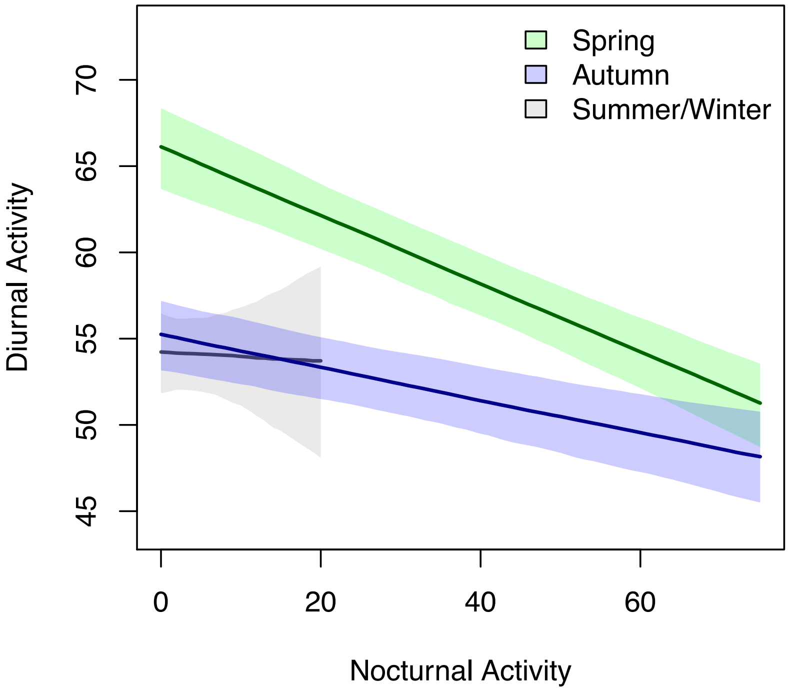


Figure A7. Daily association between nocturnal and diurnal activity during spring and autumn *Zugunruhe* periods and during summer and winter (combined). Plotted are model predictions and bootstrap 95% confidence intervals calculated with the *bootMer* function in the R package *lme4* (Bates et al. 2015). Nocturnal activity covaried negatively with diurnal activity during spring and autumn, but not in summer and winter. For summer and winter, there was a significant effect of sex on diurnal activity; predictions shown are for males only.

B

Supplementary material for chapter 5

Table S1. Representative parameterizations of the simulation model, including the best fit parameters.

	Disorientation probability	Disoriented flight directionality	Disorientation distance (σ)	Stabilization time [min]	Density increase factor
Model 1 (best fit)	High (a=0.95)	Weak (κ=0.1)	1500	34	19
Model 2	High (a=0.95)	Moderate (κ=0.2)	1500	51	42
Model 3	High (a=0.95)	None (κ=0)	1500	24	8.0
Model 4	Low (a=0.5)	Moderate (κ=0.2)	1500	6.5	3.0
Model 5	Low (a=0.5)	Weak (κ=0.1)	1500	6.7	2.3

Stabilization time is defined as the time required to reach 95% of the steady state peak density at the lights, for a migratory ground speed of 10 m/s. Density increase factor is a multiplicative factor relative to the baseline migration density ρ.

Table S2. Ranking of parameterizations of the migratory flow model (see Equation 2 for parameter definitions).

Rank	a	σ	κ	Explained variance
1	0.95	1500	0.1	0.513
2	0.95	1750	0.1	0.511
3	0.98	1250	0.1	0.510
4	0.95	1250	0.1	0.506
5	0.95	2000	0.1	0.506
6	0.98	1500	0.1	0.505
7	0.98	1000	0.1	0.502
8	0.98	1750	0.1	0.497
9	0.98	2000	0.1	0.489
10	0.95	1000	0.1	0.484
11	0.85	1250	0.2	0.480
12	0.85	1500	0.2	0.478
13	0.85	1750	0.2	0.473
14	0.85	1000	0.2	0.470
15	0.75	2000	0.3	0.469
16	0.85	2000	0.2	0.467
17	0.75	1750	0.3	0.466
18	0.75	1500	0.3	0.463
19	0.98	750	0.1	0.461
20	0.75	1250	0.3	0.457
21	0.98	500	0.2	0.449
22	0.65	2000	0.4	0.448
23	0.75	1000	0.3	0.443
24	0.65	1750	0.4	0.443
25	0.95	750	0.2	0.439
26	0.65	1500	0.4	0.436
27	0.95	750	0.1	0.435
28	0.75	750	0.4	0.434
29	0.65	1000	0.5	0.434
30	0.85	750	0.2	0.433
31	0.95	500	0.2	0.432
32	0.75	2000	0.2	0.431
33	0.55	1500	0.7	0.431
34	0.65	1250	0.5	0.430
35	0.55	1250	0.7	0.430
36	0.75	500	0.5	0.430
37	0.55	1750	0.7	0.429
38	0.85	2000	0.1	0.429
39	0.55	2000	0.6	0.429
40	0.95	250	0.6	0.429
41	0.85	1750	0.1	0.427
42	0.65	750	0.6	0.427
43	0.55	2000	0.7	0.427
44	0.85	250	0.8	0.426
45	0.55	1750	0.6	0.425

46	0.55	1000	0.8	0.425
47	0.65	1250	0.4	0.425
48	0.65	500	0.7	0.425
49	0.75	1750	0.2	0.425
50	0.85	500	0.4	0.424
51	0.98	250	0.5	0.424
52	0.55	1000	0.7	0.423
53	0.55	750	0.8	0.423
54	0.85	500	0.3	0.421
55	0.65	1500	0.5	0.421
56	0.98	250	0.6	0.421
57	0.85	1500	0.1	0.420
58	0.55	1500	0.6	0.420
59	0.85	750	0.3	0.419
60	0.65	500	0.8	0.419
61	0.65	750	0.5	0.418
62	0.85	250	0.7	0.417
63	0.75	1500	0.2	0.415
64	0.98	1250	0	0.413
65	0.95	500	0.3	0.413
66	0.98	1500	0	0.412
67	0.95	250	0.5	0.412
68	0.65	1750	0.5	0.412
69	0.55	1250	0.6	0.411
70	0.75	750	0.3	0.410
71	0.55	1250	0.8	0.409
72	0.65	1000	0.4	0.407
73	0.85	1250	0.1	0.404
74	0.65	2000	0.5	0.404
75	0.98	1750	0	0.403
76	0.65	500	0.6	0.401
77	0.55	750	0.7	0.401
78	0.75	500	0.4	0.400
79	0.98	1000	0	0.399
80	0.75	1250	0.2	0.399
81	0.75	500	0.6	0.395
82	0.55	1000	0.6	0.395
83	0.95	250	0.7	0.394
84	0.45	2000	0.8	0.392
85	0.55	2000	0.5	0.391
86	0.75	1000	0.4	0.391
87	0.75	250	0.8	0.389
88	0.65	2000	0.3	0.389
89	0.85	250	0.6	0.388
90	0.55	1500	0.8	0.388
91	0.98	2000	0	0.388
92	0.45	1750	0.8	0.387
93	0.98	250	0.4	0.387
94	0.55	1750	0.5	0.386
95	0.65	1750	0.3	0.384
96	0.65	1000	0.6	0.381
97	0.55	1500	0.5	0.379
98	0.45	1500	0.8	0.379
99	0.95	1500	0	0.378
100	0.95	1250	0	0.378
101	0.65	1500	0.3	0.377
102	0.55	500	0.8	0.377
103	0.85	1000	0.1	0.377
104	0.98	500	0.1	0.375
105	0.75	1000	0.2	0.374
106	0.65	750	0.4	0.374
107	0.95	1750	0	0.370
108	0.98	750	0.2	0.369
109	0.55	1250	0.5	0.369
110	0.95	250	0.4	0.369
111	0.45	1250	0.8	0.368
112	0.55	1750	0.8	0.368
113	0.98	750	0	0.366
114	0.95	1000	0	0.366
115	0.55	750	0.6	0.366
116	0.65	1250	0.3	0.365
117	0.65	750	0.7	0.365
118	0.65	500	0.5	0.361
119	0.45	2000	0.7	0.358
120	0.75	250	0.7	0.358
121	0.95	2000	0	0.358
122	0.85	500	0.2	0.355
123	0.45	1750	0.7	0.353
124	0.95	500	0.1	0.353
125	0.55	1000	0.5	0.352
126	0.45	1000	0.8	0.352
127	0.98	500	0.3	0.350
128	0.85	250	0.5	0.350
129	0.55	2000	0.8	0.350

130	0.65	1000	0.3	0.347
131	0.45	1500	0.7	0.346
132	0.55	500	0.7	0.345
133	0.75	500	0.3	0.343
134	0.98	250	0.3	0.340
135	0.95	750	0	0.338
136	0.75	750	0.2	0.338
137	0.98	250	0.7	0.337
138	0.85	750	0.1	0.337
139	0.55	2000	0.4	0.336
140	0.45	1250	0.7	0.335
141	0.55	1750	0.4	0.332
142	0.55	1500	0.4	0.327
143	0.45	750	0.8	0.326
144	0.55	750	0.5	0.324
145	0.75	250	0.6	0.322
146	0.95	250	0.3	0.322
147	0.45	1000	0.7	0.320
148	0.45	2000	0.6	0.320
149	0.65	250	0.8	0.319
150	0.75	750	0.5	0.319
151	0.55	1250	0.4	0.318
152	0.45	1750	0.6	0.315
153	0.65	750	0.3	0.315
154	0.65	500	0.4	0.314
155	0.98	500	0	0.312
156	0.55	500	0.6	0.311
157	0.45	1500	0.6	0.309
158	0.85	250	0.4	0.307
159	0.75	1250	0.4	0.305
160	0.65	1250	0.6	0.304
161	0.55	1000	0.4	0.304
162	0.75	1750	0.1	0.304
163	0.75	2000	0.1	0.303
164	0.65	2000	0.2	0.303
165	0.65	1750	0.2	0.302
166	0.75	1500	0.1	0.301
167	0.45	1250	0.6	0.300
168	0.65	1500	0.2	0.298
169	0.45	750	0.7	0.297
170	0.75	1250	0.1	0.295
171	0.65	1250	0.2	0.292
172	0.95	500	0	0.291
173	0.98	250	0.2	0.291
174	0.65	250	0.7	0.291
175	0.45	1000	0.6	0.287
176	0.75	250	0.5	0.285
177	0.75	1000	0.1	0.282
178	0.85	500	0.1	0.282
179	0.45	500	0.8	0.281
180	0.55	750	0.4	0.280
181	0.75	500	0.2	0.279
182	0.45	2000	0.5	0.279
183	0.65	1000	0.2	0.279
184	0.85	1250	0	0.278
185	0.95	250	0.2	0.276
186	0.85	1500	0	0.276
187	0.55	2000	0.3	0.276
188	0.45	1750	0.5	0.276
189	0.55	500	0.5	0.275
190	0.55	1750	0.3	0.274
191	0.85	1000	0	0.273
192	0.35	2000	0.8	0.272
193	0.55	1500	0.3	0.271
194	0.45	1500	0.5	0.271
195	0.95	250	0.8	0.271
196	0.85	1750	0	0.271
197	0.35	1750	0.8	0.269
198	0.65	500	0.3	0.267
199	0.45	750	0.6	0.267
200	0.55	1250	0.3	0.266
201	0.85	250	0.3	0.265
202	0.45	1250	0.5	0.264
203	0.35	1500	0.8	0.264
204	0.85	2000	0	0.263
205	0.65	250	0.6	0.262
206	0.85	750	0	0.259
207	0.75	750	0.1	0.259
208	0.45	500	0.7	0.257
209	0.35	1250	0.8	0.256
210	0.65	750	0.2	0.256
211	0.55	1000	0.3	0.256
212	0.55	250	0.8	0.254
213	0.45	1000	0.5	0.253

214	0.75	250	0.4	0.252
215	0.85	1000	0.3	0.250
216	0.98	250	0.1	0.248
217	0.35	2000	0.7	0.247
218	0.35	1000	0.8	0.245
219	0.35	1750	0.7	0.244
220	0.95	1000	0.2	0.242
221	0.55	500	0.4	0.240
222	0.35	1500	0.7	0.240
223	0.45	2000	0.4	0.239
224	0.85	500	0.5	0.238
225	0.55	750	0.3	0.238
226	0.45	1750	0.4	0.237
227	0.45	750	0.5	0.237
228	0.95	250	0.1	0.236
229	0.45	1500	0.4	0.234
230	0.75	500	0.7	0.234
231	0.65	250	0.5	0.234
232	0.35	1250	0.7	0.234
233	0.85	500	0	0.233
234	0.55	250	0.7	0.233
235	0.45	500	0.6	0.232
236	0.85	250	0.2	0.232
237	0.45	1250	0.4	0.229
238	0.35	750	0.8	0.229
239	0.75	500	0.1	0.225
240	0.65	1500	0.6	0.224
241	0.35	1000	0.7	0.224
242	0.65	1500	0.1	0.224
243	0.65	1750	0.1	0.223
244	0.35	2000	0.6	0.222
245	0.65	1250	0.1	0.222
246	0.65	500	0.2	0.222
247	0.98	250	0	0.221
248	0.45	1000	0.4	0.221
249	0.65	2000	0.1	0.221
250	0.75	250	0.3	0.221
251	0.55	1750	0.2	0.220
252	0.55	2000	0.2	0.220
253	0.35	1750	0.6	0.220
254	0.55	1500	0.2	0.220
255	0.55	1250	0.2	0.217
256	0.35	1500	0.6	0.216
257	0.65	1000	0.1	0.216
258	0.55	250	0.6	0.212
259	0.35	1250	0.6	0.212
260	0.95	250	0	0.211
261	0.75	1250	0	0.211
262	0.55	1000	0.2	0.211
263	0.75	1500	0.4	0.211
264	0.75	1000	0	0.210
265	0.35	750	0.7	0.210
266	0.45	500	0.5	0.209
267	0.75	1500	0	0.208
268	0.45	750	0.4	0.208
269	0.55	500	0.3	0.208
270	0.65	250	0.4	0.207
271	0.35	500	0.8	0.204
272	0.75	750	0	0.204
273	0.35	1000	0.6	0.204
274	0.65	750	0.1	0.204
275	0.75	1750	0	0.204
276	0.45	2000	0.3	0.202
277	0.85	250	0.1	0.202
278	0.45	1750	0.3	0.201
279	0.45	250	0.8	0.200
280	0.45	1500	0.3	0.200
281	0.55	750	0.2	0.198
282	0.75	2000	0	0.198
283	0.35	2000	0.5	0.198
284	0.45	1250	0.3	0.196
285	0.35	1750	0.5	0.196
286	0.75	250	0.2	0.194
287	0.35	1500	0.5	0.194
288	0.35	750	0.6	0.192
289	0.55	250	0.5	0.192
290	0.45	1000	0.3	0.191
291	0.35	1250	0.5	0.190
292	0.75	500	0	0.190
293	0.35	500	0.7	0.189
294	0.45	500	0.4	0.186
295	0.45	250	0.7	0.186
296	0.65	250	0.3	0.184
297	0.35	1000	0.5	0.184

298	0.25	2000	0.8	0.184
299	0.65	500	0.1	0.183
300	0.85	250	0	0.183
301	0.45	750	0.3	0.182
302	0.25	1750	0.8	0.182
303	0.65	750	0.8	0.180
304	0.25	1500	0.8	0.179
305	0.55	500	0.2	0.178
306	0.25	1250	0.8	0.175
307	0.35	750	0.5	0.175
308	0.35	2000	0.4	0.175
309	0.35	500	0.6	0.174
310	0.55	1500	0.1	0.174
311	0.55	1250	0.1	0.174
312	0.35	1750	0.4	0.174
313	0.75	250	0.1	0.173
314	0.55	250	0.4	0.173
315	0.55	1750	0.1	0.173
316	0.35	1500	0.4	0.172
317	0.45	250	0.6	0.172
318	0.55	2000	0.1	0.171
319	0.55	1000	0.1	0.171
320	0.25	2000	0.7	0.170
321	0.25	1000	0.8	0.170
322	0.35	1250	0.4	0.170
323	0.65	1000	0	0.169
324	0.65	1250	0	0.169
325	0.25	1750	0.7	0.169
326	0.45	1750	0.2	0.168
327	0.45	1500	0.2	0.168
328	0.45	2000	0.2	0.168
329	0.45	1250	0.2	0.167
330	0.25	1500	0.7	0.166
331	0.65	1500	0	0.166
332	0.65	750	0	0.166
333	0.65	1000	0.7	0.166
334	0.35	1000	0.4	0.165
335	0.45	500	0.3	0.165
336	0.55	750	0.1	0.164
337	0.65	250	0.2	0.164
338	0.45	1000	0.2	0.164
339	0.25	1250	0.7	0.163

340	0.65	1750	0	0.162
341	0.25	750	0.8	0.162
342	0.35	500	0.5	0.160
343	0.25	1000	0.7	0.159
344	0.75	250	0	0.159
345	0.65	2000	0	0.158
346	0.35	750	0.4	0.158
347	0.45	250	0.5	0.158
348	0.65	500	0	0.158
349	0.35	250	0.8	0.158
350	0.45	750	0.2	0.158
351	0.25	2000	0.6	0.157
352	0.25	1750	0.6	0.156
353	0.55	250	0.3	0.155
354	0.25	1500	0.6	0.154
355	0.35	2000	0.3	0.153
356	0.35	1750	0.3	0.153
357	0.35	1500	0.3	0.152
358	0.65	1750	0.6	0.152
359	0.55	500	0.1	0.152
360	0.25	750	0.7	0.152
361	0.25	1250	0.6	0.152
362	0.35	1250	0.3	0.151
363	0.65	250	0.1	0.150
364	0.25	500	0.8	0.149
365	0.35	250	0.7	0.149
366	0.25	1000	0.6	0.148
367	0.35	1000	0.3	0.148
368	0.35	500	0.4	0.146
369	0.45	500	0.2	0.146
370	0.45	250	0.4	0.145
371	0.25	2000	0.5	0.144
372	0.25	1750	0.5	0.143
373	0.35	750	0.3	0.143
374	0.25	1500	0.5	0.142
375	0.25	750	0.6	0.142
376	0.55	250	0.2	0.142
377	0.45	1250	0.1	0.141
378	0.25	500	0.7	0.141
379	0.55	1000	0	0.141
380	0.45	1500	0.1	0.141
381	0.25	1250	0.5	0.140

382	0.55	1250	0	0.140
383	0.35	250	0.6	0.140
384	0.45	1000	0.1	0.140
385	0.45	1750	0.1	0.139
386	0.55	750	0	0.139
387	0.65	250	0	0.139
388	0.45	2000	0.1	0.138
389	0.55	1500	0	0.138
390	0.25	1000	0.5	0.137
391	0.45	750	0.1	0.136
392	0.55	1750	0	0.135
393	0.55	500	0	0.135
394	0.35	1500	0.2	0.134
395	0.35	1750	0.2	0.134
396	0.35	500	0.3	0.133
397	0.35	2000	0.2	0.133
398	0.45	250	0.3	0.133
399	0.35	1250	0.2	0.133
400	0.25	500	0.6	0.133
401	0.55	2000	0	0.132
402	0.25	750	0.5	0.132
403	0.25	2000	0.4	0.132
404	0.35	1000	0.2	0.131
405	0.25	1750	0.4	0.131
406	0.35	250	0.5	0.131
407	0.55	250	0.1	0.131
408	0.25	1500	0.4	0.131
409	0.25	1250	0.4	0.129
410	0.45	500	0.1	0.129
411	0.35	750	0.2	0.128
412	0.25	1000	0.4	0.127
413	0.25	250	0.8	0.125
414	0.25	500	0.5	0.125
415	0.75	1750	0.4	0.123
416	0.25	750	0.4	0.123
417	0.45	250	0.2	0.123
418	0.35	250	0.4	0.123
419	0.55	250	0	0.123
420	0.35	500	0.2	0.121
421	0.45	1000	0	0.120
422	0.25	2000	0.3	0.120
423	0.25	1750	0.3	0.120
424	0.25	250	0.7	0.120
425	0.25	1500	0.3	0.119
426	0.45	750	0	0.119
427	0.45	1250	0	0.119
428	0.25	1250	0.3	0.119
429	0.45	1500	0	0.118
430	0.25	1000	0.3	0.117
431	0.35	1250	0.1	0.117
432	0.25	500	0.4	0.117
433	0.35	1500	0.1	0.117
434	0.35	1000	0.1	0.117
435	0.45	500	0	0.117
436	0.35	1750	0.1	0.116
437	0.45	1750	0	0.116
438	0.35	2000	0.1	0.116
439	0.45	250	0.1	0.115
440	0.35	250	0.3	0.115
441	0.35	750	0.1	0.115
442	0.25	250	0.6	0.115
443	0.25	750	0.3	0.114
444	0.45	2000	0	0.114
445	0.98	250	0.8	0.112
446	0.35	500	0.1	0.111
447	0.25	500	0.3	0.110
448	0.25	250	0.5	0.109
449	0.45	250	0	0.109
450	0.25	1500	0.2	0.109
451	0.25	1750	0.2	0.109
452	0.25	1250	0.2	0.109
453	0.25	2000	0.2	0.109
454	0.25	1000	0.2	0.108
455	0.35	250	0.2	0.107
456	0.25	750	0.2	0.106
457	0.35	1000	0	0.105
458	0.25	250	0.4	0.104
459	0.35	750	0	0.104
460	0.35	1250	0	0.104
461	0.35	1500	0	0.103
462	0.25	500	0.2	0.103
463	0.35	500	0	0.103
464	0.35	250	0.1	0.102
465	0.35	1750	0	0.102

466	0.35	2000	0	0.100
467	0.25	1250	0.1	0.100
468	0.25	1000	0.1	0.100
469	0.25	1500	0.1	0.100
470	0.25	250	0.3	0.100
471	0.25	1750	0.1	0.099
472	0.25	2000	0.1	0.099
473	0.25	750	0.1	0.099
474	0.35	250	0	0.098
475	0.25	500	0.1	0.097
476	0.25	250	0.2	0.095
477	0.25	1000	0	0.093
478	0.25	750	0	0.092
479	0.25	1250	0	0.092
480	0.25	500	0	0.092
481	0.25	250	0.1	0.092
482	0.25	1500	0	0.091
483	0.25	1750	0	0.091
484	0.65	2000	0.6	0.090
485	0.25	2000	0	0.090
486	0.25	250	0	0.089
487	0.75	2000	0.4	0.048
488	0.95	500	0.4	0.000
489	0.75	1000	0.5	-0.009
490	0.85	750	0.4	-0.017
491	0.85	1250	0.3	-0.024
492	0.98	1000	0.2	-0.036
493	0.95	1250	0.2	-0.080
494	0.65	1250	0.7	-0.095
495	0.75	750	0.6	-0.121
496	0.75	500	0.8	-0.148
497	0.85	1500	0.3	-0.330
498	0.65	1000	0.8	-0.342
499	0.95	750	0.3	-0.343
500	0.65	1500	0.7	-0.363
501	0.85	500	0.6	-0.375
502	0.98	500	0.4	-0.404
503	0.95	1500	0.2	-0.413
504	0.75	1250	0.5	-0.476
505	0.65	1750	0.7	-0.613
506	0.98	1250	0.2	-0.613
507	0.85	1750	0.3	-0.622
508	0.95	1750	0.2	-0.688
509	0.65	2000	0.7	-0.834
510	0.95	2000	0.2	-0.877
511	0.85	2000	0.3	-0.884
512	0.75	1500	0.5	-0.988
513	0.65	1250	0.8	-1.012
514	0.98	750	0.3	-1.058
515	0.98	1500	0.2	-1.152
516	0.85	1000	0.4	-1.170
517	0.75	750	0.7	-1.234
518	0.75	1000	0.6	-1.246
519	0.95	500	0.5	-1.480
520	0.75	1750	0.5	-1.485
521	0.98	1750	0.2	-1.544
522	0.85	750	0.5	-1.656
523	0.65	1500	0.8	-1.721
524	0.98	2000	0.2	-1.774
525	0.85	500	0.7	-1.849
526	0.75	2000	0.5	-1.939
527	0.95	1000	0.3	-2.342
528	0.65	1750	0.8	-2.405
529	0.75	1250	0.6	-2.866
530	0.85	1250	0.4	-2.874
531	0.98	500	0.5	-2.956
532	0.65	2000	0.8	-3.036
533	0.75	750	0.8	-3.627
534	0.95	750	0.4	-3.947
535	0.75	1000	0.7	-4.327
536	0.98	1000	0.3	-4.512
537	0.75	1500	0.6	-4.726
538	0.85	1500	0.4	-4.827
539	0.85	500	0.8	-4.907
540	0.95	1250	0.3	-5.230
541	0.95	500	0.6	-5.441
542	0.85	1000	0.5	-6.224
543	0.85	750	0.6	-6.239
544	0.75	1750	0.6	-6.633
545	0.85	1750	0.4	-6.778
546	0.98	750	0.4	-7.255
547	0.95	1500	0.3	-8.295
548	0.75	2000	0.6	-8.465
549	0.85	2000	0.4	-8.575

550	0.75	1250	0.7	-8.934
551	0.98	1250	0.3	-9.110
552	0.98	500	0.6	-9.677
553	0.95	1750	0.3	-11.025
554	0.75	1000	0.8	-11.236
555	0.85	1250	0.5	-13.151
556	0.95	2000	0.3	-13.198
557	0.95	1000	0.4	-13.471
558	0.98	1500	0.3	-13.605
559	0.95	500	0.7	-14.428
560	0.75	1500	0.7	-14.517
561	0.95	750	0.5	-15.404
562	0.85	750	0.7	-17.141
563	0.98	1750	0.3	-17.310
564	0.98	2000	0.3	-19.997
565	0.75	1750	0.7	-20.494
566	0.85	1000	0.6	-20.537
567	0.85	1500	0.5	-21.369
568	0.98	1000	0.4	-22.608
569	0.75	1250	0.8	-22.733
570	0.98	500	0.7	-24.601
571	0.98	750	0.5	-26.141
572	0.75	2000	0.7	-26.430
573	0.95	1250	0.4	-26.878
574	0.85	1750	0.5	-29.869
575	0.95	500	0.8	-32.206
576	0.75	1500	0.8	-37.081
577	0.85	2000	0.5	-37.933
578	0.85	750	0.8	-39.875
579	0.95	1500	0.4	-41.054
580	0.98	1250	0.4	-42.277
581	0.85	1250	0.6	-42.543
582	0.95	750	0.6	-44.196
583	0.95	1000	0.5	-47.127
584	0.75	1750	0.8	-52.964
585	0.98	500	0.8	-53.090
586	0.95	1750	0.4	-53.987
587	0.85	1000	0.7	-54.590
588	0.98	1500	0.4	-61.498
589	0.95	2000	0.4	-64.603
590	0.85	1500	0.6	-68.887
591	0.75	2000	0.8	-69.060
592	0.98	750	0.6	-70.780
593	0.98	1000	0.5	-73.467
594	0.98	1750	0.4	-77.936
595	0.95	1250	0.5	-89.209
596	0.98	2000	0.4	-90.429
597	0.85	1750	0.6	-96.345
598	0.95	750	0.7	-103.050
599	0.85	1250	0.7	-111.371
600	0.85	2000	0.6	-122.358
601	0.85	1000	0.8	-123.388
602	0.95	1000	0.6	-124.318
603	0.98	1250	0.5	-130.153
604	0.95	1500	0.5	-132.428
605	0.98	750	0.7	-155.340
606	0.95	1750	0.5	-171.749
607	0.85	1500	0.7	-178.203
608	0.98	1000	0.6	-180.789
609	0.98	1500	0.5	-184.610
610	0.95	750	0.8	-203.001
611	0.95	2000	0.5	-203.649
612	0.95	1250	0.6	-222.692
613	0.98	1750	0.5	-231.989
614	0.85	1250	0.8	-244.790
615	0.85	1750	0.7	-246.927
616	0.95	1000	0.7	-264.610
617	0.98	2000	0.5	-267.853
618	0.98	750	0.8	-288.022
619	0.98	1250	0.6	-303.941
620	0.85	2000	0.7	-310.405
621	0.95	1500	0.6	-320.917
622	0.98	1000	0.7	-361.090
623	0.85	1500	0.8	-383.141
624	0.95	1750	0.6	-410.141
625	0.98	1500	0.6	-422.130
626	0.95	1250	0.7	-450.091
627	0.95	1000	0.8	-477.357
628	0.95	2000	0.6	-480.191
629	0.85	1750	0.8	-522.227
630	0.98	1750	0.6	-526.678
631	0.98	1250	0.7	-582.412
632	0.98	2000	0.6	-602.974
633	0.98	1000	0.8	-617.452

634	0.95	1500	0.7	-634.218
635	0.85	2000	0.8	-645.770
636	0.95	1250	0.8	-780.255
637	0.98	1500	0.7	-799.078
638	0.95	1750	0.7	-802.104
639	0.95	2000	0.7	-927.590
640	0.98	1250	0.8	-969.468
641	0.98	1750	0.7	-992.204
642	0.95	1500	0.8	-1084.839
643	0.98	2000	0.7	-1124.301
644	0.98	1500	0.8	-1323.739
645	0.95	1750	0.8	-1361.783
646	0.95	2000	0.8	-1555.051
647	0.98	1750	0.8	-1636.593
648	0.98	2000	0.8	-1833.526

Table S3. Local climatic data from KNYC, Central Park, for 11-12 September.

