

# Patterns of vagrancy and long-distance dispersal in migratory birds



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# Abstract

## **Patterns of vagrancy and long-distance dispersal in migratory birds**

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Vagrancy, the process in which organisms travel far outside of their known species' breeding and wintering range, has long been thought to be an aberrant trait. Vagrants are hypothesised to result from a series of individual mistakes, such as inheritance of an incorrect compass bearing, or displacement by wind or weather systems. Though previous studies on vagrancy do not provide sufficient evidence to support these hypotheses, vagrancy still remains understudied. This thesis uses a combination of experimental field techniques, and indirect methods, to study how and why vagrancy occurs in migratory birds. More specifically, I investigated whether vagrants differ behaviourally from non-vagrants, and what factors drive vagrant occurrence. Firstly, I tested the orientation behaviour of vagrant and non-vagrant passerines to determine whether vagrants are capable of selecting a preferred migratory bearing. That is, are vagrants capable of initiating directed migratory flights? I found that not only do vagrants select a preferred orientation, but that orientation did not significantly differ from that of our non-vagrant control species, the Blackpoll Warbler (*Setophaga striata*). Both vagrants and non-vagrants oriented on a north/northwesterly heading, which is consistent with studies on post-fledging exploration of Blackpoll Warblers. This suggests that vagrancy may be linked to post-fledging exploration. Feathers from these vagrants were also assessed for the ratio of stable-hydrogen isotope (deuterium;  $\delta^2H$ ) to pinpoint their natal origin. The majority of vagrants were found to originate from the edge of their breeding range, which has been associated with increased exploratory behaviour in other species of passerines. External factors that may drive vagrant occurrence were also examined. For vagrant New World warblers, the size of the overall breeding population and vagrant distance were found to best predict vagrancy. Furthermore, when examined at the regional level, each species was best predicted by the annual variation in population size and growth at the edge of their breeding range, supporting my results that vagrants originate along the range edge. Additionally, this relationship was negative, suggesting quadratic density-dependence, whereby vagrants irrupt in years of plentiful resources as the population increases, and erupt in years of depleting resources, when the population exceeds available food or habitat. I tested whether this relationship could be used to infer the source population of vagrants indirectly, using vagrant Lesser Black-backed Gulls (*Larus fuscus*). Though it was possible to infer their origin, increased survey efforts are needed to improve predictions. Finally, since vagrants are irruptive, I investigated irruptions in the Northern Saw-whet Owl (*Aegolius acadicus*) to determine drivers of irruption cycles in this species. Irruptions were strongly influenced by prey abundance, which suggests that vagrants may respond to food availability. Overall, this thesis challenges the idea that vagrants are aberrant, and instead suggests that this behaviour is within the scope of the normal migratory programme.

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# Declaration and Author Contributions

All work presented in this thesis is primarily my own.

Eight other authors contributed to the work in this thesis, and their contributions are listed below:

Tim Guilford contributed ideas and feedback during the design and analysis of each study, and contributed to manuscript preparation for all chapters.

Phil Taylor helped design and plan experiments in chapter 2 and assisted with data analysis.

Richard R. Veit contributed ideas and feedback to the design and analysis of all chapters, participated in fieldwork for chapters 2 and 3, and assisted with analysis and manuscript preparation for chapter 5.

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*"...the occurrence of individual birds a greater or less distance beyond the bounds of the plentiful existence of the species to which they belong is the regular thing, to be expected. There is nothing really 'accidental' about it; the process is part of the ordinary evolutionary program."*

–Joseph Grinnell, 1922.

*"Birds hardly ever become lost, vagrants being birds...involved in long-distance exploration beyond their normal range."*

–R.R. Baker, 1980.

*"Not all those who wander are lost."*

–J.R.R. Tolkien, *The Fellowship of the Ring*, 1954.

To my mom, my sister, my brother, and, of course, the birds.

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# 1

## Introduction

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### 1.1 Introduction

Organisms, particularly birds, are capable of engaging in extreme long-distance movements, travelling far outside of their known species' breeding, wintering, or migratory distributions (Hengeveld 1989, Koenig et al. 1996). Known as vagrancy, these

large-scale movements have fascinated scientists for well over a century (Clarke 1912, Grinnell 1922). Though many have speculated about the cause of this behaviour, the reason behind it is still a topic of much debate. Typically, it has been posited that any individuals that appear outside of their range are aberrant (Clarke 1912), or possess a “physiological flaw” (Cottridge and Vinicombe 1996), that puts them at a distinct evolutionary disadvantage compared to other individuals in the population that follow the ‘normal’ migratory pathway (Able 1977, Wilson 1988). The term ‘vagrant’ itself means ‘wanderer’ (Merriam-Webster 2021), evoking images of one who explores, albeit aimlessly. This implies that vagrant movements occur idly and without intent, and is likely why vagrants were previously referred to as ‘accidentals’ (Grinnell 1922), suggesting that their arrival at these distant locations is a mistake.

This idea that vagrants are abnormal has served as the premise for the majority of theories proposed about vagrancy (Lees and Gilroy 2009). Vagrancy is thought to arise from various intrinsic or extrinsic factors, ranging from inheritance of an incorrect compass bearing (e.g. Rabøl 1969), to displacement by wind or weather systems (e.g. Elkins 1979, 2005, 2008). These theories imply that vagrancy results from errors in navigation due to influences that are outside of an individual’s control, though this does not explain the extensive number of vagrants seen annually for a multitude of migratory species. Furthermore, many studies on vagrancy have been descriptive in nature, and fail to provide sufficient evidence to support claims that proposed factors actually drive vagrant movements (Cottridge and Vinicombe 1996; Williamson 1959, 1961, 1969; Lack 1959, 1960a, 1960b; Baker 1977; Elkins 1979, 2005, 2008; McLaren 1981). Other studies have proposed that vagrant movements are not aberrant, but are rather exploratory, whereby individuals will disperse outside of their range in search of suitable new habitat (Baker 1978, 1980, 1993). This may lead to range expansion and colonisation in some species (DeBenedictis 1971). Additionally, correlations between vagrancy and population size and growth suggest that vagrancy is driven by population dynamics (DeBenedictis 1971; DeSante 1983b; Veit 1997, 2000; Thorup 2004; McLaren et al. 2006; Pfeifer et al. 2007; De Juana and Garcia 2010; Ralph and Wolfe 2018; Zawadzki et al. 2019), and may be linked to either habitat condition (DeBenedictis 1971, DeSante 1983b, Patten and

Marantz 1996), or resource availability in the species' range (Grinnell 1922, Williamson 1963). This would better explain the prevalence of vagrancy within avian taxa, though more study in this area is needed.

This thesis aims to study patterns of vagrancy in a variety of migratory birds, from passerines, to shorebirds and raptors. Through a combination of field studies, and regression modelling, I quantitatively assess orientation behaviour of vagrants, as well as the factors that drive broad-scale patterns in vagrant occurrence, to determine whether vagrants differ behaviourally from non-vagrants, and to assess possible factors that predict occurrence of vagrants in a number of species. Though I study birds exclusively in this thesis, due to a wealth of easily accessible data, these ideas are applicable to a variety of organisms. It is well-known that many species engage in highly-mobile long-distance dispersive movements (Baker 1978, Hengeveld 1989, Kot et al. 1996), including insects (e.g. Monarch butterfly (*Danaus plexippus*), Zhan et al. 2014), fish (e.g. Chevron butterflyfish (*Chaetodon trifascialis*), Franklin 2017), and amphibians (Cane toads (*Rhinella marina*), Phillips et al. 2010).

Due to the rarity and unpredictability of vagrant occurrence, vagrancy can be difficult to study, and thus remains poorly understood. This thesis serves as a starting point to fill gaps in the literature on vagrancy, and draw attention to the importance of this behaviour within the migratory programme. Insights into vagrancy can help us better understand migratory movements, as well as range expansion and colonisation in species.