Year	Time (EDT)	Temp.	Dew Point	Humidity	Pressure	Visibility	Wind Dir	Wind Speed	Precip	Conditions
2008	7:51 PM	17.78	12.22	54%	1026	16.09	SE	9.33	N/A	Clear
	8:51 PM	18.28	12.22	63%	1027	16.09	SSE	Calm	N/A	Clear
	9:51 PM	18.28	12.22	63%	1026	16.09	Variable	7.40	N/A	Clear
	10:51 PM	18.89	12.22	68%	1026	16.09	Variable	7.40	N/A	Clear
	11:51 PM	18.28	12.78	68%	1026	16.09	Variable	9.33	N/A	Scattered Clouds
	12:51 AM	18.28	12.22	68%	1025	16.09	Variable	11.10	N/A	Overcast
	1:51 AM	18.89	12.22	73%	1025	16.09	SSE	5.63	N/A	Scattered Clouds
	2:51 AM	18.28	12.78	70%	1024	16.09	Variable	7.40	N/A	Scattered Clouds
	3:51 AM	18.89	12.22	73%	1024	16.09	Variable	7.40	N/A	Clear
	4:51 AM	18.89	12.78	73%	1023	16.09	Variable	5.63	N/A	Clear
	5:51 AM	18.89	12.22	73%	1024	16.09	Variable	Calm	N/A	Clear
2010	7:51 PM	20.61	11.11	54%	1015	16.09	SE	13.04	N/A	Clear
	8:51 PM	19.39	12.22	63%	1016	16.09	SSE	13.04	N/A	Clear
	9:51 PM	20.00	12.78	63%	1017	16.09	Variable	11.10	N/A	Clear
	10:51 PM	19.39	13.28	68%	1017	16.09	Variable	9.33	N/A	Clear
	11:51 PM	19.39	13.28	68%	1018	16.09	Variable	5.63	N/A	Scattered Clouds
	12:51 AM	19.39	13.28	68%	1018	16.09	Variable	9.33	N/A	Overcast
	1:51 AM	18.28	13.28	73%	1017	16.09	SSE	13.04	N/A	Scattered Clouds
	2:51 AM	18.89	13.28	70%	1017	16.09	Variable	5.63	N/A	Scattered Clouds
	3:51 AM	18.28	13.28	73%	1016	16.09	Variable	9.33	N/A	Clear
	4:51 AM	18.28	13.28	73%	1017	16.09	Variable	11.10	N/A	Clear
	5:51 AM	17.78	12.78	73%	1017	16.09	Variable	9.33	N/A	Clear
2012	7:51 PM	18.89	6.72	55%	1025	16.09	Variable	5.63	N/A	Mostly Cloudy
	8:51 PM	18.89	6.11	59%	1025	16.09	North	Calm	N/A	Clear
	9:51 PM	18.28	8.28	61%	1025	16.09	SW	Calm	N/A	Clear
	10:51 PM	18.28	9.39	63%	1025	16.09	Variable	5.63	N/A	Scattered Clouds
	11:51 PM	18.28	8.89	67%	1025	16.09	Variable	5.63	N/A	Clear
	12:51 AM	18.28	8.28	67%	1026	16.09	SW	7.40	N/A	Clear
	1:51 AM	17.78	10.00	65%	1026	16.09	SW	Calm	N/A	Clear
	2:51 AM	17.22	8.89	69%	1026	16.09	Variable	Calm	N/A	Clear
	3:51 AM	17.22	9.39	69%	1026	16.09	Variable	Calm	N/A	Mostly Cloudy

	4:51 AM	16.11	10.00	71%	1027	16.09	SW	5.63	N/A	Partly Cloudy
	5:51 AM	15.61	11.11	74%	1011	16.09	Variable	Calm	N/A	Clear
2013	7:51 PM	31.11	21.11	55%	1017	12.87	Variable	5.63	N/A	Mostly Cloudy
	8:51 PM	30.00	21.11	59%	1017	12.87	North	7.24	N/A	Clear
	9:51 PM	29.39	21.11	61%	1016	14.48	SW	11.10	N/A	Clear
	10:51 PM	28.89	21.11	63%	1017	12.87	Variable	7.40	N/A	Scattered Clouds
	11:51 PM	27.78	21.11	67%	1016	12.87	Variable	9.33	N/A	Clear
	12:51 AM	27.78	21.11	67%	1015	12.87	SW	9.33	N/A	Clear
	1:51 AM	27.22	20.00	65%	1014	12.87	SW	9.33	N/A	Clear
	2:51 AM	26.11	20.00	69%	1014	11.27	Variable	7.40	N/A	Clear
	3:51 AM	26.11	20.00	69%	1014	11.27	Variable	5.63	N/A	Mostly Cloudy
	4:51 AM	25.61	20.00	71%	1014	11.27	SW	5.63	N/A	Partly Cloudy
	5:51 AM	25.00	20.00	74%	1014	11.27	Variable	9.33	N/A	Clear
2014	7:51 PM	26.11	19.39	54%	1012	16.09	Calm	5.63	N/A	Scattered Clouds
	8:51 PM	26.11	19.39	57%	1012	16.09	Variable	Calm	N/A	Clear
	9:51 PM	26.11	19.39	57%	1013	16.09	Calm	11.10	N/A	Clear
	10:51 PM	24.39	15.61	57%	1014	16.09	Calm	5.63	N/A	Clear
	11:51 PM	22.22	12.78	66%	1015	16.09	Calm	7.40	N/A	Clear
	12:51 AM	21.11	11.72	71%	1015	16.09	Calm	13.04	N/A	Clear
	1:51 AM	20.00	11.72	73%	1016	16.09	Calm	9.33	N/A	Clear
	2:51 AM	19.39	11.11	78%	1016	16.09	NE	7.40	N/A	Clear
	3:51 AM	18.28	11.11	81%	1018	16.09	Calm	5.63	N/A	Clear
	4:33 AM	17.78	10.61	84%	1017	16.09	Calm	9.33	N/A	Clear
	4:51 AM	17.78	10.61	81%	1018	16.09	West	7.40	N/A	Clear
	5:51 AM	17.22	10.00	37%	0	0.00	Variable	0.00	N/A	Clear
2015	7:51 PM	24.39	14.39	54%	1009	16.09	Calm	Calm	N/A	Scattered Clouds
	8:51 PM	23.89	15.00	57%	1009	16.09	Variable	5.63	N/A	Clear
	9:51 PM	23.89	15.00	57%	1009	16.09	Calm	Calm	N/A	Clear
	10:51 PM	23.89	15.00	57%	1010	16.09	Calm	Calm	N/A	Clear
	11:51 PM	23.28	16.72	66%	1010	16.09	Calm	Calm	N/A	Clear
	12:51 AM	22.78	17.22	71%	1010	16.09	Calm	Calm	N/A	Clear
	1:51 AM	22.22	17.22	73%	1009	16.09	Calm	Calm	N/A	Clear
	2:51 AM	21.72	17.78	78%	1009	16.09	NE	5.63	N/A	Clear

	3:51 AM	21.72	18.28	81%	1009	16.09	Calm	Calm	N/A	Clear
	4:51 AM	21.11	18.28	84%	1009	16.09	Calm	Calm	N/A	Clear
	5:51 AM	21.11	17.78	81%	1010	16.09	West	5.63	N/A	Clear
2016	7:51 PM	24.39	8.89	37%	1019	16.09	Variable	5.63	N/A	Clear
	8:51 PM	23.89	8.89	38%	1020	16.09	Variable	7.40	N/A	Clear
	9:51 PM	22.22	8.28	41%	1020	16.09	Variable	5.63	N/A	Clear
	10:51 PM	21.11	7.78	42%	1021	16.09	Variable	7.40	N/A	Clear
	11:51 PM	20.61	7.78	44%	1021	16.09	NNW	9.33	N/A	Clear
	12:51 AM	20.00	7.78	45%	1022	16.09	Variable	7.40	N/A	Clear
	1:51 AM	19.39	7.78	47%	1022	16.09	Variable	7.40	N/A	Clear
	2:51 AM	18.89	7.78	48%	1022	16.09	ENE	11.10	N/A	Clear
	3:51 AM	18.28	7.22	48%	1022	16.09	ENE	13.04	N/A	Clear
	4:51 AM	16.72	8.28	58%	1023	16.09	East	13.04	N/A	Clear
	5:51 AM	17.22	8.28	56%	1023	16.09	ENE	9.33	N/A	Clear

Table S4. METARS data from KEWR, Newark Liberty International Airport, for 11-12 September. UTC refers to Coordinated Universal Time.

Year	UTC	Full METAR
2008	23:51	18008KT 10SM FEW070 SCT250 20/12 A3031 RMK AO2 SLP263 T02000117 10228 20200 53001
	00:51	19006KT 10SM BKN060 BKN250 19/12 A3031
	01:51	19006KT 10SM BKN060 BKN250 19/12 A3032 RMK AO2 SLP266 T01940122
	02:51	18006KT 10SM SCT055 BKN250 19/12 A3031 RMK AO2 SLP262 T01890117 58000
	03:51	19005KT 10SM BKN060 BKN250 19/12 A3030 RMK AO2 SLP259 T01890117
	04:51	20006KT 10SM BKN060 19/12 A3029 RMK AO2 SLP257 T01890117 402280161
	04:58	19006KT 10SM SCT055 OVC070 19/12 A3027 RMK AO2 SLP250 T01890122 10200 20189 58012
	05:13	19004KT 10SM BKN050 OVC070 19/12 A3026 RMK AO2 SLP245 T01890117
	05:51	20007KT 10SM OVC048 19/12 A3025 RMK AO2 SLP242 T01890117
	06:51	21005KT 10SM OVC044 19/12 A3024 RMK AO2 SLP238 T01890122 56013
	07:51	20005KT 10SM FEW030 OVC042 19/12 A3022 RMK AO2 SLP232 T01890122
2010	23:51	13007KT 10SM FEW070 BKN250 22/12 A2998 RMK AO2 SLP150 T02170122 10278 20211 53010
	00:51	13007KT 10SM BKN250 21/13 A3000 RMK AO2 SLP157 T02110128
	01:51	17005KT 10SM BKN250 20/13 A3002 RMK AO2 SLP166 T02000128
	02:51	17004KT 10SM BKN250 20/13 A3004 RMK AO2 SLP170 T02000133 51020
	03:51	16005KT 10SM FEW035 BKN250 20/13 A3004 RMK AO2 SLP172 T02000133
	04:51	14007KT 10SM BKN035 BKN250 20/14 A3004 RMK AO2 SLP171 T02000144 402780144
	04:58	14007KT 10SM BKN027 BKN037 20/14 A3004 RMK AO2
	05:13	14007KT 10SM SCT027 BKN035 20/14 A3004 RMK AO2
	05:51	14007KT 10SM FEW027 SCT035 19/14 A3004 RMK AO2 SLP171 T01940139 10217 20194 51001
	06:51	13006KT 10SM FEW037 19/14 A3003 RMK AO2 SLP168 T01940139
	07:51	11005KT 10SM FEW037 SCT090 BKN250 19/14 A3000 RMK AO2 SLP159 T01940144
	08:51	11007KT 10SM FEW027 SCT110 BKN250 19/13 A3001 RMK AO2 SLP162 T01890133 55009
	09:51	11004KT 10SM FEW027 BKN110 BKN250 19/13 A3001 RMK AO2 SLP162 T01890133
2012	23:51	25006KT 10SM SCT260 22/08 A3024 RMK AO2 SLP240 T02170083 10250 20211 53006
	00:51	25005KT 10SM FEW260 21/08 A3026 RMK AO2 SLP248 T02110083
	01:51	24003KT 10SM FEW250 19/09 A3027 RMK AO2 SLP250 T01940089
	02:51	25006KT 10SM FEW250 19/09 A3027 RMK AO2 SLP251 T01890094 51011
	03:51	21003KT 10SM CLR 18/09 A3028 RMK AO2 SLP252 T01780094
	04:51	23005KT 10SM CLR 16/10 A3028 RMK AO2 SLP254 T01610100 402500117

	05:51	23004KT 10SM CLR 16/10 A3029 RMK AO2 SLP257 T01560100 10217 20156 53006
	06:51	00000KT 10SM CLR 16/11 A3030 RMK AO2 SLP258 T01560106
	07:51	22004KT 10SM CLR 14/11 A3030 RMK AO2 SLP258 T01440106
	08:51	27003KT 10SM CLR 15/11 A3031 RMK AO2 SLP262 T01500106 53004
	09:51	00000KT 10SM FEW250 14/11 A3032 RMK AO2 SLP266 T01390106
2013	23:51	22011KT 10SM FEW050 SCT200 BKN250 31/21 A3001 RMK AO2 SLP162 T03110211 10356 20311 53012
	00:51	19008KT 10SM FEW015 SCT050 OVC250 31/22 A3002 RMK AO2 SLP165 T03060217
	01:51	20010KT 10SM OVC250 29/22 A3001 RMK AO2 SLP162 T02940217
	02:51	22006KT 10SM SCT038 OVC250 29/22 A3001 RMK AO2 SLP163 T02890217 51001
	03:51	22009KT 10SM SCT045 OVC250 28/22 A2999 RMK AO2 SLP156 T02780217
	04:51	20009KT 9SM FEW050 OVC250 27/22 A2997 RMK AO2 SLP148 T02670217 403560239
	05:51	20008KT 9SM BKN250 26/21 A2995 RMK AO2 SLP142 T02610211 10311 20261 56021
	06:51	19006KT 9SM BKN250 26/21 A2995 RMK AO2 SLP141 T02560211
	07:51	20008KT 8SM SCT055 BKN250 25/21 A2994 RMK AO2 SLP139 T02500211
	08:51	21006KT 8SM SCT055 BKN250 24/21 A2994 RMK AO2 SLP136 T02440211 58005
	09:51	21006KT 7SM FEW055 BKN250 24/21 A2994 RMK AO2 SLP136 T02390211
2014	23:51	25007KT 10SM FEW040 SCT120 SCT250 27/20 A2985 RMK AO2 SLP107 T02720200 10300 20272 53009
	00:51	26007KT 10SM FEW040 SCT120 SCT250 27/20 A2987 RMK AO2 SLP114 T02670200
	01:51	29010KT 10SM FEW045 SCT250 26/20 A2989 RMK AO2 SLP121 T02610200
	02:51	33013G19KT 10SM FEW045 SCT250 24/17 A2992 RMK AO2 SLP131 T02440167 53024
	03:51	35014G19KT 10SM FEW045 SCT250 22/14 A2995 RMK AO2 SLP141 T02220139
	04:51	34009KT 10SM FEW050 SCT250 21/12 A2997 RMK AO2 SLP147 T02060122 403000189
	05:51	34010G19KT 10SM FEW250 20/12 A2997 RMK AO2 SLP149 T02000122 10272 20200 51018
	06:51	34012KT 10SM FEW050 SCT250 19/12 A2999 RMK AO2 SLP154 T01890122
	07:51	34013KT 10SM FEW025 SCT050 SCT250 18/12 A3002 RMK AO2 SLP164 T01830117
	08:51	34009KT 10SM FEW025 SCT050 SCT250 17/11 A3003 RMK AO2 SLP168 T01720111 51020
	09:51	34012G18KT 10SM FEW025 17/11 A3005 RMK AO2 SLP175 T01670106
2015	23:51	VRB04KT 10SM FEW045 SCT250 27/16 A2978 RMK AO2 SLP084 T02670156 10289 20256 53012
	00:51	00000KT 10SM FEW045 SCT250 25/17 A2980 RMK AO2 SLP091 T02500167
	01:51	11004KT 10SM FEW045 SCT250 24/17 A2981 RMK AO2 SLP093 T02440167
	02:51	00000KT 10SM FEW045 SCT250 23/19 A2981 RMK AO2 SLP095 T02330189 51011
	03:51	00000KT 10SM FEW050 23/19 A2982 RMK AO2 SLP096 T02280189
	04:51	17003KT 10SM FEW050 22/18 A2982 RMK AO2 SLP096 T02170183 402890189

	05:51	15003KT 10SM FEW050 21/18 A2981 RMK AO2 SLP094 T02110183 10267 20206 58001
	06:51	19004KT 10SM FEW050 20/18 A2981 RMK AO2 SLP093 T02000178
	07:51	18003KT 10SM FEW050 SCT250 20/18 A2981 RMK AO2 SLP094 T02000183
	08:51	00000KT 10SM FEW050 SCT250 19/18 A2981 RMK AO2 SLP094 T01940178 56000
	09:51	00000KT 10SM SCT050 SCT250 19/17 A2982 RMK AO2 SLP098 T01890172
2016	23:51	32013KT 10SM BKN250 25/08 A3008 RMK AO2 SLP185 T02500078 10300 20250 53023
	00:51	32012KT 10SM BKN250 24/07 A3011 RMK AO2 SLP195 T02390072
	01:51	34011KT 10SM BKN250 23/07 A3013 RMK AO2 SLP202 T02280072
	02:51	35009KT 10SM BKN250 22/08 A3015 RMK AO2 SLP208 T02170078 51023
	03:51	34011KT 10SM SCT250 21/08 A3016 RMK AO2 SLP212 T02060078
	04:51	36008KT 10SM SCT250 19/08 A3017 RMK AO2 SLP217 T01890078 403000189
	05:51	02007KT 10SM SCT250 17/08 A3017 RMK AO2 SLP216 T01670078 10250 20167 50008
	06:51	01007KT 10SM SCT250 17/08 A3018 RMK AO2 SLP220 T01670078
	07:51	02007KT 10SM FEW250 15/08 A3019 RMK AO2 SLP222 T01500078
	08:51	01006KT 10SM CLR 14/08 A3020 RMK AO2 SLP227 T01440083 53011
	09:51	36007KT 10SM FEW250 16/09 A3022 RMK AO2 SLP231 T01610089

Full details of the codes and abbreviations for METARS data are available from http://www.ofcm.gov/publications/fmh/FMH1/FMH1.pdf.

Model Information and Additional Calculations

Contents

Peak effects **2**

Standardized peak density **2**
0.5º elevation angle 2
1.5º elevation angle 4

Max number of birds within 500 m of the TiL **7**
0.5º elevation angle 7
1.5º elevation angle 8

Average effects **11**

Numbers of birds **11**
0.5º elevation angle 11
1.5º elevation angle 13

Standardized peak density **17**
0.5º elevation angle 17
1.5º elevation angle 19

Radial velocity **23**
0.5º elevation angle 23

Number of flight calls **26**

Number of birds affected by the lights **29**

This document presents detailed results for all non-simulation analyses, focusing on linear model output and diagnostics.

```
library(mgcv)      # v 1.8-17 - gam
library(regr0)     # v 1.0-5 - logst
library(lattice)
library(Hmisc)
library(ggplot2)
library(cowplot)
```

Note on transformations: We use the *logst* function in the *regr0* package to log-transform our data when necessary. This function is equivalent to a log_{10} transformation for all but the smallest values, which are scaled such that the transformation yields finite values (e.g. because $log_{10}(0)$ is undefined). We chose this option because, unlike adding an arbitrary constant value of 1 to all observations, this method of scaling small values is determined by the distribution of the data, and importantly it only modifies the smallest observations, leaving all others unchanged.

Peak effects

The following models include one data point for each continous period of illumination or darkness: the maximum value observed during that period.

Standardized peak density

Standardized peak density is defined as:

$$\frac{max(\eta_{0-0.5km}) - mean(\eta_{2-20km})}{sd(\eta_{2-20km})}$$

Where $\eta_{0-0.5km}$ is the set of bird density values within 0.5 km of the Tribute and η_{2-20km} is the set of bird density values between 2-20 km from the Tribute.

In all cases, we compare three models with the following parametric effects using AIC:

1. $light + year + light \times year$
2. $light + year$
3. $light$

Here, *light* is a two-level categorical variable describing whether the Tribute was illuminated or not, and *year* is a four-level categorical variable describing the year in which that observation occurred.

We used the model with the lowest AIC score, unless there was a difference of less than 1 AIC unit separating the models. In this case, we used the model with the fewest parametric effects.

0.5º elevation angle

```
m1 = gam(logst(val)~light*year,data=light.df.g %>% filter(elev==1 & the.type=="max.peak.std"))
m2 = gam(logst(val)~light+year,data=light.df.g %>% filter(elev==1 & the.type=="max.peak.std"))
m3 = gam(logst(val)~light,data=light.df.g %>% filter(elev==1 & the.type=="max.peak.std"))
AIC(m1,m2,m3)
```

```
##    df      AIC
## m1 11 116.7996
## m2  7 120.8748
## m3  3 116.3087
```

```
bm = m3
```

The best model is model 3, which includes *light* only.

```
summary(bm)
```

```
##
## Family: gaussian
## Link function: identity
##
## Formula:
## logst(val) ~ light
##
## Parametric coefficients:
##             Estimate Std. Error t value Pr(>|t|)
## (Intercept)  -0.2890     0.1555  -1.858    0.069 .
## light         1.1487     0.2014   5.703 6.32e-07 ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
##
## R-sq.(adj) =  0.382   Deviance explained = 39.4%
## GCV = 0.52829  Scale est. = 0.50797   n = 52
```

The main effect of *light* is 1.149, which can be back-transformed as $10^{1.149}$ and interpreted as a multiplicative factor. In other words, the model indicates that the maximum standardized peak bird density observed during an illuminated period was $10^{1.149} = 14$ times greater than during dark periods, on average.

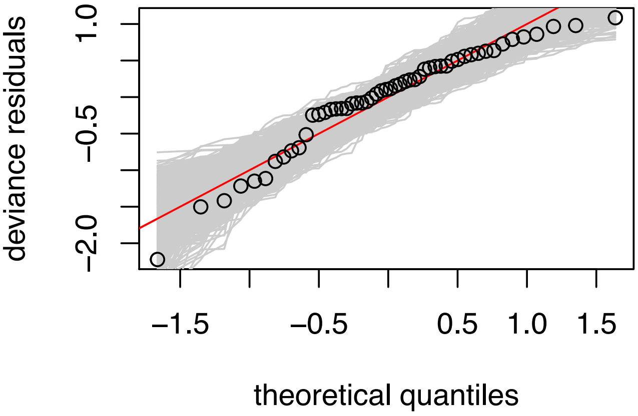
Results summarized for the main text:

```
res = summary(bm)$p.table
res = cbind(res,Factor=10^(res[,"Estimate"]))
# Effect of light after exponentiating the coefficient to get multiplicative factor
print.model.summary(res[2,5],res[2,3],res[2,4],units="x",effect.word="factor")
```

```
## [1] "factor = 14x, t = 5.70, P < 0.0001"
```

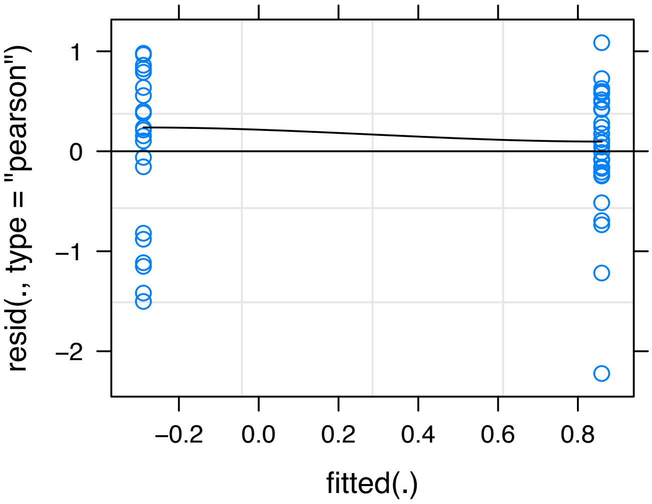
We now examine two important model diagnostic plots. The first is a standard quantile-quantile (or ‘qq’) plot, showing the distribution of the residuals compared to the quantiles of a normal distribution. Also plotted are the distributions of 1000 datasets simulated under the model, to show how much variation is expected if all assumptions are fulfilled. In this instance, all points are well within the gray lines; there is no evidence for a deviation from this assumption.

```
qq.gam(bm,rep=1000,pch=1,level=1)
```



Next, we examine a Tukey-Anscombe plot, the model residuals vs. the fitted values. There doesn't appear to be significant structure left in the data, and the variance of the residuals appears constant throughout, so there is no evidence for any deviation.

```
plot.lme(bm,type=c("p","smooth"),col.line="black")
```



1.5º elevation angle

This section runs the same models as the previous section, but with data from the high-altitude radar sweep (~1.5º elevation angle).

```
m1 = gam(logst(val)~light*year,
         data=light.df.g %>% filter(elev==1.5 & the.type=="max.peak.std"))
m2 = gam(logst(val)~light+year,
         data=light.df.g %>% filter(elev==1.5 & the.type=="max.peak.std"))
m3 = gam(logst(val)~light,
         data=light.df.g %>% filter(elev==1.5 & the.type=="max.peak.std"))
AIC(m1,m2,m3)
```

```
##    df      AIC
## m1 11 116.2694
## m2  7 113.1496
```

```
## m3  3 111.4823
```

```
bm = m3
```

Again, the best model is model 3, which includes *light* only.

```
summary(bm)
```

```
##
## Family: gaussian
## Link function: identity
##
## Formula:
## logst(val) ~ light
##
## Parametric coefficients:
##             Estimate Std. Error t value Pr(>|t|)
## (Intercept)  -0.6449     0.1365  -4.723  1.8e-05 ***
## light         0.5859     0.1802   3.251  0.00202 **
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
##
## R-sq.(adj) =  0.153   Deviance explained = 16.9%
## GCV = 0.44529  Scale est. = 0.4288    n = 54
```

Here there is one main effect of *light*, and the model indicates that maximum standardized peak bird densities were $10^{0.58} = 3.9$ times higher during illuminated periods, on average.