## 1.2 What is vagrancy?

**Vagrancy** is the long-distance dispersal movement by individuals far outside of their known breeding, wintering, or migratory ranges (Grinnell 1922, DeSante 1973, Newton 2008, Veit et al. 2021), and **vagrants** are any individual that has dispersed outside of their defined species' range at any period during their annual cycle. In this context, **dispersal** does not need to end with a breeding event as it is commonly defined in

population genetics (Matthysen 2012), but is rather just “outward movement from a point source” (Veit et al. 2021). Consequently, **migration** is annual dispersal, which includes both a spring movement towards breeding grounds, and an autumn movement towards wintering grounds, and a **migrant** is an individual that annually disperses. Under this terminology, ‘vagrancy’ is actually a part of the normal migratory programme, since it is dispersal that can occur during the migratory period. Vagrancy occurs in a wide variety of migratory bird species and families (Lees and Gilroy 2021), and though the patterns of vagrancy that are observed across these species may differ, vagrants are often pre-breeders, typically juveniles on their first autumn migration for passerines (Williamson 1959, 1969; DeSante 1973; Baker 1977; Ralph 1971, 1978; Elkins 1979), or immatures for non-passerines (Lees and Gilroy 2009).

### 1.3 Vagrant theories

Well-known theories to describe vagrancy have largely been based on the premise that vagrants are aberrant, and that vagrancy itself is a mistake (Phillips 2000). These theories suggest that vagrancy either arises from navigational errors (e.g. Rabøl 1969), or displacement by wind or weather systems (e.g. Elkins 1979). Another theory that has received increasing attention in recent decades is based on the premise that vagrancy is linked to population growth in the species’ breeding range (e.g. DeBenedictis 1971). It hypothesises that vagrancy occurs in response to high population pressure in the breeding range, and is highly density-dependent. These theories are not mutually exclusive, and it is possible that one or a combination of these may lead to or drive vagrant movements. Unfortunately, many studies on vagrancy have been descriptive in nature (Cottridge and Vinicombe 1996; Williamson 1959, 1961, 1969; Lack 1959, 1960a, 1960b; Baker 1977; Elkins 1979, 2005, 2008; McLaren 1981), and as a result, there are few studies that quantitatively test for navigational errors or displacement by wind or weather (see Sections 1.3.1 and 1.3.2). While studies on population growth have strong statistical support, there is still much to be studied in this area (see Section 1.3.3).

### 1.3.1 Navigational errors

Navigational errors proposed to cause vagrancy are thought to involve the inheritance of a faulty navigational system, or incorrect calibration of compass systems via extrinsic factors, such as magnetic anomalies (Alerstam 1987, 1991; Wiltschko and Wiltschko 2005; Winklhofer et al. 2013). The two main mechanisms put forth for errors in navigation are disorientation, which is the inability to orient in any sensible direction, or misorientation, which is the inability to orient in the correct direction. Misorientation is thought to either present as reverse migration, or mirror-image misorientation.

#### *Disorientation*

Disorientation is often proposed as the reason for occurrence of coastal migrants in North America. Coastal migrants are thought to disorient and drift offshore to nearby islands, resulting in mortality over open ocean (Able 1977, Ralph 1978). However, both Able (1977) and Ralph (1978) found that coastal migrants showed directed activity in orientation cages. Ralph further demonstrated that wind drift cannot explain the large percentage of young along the coast, suggesting that 67% of coastal migrants that travelled there were directed with a preferred orientation. Furthermore, DeSante (1973, 1983a) believed vagrants were actively misoriented rather than disoriented, since the average arrival date of most vagrants to California in his studies coincided with their predicted arrival dates if they had travelled on the same dates, and at a similar wind speed, to migrants on their normal migratory route.

#### *Reverse migration*

Reverse migration is hypothesised to occur when individuals perform a migratory flight at a 180° deviation from their normal migratory pathway. This has often been used to explain autumn vagrancy of Palearctic passerines to Europe. For example, Yellow-browed Warblers (*Phylloscopus inornatus*), a Siberian migrant, should travel on an east/south-easterly bearing to their wintering grounds in Asia, but instead, some will travel in the opposite direction along a west/north-westerly bearing towards Europe.

The first published study on reverse migration was conducted by Rabøl (1969) on four species of *Phylloscopus* warblers, in which he assessed patterns of occurrence of these species in Britain and Ireland (hereafter, "BR-IR") to determine whether individuals arrived via random dispersal or some other mechanism. Rabøl found that patterns of occurrence of these migrants mirrored the species breeding ranges around the east-west axis, and concluded that their arrival did not result from random dispersal, but rather from reverse migration. He suggested that this may explain a significant number of vagrant passerines to Europe. Particularly for Pallas's Leaf Warbler (*Phylloscopus proregulus*), vagrant movements may involve reverse bicoordinate navigation along a great circle route, rather than a series of 180° mistakes (Rabøl 1976). Van Impe and Derasse's (1994) study on patterns of occurrence of vagrant Yellow-browed and Pallas's Leaf Warbler concluded that the occurrence of these Siberian vagrants was in favour of Rabøl's (1969, 1976) reverse migration hypothesis, since individuals arrived early to the Baltic coast, and were not influenced by weather. Cottridge and Vinicombe (1996) contributed additional support to this hypothesis, and found that patterns of occurrence of Red-breasted (*Ficedula parva*) and Collared Flycatchers (*F. albicollis*) to BR—IR reflected locations of their vagrant shadows (areas where vagrants are expected to occur if they travel on a reverse heading).

In 1998, orientation experiments by Thorup on Christiansø, Denmark found that both Yellow-browed (*P. inornatus*) and Pallas's Leaf Warblers oriented on predominantly southwesterly headings. These results best matched the hypothesis that both species misoriented along a reverse great circle route in order to reach the study site, whereby individuals first oriented along the reverse migratory bearing from the breeding range, and switched to a southwesterly bearing along the route to reach Christiansø. Thorup suggested that reverse migration may result from birds failing to properly reset their internal clock. Thorup et al.'s (2011, 2012) additional orientation studies on vanishing bearings of vagrant passerines on the Faroe Islands found that species with southeasterly migratory routes (SE-group) oriented towards the west, while species with southwesterly migratory routes (SW-group) oriented towards south-southeast. Thorup et al. concluded that species in the SE-group actively flew to the Faroe Islands along this reverse route, while the SW-group likely occurred on the Faroe Islands due to wind-drift, since their

demonstrated orientation would not have directed them towards the Faroe Islands. Based on these findings, the authors suggested that autumn vagrancy in species with more east-west migrations occurs as a result of reverse migration, potentially caused by an inability to separate east from west. This could also explain mirror-image misorientation in Nearctic passerines (DeSante 1973).

Recent regression analyses have attempted to provide additional support for the reverse migration hypothesis (Thorup 2004, Pfeifer et al. 2007). Thorup (2004) found that the occurrence of Palearctic vagrants was strongly correlated with migratory direction - vagrants with easterly migratory routes were more likely to occur in northwest Europe than those with more southerly routes - as well as population size, and detectability. These results suggest that species with more east-west migratory routes are more likely to reverse orient than those with southerly migratory routes, which explains observed patterns of abundance for these species in northwest Europe. Based on Thorup's (2004) findings, Pfeifer et al. (2007) aimed to address the mechanism behind reverse migration. They hypothesised that if migratory direction influences vagrancy, only species with long enough migratory distances (and increased migratory restlessness; *Zugunruhe*) will arrive in Central Europe as vagrants. Results of this study found that vagrant abundance was positively correlated with the size of the distributional range, migratory distance, and the ratio of the migratory distance to the distance required to reach Central Europe. The migratory programme thus influences which species will occur as vagrants.