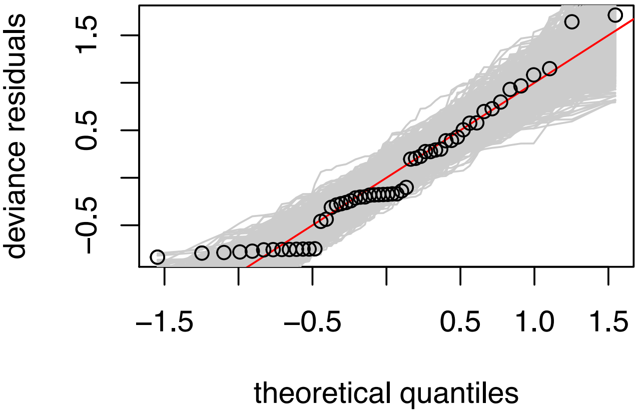
Results for the main text:

```
res = summary(bm)$p.table
res = cbind(res,Factor=10^(res[,"Estimate"]))
# Effect of light after exponentiating the coefficient to get multiplicative factor
print.model.summary(res[2,5],res[2,3],res[2,4],units="x",effect.word="factor")
```

```
## [1] "factor = 3.9x, t = 3.25, P = 0.0020"
```

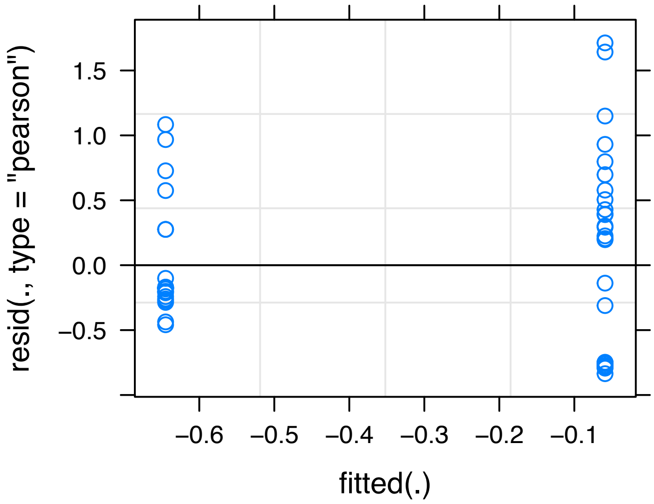
All points are within the gray simluated lines.

```
qq.gam(bm,rep=1000,pch=1,level=1)
```



The Tukey-Anscombe plot suggests that the variance may be increasing, but the difference is not extreme.

```
plot.lme(bm,type=c("p","r"),col.line="black")
```



Max number of birds within 500 m of the TiL

This section performs the same analysis as the previous section, except the response variable is the maximum number of birds detected within 500 m of the TiL during a continuous illuminated/dark period.

0.5º elevation angle

```
m1 = gam(logst(val)~light*year,data=light.df.g %>% filter(elev==1 & the.type=="max.nbirds"))
m2 = gam(logst(val)~light+year,data=light.df.g %>% filter(elev==1 & the.type=="max.nbirds"))
m3 = gam(logst(val)~light,data=light.df.g %>% filter(elev==1 & the.type=="max.nbirds"))
AIC(m1,m2,m3)
```

```
##    df      AIC
## m1 11 83.99201
## m2  7 78.16597
## m3  3 94.05718
```

```
bm = m2
```

The best model is model 2, which includes the *light* and *year* but not their interaction.

```
summary(bm)
```

```
##
## Family: gaussian
## Link function: identity
##
## Formula:
## logst(val) ~ light + year
##
## Parametric coefficients:
##             Estimate Std. Error t value Pr(>|t|)
## (Intercept)  2.08254    0.15619  13.333  < 2e-16 ***
## light        0.52534    0.13506   3.890 0.000321 ***
## year2012    -0.21004    0.23543  -0.892 0.376952
## year2013    -0.01684    0.20056  -0.084 0.933460
## year2015     0.70110    0.17818   3.935 0.000279 ***
## year2016     0.07999    0.22361   0.358 0.722184
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
##
## R-sq.(adj) =  0.406   Deviance explained = 46.4%
## GCV = 0.25699  Scale est. = 0.22734   n = 52
```

Here there is one main effect of *light*, and the model indicates that maximum number of birds within 500 m of the TiL was $10^{0.53} = 3.4$ times higher during illuminated periods, on average.

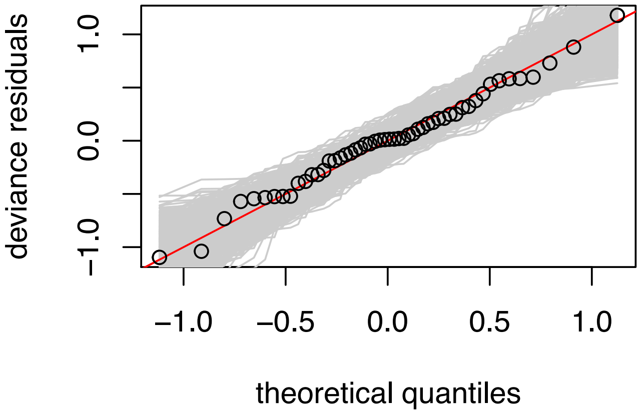
Results for the main text:

```
res = summary(bm)$p.table
res = cbind(res,Factor=10^(res[,"Estimate"]))
# Effect of light after exponentiating the coefficient to get multiplicative factor
print.model.summary(res[2,5],res[2,3],res[2,4],units="x",effect.word="factor")
```

```
## [1] "factor = 3.4x, t = 3.89, P = 0.0003"
```

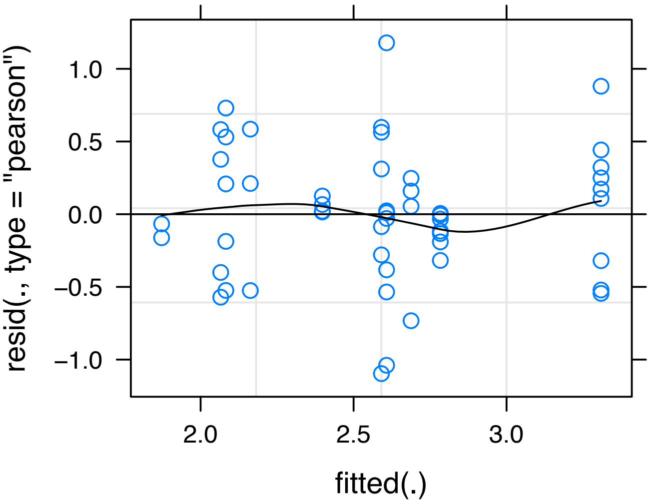
No evidence for any deviation.

```
qq.gam(bm,rep=1000,pch=1,level=1)
```



Negligible structure in the residuals.

```
plot.lme(bm,type=c("p","smooth"),col.line="black")
```



1.5º elevation angle

This section runs the same models as the previous section, but with data from the high-altitude radar scan.

```
m1 = gam(logst(val)~light*year,data=light.df.g %>% filter(elev==1.5 & the.type=="max.nbirds"))
m2 = gam(logst(val)~light+year,data=light.df.g %>% filter(elev==1.5 & the.type=="max.nbirds"))
m3 = gam(logst(val)~light,data=light.df.g %>% filter(elev==1.5 & the.type=="max.nbirds"))
AIC(m1,m2,m3)
```

```
##    df      AIC
## m1 11 141.5482
## m2  7 136.9647
## m3  3 141.4726
```

```
bm = m2
```

The best model is model 2, which includes *light* and *year*, but not their interaction.

```
summary(bm)
```

```
##
## Family: gaussian
## Link function: identity
##
## Formula:
## logst(val) ~ light + year
##
## Parametric coefficients:
##             Estimate Std. Error t value Pr(>|t|)
## (Intercept) -0.05014    0.26089  -0.192  0.84840
## light        0.51996    0.22204   2.342  0.02339 *
## year2012    -0.52410    0.39566  -1.325  0.19156
## year2013    -0.69052    0.33707  -2.049  0.04599 *
## year2015    -0.06806    0.29279  -0.232  0.81717
## year2016    -1.07497    0.37580  -2.861  0.00625 **
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
##
## R-sq.(adj) =  0.191   Deviance explained = 26.7%
## GCV = 0.72239  Scale est. = 0.64213   n = 54
```

Here there is one main effect of *light*, and the model indicates that maximum number of birds within 500 m of the TiL was $10^{0.52} = 3.3$ times higher during illuminated periods, on average.

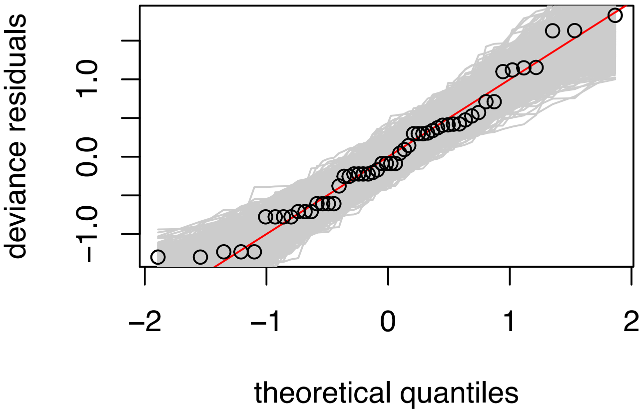
Results for the main text:

```
res = summary(bm)$p.table
res = cbind(res,Factor=10^(res[,"Estimate"]))
# Effect of light after exponentiating the coefficient to get multiplicative factor
print.model.summary(res[2,5],res[2,3],res[2,4],units="x",effect.word="factor")
```

```
## [1] "factor = 3.3x, t = 2.34, P = 0.0234"
```

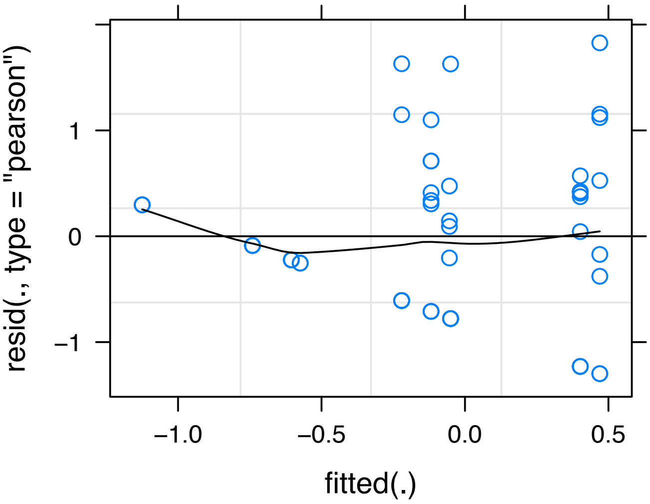
No evidence for any deviation.

```
qq.gam(bm,rep=1000,pch=1,level=1)
```



The variance may be increasing, although the sample size of points at low x-values is small. No other structure is apparent in the data, which have already been log-transformed. Furthermore, if anything, this would likely make our test conservative.

```
plot.lme(bm,type=c("p","smooth"),col.line="black")
```



Average effects

The following models include all data points (not just one per light/dark period). To account for any autocorrelation in the data, we introduce two additional predictor variables as smooth terms: time of night (*TIME*) and baseline bird density (*BIRD_DENSITY*). These smooth terms account for variation explained by temporal changes in bird numbers through the night and as a result of changes in baseline bird density—separate from any effect of the Tribute in Light (*LIGHT*).

Numbers of birds

0.5º elevation angle

We test for effect of light on the total number of birds present in the cylinder with radius 500 m and height 4.5 km, calculated from the 0.5º elevation angle sweep.

```
# 'stationary.radar.model.light' is a custom function to construct the necessary models
# and compare AIC values
n.birds.e1.model = stationary.radar.model.light(response.name="logst(n.birds.cyl.e1)",
                    the.data=dt1,elev="e1")
```

```
##                        df       AIC
## mod.light      23.37065  98.69452
## mod.light.year 24.82408 101.31629
## mod.interact   29.16755 105.87983
```

```
bm = n.birds.e1.model
```

The best model includes *light* only.

```
summary(bm)
```

```
##
## Family: gaussian
## Link function: identity
##
## Formula:
## eval(parse(text = response.name)) ~ eval(LIGHT) + s(as.numeric(eval(TIME)),
##     by = year) + s(eval(BIRD_DENSITY), by = year)
##
## Parametric coefficients:
##                Estimate Std. Error t value Pr(>|t|)
## (Intercept)  -718.92637  230.15140  -3.124  0.00207 **
## eval(LIGHT)1    0.52562    0.05628   9.339  < 2e-16 ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## Approximate significance of smooth terms:
##                                     edf Ref.df      F  p-value
## s(as.numeric(eval(TIME))):year2010 1.034  1.057  8.904  0.00238 **
## s(as.numeric(eval(TIME))):year2012 1.026  1.051  9.156  0.00230 **
## s(as.numeric(eval(TIME))):year2013 1.848  1.968  5.132  0.00967 **
## s(as.numeric(eval(TIME))):year2015 1.000  1.000  9.802  0.00201 **
## s(as.numeric(eval(TIME))):year2016 1.000  1.000  9.790  0.00203 **
## s(eval(BIRD_DENSITY)):year2010     6.049  6.942 14.895 3.52e-16 ***
```

```
## s(eval(BIRD_DENSITY)):year2012     1.000  1.000  0.000  0.99561
## s(eval(BIRD_DENSITY)):year2013     1.919  2.017 36.520 1.34e-13 ***
## s(eval(BIRD_DENSITY)):year2015     3.307  4.055 21.332 5.33e-15 ***
## s(eval(BIRD_DENSITY)):year2016     2.187  2.583 19.321 1.02e-05 ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## R-sq.(adj) =  0.806   Deviance explained = 82.6%
## GCV = 0.094149  Scale est. = 0.084072  n = 209
```

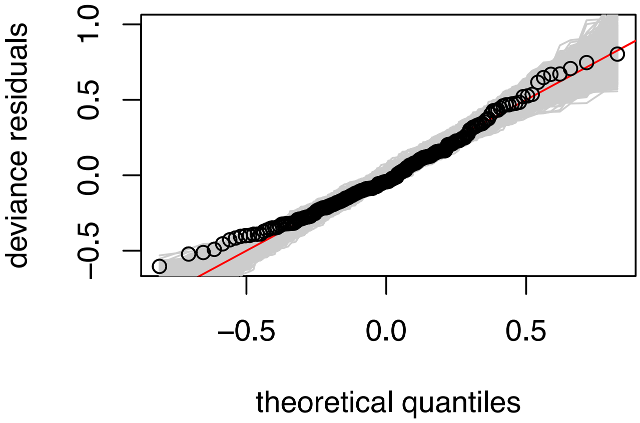
Results for the main text:

```
res = summary(bm)$p.table
res = cbind(res,Factor=10^(res[,"Estimate"]))
# Exponentiating the coefficient to get multiplicative factor
print.model.summary(res[2,5],res[2,3],res[2,4],units="x",effect.word="factor")
```

```
## [1] "factor = 3.4x, t = 9.34, P < 0.0001"
```

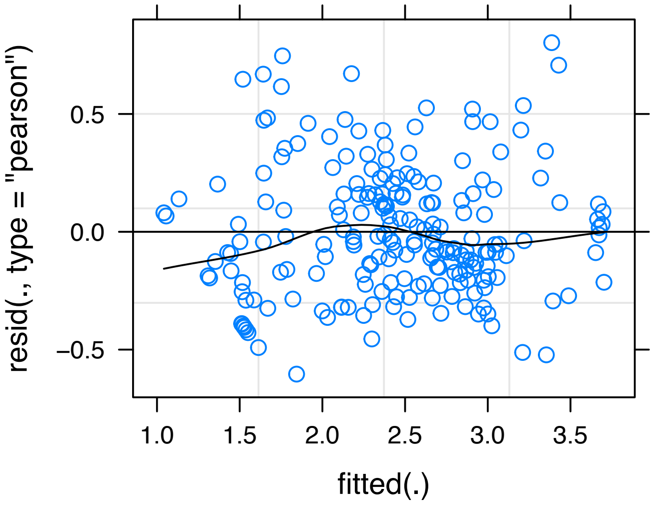
No evidence of any deviation; all points within the bounds of the simulated datasets.

```
qq.gam(bm,rep=1000,pch=1,level=1)
```



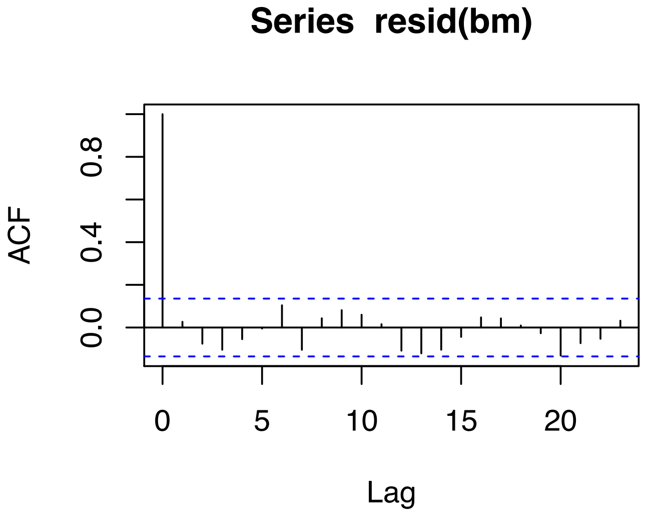
No evidence of any deviation or structure.

```
plot.lme(bm,type=c("p","smooth"),col.line="black")
```



No autocorrelation of residuals.

```
acf(resid(bm))
```



1.5º elevation angle

```
n.birds.e2.model = stationary.radar.model.light("logst(n.birds.cyl.e2)",dt2,elev="e2")
```

```
##                       df      AIC
## mod.light.year 26.01437 275.0162
## mod.interact   29.86173 275.4296
## mod.light      20.52622 283.4821
```

```
bm = n.birds.e2.model
```

The best model includes *light* and *year* but not their interaction.

```
summary(bm)
```

```
##
```

```
## Family: gaussian
## Link function: identity
##
## Formula:
## eval(parse(text = response.name)) ~ eval(LIGHT) + year + s(as.numeric(eval(TIME)),
##     by = year) + s(eval(BIRD_DENSITY), by = year)
##
## Parametric coefficients:
##                Estimate Std. Error t value Pr(>|t|)
## (Intercept)  -8583.0276  2640.8272  -3.250 0.001367 **
## eval(LIGHT)1     0.2875     0.0823   3.493 0.000595 ***
## year2012      5897.7775  2897.5004   2.035 0.043207 *
## year2013      8598.2387  2802.0783   3.069 0.002469 **
## year2015      6196.6699  2802.1699   2.211 0.028215 *
## year2016      8943.6367  3350.9547   2.669 0.008273 **
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## Approximate significance of smooth terms:
##                                     edf Ref.df      F  p-value
## s(as.numeric(eval(TIME))):year2010 0.9999  1.000 10.563 0.001362 **
## s(as.numeric(eval(TIME))):year2012 1.0000  1.000  5.035 0.025978 *
## s(as.numeric(eval(TIME))):year2013 1.0000  1.000  0.000 0.999937
## s(as.numeric(eval(TIME))):year2015 1.0000  1.000  6.445 0.011917 *
## s(as.numeric(eval(TIME))):year2016 1.0000  1.000  0.031 0.860547
## s(eval(BIRD_DENSITY)):year2010     7.4971  8.390  2.987 0.003818 **
## s(eval(BIRD_DENSITY)):year2012     1.0000  1.000  0.257 0.612484
## s(eval(BIRD_DENSITY)):year2013     1.3293  1.550  1.468 0.168807
## s(eval(BIRD_DENSITY)):year2015     3.1880  3.898  6.019 0.000165 ***
## s(eval(BIRD_DENSITY)):year2016     1.0000  1.000  0.163 0.686857
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## R-sq.(adj) =  0.728   Deviance explained = 75.8%
## GCV = 0.21414  Scale est. = 0.18899   n = 213
```

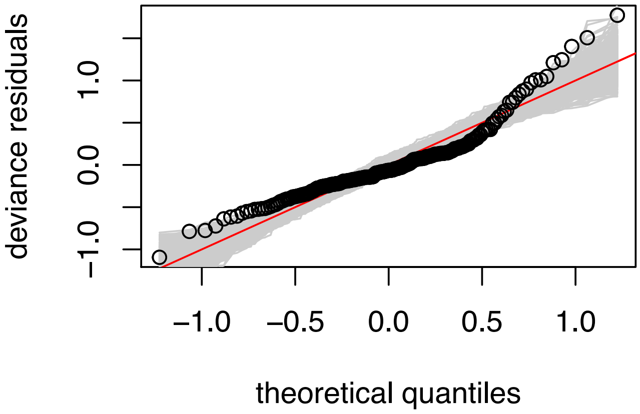
Results for the main text:

```
res = summary(bm)$p.table
res = cbind(res,Factor=10^(res[,"Estimate"]))
# Exponentiating the coefficient to get multiplicative factor
print.model.summary(res[2,5],res[2,3],res[2,4],units="x",effect.word="factor")
```

```
## [1] "factor = 1.9x, t = 3.49, P = 0.0006"
```

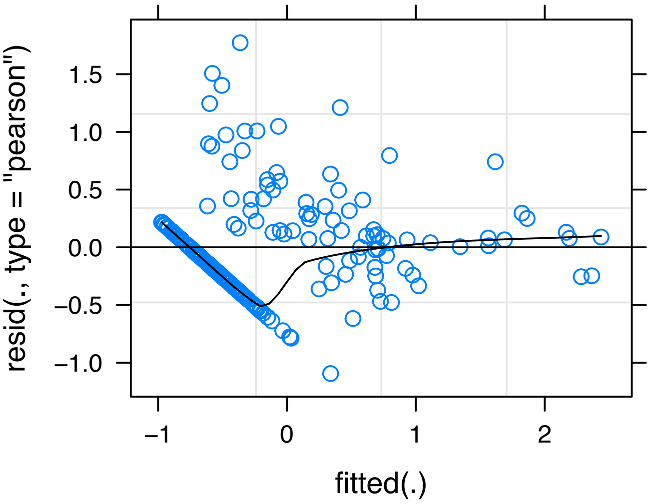
Some deviation from the normal line, but all points within the bounds of the simulated datasets, or very close.

```
qq.gam(bm,rep=1000,pch=1,level=1)
```



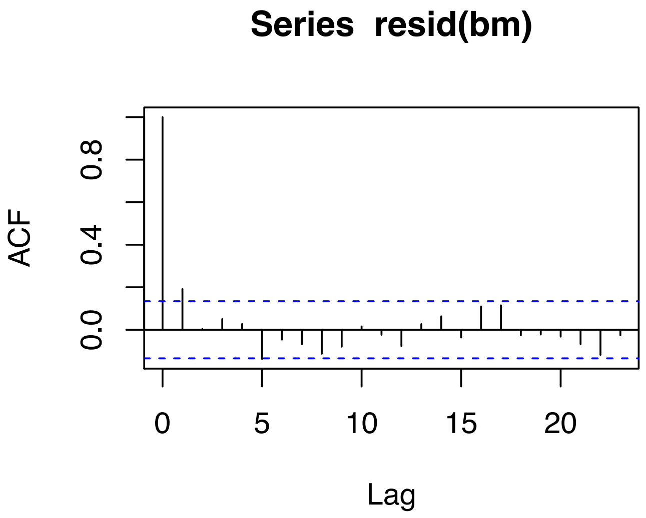
Some structure due to the large number of near-zero values in the dataset.

```
plot.lme(bm,type=c("p","smooth"),col.line="black")
```



Negligible autocorrelation of residuals.

```
acf(resid(bm))
```


Series resid(bm)
ACF
0.0
0.4
0.8
0
5
10
15
20
Lag

Standardized peak density

As previous section, but for standardized peak density.

0.5º elevation angle

```
peak.std.e1.model = stationary.radar.model.light("logst(peak.std.e1)",dt1,elev="e1")
```

```
##                       df      AIC
## mod.interact   25.88700 369.4469
## mod.light      19.87233 375.6902
## mod.light.year 22.19399 378.8855
```

```
bm = peak.std.e1.model
```

Best model includes *light* × *year* interaction.

```
summary(bm)
```

```
##
## Family: gaussian
## Link function: identity
##
## Formula:
## eval(parse(text = response.name)) ~ eval(LIGHT) * year + s(as.numeric(eval(TIME)),
##     by = year) + s(eval(BIRD_DENSITY), by = year)
##
## Parametric coefficients:
##                          Estimate Std. Error t value Pr(>|t|)
## (Intercept)            -1.146e+04  5.042e+03  -2.273  0.02419 *
## eval(LIGHT)1            8.075e-01  2.168e-01   3.724  0.00026 ***
## year2012                1.077e+04  5.160e+03   2.088  0.03818 *
## year2013                1.142e+04  5.166e+03   2.210  0.02836 *
## year2015                1.044e+04  5.070e+03   2.059  0.04093 *
## year2016                4.154e+03  8.692e+03   0.478  0.63329
## eval(LIGHT)1:year2012  4.105e-01  4.072e-01   1.008  0.31468
## eval(LIGHT)1:year2013 -1.998e-01  3.146e-01  -0.635  0.52623
## eval(LIGHT)1:year2015  8.522e-01  2.929e-01   2.910  0.00406 **
## eval(LIGHT)1:year2016 -1.305e-01  3.485e-01  -0.374  0.70858
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## Approximate significance of smooth terms:
##                                    edf Ref.df     F p-value
## s(as.numeric(eval(TIME))):year2010 1.000  1.000 5.166  0.0242 *
## s(as.numeric(eval(TIME))):year2012 1.000  1.000 0.386  0.5351
## s(as.numeric(eval(TIME))):year2013 1.000  1.000 0.001  0.9757
## s(as.numeric(eval(TIME))):year2015 1.000  1.000 3.702  0.0559 .
## s(as.numeric(eval(TIME))):year2016 1.000  1.000 1.064  0.3035
## s(eval(BIRD_DENSITY)):year2010     4.175  5.107 2.813  0.0129 *
## s(eval(BIRD_DENSITY)):year2012     1.000  1.000 0.289  0.5917
## s(eval(BIRD_DENSITY)):year2013     1.540  1.790 2.358  0.1221
## s(eval(BIRD_DENSITY)):year2015     1.383  1.667 3.197  0.0661 .
## s(eval(BIRD_DENSITY)):year2016     1.788  2.153 1.120  0.4872
```

```
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## R-sq.(adj) =  0.453   Deviance explained = 51.6%
## GCV = 0.34495  Scale est. = 0.30388   n = 209
```

Results for main text:

```
res = summary(bm)$p.table
res = cbind(res,Factor=10^(res[,"Estimate"]))
# Exponentiating the coefficients to get multiplicative factor
print.model.summary(res[2,5],res[2,3],res[2,4],units="x",effect.word="factor")
```

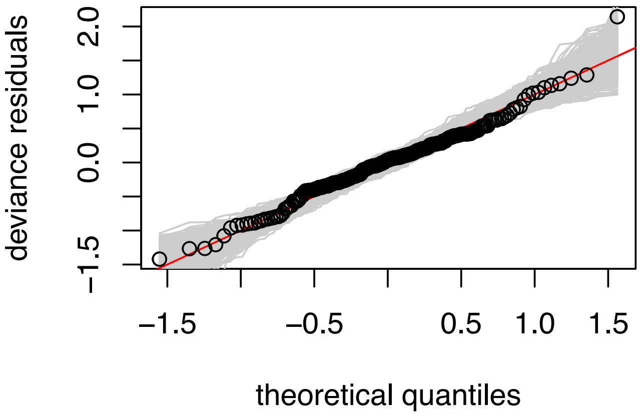
```
## [1] "factor = 6.4x, t = 3.72, P = 0.0003"
```

```
# Interaction
print.model.summary(10^(res[9,1]+res[2,1]),res[9,3],res[9,4],units="x",effect.word="factor")
```

```
## [1] "factor = 46x, t = 2.91, P = 0.0041"
```

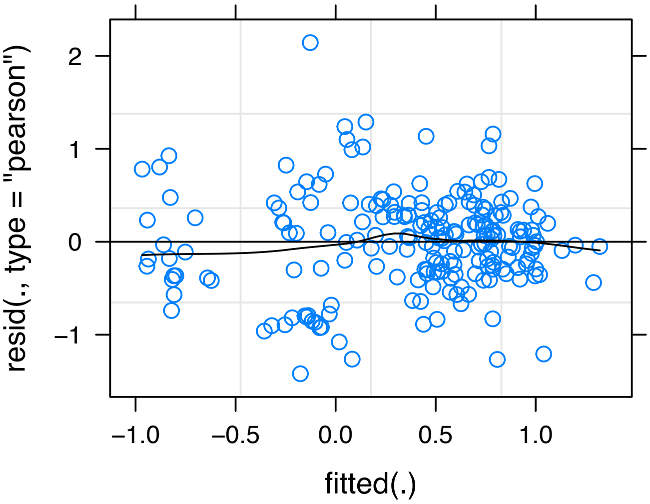
No evidence of any deviation; all points within the bounds of the simulated datasets.

```
qq.gam(bm,rep=1000,pch=1,level=1)
```



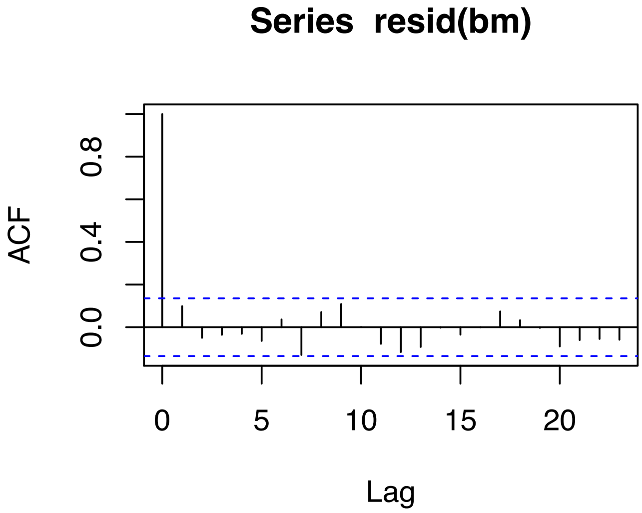
No evidence of any deviation or structure.

```
plot.lme(bm,type=c("p","smooth"),col.line="black")
```



Negligible autocorrelation of residuals.

```
acf(resid(bm))
```



1.5º elevation angle

```
peak.std.e2.model = stationary.radar.model.light("logst(peak.std.e2)",dt2,elev="e2")
```

```
##                        df      AIC
## mod.light.year 20.35718 523.5451
## mod.interact   24.43069 524.0113
## mod.light      16.56379 525.4860
```

```
bm = peak.std.e2.model
```

The best model includes *light* and *year*, but not their interaction.

```
summary(bm)
```

```
##
```

```
## Family: gaussian
## Link function: identity
##
## Formula:
## eval(parse(text = response.name)) ~ eval(LIGHT) + year + s(as.numeric(eval(TIME)),
##     by = year) + s(eval(BIRD_DENSITY), by = year)
##
## Parametric coefficients:
##                Estimate Std. Error t value Pr(>|t|)
## (Intercept)  -9104.3033  3624.2956  -2.512   0.0128 *
## eval(LIGHT)1     0.6030     0.1508   3.997 9.17e-05 ***
## year2012      3548.9179  4249.1148   0.835   0.4046
## year2013      9179.5991  4062.8409   2.259   0.0250 *
## year2015      6153.2760  3960.3706   1.554   0.1219
## year2016      7001.7664  5347.7746   1.309   0.1920
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## Approximate significance of smooth terms:
##                                      edf Ref.df     F p-value
## s(as.numeric(eval(TIME))):year2010 1.000  1.000 6.287  0.0128 *
## s(as.numeric(eval(TIME))):year2012 1.000  1.000 6.248  0.0133 *
## s(as.numeric(eval(TIME))):year2013 1.000  1.000 0.000  0.9982
## s(as.numeric(eval(TIME))):year2015 1.000  1.000 3.408  0.0664 .
## s(as.numeric(eval(TIME))):year2016 1.000  1.000 0.286  0.5932
## s(eval(BIRD_DENSITY)):year2010     1.873  2.358 1.040  0.3603
## s(eval(BIRD_DENSITY)):year2012     1.000  1.000 1.462  0.2281
## s(eval(BIRD_DENSITY)):year2013     1.790  1.956 0.313  0.6989
## s(eval(BIRD_DENSITY)):year2015     2.573  3.188 2.310  0.0881 .
## s(eval(BIRD_DENSITY)):year2016     1.122  1.231 0.080  0.7182
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## R-sq.(adj) =  0.291   Deviance explained = 35.4%
## GCV = 0.71656  Scale est. = 0.65019   n = 209
```

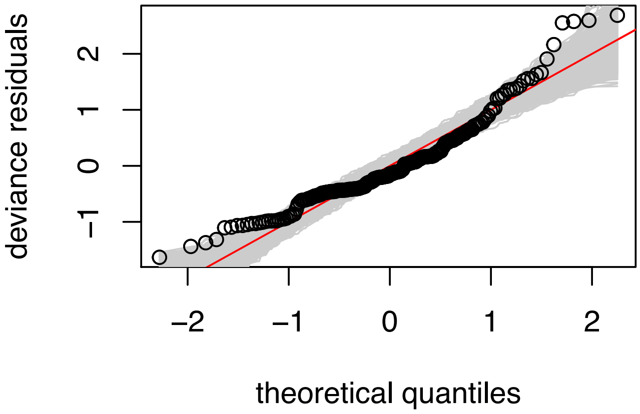
Results for the main text:

```r
res = summary(bm)$p.table
res = cbind(res,Factor=10^(res[,"Estimate"]))
# Effect of light after exponentiating the coefficient to get multiplicative factor
print.model.summary(res[2,5],res[2,3],res[2,4],units="x",effect.word="factor")
```

```
## [1] "factor = 4x, t = 4.00, P < 0.0001"
```

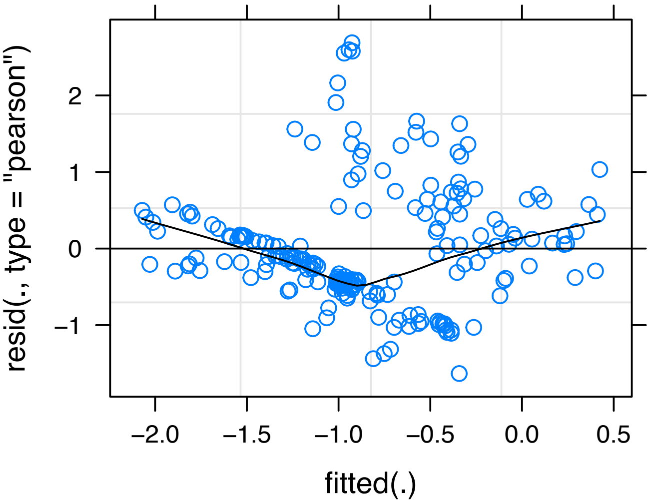
Some deviation from the normal line, but all points are either within the bounds of the simulated datasets or very close.

```r
qq.gam(bm,rep=1000,pch=1,level=1)
```



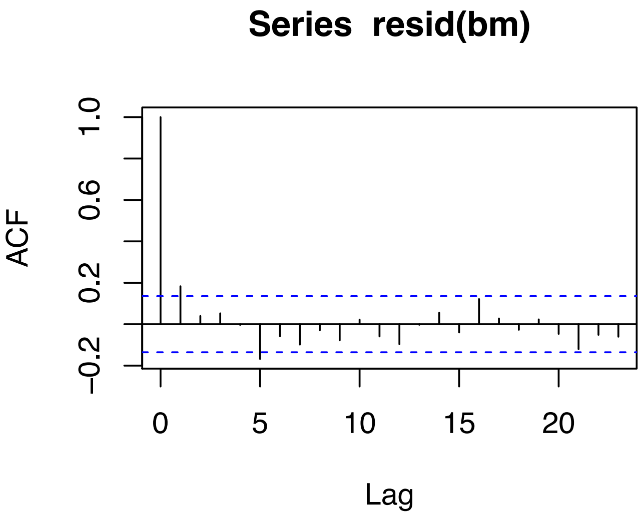
Appears to be some structure (likely due to large numbers of near-zero values), but not dramatic.

```
plot.lme(bm,type=c("p","smooth"),col.line="black")
```



Negligible autocorrelation of residuals.

```
acf(resid(bm))
```


Series resid(bm)
ACF
1.0
0.6
0.2
−0.2
0
5
10
15
20
Lag

Radial velocity

Note that radial velocity data have *not* been log-transformed.

0.5º elevation angle

```
velocity.e1.model = stationary.radar.model.light("velocity.cyl.e1",dt1,elev="e1")
```

```
##                       df      AIC
## mod.interact    29.28329 814.1776
## mod.light.year 25.70874 817.0279
## mod.light       23.24699 819.2017
```

```
bm = velocity.e1.model
```

The best model includes the *light* × *year* interaction term.

```
summary(bm)
```

```
##
## Family: gaussian
## Link function: identity
##
## Formula:
## eval(parse(text = response.name)) ~ eval(LIGHT) * year + s(as.numeric(eval(TIME)),
##     by = year) + s(eval(BIRD_DENSITY), by = year)
##
## Parametric coefficients:
##                          Estimate Std. Error t value Pr(>|t|)
## (Intercept)             5.221e+04  2.260e+04   2.310   0.0221 *
## eval(LIGHT)1           -1.670e+00  7.951e-01  -2.101   0.0372 *
## year2012               -5.063e+04  2.314e+04  -2.188   0.0301 *
## year2013               -5.197e+04  2.286e+04  -2.274   0.0243 *
## year2015               -4.947e+04  2.287e+04  -2.163   0.0320 *
## year2016               -9.960e+03  3.079e+04  -0.323   0.7468
## eval(LIGHT)1:year2012 -3.714e+00  1.558e+00  -2.384   0.0183 *
## eval(LIGHT)1:year2013 -1.773e+00  1.496e+00  -1.185   0.2376
## eval(LIGHT)1:year2015 -2.678e+00  1.062e+00  -2.521   0.0127 *
## eval(LIGHT)1:year2016 -5.909e-01  1.223e+00  -0.483   0.6296
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## Approximate significance of smooth terms:
##                                       edf Ref.df     F p-value
## s(as.numeric(eval(TIME))):year2010 1.000  1.000 5.337 0.02212 *
## s(as.numeric(eval(TIME))):year2012 1.000  1.000 0.012 0.91154
## s(as.numeric(eval(TIME))):year2013 1.000  1.000 0.013 0.91010
## s(as.numeric(eval(TIME))):year2015 1.000  1.000 0.600 0.44006
## s(as.numeric(eval(TIME))):year2016 1.000  1.000 4.078 0.04511 *
## s(eval(BIRD_DENSITY)):year2010     3.358  4.210 4.221 0.00181 **
## s(eval(BIRD_DENSITY)):year2012     2.853  2.986 3.346 0.02230 *
## s(eval(BIRD_DENSITY)):year2013     1.769  1.951 0.475 0.64828
## s(eval(BIRD_DENSITY)):year2015     4.303  5.233 3.661 0.00322 **
## s(eval(BIRD_DENSITY)):year2016     1.000  1.000 0.493 0.48343
```

```
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## R-sq.(adj) =  0.601   Deviance explained = 65.9%
## GCV = 4.4118  Scale est. = 3.7515    n = 189
```

Results for main text:

```
res = summary(bm)$p.table
print.model.summary(res[2,1],res[2,3],res[2,4],units="m/s",effect.word="effect")
```

```
## [1] "effect = -1.7 m/s, t = -2.10, P = 0.0372"
```

```
# Interaction - 2012
print.model.summary(res[7,1]+res[2,1],res[7,3],res[7,4],units="m/s",
                    effect.word="effect with interaction")
```

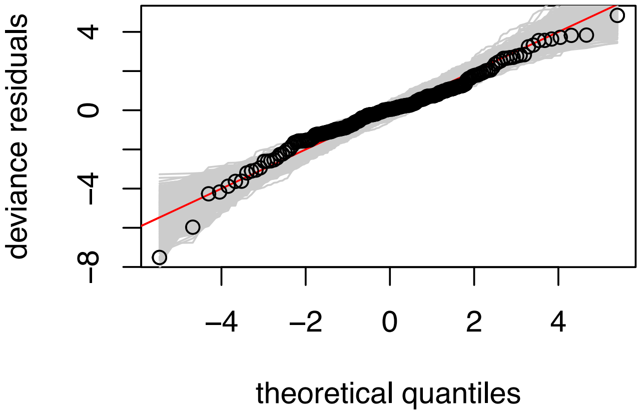
```
## [1] "effect with interaction = -5.4 m/s, t = -2.38, P = 0.0183"
```

```
# Interaction - 2015
print.model.summary(res[9,1]+res[2,1],res[9,3],res[9,4],units="m/s",
                    effect.word="effect with interaction")
```

```
## [1] "effect with interaction = -4.3 m/s, t = -2.52, P = 0.0127"
```

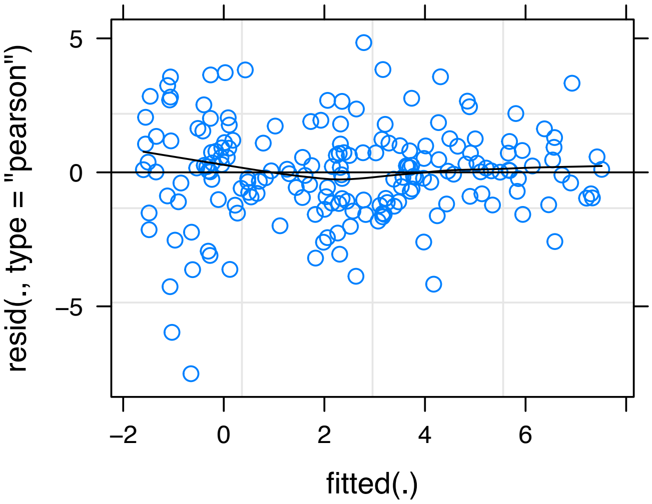
No strong evidence of any deviation; all points within the bounds of the simulated datasets.

```
qq.gam(bm,rep=1000,pch=1,level=1)
```



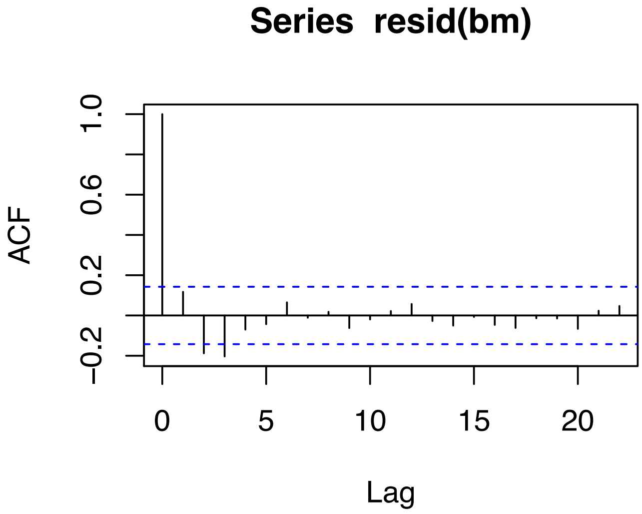
No evidence of any deviation or structure.

```
plot.lme(bm,type=c("p","smooth"),col.line="black")
```



Negligible autocorrelation of residuals.

```r
acf(resid(bm))
```



Number of flight calls

```
response.name="logst(n.calls)"
elev="e1"
```

```
aic = AIC(mod.interact,
          mod.light.year,
          mod.light); aic
```

```
##                      df       AIC
## mod.interact   26.22691 -364.0446
## mod.light.year 22.57075 -276.7783
## mod.light      22.52872 -276.8101
```

```
calls.e1.model = eval(parse(text=rownames(aic)[which.min(aic$AIC)]))
bm = calls.e1.model
```

The best model includes the *light* × *year* interaction term.

```
summary(bm)
```

```
##
## Family: gaussian
## Link function: identity
##
## Formula:
## eval(parse(text = response.name)) ~ eval(LIGHT) * year + max_eta.e1 +
##     s(as.numeric(eval(TIME)), by = year) + s(eval(BIRD_DENSITY),
##     by = year)
##
## Parametric coefficients:
##                          Estimate Std. Error t value Pr(>|t|)
## (Intercept)            -2.342e+01  2.880e+00  -8.134 1.38e-13 ***
## eval(LIGHT)1            1.519e-01  3.356e-02   4.527 1.20e-05 ***
## year2013                7.632e+00  3.756e+00   2.032  0.04390 *
## year2015               -5.346e+01  5.492e+00  -9.733  < 2e-16 ***
## year2016                9.635e+00  3.070e+00   3.138  0.00204 **
## max_eta.e1              4.233e-07  1.427e-06   0.297  0.76706
## eval(LIGHT)1:year2013 -1.087e-01  4.737e-02  -2.296  0.02306 *
## eval(LIGHT)1:year2015  3.107e-01  4.517e-02   6.877 1.49e-10 ***
## eval(LIGHT)1:year2016 -9.658e-02  5.088e-02  -1.898  0.05957 .
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## Approximate significance of smooth terms:
##                                    edf Ref.df      F  p-value
## s(as.numeric(eval(TIME))):year2010 0.8308 0.8309 99.157  < 2e-16 ***
## s(as.numeric(eval(TIME))):year2013 1.0912 1.2291 35.199 0.001458 **
## s(as.numeric(eval(TIME))):year2015 1.5598 1.5603 69.656  < 2e-16 ***
## s(as.numeric(eval(TIME))):year2016 0.5385 0.5388 23.884 0.000447 ***
## s(eval(BIRD_DENSITY)):year2010     6.2036 7.0849  7.762 2.59e-08 ***
## s(eval(BIRD_DENSITY)):year2013     1.0000 1.0000  0.638 0.425828
## s(eval(BIRD_DENSITY)):year2015     6.0761 7.0266 17.366  < 2e-16 ***
## s(eval(BIRD_DENSITY)):year2016     1.1145 1.2185  0.129 0.629785
## ---
```

```
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## Rank: 65/81
## R-sq.(adj) =  0.949   Deviance explained = 95.6%
## GCV = 0.0075709  Scale est. = 0.0064918  n = 177
```

Results for the main text:

```
res = summary(bm)$p.table
res = cbind(res,Factor=10^(res[,"Estimate"]))
# Effect of light after exponentiating the coefficient to get multiplicative factor
print.model.summary(res[2,5],res[2,3],res[2,4],units="x",effect.word="factor")
```

```
## [1] "factor = 1.4x, t = 4.53, P < 0.0001"
```

```
# Interaction - 2013
print.model.summary(10^(res[7,1]+res[2,1]),res[7,3],res[7,4],units="x",
                    effect.word="factor with interaction")
```

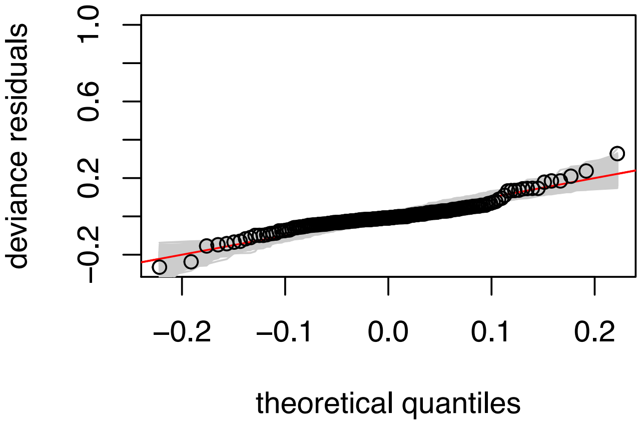
```
## [1] "factor with interaction = 1.1x, t = -2.30, P = 0.0231"
```

```
# Interaction - 2015
print.model.summary(10^(res[8,1]+res[2,1]),res[8,3],res[8,4],units="x",
                    effect.word="factor with interaction")
```

```
## [1] "factor with interaction = 2.9x, t = 6.88, P < 0.0001"
```

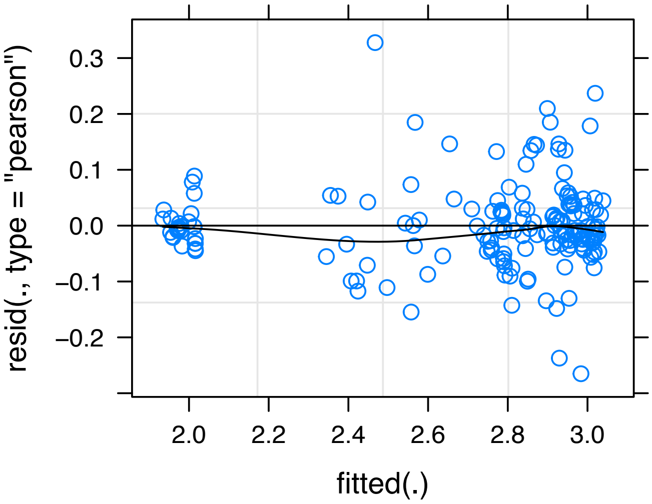
No strong evidence of any deviation; all points within the bounds of the simulated datasets.

```
qq.gam(bm,rep=1000,pch=1,level=1)
```



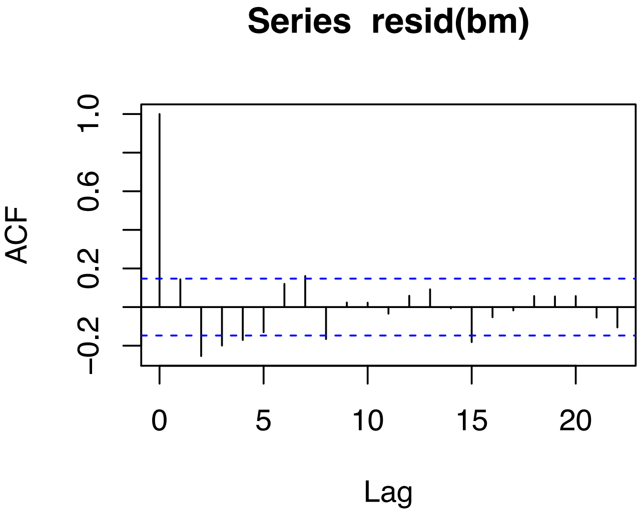
Although the variance increases, this does not affect the regression coefficients; it may make the test more conservative (i.e. more difficult to detect a statistical difference between illuminated and dark periods or between years).

```
plot.lme(bm,type=c("p","smooth"),col.line="black")
```



Negligible autocorrelation of residuals.

```
acf(resid(bm))
```



Number of birds affected by the lights

Here we estimate the total number of birds affected by the lights. Our best estimate of turnover time comes from the simulations, where the stabilization time is 34 minutes. Since on average there should be complete turnover within that period of time, we use 34 minutes as our best estimate of the turnover time. Then we find the median time between radar scans in minutes

```
time.between.scans = as.numeric(median(diff(data.m$sweep.time.e1))); time.between.scans
```

```
## [1] 9.466667
```

Next we divide the time between scans by the turnover time to find the proportion of samples that can be treated as 'independent.' We will therefore calculate total numbers of birds only from a subset of the dataset of this size.

```
retain.proportion = time.between.scans/34; retain.proportion
```

```
## [1] 0.2784314
```

To accomplish this, we subsample the dataset 10000 times with the probablity of keeping a data point equal to 'retain.proportion.'

```
set.seed(123)
yrs = sort(unique(data.m$year))
n.sim = 1e4
res.array = array(dim=c(n.sim,length(yrs)))
# xx = rep(NA,n.sim)
for (i in 1:n.sim) {
res.array[i,] = with(data.m[sample.int(nrow(data.m),size=nrow(data.m)*retain.proportion),],
             tapply(n.birds.difference.5k.e1,year,sum,na.rm=T)) # %>% sum
}
colnames(res.array) = levels(data.m$year)
```

We take the mean value of these 10000 iterations as our best estimate of number of the total number of birds affected by the lights during the study period, rounded to nearest hundred thousand.

```
# All years combined
apply(res.array,2,mean) %>% sum %>% round(-5)
```

```
## [1] 1100000
```

```
# Breakdown by year
apply(res.array,2,mean) %>% round(-3)
```

```
##   2008   2010   2012   2013   2014   2015   2016
##  21000 669000  29000 198000   5000 130000  34000
```

```
# Mean year
apply(res.array,2,mean) %>% mean %>% round(-4)
```

```
## [1] 160000
```

```
# Standard deviation
apply(res.array,2,mean) %>% sd %>% round(-4)
```

```
## [1] 240000
```

```
# Median year
apply(res.array,2,mean) %>% median %>% round(-4)
```

```
## [1] 30000
```

Finally, we calculate a 95% confidence interval for this estimate by finding the 0.025 and 0.975 quantiles of the 10000 iterations.

```
# All years combined
round(quantile(apply(res.array,1,sum),probs=c(.025,.975)),-5)
```

```
##    2.5%   97.5%
##  600000 1600000
```

```
# By year
apply(res.array,2,quantile,probs=c(.025,.975)) %>% round(-3)
```

```
##        2008    2010  2012   2013  2014   2015  2016
## 2.5%   9000  217000 13000 110000     0  47000 15000
## 97.5% 34000 1178000 47000 298000 12000 229000 55000
```

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Little change in intensity or timing of bird migration over the Gulf of Mexico

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PRIMARY RESEARCH ARTICLE

WILEY Global Change Biology

Holding steady: Little change in intensity or timing of bird migration over the Gulf of Mexico

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Abstract

Quantifying the timing and intensity of migratory movements is imperative for understanding impacts of changing landscapes and climates on migratory bird populations. Billions of birds migrate in the Western Hemisphere, but accurately estimating the population size of one migratory species, let alone hundreds, presents numerous obstacles. Here, we quantify the timing, intensity, and distribution of bird migration through one of the largest migration corridors in the Western Hemisphere, the Gulf of Mexico (the Gulf). We further assess whether there have been changes in migration timing or intensity through the Gulf. To achieve this, we integrate citizen science (eBird) observations with 21 years of weather surveillance radar data (1995–2015). We predicted no change in migration timing and a decline in migration intensity across the time series. We estimate that an average of 2.1 billion birds pass through this region each spring en route to Nearctic breeding grounds. Annually, half of these individuals pass through the region in just 18 days, between April 19 and May 7. The western region of the Gulf showed a mean rate of passage 5.4 times higher than the central and eastern regions. We did not detect an overall change in the annual numbers of migrants (2007–2015) or the annual timing of peak migration (1995–2015). However, we found that the earliest seasonal movements through the region occurred significantly earlier over time (1.6 days decade^{-1}). Additionally, body mass and migration distance explained the magnitude of phenological changes, with the most rapid advances occurring with an assemblage of larger-bodied shorter-distance migrants. Our results provide baseline information that can be used to advance our understanding of the developing implications of climate change, urbanization, and energy development for migratory bird populations in North America.

KEYWORDS
climate change, eBird, Gulf of Mexico, migratory birds, phenology, weather surveillance radar

1 | INTRODUCTION

Avian migration is a global phenomenon with movements spanning thousands of kilometers through diverse environments (Newton, 2003), but quantifying first-principle parameters of migration, such as volume and timing, to characterize this phenomenon at large spatial extents has proven challenging. These measures are critical for quantifying animal movement responses to changing landscapes and climates (Kelly & Horton, 2016). With mounting evidence of phenological shifts and population declines, there is an immediate need for testing hypotheses within and among migratory systems (Both, Bouwhuis, Lessells, & Visser, 2006; Cohen, Lajeunesse, & Rohr, 2018; Parmesan & Yohe, 2003; Thackeray et al., 2016; Visser, Perdeck, Balen, & Both, 2009; Walther et al., 2002).