The validity of this theory has been questioned by Phillips (2000), Gilroy and Lees (2003), and Newton (2008), and has been called "counterproductive" (Gilroy and Lees 2003) and an "untested hypothesis" (Newton 2008). Phillips (2000) did not agree that reverse migration hinges on the premise that vagrants are aberrant, since vagrancy should occur less frequently than it does if vagrants were actually defective. That is, it should be selected against if it is truly defective. Gilroy and Lees (2003) and Newton (2008) also questioned whether patterns of vagrants actually reflect observer bias rather than reverse migration, since the vagrant shadow of most species falls within northwestern Europe, which has a large number of observers, while areas outside of this region are less heavily

birded and may have unrecorded vagrants. De Juana (2008), however, did not agree that observational bias was an issue (specifically in Iberia) because, although sightings of vagrants are low, ringing efforts are similar to the rest of Europe. This may only be true in a few places, however, where ringing efforts can make up for lack of observers.

### *Mirror-image misorientation*

Mirror-image misorientation is hypothesised to occur when individuals travel on the mirror-image track (i.e. a 90° deviation reflected over the y-axis) of their normal migratory route, and has often been used to explain vagrancy of Nearctic birds. For example, a Blackpoll Warbler (*Setophaga striata*) should travel on an east-southeasterly bearing, approximately 125°, from their breeding grounds in California to their wintering grounds in the Greater Antilles, but instead will travel on a west-southwesterly track, approximately 215°, to islands off the coast of California. This theory was developed by DeSante (1973, 1983a, 1983b) (and described by Diamond (1982)) based on orientation-cage testing of vagrant Blackpoll Warblers on the Southeast Farallon Islands in California. DeSante (1973) found that vagrant Blackpoll Warblers oriented in the expected mirror-image direction (WSW), but also in the correct migratory direction (ESE), suggesting that misoriented vagrants are unable to distinguish between east and west (e.g. Corballis and Beale 1971, 2020), and display both directions simultaneously under stressful conditions. There has yet to be any further testing of this as a valid cause of vagrancy, possibly owing to the difficulty posed by capturing and studying vagrants directly in the field. A new migratory route in Richard's Pipit (*Anthus richardi*), however, visually suggests that the vagrants that established this route may have oriented on a mirror-image track to their normal migratory route (Dufour et al. 2021) to reach their new wintering location (though this may not in fact be a "new" route since Richard's Pipits have historically been known to occur in Europe; Gätke 1895, Lees and Gilroy 2021).

### 1.3.2 Wind and weather systems

Extrinsic factors are by far the most cited reason for vagrancy, through either displacement by wind (Williamson 1952, 1955, 1959, 1961, 1963, 1969; Lack 1959, 1960a, 1960b; Baker 1977; Elkins 1979, 2005, 2008; McLaren 1981), or intense weather systems, like hurricanes or cyclones (Elkins 2005, Farnsworth and Iliff 2012, Farnsworth et al. 2015). Wind-driven vagrants, particularly Palearctic species, are thought to be driven by anticyclonic weather (i.e. fine weather associated with cold fronts in the winter) (see Williamson (1952, 1955, 1959, 1961, 1963, 1969) and Lack (1959, 1960a, 1960b) for an in-depth explanation of how anticyclonic weather influences vagrancy). Williamson hypothesised that anticyclonic weather displaces vagrants downwind along easterlies, while Lack suggested easterlies displace oriented birds laterally. Studies comparing synoptic weather maps to timing of occurrence of Siberian passerines to BR—IR have found that vagrancy is associated with anticyclonic activity in the breeding grounds (Williamson 1959, 1961; Baker 1977), suggesting that anticyclones are responsible for vagrancy. Lack (1960a, 1960b), on the other hand, found no correlation with southeast winds in the North Sea, and rejected both Williamson's (1952, 1955, 1959, 1961, 1969), and his own (1959), hypothesis. Van Impe and Derasse (1994) also found no association between anticyclonic weather and occurrence of Siberian vagrants.

Studies using similar techniques to Williamson (1959, 1961), Lack (1960a, 1960b), and Baker (1977) have found that transatlantic vagrants to BR—IR are associated with synoptic weather, particularly strong southwesterlies of warm sectors (Elkins 1979, 2008). However, Elkins (1979, 2008) broadly assumed that any individuals that did not follow this pattern must have been ship-assisted, or must have arrived earlier than they were observed. McLaren (1981) also compared synoptic weather maps to arrival of vagrants to Nova Scotian islands, and found similarly to Williamson (1959, 1961) and Baker (1977) that vagrants generally occurred during fine weather (i.e. slack winds and high pressure), rather than from “propulsion northeastward by winds”. Individuals were not blown off-course to Nova Scotia by winds, but rather may have voluntarily flown outside of their range, or

“chose” to fly towards Nova Scotia. However, despite these results, McLaren concluded that western species in autumn are “swept-up the coast” by prevailing southwesterlies.

Though vagrants are frequently described as being “blown off course” (Lees and Gilroy 2009), sufficient evidence does not exist to classify vagrants as wind-blown, and the migratory acumen of birds makes it implausible that vagrants do not compensate for wind (Liechti 2006, Kok et al. 2020). The majority of studies on weather and vagrancy are qualitative, and do not provide sufficient evidence for or against the claim that wind drives vagrant movements. Previous methods have involved visual comparison between timing of vagrant occurrence and synoptic weather maps in the supposed region of origin, under the premise that vagrants are entrained by winds 1 to 3 days before their arrival at the vagrant site (Williamson 1959, 1961; Lack 1960a, 1960b; Nisbet 1962; Elkins 1979, 2008; McLaren 1981). However, conditions presented in these studies as the cause of vagrancy also occur without the arrival of vagrants. Concurrently, vagrants still occur in years when these conditions are not present (Pfeifer et al. 2007). Conditions thought to drive vagrancy are therefore not novel, or “unusual”, and can be used to explain almost any type of migratory movement, though that would be incorrect (Veit 1989).

Additionally, Williamson specified in his papers that vagrants *actively* fly downwind (1959, p. 363), and may be “drift-aided” by winds (1959, p. 372), rather than blown by them. Baker (1977) also hypothesised that vagrancy was not *due* to drift on anticyclonic easterlies, but was rather a consequence of random dispersal facilitated by wind (Holt 1978). Therefore, wind-drift is not thought to be the mechanism behind vagrant movement, but rather, vagrant movements may be aided by tail winds, which is why correlations between wind direction and vagrancy are sometimes detected (Veit 2008, Zawadzki et al. 2019). Individuals will select nights with favourable tail winds to migrate, using the wind to facilitate their movements (Veit 1989). Regardless, the idea that vagrants are swept away is so pervasive in the literature and in birding circles, that studies that do not even analyse how wind drives vagrancy (e.g. McLaren et al. 2006, Farnsworth et al. 2015) still conclude that vagrants are transported by wind.

Only three papers have attempted to quantitatively test for the effect of wind on vagrant movements (Nisbet 1962, Van Impe and Derasse 1994, Zawadzki et al. 2019), all of which show a distinct lack of statistical support for wind on vagrancy. Nisbet's (1962) reanalysis of Lack's (1960b) data found that Palearctic vagrants to Fair Isle coincided with high temperatures, but not with south-east winds in the North Sea, denoting that vagrants are not affected by drift, but will reverse orient to BR—IR in response to high temperatures. Van Impe and Derasse (1994), who also studied Palearctic vagrants, did not find any relationship between wind or high temperatures and occurrence of Yellow-browed or Pallas's Leaf Warblers to Europe. For Nearctic vagrants, Zawadzki et al. (2019) showed that southwesterly airflow was of secondary importance to population growth in predicting occurrence of vagrant Ash-throated Flycatchers (*Myiarchus cinerascens*) to the east coast of North America.

Furthermore, the hypothesis that *all* vagrants are storm-driven is not plausible. While it is certainly possible that some vagrants are, and have been, displaced by storms (Kinsky 1968, Bugoni et al. 2007), the sheer number of vagrant records makes it extraordinarily unlikely that storms have caused every single occurrence, and few vagrants are actually recorded after passage of storms (McLaren 1981). Additionally, many birds are known to be able to combat winds that are produced under storm conditions (Veit 1989), and anecdotal evidence suggests that some vagrants are capable of flying directly into headwinds (Vernimmen 2017).

A few studies have also looked at how environmental conditions, rather than wind, may impact vagrant movements. Vagrancy has been found to be positively correlated with the North Atlantic Oscillation (NAO) index for autumn transatlantic vagrants to BR—IR (Elkins 2008), and vagrant pelicans in Europe (Jiguet et al. 2008). However, transatlantic American teals do not respond to NAO (De Juana and Garcia 2010). El Niño—Southern Oscillation (ENSO) has also been correlated with vagrant occurrence, negatively for autumn transatlantic vagrants (Elkins 2008), and positively for drifted Asiatic migrants to Attu Island in the autumn (Hameed et al. 2009). Asiatic migrants were also correlated with sea surface temperatures in the previous autumn in the eastern equatorial Pacific. Warmer

temperatures have been linked to vagrant occurrence of Purple Gallinules (*Porphyrio martinicus*) in North America (Farnsworth et al. 2015), and rainfall has been correlated with occurrence of vagrant pelicans to Europe (Jiguet et al. 2008).

## 1.4 Factors that influence vagrancy

A variety of other factors have been studied to determine plausible influences of vagrancy. Factors include **(1) migratory factors** such as migratory distance (DeBenedictis 1971, Hampton 1997, Robbins 1980, McLaren et al. 2006, Pfeifer et al. 2007, Umegaki 2014, Ralph and Wolfe 2018), migratory direction (Thorup 2004, Umegaki 2014), vagrant distance (i.e. the distance between the breeding range and vagrant site) (Hampton 1997, Pfeifer et al. 2007, Umegaki 2014), and angular deviation from the migratory route (DeBenedictis 1971, Ralph and Wolfe 2018), **(2) morphological factors** such as body mass (Robbins 1980, McLaren et al. 2006, Pfeifer et al. 2007), and wing length (McLaren et al. 2006, Pfeifer et al. 2007), and **(3) population factors** such as population size (DeBenedictis 1971; DeSante 1983b; Hampton 1997; Veit 1990, 1997, 2000; Elkins 1999; Thorup 2004; Jiguet et al. 2008; De Juana and Garcia 2010; Farnsworth et al. 2015, Ralph and Wolfe 2018), population growth (McLaren et al. 2006, Zawadzki et al. 2019), and the size of the species' range (Pfeifer et al. 2007, Umegaki 2014).

### 1.4.1 Migratory factors

Studies that analyse migratory distance in relation to vagrant abundance have all found that the longer the migratory distance, the more likely an individual will occur as a vagrant (DeBenedictis 1971, Robbins 1980, Hampton 1997, Thorup 2004, McLaren et al. 2006, Pfeifer et al. 2007, Umegaki 2014). It seems logical that species which are already capable of long-distance flights will be more likely to occur as vagrants outside of their range (Lees and Gilroy 2014). However, DeBenedictis (1971) found a weak relationship between migratory distance and vagrancy, which he theorised resulted from short-distance migrants being less common everywhere.

Ralph and Wolfe (2018) also found that the longer the distance between the breeding grounds and the vagrant site (i.e. the vagrant distance), the more likely an individual would occur as a vagrant. On the other hand, Hampton (1997), Pfeifer et al. (2007), and Umegaki (2014) did not find any correlation between vagrant distance and vagrant occurrence. When the ratio of the migratory distance to the vagrant distance was compared to vagrant occurrence instead, a significant positive relationship was detected (Pfeifer et al. 2007, Umegaki 2014). That is, the closer in length the migratory distance and vagrant distance are, the more likely an individual will occur as a vagrant at locations at that distance.

Furthermore, it was found that the smaller the angular deviation between the migratory route and the suspected vagrant route, the more likely a species would occur as a vagrant (DeBenedictis 1971, Ralph and Wolfe 2018). Migratory direction was only analysed in Thorup (2004) and Umegaki (2014), and was specific for vagrants to northern Europe and Japan, respectively. Thorup (2004) found that vagrants with more easterly migratory routes occurred more often as vagrants in northern Europe than those with more southerly/southwesterly routes, while Umegaki (2014) did not find any effect of migratory direction on vagrancy.

#### **1.4.2 Morphological factors**

Robbins (1980) and McLaren et al. (2006) found that larger species are more likely to occur as transatlantic vagrants. Larger species may morphologically have a greater capacity for flight (larger wing span and body size), and will be able to maintain greater fat stores for increased flight distances, which is essential for ocean crossings. Pfeifer et al. (2007), on the other hand, found that Palearctic vagrants were not influenced by body size or wing length.

### 1.4.3 Population factors and density-dependence

It has been widely hypothesised that a link exists between population size and occurrence of vagrants (Grinnell 1922; Williamson 1963, 1969; Holt 1978; Veit 1990, 2005, 2008; Phillips 2000). Grinnell (1922) first theorised that as individuals continues to reproduce, the pressure becomes so great that it forces individuals (i.e. vagrants) to disperse outwards. Williamson (1963, 1969) also hypothesised that all vagrancy may be driven by high population pressure that pushes individuals out of overpopulated areas, and that vagrancy is much more dependent upon population density than displacement via wind drift. This link has been strongly supported by quantitative models on factors that influence annual occurrence of vagrants. The majority of studies have shown that population size (DeBenedictis 1971; DeSante 1983b; Veit 1990, 1997, 2000; Thorup 2004; Pfeifer et al. 2007 (by proxy of range size); Jiguet et al. 2008; De Juana and Garcia 2010; Ralph and Wolfe 2018; Zawadzki et al. 2019) or population growth (Veit 1997; McLaren et al. 2006; Zawadzki et al. 2019) are significantly correlated with annual variation in vagrant abundance. Studies have predominantly focused on Nearctic vagrants (DeBenedictis 1971; DeSante 1983b; Veit 1990, 1997, 2000; Ralph and Wolfe 2018; Zawadzki et al. 2019), though transatlantic vagrants (Robbins 1990, Elkins 1999, McLaren et al. 2006) and Palearctic vagrants (Thorup 2004, Pfeifer et al. 2007, Umegaki 2014) have also been studied.

In fact, studies on vagrancy that focus mainly on navigational errors or wind, often state that vagrants belong to large and growing populations, and that increased vagrancy may result from increased population sizes and range expansion (Williamson 1959, 1963, 1969; McLaren 1981; Elkins 1979, 2005). This idea, however, is often buried in the discussion of these papers, and subsequently overlooked (Williamson 1959, 1963, 1969; Baker 1977; Elkins 1979, McLaren 1981; DeSante 1983b; Thorup 2004; McLaren et al. 2006). Consequently, the idea that vagrants are aberrant remains pervasive in the literature, masking plausible causes of vagrancy. Vagrancy is not a series of individual “mistakes”, but rather a property of populations (Veit 2008), whereby vagrant patterns are influenced by population dynamics and population-level effects. Time series on

vagrants show that vagrants occur in episodic irruptions (e.g. Veit 1990, Patten and Marantz 1996, Patten and Burger 1998, Hamilton et al. 2007, White and Kehoe 2014), strongly suggesting a link between population growth and incidence of vagrancy, since populations of birds are known to fluctuate episodically (Williamson 1963, Perrins et al. 1991, Böhning-Gaese et al. 1994).