Estimates of the numbers of individual birds involved in nocturnal migration—the primary diel period of movement for most terrestrial species—range in the millions (Van Doren & Horton, 2018; Gauthreaux, 1971; Horton, Van Doren, Stepanian, Hochachka, et al., 2016) and may approach the billions when accounting for full season movements across broad geographic regions (Dokter et al., 2018; Hahn, Bauer, & Liechti, 2009). However, objective estimates of the number of individuals that undertake nocturnal migration within North America are largely unavailable (Rich et al., 2004). The importance of estimating the passage of migrants cannot be overemphasized, with a large body of literature highlighting recent declines in migratory bird populations (Askins, Lynch, & Greenberg, 1990; Both et al., 2006; Gauthreaux, 1992; Møller, Rubolini, & Lehikoinen, 2008; Nebel, Mills, McCracken, & Taylor, 2010; Robbins, Sauer, Greenberg, & Droege, 1989). Natural and anthropogenic obstacles abound for migrating birds, including predation (Cimprich & Moore, 1999; Loss, Will, & Marra, 2013b), habitat degradation and destruction (Norris & Marra, 2007; Norris, Marra, Kyser, Sherry, & Ratcliffe, 2004), collisions with structures (e.g., buildings, communication towers, wind turbines) (Loss, Will, Loss, & Marra, 2014; Loss, Will, & Marra, 2013a), and attraction to artificial light at night (Cabrera-Cruz, Smolinsky, & Buler, 2018; Van Doren et al., 2017; McLaren et al., 2018; La Sorte, Fink, Buler, Farnsworth, & Cabrera-Cruz, 2017). In addition to these factors, another fundamental challenge for migratory birds is shifts in resource availability induced by global climate change (IPCC, 2013), which has the potential to affect all aspects of their annual life cycle, including migration (Møller, Fiedler, & Berthold, 2010).

Within North America, the northern coast of the Gulf of Mexico (hereafter the Gulf) is an ecologically important region for the passage of spring migrants. Migrants leaving the Caribbean and Central and South America cross the Gulf (trans-Gulf) or travel around the Gulf (circum-Gulf) (Gauthreaux & Belser, 1999; Lowery, 1946; Stevenson, 1957). These coastal regions are vital for birds to make successful journeys, as they provide the first possible terrestrial stopover locations following overwater flights, allowing birds to replenish depleted fat stores and take shelter in adverse conditions (Moore, 2018). With the vast majority of long-distance migrants (i.e., migrants wintering south of the Gulf of Mexico) passing through this geographic region, quantifying where and when migrants move over and around the Gulf is fundamental for understanding how these patterns may be changing, particularly important given increased anthropogenic threats, including habitat and climate change, with which migrant populations must contend.

Migratory birds may be particularly vulnerable to climate change in the geographically disparate areas they use throughout their annual cycle (Bairlein & Winkler, 2001). For example, decreasing rainfall, and consequently diminished food abundance and body condition, at tropical wintering areas can delay the timing of departure for spring migration (Cooper, Sherry, & Marra, 2015; Gordo, 2007; Saino et al., 2007; Studds & Marra, 2011). Furthermore, phenologies of resources in temperate breeding areas are advancing, many species are arriving earlier (Cohen et al., 2018; Usui, Butchart, & Phillimore, 2017), and behavioral changes may be insufficient to match changes in resources (Mayor et al., 2017); moreover, there may be fitness consequences associated with arrival timing (e.g., Gienapp & Bregnballe, 2012; Møller, Balbontín, Cuervo, Hermosell, & Lope, 2009; Smith & Moore, 2005). Therefore, it is possible that Nearctic–Neotropical migrants are under pressure to increase rates of spring migration. Evidence shows that these migrants can adjust their speeds of migration within eastern North America as they encounter warmer spring temperatures (Marra, Francis, Mulvihill, & Moore, 2005). One long-term analysis of spring phenology at a single location along the Gulf of Mexico found annual variability but no advancement of passage timing, while some species have delayed passage by a few days over the 20-year period (1993–2012; Cohen et al., 2015). Cohen et al. (2015) also found annual tropical resource phenology was a poor indicator of temperate resource phenology, suggesting that migrants may adjust the rate of migration after crossing the Gulf of Mexico into continental North America. However, this study was done at a single location and no study has comprehensively measured the timing of migration across this critical passage region.

Variation in the arrival time of avian migrants has served as a useful framework for understanding how natural systems are responding to climate change (Both & Visser, 2001; Hüppop & Winkel, 2006; Hurlbert & Liang, 2012; Jonzén et al., 2006; Marra et al., 2005; Strode, 2003), but the number of large-scale examinations of phenological change in migratory birds is limited. Using data from the broadscale citizen science project eBird (Sullivan et al., 2014), the quantifications of system-wide phenological change, asynchrony in primary production, and migrant arrival are becoming clearer (Hurlbert & Liang, 2012; Mayor et al., 2017). However, much variation exists geographically and across species. With such variation, it is difficult to make general conclusions across species without standardized abundance measures. Weather surveillance radars (WSR) offer an opportunity to address this problem, as it is a standardized tool for quantifying the abundance of aerial migrants (Kelly & Horton, 2016). Furthermore, although radar data have limited utility for representing species identities, we can build an index of system-based phenology by integrating eBird and WSR data. The integration of these datasets is revealing new insights into macroscale movements (Horton et al., 2018; Kelly et al., 2016; La Sorte, Hochachka, Farnsworth, Sheldon, Van Doren, et al., 2015; La Sorte, Hochachka, Farnsworth, Sheldon, Fink, et al., 2015) and can add taxonomic resolution to the rich archive of WSR data. To date, such efforts have been primarily proofs-of-concept that this approach can capture properties of complex assemblages of biotic and abiotic factors that characterize multidimensional systems, heralding a new paradigm that combines data-intensive science and ecology (Hochachka et al., 2012; Kelling et al., 2009).

Here, we integrate data from eBird and weather surveillance radars to quantify the (a) timing, (b) intensity, (c) distribution, and (d) trends in migration timing and intensity of birds passing through the primary migratory corridor in the Western Hemisphere, the Gulf of Mexico. We predict declines in migration intensity through the Gulf of Mexico (Askins et al., 1990; Both et al., 2006; Robbins et al., 1989) and no change in the timing of migratory movements across the time series of years analyzed (Cohen et al., 2015).

2 | MATERIALS AND METHODS

2.1 | Weather surveillance radar

2.1.1 | Data processing

We used unfiltered (i.e., level-II) weather surveillance radar data from 11 stations surrounding the Gulf (Figure 1), acquired from NOAA's National Centers for Environmental Information, for the period March 1 to May 31 for each year from 1995 to 2015. We retained data between evening and morning civil twilight (i.e., when the sun angle was at least 6° below the horizon) and discarded any aerial samples containing precipitation that could obscure bird movements. We only used nights if at least half of the nocturnal period yielded clear samples for biological interpretation. For the characterization of movements, we categorized WSR stations into three regions: western (KCRP, KBRO, KHGX), central (KLCH, KLIX, KMOB, KEVX), and eastern (KTLH, KTBW, KBYX, KAMX).

We determined migrant flight direction (i.e., track) and groundspeed from radial velocity following Browning and Wexler (1968) and migration traffic from reflectivity from 0 to 3,000 m above ground level (a.g.l.), at 100 m altitudinal bins, following Farnsworth et al. (2016) and Horton, Van Doren, Stepanian, Farnsworth, and Kelly (2016b). We constructed height profiles of migrant track and intensity from the lowest elevation sweeps (0.5–4.5°) from 5 to 37.5 km. Elevation sweeps are completed every 5–10 min, and the assemblage of sweeps represents a volume scan, the sampling unit of our processing. When necessary, we dealiased radial velocity measures following Sheldon et al. (2013) through the WSRLIB package (Sheldon, 2015). To limit insect contamination, we excluded altitudinal bins with velocity azimuth displays with RMSE (root mean squared error) <1, and we removed samples with RMSE >5 to limit poor fits (Dokter et al., 2011; Horton, Van Doren, Stepanian, Farnsworth, & Kelly, 2016a; Horton, Van Doren, Stepanian, Hochachka, et al., 2016). We used samples with northward tracks only (<90° and>270°, Figure S1), resulting in an elimination of 14.1% of the data that remained after filtering protocols.

2.1.2 | Stationary clutter mitigation

Prior to the construction of height profiles of activity, we constructed masks to remove stationary clutter from the lowest elevational sweep for each radar for each year. We summed 500 (if available) low elevation scans (0.5°), starting on March 1 (00:00 UTC) and selected every 5th scan (day and night). We classified any pixel above the 85th percentile of the summed reflectivity as clutter and masked it from our analysis. As an additional precaution, we replaced the 0-m height bin with the 100-m height bin to reduce clutter contamination but still approximate the complete coverage to the ground.

2.1.3 | Data selection

To discriminate unsuitable volume scans for analysis (e.g., contaminated with precipitation or ground clutter from anomalous beam propagation) from suitable scans (i.e., empty airspace or biologically dominated reflectivity), we designed a random forest classifier using package "randomForest" (Liaw & Wiener, 2002). We trained the classifier on 22,172 manually classified nocturnal volume scans (e.g.,

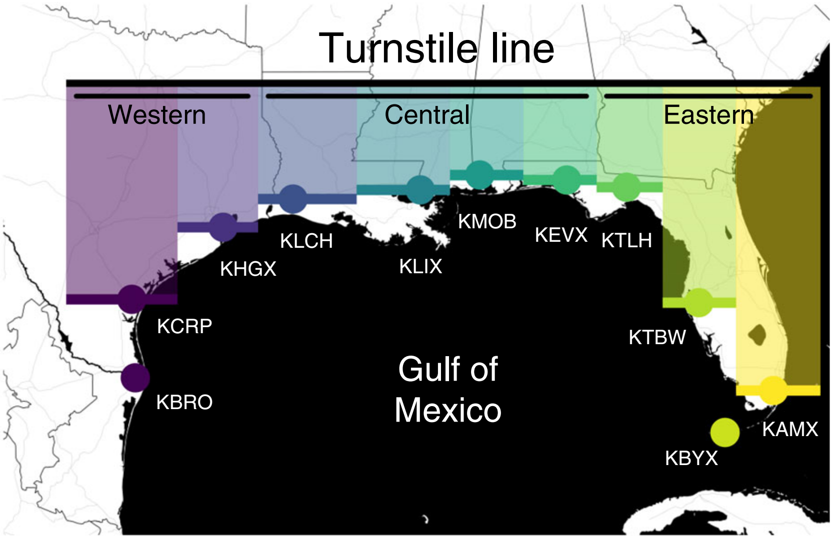

FIGURE 1 Locations of weather surveillance radar (WSR) stations and segments used for calculating nocturnal migration traffic through the Gulf of Mexico region. WSR stations were categorized into three regions, western (KCRP, KBRO, KHGX), central (KLCH, KLIX, KMOB, KEVX), and eastern (KTLH, KTBW, KBYX, KAMX), listed by increasing longitude. Stations and segments are shaded by longitude [Colour figure can be viewed at wileyonlinelibrary.com]

Figure S2), independently classified by KGH and BVD. We used samples with common classification agreement in the training set (93.7% of scans). We randomly selected scans for the training set in sequence sets for each radar for each year (mean samples per radar 102 year^{-1}). We extracted derived predictor variables from profiles of reflectivity, groundspeed, and summaries of the number of sampling volumes above 35 dBZ (see Table S1 for predictor descriptors). We generated 1,000 trees and restricted terminal node size to 50 scans to limit overfitting. The model resulted in 2.64% classification error (see Table S2). As an additional step to reduce the inclusion of false positives (i.e., unsuitable samples classified as suitable), we only used scans with a probability of being uncontaminated of 75% or higher. We processed 1,481,063 nocturnal scans from 1995 to 2015, and 1,161,029 were classified as suitable.

2.1.4 | Insect mitigation

To limit insect contamination, we eliminated data from height bins with airspeeds <5 m/s (Van Doren & Horton, 2018; Gauthreaux & Belser, 1998; Larkin, 1991). We calculated airspeeds through vector subtraction using measures of migrant groundspeed, wind direction, and wind speed. We quantified wind direction aloft using the North American Regional Reanalysis (NARR) dataset (Mesinger et al., 2006). NARR models zonal and meridional wind components every 3 hr at 25 hPa increments at a gridded 32-km spatial resolution. We aligned the nearest radar measures by time and height above ground level.

2.2 | eBird

To build a species-based perspective of migratory communities moving through the Gulf region, we used spatio-temporal exploratory models (STEM) (Fink et al., 2010) to estimate weekly probabilities of occurrence of nocturnally migrating bird species using bird observations from eBird (Sullivan et al., 2014) compiled during the period 2004 to 2011. From 446 species with reliable occurrence maps, we classified 143 as nocturnal migrants having probabilities of occurrence >0 in our sampling area (see Table S3). STEM use underlying landscape (land cover, elevation), temporal (year, day of year, time of day), and effort (duration, distance, number of observers) information to produce probabilities of species occurrence. For the STEM analysis, eBird data were limited to stationary and traveling counts (≤8.1 km) with local start times between 05:00 and 20:00 and counts that were <3 hr in duration. We rendered weekly estimates of probability of occurrence for each species at 130,751 points at a density of *ca*. 15 per 30 × 30 km within the contiguous United States using a geographically stratified random design (SRD). We used previously described methods to remove SRD points that contained very low probabilities of occurrence (La Sorte et al., 2014). Specifically, we converted weekly estimates of probability of occurrence to zero that were less than or equal to the 80th percentile of the nonzero occurrence probabilities for that week, and if the 80th percentile was <0.0175, which defined our minimum probability threshold, the probability threshold was set to 0.0175.

2.3 | Migrant distance

To estimate migrant distance, we used NatureServe breeding and nonbreeding range maps for 143 species (Ridgely et al., 2007). We first converted breeding and wintering range map polygons to collections of equal-area hexagons (cell size of 12,452 km^2, Sahr, 2011; Sahr, White, & Kimerling, 2003). Following this step, total migration distance was calculated as the great circle (orthodromic) distance between the geographic centroids of the breeding and nonbreeding ranges for each species. Geographic centroids were estimated by averaging the geographic locations of the hexagon cell centers occurring within each species' breeding and nonbreeding ranges (La Sorte, Hochachka, Farnsworth, Dhondt, & Sheldon, 2016). We weighted distances by the probability of occurrence of each species to emphasize distance measures of migrants moving through the radar sampling area.

2.4 | Estimating the number of migrants

To estimate the number of migrants passing, we first converted reflectivity factor (dBZ) to reflectivity (dBη) following: $\eta[\mathrm{dB}] = Z[\mathrm{dBZ}] + \beta$, where $\beta = 10\log_{10}(10^3\pi^5|K_m|^2/\lambda^4)$ (Chilson et al., 2012). We used an average WSR-88D wavelength (λ) of 10.7 cm and $|K_m|^2$ for liquid water of 0.93, the dielectric constant. This yielded $\beta = 13.37$. Converting reflectivity factor (Z) to reflectivity (η) resulted in units of cm^2 km^{-3}. We converted reflectivity (η) to birds km^{-3} by dividing by the radar cross-sectional (RCS) area of an average-sized migrant passing through the region, as indicated by ground-based observations (see below for RCS quantification).

To account for the flow of migrants over the sampling area and to limit the potential for double counting of migrants between radars, we multiplied birds km^{-3} by the northward component of the measured groundspeed (km h^{-1}) and integrated through the night to account for the nightly passage using linear interpolation for area under the curve, resulting in birds km^{-2}. We multiplied by the altitudinal resolution (0.1 km) of each altitudinal bin, resulting in birds km^{-1}.

Empirically measured radar cross-sections, a measure needed to convert radar reflectivity to number of birds, are difficult to acquire, and the number of unique species measured is limited. For this reason, we used previously measured S-band (~10 cm wavelength) radar cross-sections of known species to relate migrant body size (grams) to RCS (Table S4) (Eastwood, 1967; Houghton, Blackwell, Ogilvie, & Wilmot, 1975). Whereas radar theory predicts a complex, nonlinear relationship between RCS and reflector size (Stepanian, Horton, Melnikov, Zrnić, & Gauthreaux, 2016), especially of large scatters, like birds, we believe the number of species and variation in aspect relative to the radar will generalize effects of resonance to a broadly linear relationship. We found that body mass explained 89.9% of the variance in RCS measures ($\log_{10}$ (cross-section) = 0.670 ($\log_{10}$ (body mass), $p < 0.001$, $df = 10$, Figure 2a). Using this relationship, we converted the average mass of each species likely to pass through the region to a species-specific RCS (Figure 2b, Table S3).

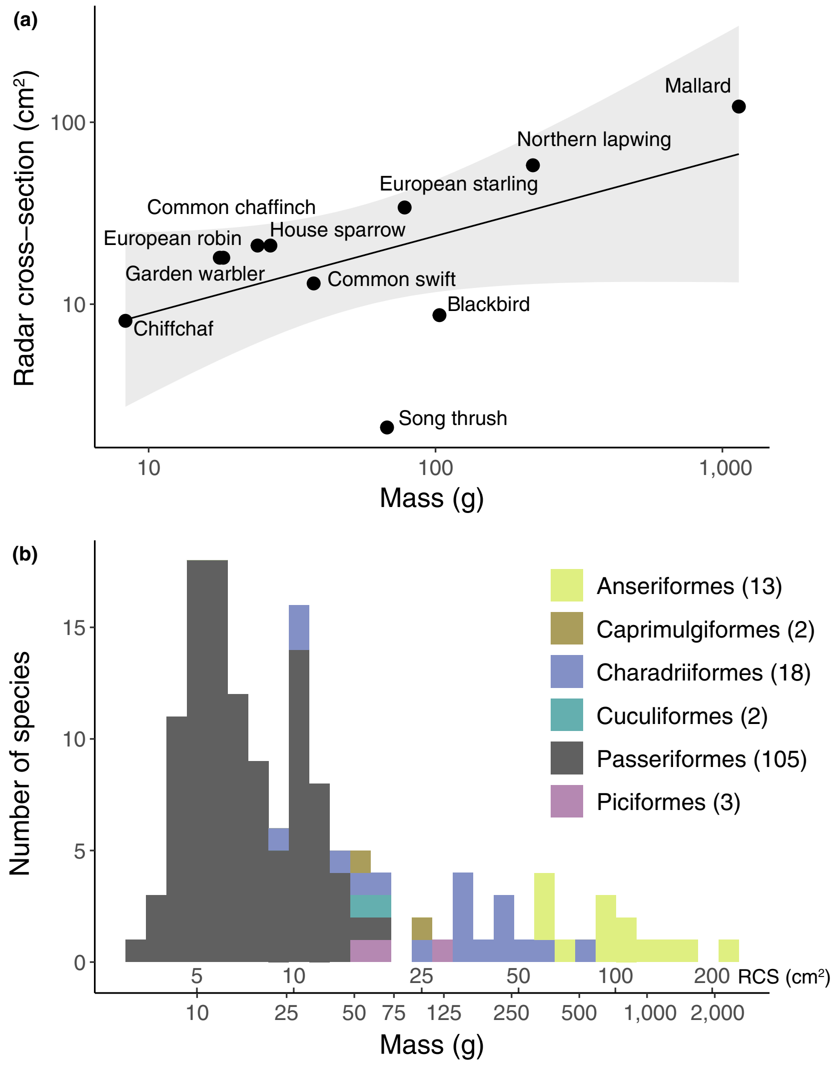

FIGURE 2 (a) Radar cross-section (cm^2) relationship with average species body mass (g). Body masses derived from Dunning (2008) and radar cross-sections from Eastwood (1967) and Houghton et al. (1975). (b) Average body mass (gram, log-scale) of nocturnal species by order and their corresponding radar cross-section (RCS, cm^2, log-scale) as predicted by (a). The number of species within each order is shown in parentheses [Colour figure can be viewed at wileyonlinelibrary.com]

We weighted our calculations of mean RCS by the probability of occurrence of each species to emphasize RCS measures of migrants moving through the radar sampling area. We calculated weekly mean probability of occurrence for each species from eBird at each WSR station using the SRD points that occurred within the biological range (80-km radius) of each WSR station. Our weights were the absolute value of the derivative of occurrence, to capture actively migrating species whose rates of detection in an area were therefore either increasing or decreasing. We used a square root transformation on the occurrence values to reduce the skewness of the distribution, but not completely remove it, as in a log-transformation (Horton et al., 2018). We log-transformed species RCS values before averaging to reduce bias from large-bodied species. We used the weekly estimate of RCS to predict nightly RCS by fitting a generalized additive model (GAM) to ordinal date for each WSR station. To determine the sensitivity of our estimates of migrant passage to our calculation of RCS, we made estimates using fixed RCS values and a range of transformations on RCS and species probability of occurrence (Table S5). Because KBYX is located on Key West and samples migrating birds primarily over marine environments where STEM estimates do not exist, we used the next closest radar installation (KAMX) to retain KBYX in our analysis. KBYX and KAMX are separated by roughly 210 km.

Lastly, to measure the total number of birds passing through the region, we used a transect, or turnstile line, spanning the entire Gulf region (1,954 km, Figure 1). We determined individual radar segments by measuring the distance between the midpoints of the radar locations. Multiplying the northward component of bird traffic at each station (birds km^{-1}) by the segment length resulted in the northward component of traffic estimates (i.e., number of birds) for each segment. To encompass the full scope of the movements, we extended the turnstile line beyond the western- and easternmost locations, using 1.75° and 1.25° length segments, respectively. As an additional precaution, we excluded KBRO and KBYX from our estimate of total passage to limit true double counting of migrants (i.e., the same migrant counted on two different radars). We removed these radars because they are positioned at comparable longitudes

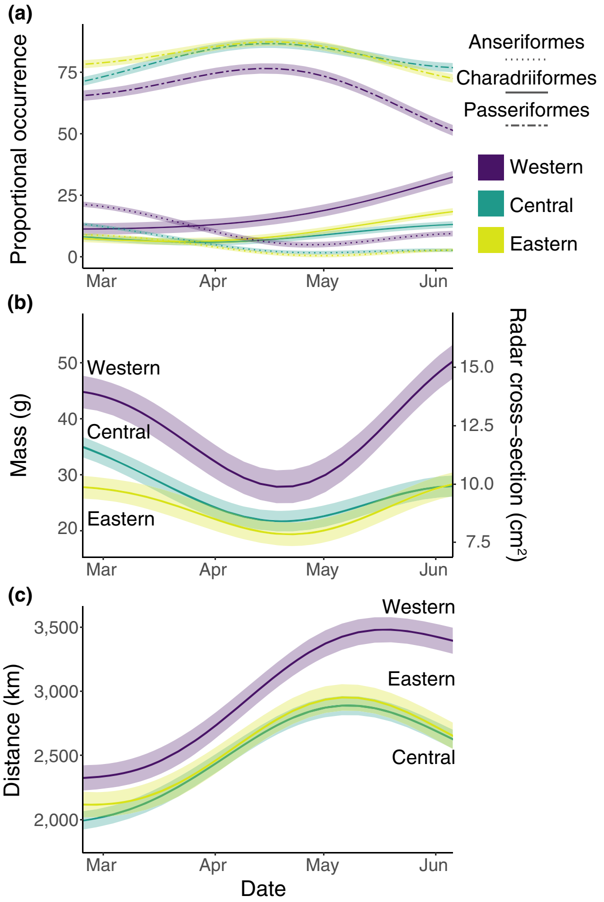

FIGURE 3 (a) Spring proportional occurrence of the top three species-rich orders in the western, central, and eastern regions. (b) Mean mass (g) and predicted radar cross-section (cm^2) for each region based on body mass weighted by STEM probability of occurrence. (c) Mean migration distance (km) for each region weighted by STEM probability of occurrence. Lines of (a–c) were generated by generalized additive models. Shaded regions show 95% confidence intervals from generalized additive models [Colour figure can be viewed at wileyonlinelibrary.com]

and proximity of more northerly radars. We must note that we use nocturnal measures only, likely resulting in a more conservative estimate of passage, as some nocturnal migrants may pass our stations during diurnal periods.

2.5 | Migration traffic and phenology analyses

We examined two primary signals annually, migration intensity (i.e., number of migrants and traffic rate) and migration timing (i.e., the dates at which 5%, 25%, 50%, 75%, and 95% of migrants passed).

We determined the average overall number of migrants passing through the entire region by fitting separate generalized additive mixed-models (GAMM) to the data from each radar station, specifying ordinal date as a smooth term and year as a random effect. We used the “quasipoisson” distribution family with log link function to restrict predictions to positive values and generated discrete predictions for each day for each radar, summing all nights to total number of migrants passing the entire region. To determine the magnitude of annual change in migration traffic, we constructed yearly models for each WSR station, fitting a GAM to each radar for each year, fitting a spline to ordinal date. We made nightly predictions and summed estimates to calculate the cumulative migration traffic rate (birds km^{-1}). We regressed cumulative migration traffic rate on year. We examined annual change at three levels: the entire Gulf, regional (western, central, and eastern), and individual WSR station.

Because precipitation contamination occluded our ability to make viable traffic estimates on some nights, our dataset contained gaps in the time series, to which we filled with GAM predictions. These gaps have the potential to bias our traffic estimate if migrant activity correlates with precipitation contamination (e.g., if proportionally fewer birds migrate in the presence of precipitation). To quantify how this distribution of missing data could influence our passage estimates, we randomly subsampled our dataset to demonstrate two extremes: (a) nights with precipitation were more likely to have low bird densities and (b) nights with precipitation were more likely to have high bird densities. Additionally, we examined our assumption that nights excluded due to precipitation show the same distribution of bird densities as clear nights. We employed these three sampling strategies by weighting the random selection by the inverse of the square root of the number of birds, square root of the number of birds, and an unweighted random selection.

To determine whether migration phenology changed from 1995 to 2015, we calculated the date of peak migration, defined as the date at which half the number of migrants had passed through the region. Additionally, we examined the dates when 5%, 25%, 75%, and 95% of migrants passed. We fit a GAM for each year for each radar and calculated the 5%, 25%, 50%, 75%, and 95% passage dates from model predictions. Because seasonal radar samples were at times sparse (See Figure S2), especially in the early years of the radar archive, we only used radars in years when at least five nights in March, April, and May and at least one third of the possible nights (total 92 nights) were sampled (~30 nights). Changes in phenology were calculated by regressing dates of cumulative activity (5%, 25%, 50%, 75%, and 95%) on year. To examine whether body size and migrant distance were predictive of the rate of phenological change, we regressed mass, distance, and the interaction of mass and distance on phenological change using a linear mixed-effects model with WSR station as a random effect. We calculated 95% confidence intervals from 1,000 bootstrapped samples.

In the history of the NEXRAD network, NOAA has implemented a series of upgrades. One subtle, but important, change occurred from November 2005 to September 2006, altering how stationary clutter (e.g., buildings, trees) and potentially low-speed targets, like birds, were filtered (Gaussian Model Adaptive Processing, Chrisman & Ray, 2005). Therefore, out of caution, we use data from 2007 to 2015 (9 years) for trend analysis of intensity. We use the full time series (1995–2015) to make phenological estimates, because they are insensitive to these changes.