It is evident that vagrancy may be driven by population dynamics, whereby young disperse during periods of high density in the breeding range (Lack 1954, Williamson 1963). Pressure to leave the population range has been hypothesised to result from either the population exceeding the available food supply, in a similar manner to irruptions (Grinnell 1922, Williamson 1963, Veit 1990, Baker 1978, Newton 2006, Veit 2008, Lees and Gilroy 2009), or from loss of habitat (DeBenedictis 1971, DeSante 1983b, Patten and Marantz 1996). Vagrants may increase in years when food is abundant as the source population increases (i.e. irruptions; an increase in vagrants due to an increase in population), but may also increase in years of low food density to find new resources (i.e. eruptions; an increase in emigrating individuals to find new resources) (Newton 2006, Lees and Gilroy 2009). Evidence that vagrants respond to food availability was discovered by Patten and Burger (1998), who found that spruce budworm (*Chorisonneura fumiferana*) populations in the spring were excellent predictors of vagrant New World warblers the following autumn. As for habitat change, DeBenedictis (1971) found that species that occupy early seral stages of habitat, which are subject to increased rates of habitat change, are much more likely to occur as vagrants than those in later seral stages. DeSante (1983b) hypothesised that vagrants would increase as the rate of habitat change increases (to become more unsuitable), since dispersers are often selected for when habitats change (Southwood 1974). Vagrancy thus results from larger than average numbers of individuals dispersing outwards from the natal site (Williamson 1963, Veit 2008) to find suitable habitat and resources to ensure their continued individual survival (Baker 1978).

## 1.5 Consequences of vagrancy

### 1.5.1 Vagrancy as dispersal

*Zwischenzug*, or exploratory migration, has been hypothesised to be the reason for observed vagrant movements (De Juana 2008, Veit 2008). Based on Baker's (1978, 1980, 1993) "Exploratory Migration Model", *Zwischenzug* hypothesises that young birds will engage in exploratory movements immediately after fledging, known as post-fledging, or post-juvenile, dispersal, to create a familiar area map of the sites surrounding their natal area. Their first autumn migration is an extension of the post-fledging phase, to locate suitable overwintering sites. Since vagrants are mainly young birds on their first autumn migration, it is likely that their movements are linked to exploration via post-fledging dispersal. Young vagrants may disperse outwards from the natal site to overwintering sites that are not typical of the species, in response to conditions they encounter during this exploratory period. Williamson (1959), based on his observations of Barred Warblers (*Curruca nisoria*) to the Faroe Islands, suggested that vagrancy was associated with post-juvenile dispersal and was not a true migration. Vagrants will disperse randomly from the natal site to new overwintering sites, which may result in the establishment of new breeding sites at the edge of their range the following spring (Williamson 1959, 1963).

### 1.5.2 Range expansion and colonisation

Through dispersal, vagrants may colonise new areas, much like the pioneers or explorers that Grinnell (1922) and Williamson (1959, 1969) envisioned. They theorised that the purpose of vagrancy was to colonise new habitat for the benefit of the species, to ensure their continued survival. However, since selection does not occur at the species-level, this cannot be the case. Vagrants may still be pioneers, but their colonisation of new habitats is not the *function* of vagrancy, but rather a rare, and important *consequence* of it. Vagrants may colonise new areas if suitable habitat is found during their dispersal movements, and it is these dispersal movements that impart benefits at the individual-level, particularly if

individuals derive from ranges that are unpredictable, unstable, or overcrowded. While it has been speculated that vagrancy should be selected against since the risk seems far greater than the reward (Able 1977, Wilson 1988), it might actually be highly beneficial for young birds to be prone to vagrancy (DeBenedictis 1971, Ralph 1978, DeSante 1983b, Veit 1989, De Juana 2008, Veit 2008), since flexibility in the migratory programme can allow individuals to take advantage of newly available habitats (Ralph 1978), particularly when habitat in their normal range is ephemeral (Farnsworth et al. 2015). It is also possible that vagrancy is highly beneficial for the parents, rather than their offspring, through bet-hedging (Reilly and Reilly 2009). Parents may impart an array of innate migratory orientations creating within-clutch phenotypic variation in migratory orientation, which ensures that their genes get passed on. This does not detract from the hypothesis that vagrancy is evolutionarily advantageous, and will either impart fitness benefits on the parents, or its offspring, resulting in its continued presence across generations.

Examples of range expansion in vagrant species are numerous. Some examples include Cattle Egrets (*Bubulcus ibis*) (Hengeveld 1989); Little Egrets (*Egretta garzetta*) (Buckley et al. 2009); Glossy Ibis (*Plegadis falcinellus*) (Davis Jr. and Kricher 2020); Eurasian Collared Doves (*Streptopelia decaocto*) (Romagosa 2020); Lesser Black-backed Gulls (*Larus fuscus*) (Boertmann 2008); Blue-gray Gnatcatchers (*Polioptila cearulea*) (Ellison 1991, 1993); Adelaide's Warblers (*Setophaga adelaidae*) (Veit et al. 2016) and a number of species on Caribbean Islands (Lovette et al. 1999a, 1999b), which have all expanded their range as a result of repeated vagrancy. Recent studies have also demonstrated that Green-winged (*Anas carolinensis*) and Blue-winged Teals (*Anas discors*) (De Juana and Garcia 2010), Barn Swallows (*Hirundo rustica*) (Winkler et al. 2017) and Richard's Pipit (*Anthus richardi*) (Dufour et al. 2021) have established new migratory routes, which may have emerged as result of vagrant individuals.

Vagrants represent individuals at the tail-end of leptokurtic frequency distributions that are typical of mobile populations (Kot et al. 1996, Veit and Lewis 1996), and are the "extremes of dispersal" (DeSante 1983a). These individuals are part of the natural process of dispersal, and without them, the extent of species' ranges are often severely

underestimated (Veit and Lewis 1996, Winkler 2005). However, only a few studies have actually tested the ability of vagrants to colonise new areas, and of those, only vagrants to island systems were assessed. Rose and Polis (2000) speculated that vagrants only visit islands briefly and do not colonise them, however, no statistical analyses were used to confirm or deny this statement. Lees and Gilroy (2013) modelled how vagrancy may influence colonisation on islands, and found that a species' propensity for vagrancy did not predict island colonisation, though many well-known island systems in northwest Europe were excluded from their analysis. They did find, however, that a species' range size predicted colonisation of islands. Since vagrancy increases with population size, it is likely that vagrancy and colonisation are actually related, but either their index for vagrancy or colonisation did not fully capture movements in these species.

## **1.6 The importance of studying vagrancy**

Due to recent climatic changes, species of birds, and many other organisms, are disappearing at an alarming rate (Urban 2015, Román-Palacios et al. 2020). Vagrancy may be the key to understanding which species will be more likely to adapt by movement to new habitats as current habitats change and deteriorate. Recent studies have shown that species that currently demonstrate high rates of vagrancy are predicted to experience the largest range increases under climatic changes (Jiguet and Barbet-Massin 2013). This finding highlights the importance of understanding how vagrancy occurs, and what influences some species to produce more vagrants than others. If species with high rates of vagrancy will expand their ranges under climate change, knowing why this is the case will help us to pinpoint species that will persist, and those that will need further conservation protections to survive. Birds themselves are also a good indicator of ecosystem health (Gregory and Van Strien 2010). Since vagrants are linked to increases in population, patterns of vagrant occurrence may serve as our first warning of which species are likely to be at risk – i.e. species that are less prone to vagrant movements may be at a higher risk of climatic extinction than those that are more prone to vagrancy (Jiguet and Barbet-Massin 2013).

Furthermore, vagrancy itself may provide the mechanism through which individuals survive the effects of a rapidly changing climate (Gilroy et al. 2016). Davis and Watson (2018), who refer to vagrants as “climate refugees”, emphasise that long-distance dispersal and vagrancy may provide the means for individuals to escape climatic extinction. Vagrants are “potential colonists of high conservation value”, and vagrant events that lead to colonisation may offset the effects of climate change (Davis and Watson 2018). This is particularly important in the face of invasive-species policies, whereby vagrants are sometimes considered invasive and eradicated or confined as biosecurity risks. For example, the first Nicobar Pigeon (*Caloenas nicobarica*) in Australia was deemed a biosecurity risk and placed in captivity (Davis and Watson 2018). Gilroy et al. (2017) argue that cases such as these should not be considered invasive if individuals travelled to locations via “unassisted dispersal” (Gilroy et al. 2017, Davis and Watson 2018). These individuals are likely responding to changing habitat, and the possibility that they will colonise the new regions that they find is invaluable, especially for threatened species.

In light of the recent pandemic, however, vagrants are also an important public health issue since many migratory birds have been linked to the spread of a number of zoonotic diseases that can affect both humans and wildlife (Reed et al. 2003). To the best of my knowledge, vagrants themselves have not been explicitly examined for such diseases, though case studies do exist. One case study on the King Penguin (*Aptenodytes patagonicus*) in South Africa found that vagrant penguins admitted to a rehabilitation centre were diagnosed with tick-borne *Babesia peircei*, though it could not be confirmed whether they contracted the disease before or after their arrival to South Africa (Parsons et al. 2017). Nonetheless, species that do occur as vagrants are known to carry diseases, such as avian influenza (Rappole and Hubálek 2006), avian malaria (Clark and Clegg 2015), various tick-borne diseases (Smith et al. 1996, Morshed et al. 2005), and the West Nile virus (Peterson et al. 2003). Though the likelihood that they will serve as a vector is low due to their inherent rarity, it only takes one individual to spread disease. Therefore, the prevalence of disease in migratory birds, and the extreme long distances that vagrants are known to travel, emphasises that this will be an area of possible concern in the future.

Vagrants may also impact their environment in other ways. Kalwij et al. (2019) found that the colonisation of a vascular plant on Marion Island in the Southern Ocean, more than 7500 km away from its nearest natural population, was linked to dispersal by vagrant birds. This case demonstrates that vagrants can, and do, influence the habitats that they enter, and cases like this are likely to have occurred before. Vagrants, however, are often excluded from studies on population dynamics, such as species turnover, community assembly, or effects of competition (Rose and Polis 2000), as well as studies on migration, colonisation, and range expansion (Veit and Lewis 1996). This lends itself to the much larger issue that vagrancy has been relatively ignored in general ecological literature, even though the impacts that vagrancy may have on habitats and other species are significant. Rose and Polis (2000) stressed the need to study vagrants, in order to understand their role in the ecosystems that they occupy.

Lastly, vagrants have been found to generate real economic value due to the increased interest and attraction from birdwatchers (Booth et al. 2011, Callaghan et al. 2018, 2020). From a conservation standpoint, the high economic value that vagrants generate can help influence policy-makers to protect birds and conserve their habitats (Callaghan et al. 2018, 2020). Additionally, by capitalising on the interest and excitement that vagrants generate through ecotourism and other means, bird observatories and conservation organisations can increase awareness and engagement in conservation by the general public (Booth et al. 2011, Callaghan et al. 2018, 2020). This will in turn influence conservation policy since individuals are more likely to advocate for causes that they care about.

## **1.7 Objectives and aims of this thesis**

This thesis explores patterns of vagrancy and long-distance dispersal in migratory species, and investigates factors that may influence vagrant occurrence. Each chapter in this thesis has been written in a stand-alone format, with its own introduction, methods, and discussion, and can be read independently, although Chapter 3 relies partially on

methods described in Chapter 2. At the time of writing, Chapter 5 has been published in *Frontiers in Ecology and Evolution*.

The underlying premise of this thesis is that vagrants are not aberrant, and that vagrancy is part of the natural migratory programme. In **Chapter 2**, I investigate the orientation behaviour of vagrants versus non-vagrants using orientation cage experiments to determine whether vagrants and non-vagrants behaviourally differ. Motivation and methodology for this chapter were inspired by DeSante's (1973) thesis on vagrant Blackpoll Warblers (*Setophaga striata*) to Southeast Farallon Island in California. This study is the second of its kind to directly assess orientation behaviour of Nearctic vagrants in the field.

Knowing where vagrants come from would clarify theories surrounding their arrival, however, no methodology has been developed to determine the source population of vagrants when they occur. In **Chapter 3**, I analyse the deuterium content in feathers (from vagrants captured for orientation experiments in Chapter 2) using stable isotope analysis, to assess the suitability of this technique to predict the natal origin of vagrants, particularly in North America where isoscapes are more pronounced (Hobson and Wassenaar 1997, Hobson et al. 2004). This study will be the first to use stable isotope analysis to determine natal origin of vagrants in North America, and the third for vagrants globally (Fox et al. 2007, De Jong et al. 2019).

Many studies have indicated a strong relationship between vagrancy, and population size and growth (e.g. Veit 1997, 2000; Zawadzki et al. 2019). In **Chapter 4**, I expand upon analyses by Zawadzki et al. (2019) to determine whether vagrant New World warblers to eastern North America are influenced by population size, population growth, vagrant distance, and angular deviation from the normal migratory route. I also investigate how population size and population growth from different regions within the breeding range influence vagrancy for these warbler species.

Based on the relationship between population growth and vagrant occurrence, in **Chapter 5**, I conduct a case study to investigate whether the source population of a vagrant species

can be determined by examining the relationship between population growth in the breeding range and abundance of vagrants. The Lesser Black-backed Gull (*Larus fuscus*) served as the focal species for this study due to their well-documented vagrancy to North America. This approach would provide a means to study vagrancy indirectly, which is often necessary due to the rarity and unpredictability of vagrant occurrence.

Vagrants occur in regular irruptions (e.g. Veit 1990), likely as a result of population growth within the breeding range. In **Chapter 6**, I analyse irruption cycles for the Northern Saw-whet Owl (*Aegolius acadicus*) in North America. Though Northern Saw-whet Owls are not classified as a vagrant, their irruption cycles are similar to the episodic irruptions of vagrant species, and are characterised by an influx of juvenile individuals on their first autumn migration (Murray 1996, Ralph 1971). I investigate the timing of these irruptions, and whether they are influenced by prey availability in the breeding range.

Finally, in **Chapter 7**, I summarise and discuss the main findings of my thesis, and highlight areas of importance for future studies.