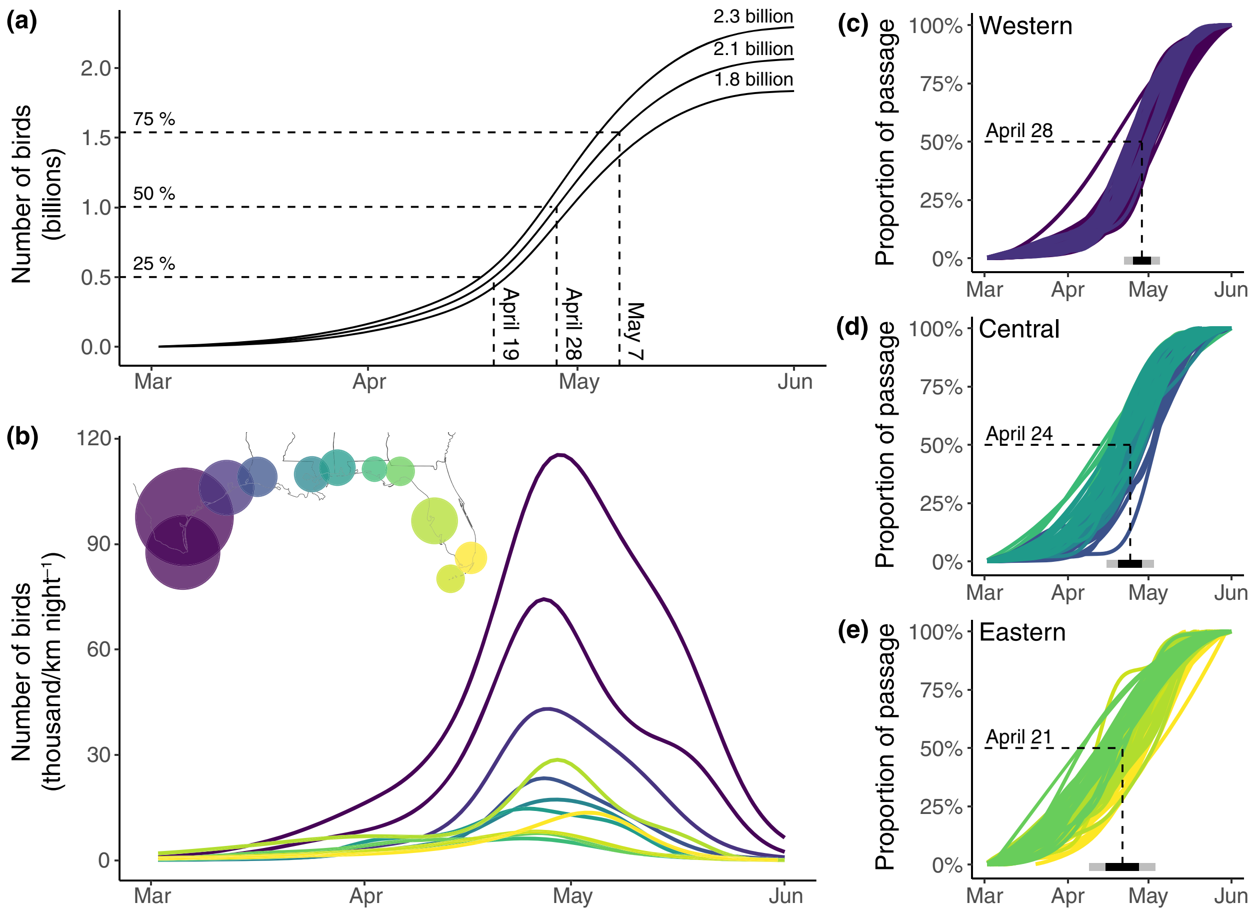

FIGURE 4 (a) Average cumulative number of nocturnal migrants passing through the northern Gulf of Mexico region from 2007 to 2015. Upper and lower lines show the standard error of generalized additive model. Dotted line and dates show the point at which 25%, 50%, and 75% of the migrants have passed. (b) Average seasonal phenology of the number of migrants passing per night at each weather surveillance (WSR) station from 2007 to 2015. Inset shows the mean seasonal activity with disk size scaled to the square root of the mean traffic rate (bird km^{-1}). (c–e) Cumulative proportion of migrants passing through the western, central, and eastern regions. Individual lines represent years for each WSR station from 1995 to 2015. Dates show the average point at which 50% of the migrants have passed and the black and gray bars show one and two standard deviations, respectively. Lines and points are shaded by WSR station longitude [Colour figure can be viewed at wileyonlinelibrary.com]

3 | RESULTS

The three most commonly occurring orders that passed through the Gulf region were Anseriformes, Charadriiformes, and Passeriformes, and occurrence varied noticeably by geographic location and more subtly over the season (Figure 3a). Through the season, we observed a higher occurrence of passerines in the central and eastern regions, with the western region showing a higher occurrence of Anseriformes and Charadriiformes. For these reasons, we observed higher body masses for birds moving over the western region. Translating body mass to average radar cross-section, we observed a seasonal range between 7.6 cm^2 (18.1 g) and 19.5 cm^2 (69.8 g) at individual stations, with the mean across the regions being 12.8 ± 2.1 cm^2 (*SD*; 38.1 g), 10.3 ± 1.6 cm^2 (*SD*; 27.9 g), and 9.2 ± 1.2 cm^2 (*SD*; 24.0 g), for western, central, and eastern, respectively (Figure 3b). Assemblage migratory distance generally increased through the season and was highest in the western region (Figure 3c).

Integrating species observations with radar measures, we estimated an average of 2.1 ± 0.2 (*SE*) billion migrants pass through the Gulf region during spring migration (range 1.7–2.6, Figure 4a, Figure S4). Our quantification of migrant passage assumed that nights excluded due to precipitation show the same distribution of bird densities as clear nights. Even with strong violations of this assumption, our estimation of traffic only changed by as much as 8.0% (mean 4.7 ± 2.4% *SD*), lending support for our methodology (Figure S5). Migration traffic was greatest over the western Gulf. Migration was particularly intense over south and central coast of Texas, and generally diminished moving eastward across the Gulf region (Figure 4b). The western region had an average migration rate of 26,224 bird km^{-1}night^{-1}, 5.4 times higher than the central and eastern regions (Figure 4b). Half of the migrants passing the Gulf region passed in an 18-day period between April 19 and May 7 (Figure 4a). Site-specific patterns of phenology were similar across the region, with peaks in late April and early May (Figure 4b). However, we

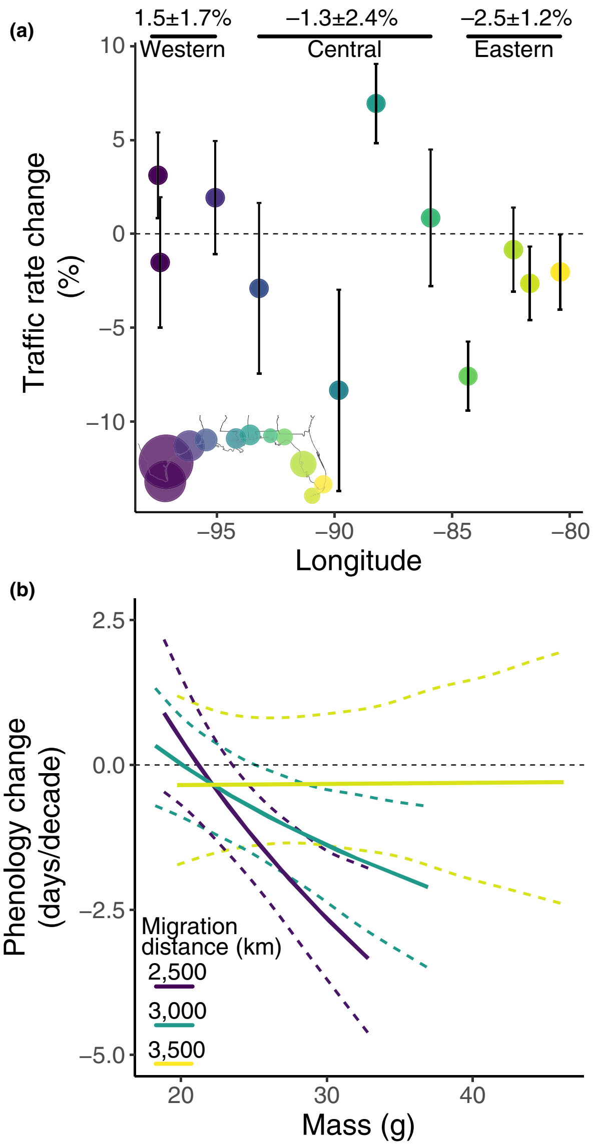

FIGURE 5 (a) Per year percent change in cumulative nocturnal migrant traffic rate from 2007 to 2015 for each weather surveillance radar (WSR) station. Error bars and average regional percent change shown with standard error. Inset reshown to emphasize the geographic disparity in traffic intensity. (b) Change in migration timing (days decade^{-1}) from 1995 to 2015 by body mass (g) and migrant distance (km) derived by eBird species probabilities of occurrence. Fitted lines shown from a linear mixed-effects model with WSR station as a random effect and the 95% confidence interval from 1,000 bootstrapped samples. Predictions only plotted for ranges for which observations were represented in our dataset [Colour figure can be viewed at wileyonlinelibrary.com]

generally observed earlier and more variable peak dates moving eastward across the Gulf region (Figure 4c–e).

We did not find a significant change in migration traffic through the entire Gulf from 2007 to 2015 ($p = 0.379$). We did find variation across sites and regions (Figure 5a), with no change detected in the western and central regions ($p = 0.286$ and $p = 0.799$, respectively) and a significant decline in the eastern region (−2.5 ± 1.2% year^{-1} *SE*, $p = 0.033$).

From 1995 to 2015, we observed a significant advancement (1.6 ± 0.7 days decade^{-1} *SE*, $p = 0.035$) in the timing of early-season migratory movements (i.e., 5% of cumulative movement, Figure S6); however, we did not see significant changes for later periods (25th, $p = 0.518$; 50th, $p = 0.588$; 75th, $p = 0.599$, 95th, $p = 0.638$, Figure S6). Body mass ($p = 0.005$) and migrant distance ($p = 0.020$) and the interaction of mass and distance ($p = 0.006$) explained the magnitude of phenological change moving through each quantile period, with the most rapid advances occurring with an assemblage of larger-bodied birds and shorter-distance migrants (Figure 5b). Moreover, the change in timing of peak migration exhibited a longitudinal trend across individual radars from earlier in the west to later in the east ($p = 0.015$, Figure S6).

4 | DISCUSSION

In a unique long-term and large-scale radar dataset, we found that between 1.7 and 2.6 billion nocturnal migrants (mean of 2.1 ± 0.2 *SE*) pass over the north coast of the Gulf of Mexico during spring migration. Half of these birds pass this important region within an 18-day window, from April 19 and May 7, and our findings indicate that neither the overall numbers of birds (2007–2015) nor their peak timing (1995–2015) has changed; however, the earliest seasonal movements (i.e., 5% of cumulative movement) advanced earlier over the duration of our study. Additionally, our findings show that migrants are not distributed evenly along the Gulf coast during spring migration, with the western Gulf used by more migrants than the eastern Gulf (Gauthreaux & Belser, 1999). The results of this study rely heavily on the integration of our two complementary datasets, radar and eBird, to estimate over broad spatial and temporal scales the number and timing of migrants moving into North America. This integration leaves no doubt that the Gulf of Mexico is a critical region for North American migratory bird populations and the changes that occur within this region—from urbanization to wind energy development—have the potential to significantly affect many migratory bird populations.

Peak spring migration passage timing was concentrated and consistent among the 21 years considered in this study. This study included long-distance migrant species that spend the winter in the Neotropics and short-distance migrant species that winter locally around the Gulf (See Table S3). While short-distance migrants may be more flexible (Calvert, Mackenzie, Flemming, Taylor, & Walde, 2012; La Sorte et al., 2016), long-distance migrants are under strong endogenous control for departure timing (Berthold, 1996). Within these areas, there is no evidence for advancing phenological changes in greenness (Cohen et al., 2015); therefore, it is not entirely surprising to see relatively consistent median passage timing when departing, crossing, and navigating around the Gulf. Similarly, long-term species-specific comparisons within this region have not found evidence of earlier passage linked with changes in en route spring greening of vegetation (NDVI) for passerines that overwinter in South America (Cohen et al., 2015). In contrast, passerines that overwinter in the Caribbean and Central America have delayed their peak passage by 2–3 days over the last 20 years, which has been linked to drier conditions on their wintering areas (Cohen et al., 2015). Consistent with this, the change in median passage at individual radar stations showed a trend of later passage in the eastern Gulf, a region dominated by smaller-bodied passerine species. However, long-distance migrants are adjusting their migration timing to arrive earlier to their breeding grounds (Usui et al., 2017), suggesting this change is occurring after they circumnavigate or cross the Gulf (Marra et al., 2005). We predict the magnitude of phenological change increases with increasing latitude across North America during spring movements. Yet, while adjustments to stopover duration can be made, the growing divide between resource availability and migration initiation may stretch the limit of this phenotypic plasticity (Schmaljohann & Both, 2017), resulting in insufficient adjustments and possibly trophic mismatches (Strode, 2015; Wood & Pidgeon, 2015). Numerous studies of plot-level phenology demonstrate that variation in phenology of individual plant species is impactful for migrant phenology (Strode, 2009; Wood, Pidgeon, Liu, & Mladenoff, 2012). Further effort to scale-up species-level phenology from standardized plot-level measurements is needed.

Our examination of the earliest seasonal movements of migration (i.e., 5% of cumulative movement) revealed earlier passage timing of first migrants at a rate of 1.6 days decade^{-1} earlier. This supports other evidence of earlier migratory movements with a warming climate (Cohen et al., 2018) and likely explained by shifts in the departure of short-distance migrants that overwinter along the northern Gulf, rather than for intercontinental long-distance migrants, since peak passage timing has not consistently shifted. We predicted the greatest changes in phenology were driven by assemblages of larger-bodied and shorter-distance migrants. This interpretation is consistent with other evidence that short-distance migrants are responding more readily to climate change (Butler, 2003; Hurlbert & Liang, 2012; La Sorte et al., 2016) and our finding that body mass explained the magnitude of phenological changes, with the most rapid advances occurring with an assemblage of larger-bodied birds supports this. In the western Gulf, where larger species, particularly waterfowl and shorebirds, were more prevalent, the change in timing of passage at individual radar stations trended toward earlier passage times. Waterfowl species have been shown to have slightly higher incidences of advancing arrival dates on their breeding grounds in Canada compared to other taxa (Murphy-Klassen, Underwood, Sealy, & Czyrnyj, 2005). Longitudinal variation in the taxonomic composition of spring migrants along the north coast of the Gulf offers a unique opportunity to better understand how phenological responses to climate change vary among different categories of migrants (e.g., migration distance, winter range location, and foraging guild).

This study provides a long-term estimate of the total numbers of nocturnal migrant passing through the GOM region. Generating these estimates required a series of advances in radar processing and analytical methods (e.g., big data analytics for the entire radar archive), species occurrence information (eBird) and distribution modeling techniques (STEM), and in the procedures for calculating bird number through the integration of these resources and methods. The characterization presented in this study represents a major leap forward for understanding the magnitude of bird migration in the Gulf region and brings us closer to achieving critical goals of monitoring in the region and understanding the role of migration in the dynamics of bird populations (Cohen et al., 2017). Our results from 2007 to 2015 did not show evidence of an overall decline in the number of migrating birds, however we did see evidence of a decline in the eastern Gulf. The lack of significant changes does not preclude the existence of troubling declines in the abundance of some migratory bird species during this time period, especially aerial insectivores and migrants that breed in grasslands and coastal habitats (Nebel et al., 2010; The State of North America's Birds, 2016). However, it is possible that these observed declines are not evident in our findings due to increases in other species, which requires further study.

Synthesizing an increasing volume and diversity of ecological data to generate relevant and reliable summaries is a grand challenge in the natural sciences. Our methodology and results emphasize the importance of integrating WSR data with species-specific information (Horton et al., 2018; Kelly et al., 2016; Shipley, Kelly, & Frick, 2017; La Sorte, Hochachka, Farnsworth, Sheldon, Fink, et al., 2015; La Sorte, Hochachka, Farnsworth, Sheldon, Fink, et al., 2015). A common criticism of using WSR data to study the patterns and behaviors of migrating birds is the lack of species specificity (Kelly & Horton, 2016). In this study, we present a path forward that can incorporate species-specific information with WSR data that substantially enhances the scientific value of each individual dataset. However, our analysis, leveraging more than one million radar samples, is still a small fraction of the entirety of the radar archive, which totals 143 WSR stations (11 used in this study, 7.7%). Examining these questions at even larger extents (e.g., continental United States) and across seasons (spring and fall) will increase our understanding of broad ecological consequences of a changing climate and bring us closer to a full annual-cycle analysis of migratory systems.

Our analysis of the timing and intensity of migration through the Gulf yields new insights necessary to address pressing global change research questions in a comprehensive and robust manner. For the first time, we can estimate where, when, and how many migrants move through this important ecological region. Our analysis showed that early migrants have advanced their movements through this region and mean body size and migrant distance was predictive of the pace of advancement. This adjustment should allow large-bodied migrants to time their arrival to the breeding grounds with changing resource phenology. However, the timing of peak migration movements has not changed, a period dominated by small long-distance songbirds which typically have less flexible migration programs (Berthold, 1996; Gwinner, 1996). While we did not detect declines over the duration of our study, this does not preclude the possibility that some declines are masked by increases in other species. This work fills a critical gap, enhancing our ability to document and understand existing consequences of global change. The resulting information is also important to inform modeling efforts designed to predict the long-term implications of different climate change scenarios and inform conservation efforts within the Gulf of Mexico region.

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AUTHORS' CONTRIBUTIONS

KGH, BVD, JFK, and AF worked to conceive and design this study. KGH, JK, and AF drafted the manuscript. KGH processed radar and wind data and generated figures. KGH and BVD conducted and designed statistical analyses. DF designed and implemented the species distribution models, and FAL and DF designed the analysis of the model products. All the authors have provided editorial advice, approved the final version of this manuscript, and agree to be accountable for all aspects of the work.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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LETTER

Navigating north: how body mass and winds shape avian flight behaviours across a North American migratory flyway

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Abstract

The migratory patterns of birds have been the focus of ecologists for millennia. What behavioural traits underlie these remarkably consistent movements? Addressing this question is central to advancing our understanding of migratory flight strategies and requires the integration of information across levels of biological organisation, e.g. species to communities. Here, we combine species-specific observations from the eBird citizen-science database with observations aggregated from weather surveillance radars during spring migration in central North America. Our results confirm a core prediction of migration theory at an unprecedented national scale: body mass predicts variation in flight strategies across latitudes, with larger-bodied species flying faster and compensating more for wind drift. We also find evidence that migrants travelling northward earlier in the spring increasingly compensate for wind drift at higher latitudes. This integration of information across biological scales provides new insight into patterns and determinants of broad-scale flight strategies of migratory birds.

Keywords

Citizen science, eBird, flight biology, macroecology, radar, remote sensing, seasonal bird migration, wind drift.

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INTRODUCTION

Migration is one dimension of a global, ecological system response to the seasonality of Earth's productivity (Mueller & Fagan 2008; Baguette *et al.* 2013; Way & Montgomery 2015). Migration is ubiquitous among a diverse array of taxonomic groups, varying in nearly as many ways as the taxa engaging in these movements. Such variation may have significant implications for individuals in terms of fitness as well as for populations of individuals and the environments in which they occur (e.g. Bonte *et al.* 2012; La Sorte *et al.* 2014a). Migratory behaviour varies among species based on mode, speed, duration, body mass and scale—all of which are dictated by the physical and natural environment in which it occurs. In turn, migration affects the structure and function of the ecosystems that these species occupy across the annual cycle (Fridley 2001; Bauer & Hoye 2014; Chapman *et al.* 2015b; Hessen *et al.* 2017). Of all the taxonomic groups that display migratory behaviour, birds have received the greatest attention (Newton 2008). During migratory journeys, which may last weeks or months, birds must decide when to fly, and once in flight make decisions on the direction, speed and duration of flight (e.g. Votier 2018).

Varying wind conditions present major challenges for aerial navigators, and understanding birds' context-dependent responses to winds aloft is fundamental to understanding avian navigation. Successful movements depend strongly on these behaviours, which directly affect survivorship and fitness. With the exception of precipitation, wind is the most important meteorological factor determining migratory behaviour (Richardson 1978, 1990). Tailwinds create the optimal migration conditions (Alerstam 1979; Akesson & Hedenström 2000), but extensive geographic variation in the strength and direction of prevailing winds may dictate migration departure during locally suboptimal conditions (Liechti 2006; Sjöberg *et al.* 2015; Horton *et al.* 2016b). Migrants must contend with getting blown off course, making constant en route adjustments that may incur proximate (e.g. energetic costs) or ultimate consequences (e.g. death or failure to breed). Documenting the relationship among migratory behaviours, traits of migrants and wind conditions at the scale of an entire migration system is a grand challenge in migration research (e.g. Klaassen *et al.* 2010; Lanzone *et al.* 2012; Sergio *et al.* 2014; Wikelski *et al.* 2015; Flack *et al.* 2016; Åkesson *et al.* 2016; Vansteelant *et al.* 2017a,b).

The ecological systems migrants inhabit are inherently complex and are not mechanistic combinations of their constituent parts (individuals; Holling 1973). Models of optimal migration behaviour have made significant progress in revealing the factors constraining broad-scale seasonal movements (Erni *et al.* 2002, 2003, 2005; Vrugt *et al.* 2007; Kranstauber *et al.* 2015). However, more efficient approaches are still needed to amass

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and analyze data that characterise rich emergent behavioural characteristics of migration systems, which remains a principal challenge (Shipley *et al.* 2017). Understanding global bird movements, and in particular, their adaptations to predictable patterns in atmospheric circulation is an area of active research (La Sorte *et al.* 2014b; Chapman *et al.* 2015a; Kranstauber *et al.* 2015). An alternative to an individual-based strategy for studying day-to-day variation in migratory behaviour is an approach where the migration system's aggregate properties themselves are studied (e.g. La Sorte *et al.* 2013). By measuring these properties directly, rather than attempting to reconstruct them from individual constituents, we can efficiently quantify dominant long-term and large scale system-level behaviours. To this end, we use a data-intensive approach to examine this interaction. Specifically, we address two long-standing ecological questions: How do migratory birds adjust their flight strategies in response to predictable large scale patterns in atmospheric conditions; and what is the role of a dominant life history trait, body mass, in this response?

Weather surveillance radar (WSR) can measure the emergent properties of avian migration systems, capturing the aggregate behaviours of millions of individual migrants moving through the atmosphere (Kelly & Horton 2016). Although WSR can detect these movements at continental extents, they cannot resolve species identities (Gauthreaux & Belser 1998), a feature that has historically imposed stark limitations on WSR-based inferences (Kelly & Horton 2016). However, the rapid growth and accessibility of citizen science data, specifically the eBird enterprise (Sullivan *et al.* 2014), have transformed our understanding of avian migration at the population scale using a species-level perspective (Silvertown 2009; Hochachka *et al.* 2012; Hurlbert & Liang 2012; La Sorte *et al.* 2013, 2016; La Sorte & Fink 2017). Furthermore, species-level information from eBird can be used to enhance the aggregate-level information available from WSR (La Sorte *et al.* 2015a,b). Although eBird observations are made primarily during diurnal periods and do not directly characterise nocturnal movements, the merger of eBird data with WSR-derived nocturnal estimates of migratory birds aloft has the potential to reveal the translation from species-specific properties to system-based properties. For instance, we can address how the aggregate migrant body mass (eBird) with the aggregate measures of migrant airspeed (radar). This merger is a natural advancement toward the growth of a macroecological sensing network for studying the broad-scale patterns and determinants of avian migration systems.

Theoretical predictions of the behaviour of migrating birds abound (Pennycuick 1969; Alerstam 1979; Alerstam & Hedenström 1998), and recent system-level investigations of stopover behaviour have mapped migration trajectories (La Sorte *et al.* 2013, 2016). The influence of prevailing winds on birds' flight strategies are well known in the context of optimal migratory movements (Liechti 2006; Chapman *et al.* 2011; Horton *et al.* 2016a); however, whether migrants need to routinely select for opposing winds in a context dependent manner remains unresolved, specifically with respect to proximity to their end destination. For this investigation, the prediction that body mass, as a driver of life history and energetics (e.g. Nagy 1987), ought to drive variable wind compensation behaviour among migrants is a key to investigating context-dependent behaviours. Indeed, at the scale of individuals there is robust evidence of body mass driving flight strategies of migrants (Alerstam *et al.* 2007). We investigate these relationships at the scale of the migration flyway, which has not been done previously.

Migration theory predicts that migrants should tolerate wind drift near the origin of their migratory route and increase the degree to which they compensate for wind drift as they near their ultimate destination (Alerstam 1979; Liechti 2006). In addition, morphological constraints (e.g. body mass and its impact on maximum flight speed) may limit species' abilities to fully compensate, with large-bodied faster flying migrants showing greater compensatory abilities. The central portion of North America offers an ideal locality to test this hypothesis. This region extends upwards of *c.* 2500 km from subtropical habitats bordering the Gulf of Mexico, across the grasslands of the Great Plains, and extending into the boreal forest near the Canadian border. This region is only minimally influenced by major ecological barriers (e.g. mountains, lakes, or deserts) or leading lines (i.e. coastlines or rivers), that may otherwise affect flight strategies (Horton *et al.* 2016c). Here, we use data from 20 WSR stations and bird observations from eBird (Sullivan *et al.* 2014) to test our optimal flight strategy predictions. In addition, we examine how the quality of our predictions are affected by two traits that dictate in-flight migratory behaviour: body mass, an important morphological trait, and migration destination, an important natural history trait.

MATERIALS AND METHODS

Weather surveillance radar

We processed unfiltered (i.e. level-II) Weather Surveillance Radar 1988 Doppler (WSR-88D) data from 20 radar stations covering a large portion of the central USA from spring 2013 to spring 2015 (21.6° of latitude; Fig. 1) (Crum & Alberty 1993). To investigate spring behaviours, we acquired radar data from NOAA's National Centers for Environmental Information (https://www.ncdc.noaa.gov) for the period 1 March to 31 May of each year. The National Weather Service (NWS) within the National Oceanic and Atmospheric Administration (NOAA) operates nineteen of these radars and the Department of Defense (DOD) operates one (KGRK). Every 5 to 10 min the radars make a series of sequential elevation observations (e.g. 0.5° above horizontal, 1.5°, … 19.5°), scanning the airspace from 0 to 359° degrees in azimuth at each elevation. The volume coverage pattern (i.e. airspace sampling routine) is tailored to the atmospheric conditions, and for this reason sampling update times can vary.

We retained data between evening and morning civil twilight (i.e. when the sun angle was at least 6° below the horizon) and discarded any aerial samples containing precipitation, which obscures bird movements. Because the number of radar sweeps (456 101 sweeps) prevented complete manual screening, we used a two-stage approach to remove weather contamination: First, we removed volume coverage

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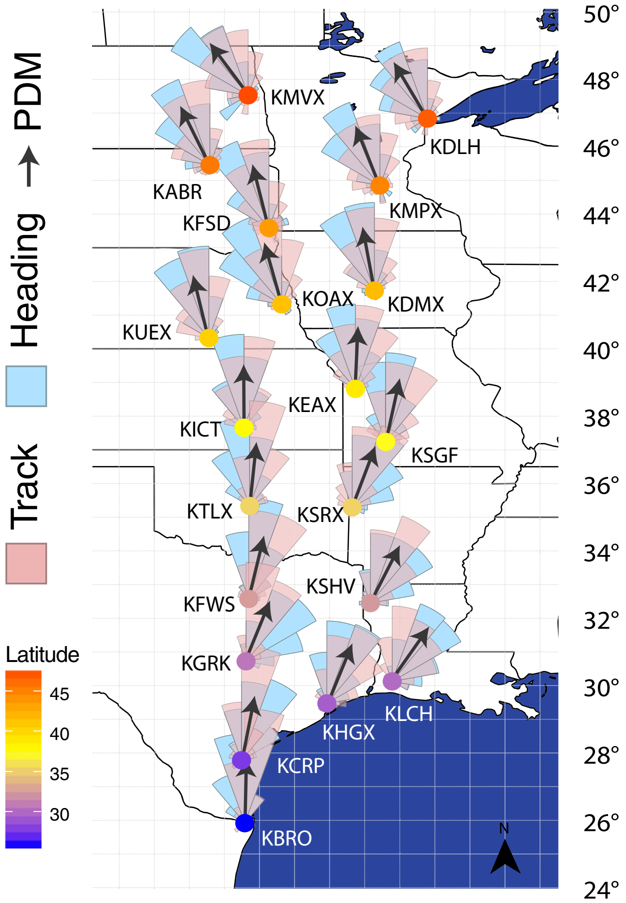

Figure 1 Rose diagram showing the distribution of migrant track (pink) and heading (blue) during spring migration (2013–2015) from 20 weather surveillance radar (WSR) stations locations in the central USA. Black arrows identify the modelled in-flight preferred direction of movement. We weighted track and heading distributions by scaled reflectivity factor and used 20° sectors for the plotting of track and heading measures. The colour of the WSR stations is based on its latitude.

patterns in which 70% of the low elevation (*c.* 0.5°) sweep volumes had correlation coefficient (a polarimetric radar variable) values > 0.90 or 70% of the sampling volumes had reflectivity measures > 35 dBZ (Stepanian *et al.* 2016). Second, we visually screened all remaining sweeps (n = 250 552) for weather contamination. Examination of a subset of images following the first automated step (KMVX 2013, n = 11 543) revealed that automated filtering by correlation coefficient and reflectivity returned a 2.7% false negative rate (203 of 7582). We deemed the false positive rate too high for our biological application (573 of 3961; 14.5%), mandating the need for manual inspection (step two) (see Fig. S1 for illustrated workflow). This two-stage process resulted in 231 241 sweeps containing weather-free data, which we retained for subsequent stages of filtering and analysis (50.7% of the total available sweeps).