## References

- Able, K. P. (1977). The orientation of passerine nocturnal migrants following offshore drift. *The Auk*, *94*(2), 320–330.
- Alerstam, T. (1987). Bird migration across a strong magnetic anomaly. *Journal of Experimental Biology*, *130*(1), 63–86.
- Alerstam, T. (1991). Ecological causes and consequences of bird orientation. In P. Berthold (Ed.), *Orientation in birds*. Birkhäuser, Basel.
- Baker, K. (1977). Westward vagrancy of Siberian passerines in autumn 1975. *Bird Study*, *24*(4), 233–242.
- Baker, R. R. (1978). *The evolutionary ecology of animal migration*. Holmes; Meier Publishers.
- Baker, R. R. (1980). The significance of the Lesser Black-backed Gull to models of bird migration. *Bird Study*, *27*(1), 41–50.
- Baker, R. R. (1993). The function of post-fledging exploration: A pilot study of three species of passerines ringed in Britain. *Ornis Scandinavica*, *24*, 71–79.
- Boertmann, D. (2008). The Lesser Black-backed Gull, *Larus fuscus*, in Greenland. *Arctic*, *61*(2), 129–133.
- Booth, J. E., Gaston, K. J., Evans, K. L., & Armsworth, P. R. (2011). The value of species rarity in biodiversity recreation: A birdwatching example. *Biological Conservation*, *144*, 2728–2732.
- Buckley, P. A., Massiah, E. B., Hutt, M. B., Buckley, F. G., & Hutt, H. F. (2009). *The Birds of Barbados* (BOU Checklist Series: 24). British Ornithologist's Union.
- Bugoni, L., Sander, M., & Costa, E. S. (2007). Effects of the first southern Atlantic hurricane on Atlantic petrels (*Pterodroma incerta*). *The Wilson Journal of Ornithology*, *119*(4), 725–729.
- Callaghan, C. T., Benson, I., Major, R. E., Martin, J. M., Longden, T., & Kingsford, R. T. (2020). Birds are valuable: The case of vagrants. *Journal of Ecotourism*, *19*(1), 82–92.
- Callaghan, C. T., Slater, M., Major, R. E., Morrison, M., Martin, J. M., & Kingsford, R. T. (2018). Travelling birds generate eco-travellers: The economic potential of vagrant birdwatching. *Human Dimensions of Wildlife*, *23*(1), 71–82.

- Clark, N. J., & Clegg, S. M. (2015). The influence of vagrant hosts and weather patterns on the colonization and persistence of blood parasites in an island bird. *Journal of Biogeography*, *42*, 641–651.
- Clarke, W. E. (1912). *Studies in bird migration*. Gurney; Jackson.
- Corballis, M. C., & Beale, I. L. (1970). Bilateral symmetry and behavior. *Psychological Review*, *77*(5), 451–464.
- Corballis, M. C., & Beale, I. L. (2020). *The psychology of left and right*. Routledge.
- Cottridge, D., & Vinicombe, K. (1996). *Rare birds in Britain and Ireland - a photographic record*. Harper Collins.
- Davis, R. A., & Watson, D. M. (2018). Vagrants as vanguards of range shifts in a dynamic world. *Biological Conservation*, *224*, 238–241.
- Davis Jr., W. E., & Kricher, J. C. (2020). Glossy Ibis (*Plegadis falcinellus*). In S. Billerman (Ed.), *Birds of the World*. Cornell Lab of Ornithology.
- De Jong, A., Tornaiainen, J., Bourski, O. V., Heim, W., & Edenius, L. (2019). Tracing the origin of vagrant Siberian songbirds with stable isotopes: the case of Yellow-browed Warbler (*Abrornis inornatus*) in Fennoscandia. *Ornis Fennica*, *96*, 90–99.
- De Juana, E. (2008). Where do Pallas's and Yellow-browed Warblers (*Phylloscopus proregulus*, *Ph. inornatus*) go after visiting northwest Europe in autumn? an Iberian perspective. *Ardeola*, *55*(2), 179–192.
- De Juana, E., & Garcia, E. F. J. (2010). Vagrancy or migration: Why do American Teals cross the Atlantic? *Ardeola*, *57*(2), 417–430.
- DeBenedictis, P. (1971). Wood warblers and vireos in California: The nature of the accidental. *California Birds*, *2*(4), 111–128.
- DeSante, D. F. (1973). *An analysis of the fall occurrences and nocturnal orientations of vagrant wood warblers (Parulidae) in California* (Doctoral dissertation). Stanford University. Stanford, California.
- DeSante, D. F. (1983a). Annual variability in the abundance of migrant landbirds on Southeast Farallon Island, California. *The Auk*, *100*(4), 826–852.
- DeSante, D. F. (1983b). Vagrants: when orientation or navigation goes wrong. *Point Reyes Bird Observatory Newsletter*, *61*, 12–16.
- Diamond, J. M. (1982). Mirror-image navigational errors in migrating birds. *Nature*, *295*, 277–278.
- Dufour, P., Franceschi, C., Doniol-Valcroze, P., Jiguet, F., Guéguen, M., Renaud, J., Lavergne, S., & Crochet, P. A. (2021). A new westward migration route in an Asian passerine bird. *Current Biology*, *31*, 1–7.

- Elkins, N. (1979). Nearctic landbirds in Britain and Ireland: A meteorological analysis. *British Birds*, 72(9), 417–433.
- Elkins, N. (1999). Recent records of Nearctic landbirds in Britain and Ireland. *British Birds*, 92, 83–95.
- Elkins, N. (2005). Weather and bird migration. *British Birds*, 98, 238–256.
- Elkins, N. (2008). Further thoughts on transatlantic vagrancy of landbirds to Britain & Ireland. *British Birds*, 101, 458–477.
- Ellison, W. G. (1991). *The mechanism and ecology of range expansion by the Blue-gray Gnatcatcher* (M.Sc. thesis). University of Connecticut. Storrs, Connecticut.
- Ellison, W. G. (1993). Historical patterns of vagrancy by Blue-gray Gnatcatchers in New England. *Journal of Field Ornithology*, 64(3), 358–366.
- Farnsworth, A., & Iliff, M. J. (2012). The changing seasons: Driven. *North American Birds*, 66(1), 16–28.
- Farnsworth, A., La Sorte, F., & Iliff, M. J. (2015). Warmer summers and drier winters correlate with more winter vagrant Purple Gallinules (*Porphyrio martinicus*) in the North Atlantic Region. *The Wilson Journal of Ornithology*, 127(4), 582–592.
- Fox, T. A. D., Christensen, T. K., Bearhop, S., & Newton, J. (2007). Using stable isotope analysis of multiple feather tracts to identify moulting provenance of vagrant birds: A case study of the Baikal Teal *Anas formosa* in Denmark. *Ibis*, 149, 622–625.
- Franklin, E. C. (2017). Vagrancy in paradise: Documentation of the chevron butterflyfish *Chaetodon trifascialis* in Kaneohe Bay, Oahu, Hawaiian islands. *Marine Biodiversity Records*, 10(1), 1–4.
- Gätke, H. (1895). *Heligoland as an Ornithological Observatory: The Result of Fifty Years' Experience*. David Douglas.
- Gilroy, J. J., Avery, J. D., & Lockwood, J. L. (2017). Seeking international agreement on what it means to be “native”. *Conservation Letters*, 10(2), 238–247.
- Gilroy, J. J., Gill, J. A., Butchart, S. H. M., Jones, V. R., & Franco, A. M. A. (2016). Migratory diversity predicts population declines in birds. *Ecology Letters*, 19, 308–317.
- Gilroy, J. J., & Lees, A. C. (2003). Vagrancy theories: Are autumn vagrants really reverse migrants? *British Birds*, 96, 427–438.
- Gregory, R. D., & Van Strien, A. (2010). Wild bird indicators: Using composite population trends of birds as measures of environmental health. *Ornithological Science*, 9, 3–22.
- Grinnell, J. (1922). The role of the “accidental”. *The Auk*, 39(3), 373–380.