We used the WSRLIB package (Sheldon 2015) to determine migrant track (flight direction with respect to the ground) and heading (orientation of body axis) from radial velocity and correlation coefficient (ρ_{HV}), respectively, from 55 to 1995 m above ground level (a.g.l.) following Browning & Wexler (1968) and Stepanian & Horton (2015). When necessary, radial velocity measures were dealiased following Sheldon *et al.* (2013). To limit insect contamination, we excluded velocity azimuth displays (a computation of the mean Doppler velocity to derive migrant track and groundspeed) with RMSE (root mean squared error) < 1, and we removed samples with RMSE > 5 to limit poor fits (Dokter *et al.* 2011; Horton *et al.* 2016a). We restricted polarimetric azimuth displays (a computation of the correlation coefficient, ρ_{HV}, to derive heading) to fits with > 15% of the variance explained (when fitting ρ_{HV} to a sinusoid) and an average standard deviation in heading direction that was < 20° (Stepanian & Horton 2015; Horton *et al.* 2016c). Profiles of track and heading were weighted by log-scaled reflectivity (a measure that scales with biological density), constructed from the lowest elevation sweeps, (0.5–4.5°) from 5 to 37.5 km (Farnsworth *et al.* 2016).

For statistical weighting of aerial movements, we calculated the large-scale (20–125 km) intensity of migratory movements for all biologically classified sweeps from the lowest elevation sweeps (~ 0.5°) of reflectivity. We calculated intensity (i.e. phenology indices) and directional data from the lowest sweep because it provides a large-scale perspective of migratory behaviours, and we constructed vertical profiles of reflectivity at closer ranges and higher elevation scales because they allow a better sampling of the altitudinal distribution of birds (Buler & Diehl 2009). We summarised radar measures to tenths of the night (i.e. deciles) to avoid sampling changes caused by the duration of the night. We only used data from individual radars on nights where two or more radars acquired usable samples (e.g. those that were dominated by biology) through the night and five or more deciles of the night were sampled at the individual radar. Overall, we retained 106 772 sweeps (23.4% of the total available sweeps) across 238 unique sampling nights (17 080 unique deciles, see Fig. S2) from three spring migratory seasons.

Winds Aloft

We quantified wind direction and variance aloft with the radar sampling range (37.5 km) using the North American Regional Reanalysis (NARR) data set (Mesinger *et al.* 2006). NARR models zonal and meridional wind components every three hours at 25-hPa increments at a gridded 32-km spatial resolution. To characterise general nocturnal wind patterns, regardless of migratory activity and precipitation conditions, we extracted the 03:00 UTC wind speeds and directions from measures between typical avian flight height ranges, 350–650 m above ground level (875–975 hPa)(La Sorte *et al.* 2015a,b; Horton *et al.* 2016b). We used 03:00 UTC because it mostly closely coincides with peak migration timing (Zehnder *et al.* 2001; Horton *et al.* 2015; Farnsworth *et al.* 2016). We weighted the prevailing directions by wind speed. All dates between 1 March and 31 May from 2013 to 2015 were used to characterise average wind patterns.

For linking biological measures with wind speeds and directions, we aligned the nearest radar measures by time and

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height above ground level (55 to 1995 m). We weighted the vertical structure of wind speed and direction by vertical profiles of reflectivity. In addition to determining the dominant wind regimes and winds used by migrants, we used winds aloft to calculate migrant airspeed (powered flight speed). Knowing groundspeed, wind direction, and wind speed, we calculated migrant airspeeds through vector subtraction. As an additional step to limit insect contamination, we eliminated individual height bins (100 m resolution) with airspeeds < 5 m/s (Larkin 1991; Gauthreaux & Belser 1998; *c.* 28.5% of altitudinal samples). Following the condensation of the data to deciles, we observed the distribution of mean airspeed measures to be long-tailed (skewed-right), and for this reason we eliminated samples with airspeeds > 30 m/s ($n = 67$ deciles, *c.* 0.99 quantile), a threshold at the upper range of a typical migrant (Alerstam *et al.* 2007).

eBird

We used spatio-temporal exploratory models (STEM) developed by Fink *et al.* (2010) to estimate weekly probability of occurrence of nocturnally migrating bird species using bird observations from the eBird database (Sullivan *et al.* 2014) compiled during the period 2004 to 2011. Because the STEM procedure is computationally very intensive, directly matching the temporal range of the radar data with the STEM estimates was not feasible. In addition, the 2004–2011 implementation is currently the most comprehensive where the largest proportion of the North America avifauna was analysed. We observed comparable wind directions and speeds across the two time periods, and thus do not feel timing differences are of concern (Fig. S3). From 446 species, we classified 157 as nocturnal migrants having probabilities of occurrence that were > 0 in our sampling area after applying the thresholding procedure describe below (see Table S1). STEM models use underlying landscape (landcover, elevation), temporal (year, day of year, time of day), location (latitude and longitude) and effort (duration, distance, number of observers) information to produce probabilities of species occurrence. For the STEM analysis, eBird data were limited to stationary and travelling counts (≤ 8.1 km) with local start times between 05:00 and 20:00 and counts that were < 3 h in duration. STEM uses an ensemble of randomised overlapping local models, which are each applied across a restricted geographical and temporal extent (Fink *et al.* 2010), to discern associations between observed patterns of bird occurrence (eBird data) and local land-cover characteristics (Fry *et al.* 2011). The assembly of these models are used to make spatial and temporal predictions for the distribution of each species throughout the year based on local land-cover characteristics. These estimates represent the probability of observing a species by an eBird participant that searches from 07:00 to 08:00 while travelling 1 km. See Fink *et al.* (2010) for additional details on the STEM procedure.

The weekly estimates of probability of occurrence for each of the 157 species were rendered at 130 751 points at a density of *c.* 15 per 30 × 30 km within the contiguous USA using a geographically stratified random design (SRD) (see Fig. S4). We used previously described methods to remove SRD points that contained very low probabilities of occurrence (La Sorte *et al.* 2014b). Specifically, we converted weekly estimates of probability of occurrence to zero that were less than or equal to the 80th percentile of the non-zero occurrence probabilities for that week, and if the 80th percentile was < 0.0175, which defined our minimum probability threshold.

We then calculated the mean probability of occurrence for species at each WSR station during each week using the SRD points that occurred within a 125-km radius of each WSR station (see Fig. S4). We defined presence/absence for the species richness calculations if the mean probability of occurrence of a species at a WSR station was < 0. We derived body mass estimates for each of the 157 species from Dunning (2008); sex- and subspecies-specific masses were averaged following La Sore *et al.* (2015b). To calculate average body mass within the radar coverage area we weighted body masses by the underlying species' STEM probability of occurrence.

We used NatureServe breeding range map polygons (Ridgely *et al.* 2007) to estimate the direction of movement between centres of species' distributions and radar locations for the 157 species. We used the angles to predict the population-level direction of movement of species reflected in the radar measures. For each radar station and each species, we calculated the angle from the station to the centre of the breeding range following formulae by Snyder (1987). We only retained distances from angles < 90° and > 270° because these species should be making progress northward towards their breeding range. For each radar station and week, we calculated the mean angle of all species (Fig. S5 and S6), weighted by the proportional occurrence from STEM models. The proportional occurrence was calculated weekly, by dividing species-specific STEM probability of occurrences within the radar domain by the weekly summed total probability of occurrence (for all species) within the radar domain. Prior to the calculation of proportional occurrence, we used a square-root transformation to reduce the range of weights, preventing conspicuous species from dominating the weighting procedure. The resulting weighted average of trajectory angles, weighted by proportional occurrence, was the eBird-derived predicted direction of movement for a given radar station and time point.

Statistical analysis

We based our approach on the methods of Green & Alerstam (2002) to determine the degree of compensation for wind drift and radar-derived preferred direction of movement (Chapman *et al.* 2011; Kemp *et al.* 2012). In brief, we used a mixed model to regress radar measures of track on the difference between track and heading (α) (Green & Alerstam 2002; Horton *et al.* 2016c; Van Doren *et al.* 2016). This model is used to derive two important metrics describing migrant flight strategy: (1) slope of α vs. track, a measure of the propensity of drift (0 = complete compensation for wind drift; 1 = no compensation, or total drift), and (2) the y-intercept of this regression, the direction at which birds align themselves downwind, which is a measure of the preferred direction of movement.

To test for effects of latitude and body mass on flight strategies, we constructed a linear mixed-effects model with α, average body mass, latitude, and day of year as fixed predictors.

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To determine proper model complexity, we constructed three models, all including the four main fixed effects but varying in the complexity of their interactions. We selected the best model using the Akaike Information Criterion (AIC). (see Table S2 and S3 for model details). We standardised (mean = 0, SD = 1) body mass after subtracting 30 g and rescaled latitudes so that the mean latitude was zero. We also standardised day of year (mean = 0, SD = 1). Therefore, the intercepts of the model would be at a body mass of 30 g, the mass of a medium-sized migratory songbird, and the mean latitude and mean time of season. Random intercept terms were station, station × year, date and station × date. We included one random slope term, of α varying on station. We weighted our analysis by scaled radar reflectivity. We used body mass to differentiate how coarse taxonomic shifts influence flight behaviour. Body mass distributions showed general separation by order (Fig. S7) and by timing of movement (Fig. S8). For model predictions, we display the 20th, 40th, 60th and 80th percentiles of the average system-based body masses: 40, 60, 80 and 140 grams.

We visualised uncertainty in model predictions by bootstrapping 95% confidence intervals of key parameters of interest. Bootstrapping is recommended by the authors of *lme4* for determining uncertainty in mixed-model predictions (Bates et al. 2015). We also elected to perform bootstrapping because the residual distribution was long-tailed, which may bias conventional *P*-values.

All statistical analyses were conducted in R version 3.3.3 (R Core Team 2017), and linear mixed models implemented using the lme4 package (Bates et al. 2015). All summary statistics are reported with 95% confidence intervals unless otherwise stated.

RESULTS

Weather surveillance radar

Migratory activity increased during the second week of April and peaked between 30 April and 20 May. Date of peak reflectivity was correlated with latitude ($r = 0.89$, $t_{18} = 8.02$, $P < 0.001$), showing a 10-day difference between latitudinal extremes (KBRO and KMVX) (Fig. 2a). Overall, track direction averaged slightly more eastward-facing (3.20 ± 5.66°) than heading (359.13 ± 6.78°) (Fig. 1). Flight directions changed systematically with latitude, with tracks shifting 2.30 ± 0.48° ($P < 0.001$) and heading 3.23 ± 0.61° ($P < 0.001$) westward with each increase in degree latitude. Across all sites, airspeeds by station averaged 10.89 ± 1.26 m/s (lowest, KHGX, 8.42 ± 1.26 m/s; highest, KABR, 13.34 ± 1.29 m/s). Through the season, airspeeds declined for 19 of 20 sites, most sharply for high latitude sites (Fig. 3a), and tended to average higher with increasing latitude (slope = 0.18 ± 0.06 m/s, $R^2 = 0.59$, d.f. = 18, $P < 0.001$). Overall, we saw a significant decline in airspeed through the season (slope = 0.026 ± 0.0023 m/s, $P < 0.001$).

eBird

Species richness generally increased throughout the season, rising more rapidly with increasing latitude (Fig. 2b). The three most speciose and highest occurring orders were Passeriformes ($n = 115$), Charadriiformes ($n = 19$), and Anseriformes ($n = 14$) (Fig. S9, Fig. S10). Average body mass of species detected at the most northern WSR stations (e.g. KMVX, KDLH; Fig. 2c) increased early in the season and then decreased for the remainder of the season. Otherwise, there was a general decline in body mass through the season, with a slight increase toward the end May. This peak in migrant body size was driven by shifts in species composition (Fig. S9, Fig. S10); large-bodied Anseriformes dominated early season occurrence patterns but gave way to small-bodied Passeriformes later in the season.

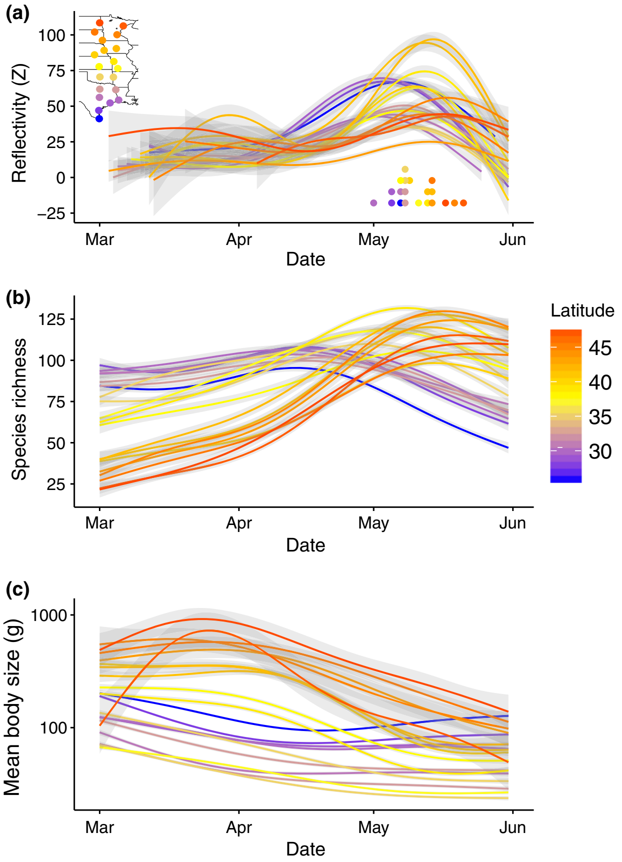

Figure 2 Bird migration characterisations by time and latitude in the central USA. (a) Reflectivity as measured by 20 weather surveillance radar (WSR) stations during spring migration (2013–2015). The fitted lines and 95% confidence bands are from generalised additive models. The coloured points are the estimated peak migration date (highest modelled reflectivity) for each WSR station. Points depicted in multiple rows because of overlapping date. (b) Weekly species richness and (c) log-scaled mean body size of migrating birds based on STEM estimates of probability of occurrence using bird observations from eBird.

Combining radar and eBird

We examine three sets of behavioural measures: (1) airspeed (radar) and body mass (eBird), (2) preferred (radar) and predicted (eBird) directions of movement, and (3) how these

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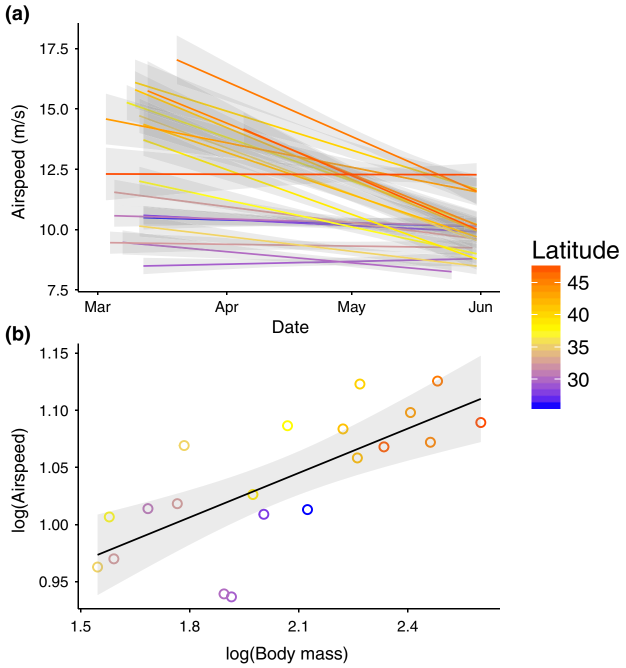

Figure 3 (a) Airspeeds of migrants measured at 20 weather surveillance radar (WSR) stations during spring migration (2013–2015). The fitted lines and 95% confidence bands are from least squares linear models. (b) Log-transformed migrant airspeed (m/s) and averaged body mass (g). The fitted line and 95% confidence band is from least squares linear models ($R^2 = 0.54$). Only airspeeds with northward track directions were considered (< 90° and > 270°). The scaling relationship is described as follows: airspeed = 5.93 × $(\text{mass})^{0.13}$. WSR station colour corresponds to its latitude.

factors influence how migrants cope with wind drift across a latitudinal gradient.

Average body mass within the radar coverage estimated from eBird STEM models explained a significant amount of variation in average airspeed (slope = 0.13 ± 0.06, $R^2 = 0.54$, d.f. = 18, $P < 0.001$; Fig. 3b). Like radar-derived preferred directions of movement (slope = 2.67 ± 0.75°, $R^2 = 0.73$, d.f. = 18, $P < 0.001$, Fig. 2), eBird-derived predicted directions of movement shifted westward with increasing latitude (slope = 2.34 ± 0.71, R^2=0.70, d.f. = 18, $P < 0.001$) (Fig. 4). Predicted direction of movement from eBird explained 84% of the variation in radar-derived preferred direction of movement estimates (d.f. = 18, $P < 0.001$; Fig. 4).

Body mass, latitude and date all significantly affected flight direction and drift strategy (Table S3). Birds generally compensated for drift to an increasing extent as latitude increased (Fig. 5). This latitudinal contrast was greatest among smaller-bodied birds and earlier in the season; the effect largely disappeared by late May. In general, larger bodied birds compensated more than smaller bodied birds. Time of season showed the strongest influence on flight strategy: birds of all body masses and across all latitudes compensated less as the season progressed. The preferred direction of migration shifted westward with increasing latitude (Fig. 1), especially later in the season (Fig. 6), and shifted eastward with increasing body mass (Fig. 6), especially early in the season.

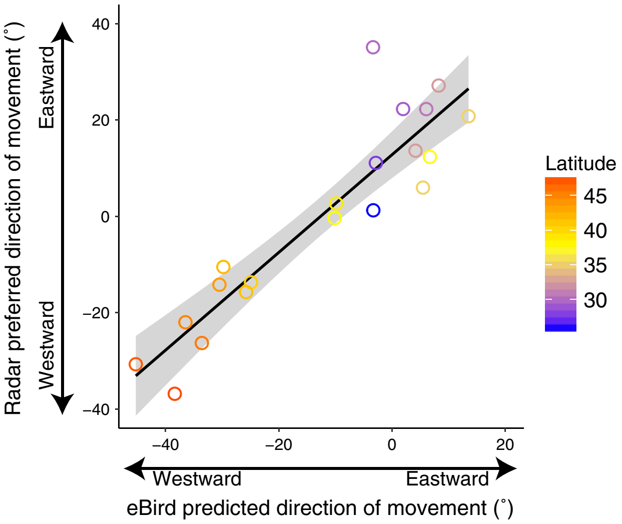

Figure 4 Radar preferred direction of movement and eBird predicted direction of movement during spring migratory periods (2013–2015) at 20 weather surveillance radar (WSR) stations. Fitted line and 95% confidence band are from a least squares linear model ($R^2 = 0.84$). WSR station color corresponds to its latitude.

Wind

Seasonal wind direction originated increasingly from the west at higher latitudes (slope = 7.37 ± 2.07°, $P < 0.001$, $R^2 =$ 0.74) and became more variable in direction at higher latitudes (slope of variance = 3.19 ± 0.93°, $P < 0.001$, $R^2 =$ 0.73). Similarly, although less dramatically, wind directions weighted by migratory activity showed a westerly shift at higher latitudes (slope = 1.38 ± 0.80°, $P < 0.01$, $R^2 = 0.38$). Winds used by migrants were more variable in direction with increasing latitude (slope = 2.36 ± 0.68°, $P < 0.001$, $R^2 = 0.72$).

DISCUSSION

We show through a process of data integration how the in-flight strategies of the migratory system change through the season and across a broad latitudinal gradient. Our results give system-level support for our optimal migration hypotheses. Across 20 WSR stations, we found evidence that nocturnal migrants increasingly compensated for wind drift as they progressed northward through the center of North America, especially early in the spring. In addition, faster-flying, larger-bodied migrants compensated more for wind drift, regardless of latitude. Our findings support our prediction that migrants compensate more for wind drift at higher latitudes during spring migration, with smaller-sized songbirds showing the strongest shifts. The multitude of significant interactions in our model highlight the complexity of these flight strategy patterns and their dependence on time of season and species composition.

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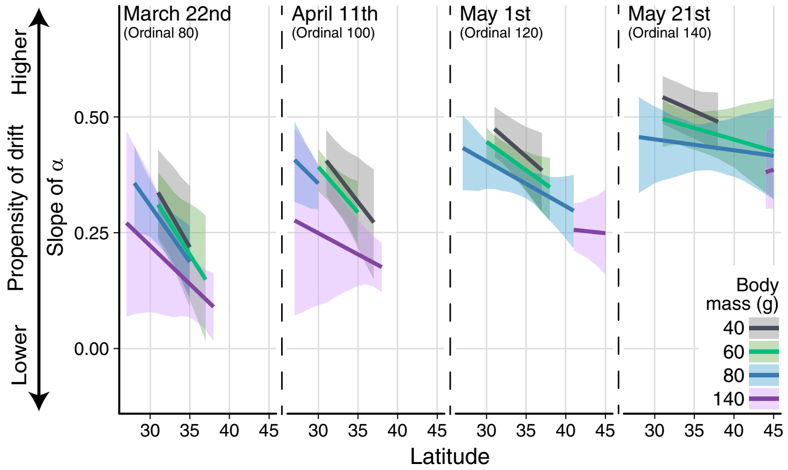

Figure 5 Wind drift propensity across latitudes at 20 weather surveillance radar stations during spring migration (2013–2015). Slope of α represents drift propensity; 0 is complete compensation for wind, 1 is complete drift with wind. Predictions of propensity of drift are shown at 20 day intervals (80, 100, 120 and 140) for the 20th, 40th, 60th and 80th percentiles of body mass (grams). The fitted lines and 95% confidence bands are from a mixed-effects model (see methods for details). Predictions only plotted for ranges for which behavioural observations were represented in our dataset.

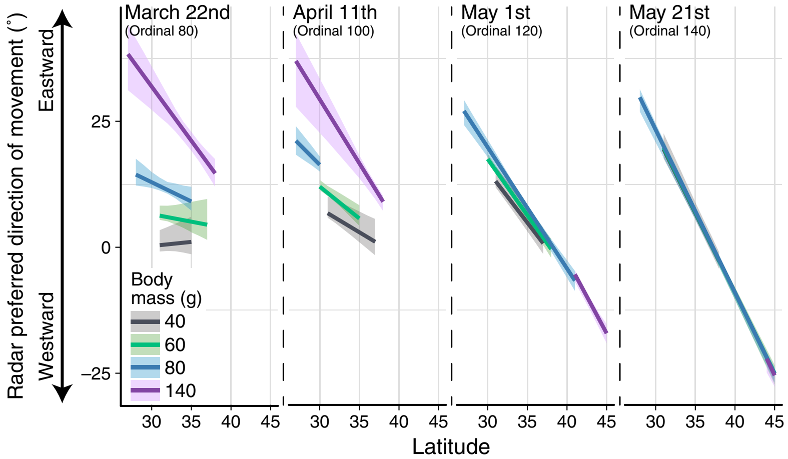

Figure 6 Radar preferred direction of movement across latitudes at 20 weather surveillance radar stations during spring migration (2013–2015). Predictions of preferred direction of movement are shown at 20 day intervals (80, 100, 120 and 140) for the 20th, 40th, 60th and 80th percentiles of body mass (grams). The fitted lines and 95% confidence bands are from a mixed-effects model (see methods for details). Predictions only plotted for ranges for which behavioural observations were represented in our dataset.

The emergent flight strategies of migrating birds are complex integrations of multiple biotic and abiotic factors. A primary component is maximum airspeed, which defines a species' ability to compensate for wind drift (Alerstam 1979; Green & Alerstam 2002). Large-bodied species, which have the morphological capacity to fly faster, have an increased capability to successfully counter wind drift (Pennycuick 1969; Alerstam & Hedenström 1998; Alerstam *et al.* 2007; Hedenström 2008). Ground-based eBird derived observations of species composition across our study region show a seasonal shift from early, large-bodied, fast-flying migrants to late, small-bodied, slow flying migrants. The positive relationship between species body mass estimated from ground-based eBird observations and WSR based estimates of in-flight nocturnal airspeeds is an exciting integration of these two independent data sets. These findings follow predictions from aerodynamic first principles based on individual behaviour (Pennycuick 1969; Alerstam 2003). We show a strong correspondence with airspeed-body mass scaling coefficients measured on individually tracked migrants (0.12, Alerstam *et al.* 2007) and at the system-level (0.13, see Fig. 3), giving additional support to our finding that aggregate eBird properties can predict large-scale migratory movements detected by weather surveillance radar. Never has this relationship been detected at a flyway scale for millions of migrating individuals. These findings suggest that body size is a critical trait

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driving migration biology, and can play an important role in advancing our understanding of broad-scale migration dynamics.

Optimal migration theory predicts that migrants should increase compensation as they approach their end destination to minimise their overall time and energy expenditure (Liechti 2006). We show that smaller-bodied and early-season migrants made systematic shifts toward greater compensation with increasing latitude. In addition, preferred directions of movements of nocturnal migrants sensed by WSR shifted to increasingly westerly directions at higher latitudes. We reproduced this pattern with information about species composition from ground-based eBird observations and directions to destination, which suggests that this phenomenon occurs because species with northerly distributions tend to have breeding ranges centered in western North America (Fig. S6). Birds moving towards the northwest must contend increasingly with westerly crosswinds at higher latitudes, compounding the effort needed to compensate for wind drift. Although we cannot confirm whether migrants are increasingly compensating for increasingly unfavourable winds or proximity to their breeding destination, our assessment shows a system-wide behavioural trend in the propensity of drift.

We recognise an important caveat here, that it remains difficult to assess the influence of pseudodrift in our findings. The non-uniformity in preferred flight directions among different species or populations and their choice to fly under different wind conditions can manifest in the appearance of enhanced levels of drift (i.e. pseudodrift) (Evans 1966; Nisbet & Drury 1967; Alerstam 1978). Our analysis was designed to minimise the effect of pseudodrift, accounting for inter-night variation in flight direction using random effects and leaving the fixed effects to describe average patterns within the migratory periods. However, without detailed knowledge of the relationship between the probability of departure and wind direction and speed (e.g. Deppe *et al.* 2015), quantifying pseudodrift remains a principle challenge. The question of the general behavioural mechanisms that enable individual migrants to cope with these unfavourable conditions and ultimately arrive precisely at their destinations remains open.

Species' body size and geographic location and how wind speed and direction vary seasonally along migration flyways are likely the primary factors affecting compensation strategies. Winds aloft, in particular, appear to be an important component determining the seasonal composition of migrants within a flyway (Kranstauber *et al.* 2015). Geographic tendencies in wind speed and direction may shape observed flight behaviours, as well as their phenologies. The low-level nocturnal jet stream of the Great Plains brings strong, southerly winds from the Gulf of Mexico, generally peaking in intensity through the mid-latitudes of the United States (Walters *et al.* 2008). The low-level jet influences spring migratory pathways (La Sorte *et al.* 2014b) and nightly flight behaviours (e.g. flight height selection; Wainwright *et al.* 2016). In addition, the behaviour of the low-level jet, in concert with the polar front and subtropical jet stream, which drive synoptic weather patterns west to east (Archer & Caldeira 2008; Pena-Ortiz *et al.* 2013), helps to explain our findings of winds originating increasingly from the west at higher latitudes, in addition to greater seasonal variation in wind directions at more northerly sites. Our findings carry significance when considering the implications of projected changes in the region's prevailing winds under global warming. The low-level jet in the south is projected to increase in strength (Cook *et al.* 2008), and the prevailing westerlies in the north are projected to decrease in strength (Francis & Vavrus 2012; Li *et al.* 2012); the former may increase migration speeds, while the latter may diminish the need for compensation (La Sorte & Fink 2016). In total, these changes may enhance flight efficiency during spring migration. It remains to be seen how these behaviours contrast with fall migratory movements, where winds are expected to be less favourable for southbound flights (La Sorte *et al.* 2014b; Wainwright *et al.* 2016).

Characterising a multi-dimensional biological system like bird migration with observational and remote sensing data highlights the power of ecological analyses in the era of big data (Hampton *et al.* 2013; Schimel & Keller 2015). Citizen scientists can collect direct observations of species on the ground that can be synthesised into state-of-the-art distribution maps. The WSR network in the USA can detect hundreds of millions, if not billions, of migrating birds each year, making it a sensor network with unparalleled potential to study and monitor migration systems. We show that it is possible to integrate these datasets representing models of concurrent species distributions derived from ground-based observations and aerial distributions of nocturnally migrating birds to advance our understanding of the patterns and dynamics of migration systems.

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AUTHORSHIP

KGH, BVD, AF and JFK worked to conceive and design this study. KGH processed radar and wind data, generated figures, and drafted the manuscript. BVD and KGH conducted statistical analyses. DF designed and implemented the species distribution models, and FAL and DF designed the analysis of the model products. BVD designed species trajectory analyses and flight behaviour models. DS designed radar-processing algorithms. All the authors have provided editorial advice, approved the final version of this manuscript, and agree to be accountable for all aspects of the work.

DATA ACCESSIBILITY

Raw data are accessible through figshare (https://knowledge.figshare.com) https://doi.org/10.6084/m9.figshare.6044693.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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Bright lights in the big cities: migratory birds' exposure to artificial light at night

Bright lights in the big cities: migratory birds' exposure to artificial light

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Many species of migratory birds have evolved the ability to migrate at night, and the recent and rapid expansion of artificial light at night has markedly altered the nighttime sky through which they travel. Migrating birds regularly pass through heavily illuminated landscapes, and bright lights affect avian orientation. But risks to migrating birds from artificial light are not spatially or temporally uniform, representing a challenge for mitigating potential hazards and developing action plans to catalog risks at continental scales. We leveraged over two decades of remote-sensing data collected by weather surveillance radar and satellite-based sensors to identify locations and times of year when the highest numbers of migrating birds are exposed to light pollution in the contiguous US. Our continental-scale quantification of light exposure provides a novel opportunity for dynamic and targeted conservation strategies to address the hazards posed by light pollution to nocturnally migrating birds.

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Trillions of flying organisms (eg birds, bats, insects) occupy the airspace within the troposphere during different periods of their annual cycles (Diehl 2013). The recent recognition of airspace as vital habitat – one that is subject to increasing modification by humans – highlights the fundamental need to understand how organisms cope with such alterations (Lambertucci *et al.* 2015), which pose numerous challenges to airborne organisms during periods of transit, including nocturnally migrating birds. Of the nearly 630 terrestrial species of birds regularly occurring in North America, approximately 70% are considered migratory, and of these more than 80% migrate at night (WebTable 1). Yet most studies of associated risks have focused on terrestrial habitats, underscoring a fundamental knowledge gap that can be addressed with recent technological (including computational) advances.

Light pollution of the airspace is a relatively recent but growing threat to nocturnally migrating birds (Longcore and Rich 2004; Van Doren *et al.* 2017; Cabrera-Cruz *et al.* 2018). Increasing urbanization has greatly amplified the amount of artificial light at night (ALAN; Kyba *et al.* 2017), with almost one-half of the contiguous US experiencing substantially photo-polluted nights (Falchi *et al.* 2016). Light sources – including streetlights, safety lights, and extensively lit buildings – can disturb wildlife in a multitude of ways (Gauthreux and Belser 2005; Hölker *et al.* 2010; Rodríguez *et al.* 2017). High-power light installations like lighthouses and communication towers are known to attract nocturnal migrants and are responsible for substantial mortality (Gauthreux and Belser 2005; Longcore *et al.* 2012). The numbers of birds attracted to or trapped by illumination depend on light wavelength (Poot *et al.* 2008) as well as weather factors such as fog and precipitation (Gauthreux and Belser 2005). High-power light installations can even attract migrants in already heavily photo-polluted areas and in skies with clear weather conditions (Van Doren *et al.* 2017).

An increasing number of artificial structures are now present in the lowest reaches of the troposphere (Davy *et al.* 2017), and their continued expansion poses an ever-increasing threat to wildlife. In the contiguous US, annual fatal bird collisions with buildings, communication towers, power lines, and wind turbines cumulatively number in the hundreds of millions (Loss *et al.* 2015). For nocturnally migrating birds, direct mortality as a result of collisions due to attraction to light (Gauthreux and Belser 2005) is the most obvious and direct effect of ALAN, but there are also more subtle effects, such as disrupted orientation (Poot *et al.* 2008) and changes in habitat selection (McLaren *et al.* 2018). There is also growing evidence that light pollution alters behavior at regional scales, with migrants occupying urban centers at higher-than-expected rates as a function of urban illumination (La Sorte *et al.* 2017). While ALAN acts as an attractant at both large (La Sorte *et al.* 2017) and local (Van Doren *et al.* 2017) scales, there is also evidence of migrating birds avoiding strongly lit areas when selecting critical resting sites needed to rebuild energy stores (McLaren *et al.* 2018).

Challenges to conservation and mitigation

To date, mitigating actions to reduce impacts of ALAN have involved directed and specific efforts, including reductions in excess lighting, the periodic switching off of high-intensity lights (Van Doren *et al.* 2017), and adjusting wavelengths in situations where lights cannot be shut down (Poot *et al.* 2008; Longcore *et al.* 2018). These actions are

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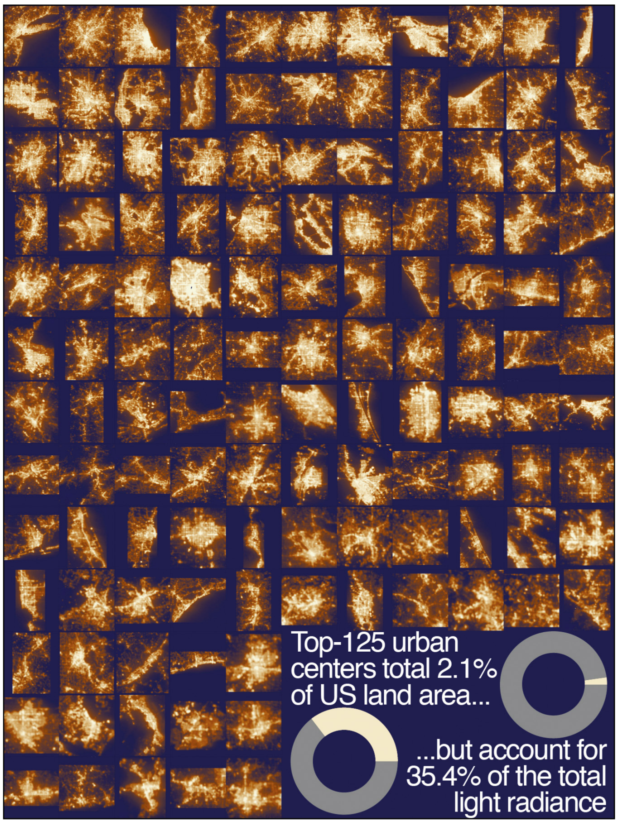

Figure 1. Log_{10}-scaled radiance of artificial light at night (ALAN) measured by the Visible Infrared Imaging Radiometer Suite (VIIRS) on the Suomi-NPP satellite of the 125 largest urban centers (by area) in the continental US. The largest urban center area is depicted in the top-left corner; the second largest area appears to its immediate right, and so forth, across the top-most row. In each successive row, urban center areas continue to decrease in size from left to right.

typically carried out at the scale of individual buildings but occasionally at much larger scales (eg Lights Out Toronto). However, as the intensity and extent of bird migrations vary considerably in space and over time (Van Doren and Horton 2018), so too may exposure risks, requiring detailed and site- and time-specific considerations when implementing mitigation actions and developing conservation plans. To this end, we used radar to quantify the passage of nocturnally migrating birds across the contiguous US, identified the areas where the greatest number of migrants are exposed to light pollution, and mapped this exposure across the US, focusing specifically on the 125 largest urban centers.

Methods

Weather surveillance radar

We used weather surveillance radar (WSR) data from 143 stations from spring (1 March to 31 May) and fall (15 August to 15 November) between spring 1995 and spring 2017 to characterize cumulative migration activity across the contiguous US. We acquired radar data through the Amazon Web Service portal, extracting data from a 30-minute window centered on 3 hours after local sunset. This time period was chosen because it represents the average peak in nocturnal migratory activity (eg Farnsworth *et al.* 2015; Horton *et al.* 2015; see Horton *et al.* [2018] and Van Doren and Horton [2018] for additional details regarding radar processing).

With respect to creating profiles of migration activity, we calculated altitude, speed, and direction using the lowest elevation scans (0.5–4.5°) at distances of 5 km to 37.5 km from the radar station (Farnsworth *et al.* 2015). We determined migration activity from reflectivity (η, $cm^2\ km^{-3}$) and flight direction and groundspeed from radial velocity between 100 m and 3000 m above ground level, at 100-m altitudinal bins using the WSRLIB package (Sheldon 2015). We excluded altitudinal bins with velocity azimuth displays with root mean squared error (RMSE) $<1\ m\ s^{-1}$ to limit contamination of radar readings by insects and removed samples with RMSE $>5\ m\ s^{-1}$ to limit poor fits. In addition, we removed slow-flying objects (airspeed $<5\ m\ s^{-1}$), which are representative of insects (Larkin 1991). To calculate airspeeds, we paired all radar measures of groundspeed and flight direction with wind measures using the North American Regional Reanalysis (NARR). Following these filtering procedures, we integrated reflectivity ($cm^2\ km^{-3}$) across the column of airspace sampled (100–3000 m) into vertically integrated reflectivity (VIR, $cm^2\ km^{-2}$), which represented our measure of migration activity.

To discriminate contaminated scans (ie with precipitation) from precipitation-free scans (ie clear or biologically dominated), we designed a random forest classifier (Horton *et al.* 2019) using the R package "randomForest" (Liaw and Wiener 2002). We trained the classifier on 318,047 (spring: 157,279; fall: 160,768) manually classified nocturnal scans, selected from a 2.5-hour period centered on 3 hours after local sunset on 15 March, 15 April, 15 May, 1 September, 1 October, and 1 November. Scans for each radar and for each year were represented in the training set. We extracted derived predictor variables from profiles of reflectivity, groundspeed, and summaries of the number of volumes above 35 decibels of reflectivity (dBZ) (a value typical of precipitation). We populated 1000 trees and restricted node size to 50 scans. The algorithm classified a total of 2,176,126 scans (spring: 979,326; fall: 1,196,800) with 5.6% classification error during the spring and 4.5% during the fall, as determined using the manually classified scans. As an additional step to reduce the inclusion of samples classified as clear but containing weather, we used only scans with a confidence of being precipitation-free of 75% or higher (rather than a majority rule; ie >50%).

To extrapolate migration activity to areas not sampled by the radars, we relied on a generalized additive model using the R package "mgcv" (Wood 2011; R Core Team 2017). We first calculated the average migration activity for each ordinal day across all years and then summed each night through the sea-

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son to estimate the cumulative migration activity for each radar station. We fit radar station latitude, longitude, and the interaction of latitude and longitude with smoothing splines to predict the cumulative seasonal activity across the contiguous US.

Artificial light at night

We used the monthly Day/Night Band (DNB) product from the Visible Infrared Imaging Radiometer Suite (VIIRS) onboard the joint National Oceanic and Atmospheric Administration (NOAA)/National Aeronautics and Space Administration Suomi-NPP satellite to quantify the magnitude of ALAN radiance (Earth Observation Group, NOAA National Geophysical Data Center; https://bit.ly/2nCjqvz). Monthly composites of radiance (nanoWatts per square centimeter per steradian; nW cm^{-2} sr^{-1}) are projected at 15 arc-second geographic resolution and are filtered to exclude data from stray light, lightning, lunar illumination, and cloud cover. However, because these data are not filtered for auroras and fires, we averaged across 3 months (October–December) over 6 years (2012–2017) to dampen the influence of episodic lighting events; these months were chosen because they fall outside the primary storm season in North America, which would obscure radiance measures. As an added step to ensure data quality, we excluded any pixel with fewer than 5 use-days prior to averaging monthly composites. Finally, we removed pixels with radiance values greater than 900 nW cm^{-2} sr^{-1} to remove wildfires and other ephemeral high-intensity lighting events (Kyba *et al.* 2017).

Exposure index calculation

To quantify migrant exposure to ALAN, we summarized exposure at two levels: (1) across the contiguous US and (2) in the top 125 largest urban centers by area (Figure 1). We used the 2017 US Census database to define the boundaries of these urban centers and used the primary city name in our presentation of urban area (eg Dallas–Fort Worth–Arlington, Texas, is presented as "Dallas"). Across the contiguous US, we calculated exposure as the product of *cumulative migration activity* × *radiance*, whereas over urban areas we calculated exposure as the product of *cumulative migration activity* × *summed radiance of the entire urban area*. To differentiate seasonal differences irrespective of increases in bird populations, we standardized cumulative migratory activity to range between 0 and 1, and standardized activity relative to the highest value across the contiguous US. Exposure difference was calculated as the product of log$_{10}$-scaled VIIRS radiance (standardized 0 to 1) and seasonal differences in migratory activity.

Results

Migration activity

Migration activity in spring was greatest in the central US (Figure 2a) and generally more widespread and more easterly in distribution in the fall (Figure 2b). In the western US, we observed greater migratory activity in the spring than in the fall. Furthermore, we observed a 63% increase in cumulative migratory activity from spring to fall. Examining the annual nightly pulses of migratory movements at each radar station, we observed that half of the cumulative migratory activity passed each station in 6.2 ± 2.5 (mean ± standard deviation [SD]) nights in spring and 7.1 ± 2.6 nights in fall.

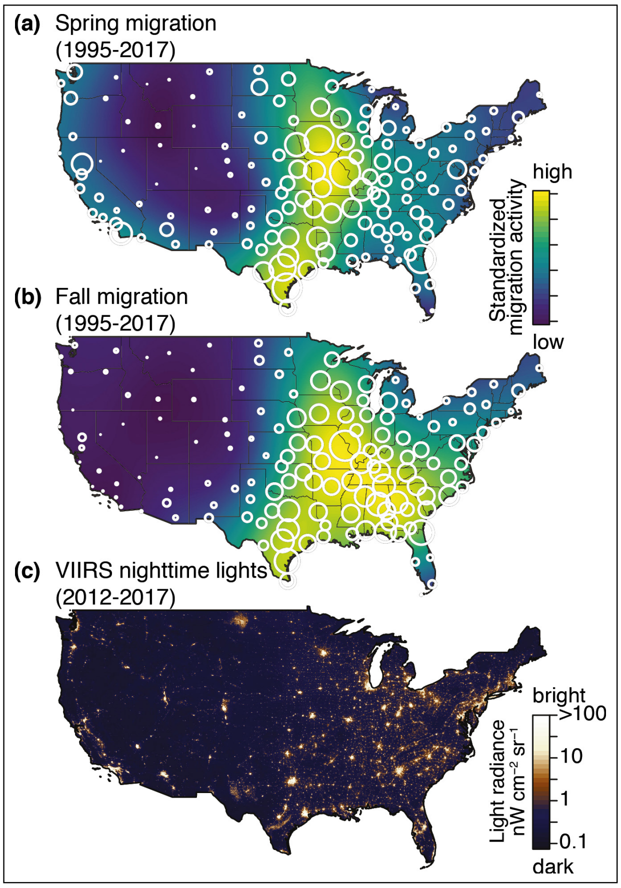

Figure 2. Average cumulative distribution of migrant birds during (a) spring and (b) fall migrations from 1995 to 2017 measured by weather surveillance radar (WSR). Circles indicate WSR station locations and are scaled to cumulative migration activity. The magnitudes of spring and fall cumulative movements are standardized to the same range. (c) Log$_{10}$-scaled mean radiance of ALAN measured by the VIIRS on the Suomi-NPP satellite.

Light pollution

The general pattern of nightly radiance showed greater average radiance in the eastern half of the US, with a few notable exceptions from urban areas in the Pacific states, Desert Southwest, and a few Rocky Mountain cities (Figure 2c). As expected, the strongest radiance values were observed

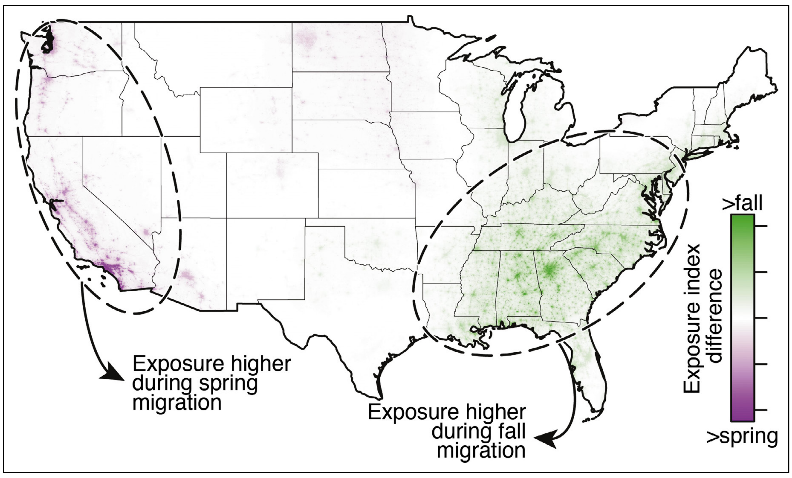

Figure 3. Seasonal differences in exposure to ALAN. The magnitude of spring and fall cumulative movements were standardized to the same range (0 to 1) to highlight seasonal differences in migratory routes. Exposure difference was calculated as the product of $\log_{10}$-scaled VIIRS radiance (standardized 0 to 1) and seasonal differences in migratory activity.

in urban areas. Across the US, 69.5% of the summed linear light radiance came from just 5% of the land area. The top 125 largest urban areas accounted for only 2.1% of total land area and 35.4% of total summed linear radiance.

Continental exposure risk

Increased migratory activity during fall was observed in almost all areas, resulting in 53.8% higher total of exposure in the fall. After standardizing for differences in overall migration activity between seasons, we determined that there was still a 13.1% higher sum of exposure in the fall, when migrants moved through more photo-polluted airspaces in the eastern half of the US (Figure 3). Departures from this trend were evident in the western half of the country, where spring movements along the Pacific coast led to higher spring exposure (Figure 3).

Urban exposure risk over the 125 largest US cites

Mean avian light exposure in cities was 24 times as high as the countrywide average. Larger cities tended toward greater exposure risk (linear regression, spring: $F_{1,123} = 135.8$, $P < 0.001$, $R^2 = 0.52$; fall: $F_{1,123} = 203.1$, $P < 0.001$, $R^2 = 0.62$), but there were notable exceptions, such as Boston (4th in size but 36th and 24th in exposure in spring and fall) and Des Moines (99th in size but 28th and 36th in exposure in spring and fall) (WebTable 2). Regardless of season, the highest levels of exposure to anthropogenic light at night were observed in Chicago, Houston, and Dallas, in descending order (Figure 4; see WebTable 2 for a complete list). These three cities showed exposure magnitudes that were 19 (spring) to 21 (fall) times as high as the median exposure of the remaining 122 cities (Figure 4a). In total, 45 and 74 urban areas exhibited higher spring exposure rankings and higher fall exposure rankings, respectively. Six areas, including Chicago, Houston, and Dallas, showed no change in ranking (Figure 4b). Of the 125 largest US cities, the top 10 greatest changes in seasonal rankings occurred in western states (eg Riverside, San Diego, San Jose; Figure 4b). Of the top 10 risks for exposure, the majority occurred in the central US: seven in spring and six in fall.

Discussion

We conducted a quantitative assessment of continent-scale exposure of actively migrating birds to nighttime light pollution. The findings leverage recent advances in data access and machine learning to capture new and rich details in characterizing bird movements aloft in relation to radiance from human population centers. With considerations for urban areas and the numbers of migrants flying above them, we can now provide the data necessary to guide conservation actions to identify locations where ALAN-reducing programs may be most effective.

Shifted seasonal distributions

Greater abundance of migrants in fall increases the number of birds at risk to ALAN, which was apparent in the general increase in exposure indices from spring to fall. However, shifts in migratory routes between spring and fall migration also affect the numbers of birds exposed to higher light levels (Figure 2). More easterly fall routes, often described as looped migration (La Sorte *et al.* 2014), take birds over more heavily photo-polluted areas than do spring routes, leading to even higher numbers of birds – and many young birds – exposed to ALAN in fall. At most sites, exposure indices are therefore higher during fall than in spring, indicating that any mitigation efforts (eg lights-out campaigns) would have a larger effect during the fall, especially with juveniles as they undertake their first migratory journey. However, while the risk of mortality for juveniles is likely to increase in the fall, any effects of ALAN on migrants in the spring will directly affect breeding activities. Birds moving along westerly routes during spring migration are the exception to this general pattern, likely related to their use of more westerly, low-elevation routes during spring as compared to fall (La Sorte *et al.* 2014). For example, the patterns in Los Angeles and other cities in California are the opposite of most East Coast cities, with higher exposure during spring migration (Figures 3 and 4).

Uneven temporal distributions

Migration periods may span more than 6 months in total, with hundreds of millions of individual migrants aloft on a

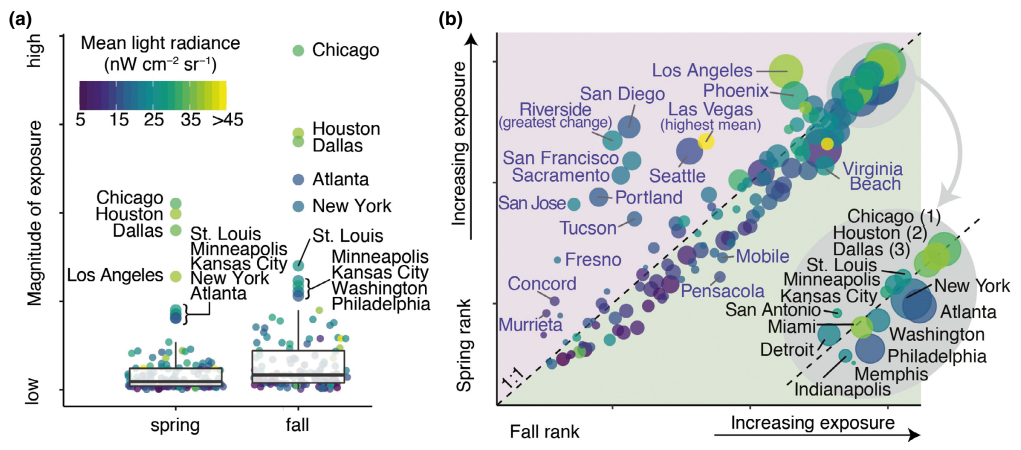

Figure 4. Seasonal (a) magnitude and (b) relative rankings of the 125 largest urban areas in the continental US. Point color shaded by the mean light radiance and sizes (in [b]) are scaled by the square root of urban area. (a) Only urban areas outside the 25th and 75th quartiles are labeled and (b) areas with a change in seasonal rank of ≥20 positions are labeled and identified in blue. Inset in (b) depicts the top 15 (spring or fall) rankings; note that Los Angeles and Phoenix show both ranking changes ≥20 and are ranked in the top 15, and therefore are not included in the inset. Urban areas in the purple shading (above the 1:1 dashed line) had higher spring exposure rankings, whereas those in the green shading (below the 1:1 dashed line) had higher fall exposure rankings.

given night; however, their passage occurs in sporadic waves, with a large majority of birds passing individual sites during just a few peak nights. We observed that half of the total number of migrants for each season passed each radar site in just 6.7 ± 2.6 (mean ± SD) nights, a notable finding when paired with the recent capacity to confidently forecast (12–72 hours in advance) these episodic events (Van Doren and Horton 2018). This advance has the potential to offer a detailed and tailored guide for mitigation actions to substantially lower the numbers of birds exposed to risks of ALAN while simultaneously minimizing adverse effects to stakeholders, including municipalities and industry. In addition, birds disproportionately use modified habitats (eg urban areas) during fall migration (Zuckerberg *et al.* 2016), and because migrants are more numerous and less experienced in fall, an emphasis on fall mitigation efforts is especially important.

Conclusions

ALAN continues to increase in many areas globally (Kyba *et al.* 2017), presenting an ever-growing ecological threat to all nocturnally active animals (Longcore and Rich 2004; Guetté *et al.* 2018), particularly migrating birds. Concerted conservation efforts at local (eg Van Doren *et al.* 2017) and continental scales are necessary to reduce exposure of migrants to light pollution. The disproportionate relationship between the land area occupied by cities and the amount of ALAN emitted leaves little doubt where conservation action is most needed: urban centers. Such efforts require balance with the needs of stakeholders. ALAN ranges from bright sources to dim stray light, and it remains an open question how conservation action should be prioritized over these widely differing sources. In addition, the extent to which species – or even populations – differentially respond to ALAN remains unclear, but could have important conservation implications. Furthermore, different datasets are available (eg a world atlas of artificial night sky brightness; Falchi *et al.* 2016), which may provide valuable information for characterizing ALAN's disruptions to aerial organismal biology (eg horizon glow versus upward radiance). Although we did not directly compare different sources of ALAN information with respect to exposure risks, we believe that such comparisons will be fundamentally important.

Reducing nighttime lights for the benefit of migrants and other wildlife represents yet another instance of anthropogenic and environmental trade-offs, in this case among avian safety, human safety, energy expenditure, and societal and psychological expectations. It is therefore important that conservation efforts and future research are directed to the times and places where they will have the largest impact. An important step in this direction is identifying where the highest numbers of birds are exposed to the highest amounts of ALAN. Here we have shown where the greatest threats exist, and how these threats vary seasonally. The combination of large amounts of nocturnal illumination and their location in the most trafficked airspace across the US elevate metropolitan Chicago, Houston, and Dallas to the top of the exposure risk ranking. While all urban areas should take care to minimize ALAN, our analysis indicates that actions taken in these particular cities would benefit the largest numbers of birds. Through our analysis, we have identified risk; however, directly linking risk with adverse effects on bird populations is a challenge, and future research is needed to fully understand the impacts of ALAN on migratory species.

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Supporting Information

Additional, web-only material may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/fee.2029/suppinfo