- Hameed, S., Norwood, H. H., Flanagan, M., Feldstein, S., & Yang, C. H. (2009). The influence of El Niño on the spring fallout of Asian bird species at Attu Island. *Earth Interactions*, *13*(7), 1–22.
- Hampton, S. (1997). Rare migrants in California: The determinants of their frequency. *Western Birds*, *28*, 30–42.
- Hengeveld, R. (1989). *Dynamics of biological invasions*. Kluwer Academic Publishers. Chapman; Hall.
- Hobson, K. A., Bowen, G. J., Wassenaar, L. I., Ferrand, Y., & Lormee, H. (2004). Using stable hydrogen and oxygen isotope measurements of feathers to infer geographical origins of migrating European birds. *Oecologia*, *141*, 477–488.
- Holt, C. W. (1978). Westward vagrancy of Siberian passerines [Letters]. *Bird Study*, *25*(2), 123–124.
- Jiguet, F., & Barbet-Massin, M. (2013). Climate change and rates of vagrancy of Siberian bird species to Europe. *Ibis*, *155*, 194–198.
- Jiguet, F., Doxa, A., & Robert, A. (2008). The origin of out-of-range pelicans in Europe: Wild bird dispersal or zoo escapes? *Ibis*, *150*, 606–618.
- Kalwij, J. M., Medan, D., Kellermann, J., Greve, M., & Chown, S. L. (2019). Vagrant birds as a dispersal vector in transoceanic range expansion of vascular plants. *Scientific Reports*, *9*(4655).
- Kinsky, F. C. (1968). An unusual seabird mortality in the southern North Island (New Zealand) April, 1968. *Notornis*, *15*, 143–155.
- Koenig, W. D., Van Vuren, D., & Hooge, P. N. (1996). Detectability, philopatry, and the distribution of dispersal distances in vertebrates. *Trends in ecology & evolution*, *11*(12), 514–517.
- Kok, E. M. A., Tibbitts, T. L., Douglas, D. C., Howey, P. W., Dekinga, A., Gnep, B., & Piersma, T. (2020). A red knot as a black swan: How a single bird shows navigational abilities during repeat crossings of the Greenland Icecap. *Journal of Avian Biology*, *51*(8), 02464.
- Kot, M., Lewis, M. A., & Driessche, P. (1996). Dispersal data and the spread of invading organisms. *Ecology*, *77*(7), 2027–2042.
- Lack, D. (1954). *The natural regulation of animal numbers*. Clarendon Press.
- Lack, D. (1959). Migration across the sea. *Ibis*, *101*, 374–399.
- Lack, D. (1960a). Autumn drift-migration on the English east coast. *British Birds*, *53*, 325–352, 379–397.
- Lack, D. (1960b). A comparison of drift-migration at Fair Isle, the Isle of May and Spurn Point. *Scottish Birds*, *1*, 295–323.

- Lees, A. C., & Gilroy, J. J. (2009). Vagrancy mechanisms in passerines and near-passerines. In R. Slack (Ed.), *Where and When: An analysis of status and distribution in Britain and Ireland. Volume 1: Sandgrouse to New World orioles*. Rare Bird Books.
- Lees, A. C., & Gilroy, J. J. (2014). Vagrancy fails to predict colonization of oceanic islands. *Global Ecology and Biogeography*, *23*, 405–413.
- Lees, A. C., & Gilroy, J. J. (2021). Bird migration: When vagrants become pioneers. *Current Biology*, *31*(24), R1568–R1570.
- Liechti, F. (2006). Birds: Blowin' by the wind? *Journal of Ornithology*, *147*, 202–211.
- Lovette, I. J., Bermingham, E., & Ricklefs, R. E. (1999a). Mitochondrial DNA phylogeography and the conservation of endangered Lesser Antillean icterus orioles. *Conservation Biology*, *13*(5), 1088–1096.
- Lovette, I. J., Seutin, G., Ricklefs, R. E., & Bermingham, E. (1999b). The assembly of an island fauna by natural invasion: Sources and temporal patterns in the avian colonization of barbados. *Biological Invasions*, *1*(1), 33–41.
- McLaren, I. A. (1981). The incidence of vagrant landbirds on Nova Scotian islands. *The Auk*, *98*(2), 243–257.
- McLaren, I. A., Lees, A. C., Field, C., & Collins, K. J. (2006). Origins and characteristics of Nearctic landbirds in Britain and Ireland in autumn: A statistical analysis. *Ibis*, *148*(4), 1–20.
- Merriam-Webster. (2021, October 28). *Vagrant*. Arlington, Massachusetts. Retrieved October 28, 2021, from <https://www.merriam-webster.com/dictionary/vagrant>
- Morshed, M. G., Scott, J. D., Fernando, K., Beati, L., Mazerolle, D. F., Geddes, G., & Durden, L. A. (2005). Migratory songbirds disperse ticks across Canada, and first isolation of the Lyme disease spirochete, *Borrelia burgdorferi*, from the avian tick, *Ixodes auritulus*. *Journal of Parasitology*, *91*(4), 780–790.
- Murray, B. G., Jr. (1966). Migration of age and sex classes of passerines on the Atlantic Coast in autumn. *The Auk*, *83*(3), 352–360.
- Newton, I. (2006). Advances in the study of irruptive migration. *Ardea*, *94*(3), 433–460.
- Newton, I. (2008). *The migration ecology of birds*. Academic Press.
- Nisbet, I. C. T. (1962). South-eastern rarities at Fair Isle. *British Birds*, *55*, 74–86.
- Parsons, N. J., Gous, T. A., Cranfield, M. R., Cheng, L. I., Schultz, A., Horne, E., Last, R. P., Lampen, F., Ludynia, K., Bousfield, B., Strauss, V., Peirce, M. A., & Vanstreels, R. E. T. (2017). Novel vagrant records and occurrence of vector-borne pathogens in King Penguins (*Aptenodytes patagonicus*) in South Africa. *Polar Biology*, *41*, 79–86.
- Patten, M. A., & Burger, J. C. (1998). Spruce budworm outbreaks and the incidence of vagrancy in eastern North American wood-warblers. *Canadian Journal of Zoology*, *76*, 433–439.

- Patten, M. A., & Marantz, C. A. (1996). Implications of vagrant southeastern vireos and warblers in California. *The Auk*, *113*(4), 911–923.
- Peterson, A. T., Viegals, D. A., & Andreasen, J. K. (2003). Migratory birds modelled as critical transport agents for West Nile Virus in North America. *Vector-borne and Zoonotic Diseases*, *3*(1), 27–37.
- Pfeifer, R., Stadler, J., & Brandl, R. (2007). Birds from the Far East in Central Europe: A test of the reverse migration hypothesis. *Journal of Ornithology*, *148*, 379–385.
- Phillips, J. (2000). Autumn vagrancy: “reverse migration” and migratory orientation. *Ringing & Migration*, *20*, 35–38.
- Rabøl, J. (1969). Reversed migration as a cause of westward vagrancy by four *Phylloscopus* warblers. *British Birds*, *62*(3), 89–92.
- Rabøl, J. (1976). The orientation of Pallas’s Leaf Warbler *Phylloscopus proregulus* in Europe. *Dansk Ornitologisk Forenings Tidsskrift*, *70*, 6–16.
- Ralph, C. J. (1971). An age differential of migrants in coastal California. *The Condor*, *73*(2), 243–246.
- Ralph, C. J. (1978). Disorientation and possible fate of young passerine coastal migrants. *Bird-banding*, *49*(3), 237–247.
- Ralph, C. J., & Wolfe, J. D. (2018). Factors affecting the distribution and abundance of autumn vagrant New World warblers in northwestern California and southern Oregon. *PeerJ*, *6*, 5881.
- Rappole, J. H., & Hubalek, Z. (2006). Birds and Influenza H5N1 virus movement to and within North America. *Emerging Infectious Diseases*, *12*(10), 1486–1492.
- Reed, K. D., Meece, J. K., Henkel, J. S., & Shukla, S. K. (2003). Birds, migration and emerging zoonoses: West Nile virus, Lyme disease, influenza A and enteropathogens. *Clinical medicine & research*, *1*(1), 5–12.
- Reilly, J. R., & Reilly, R. J. (2009). Bet-hedging and the orientation of juvenile passerines in fall migration. *Journal of Animal Ecology*, *78*, 990–1001.
- Robbins, C. S. (1980). Predictions of future Nearctic landbird vagrants to Europe. *British Birds*, *73*, 448–457.
- Romagosa, C. M. (2020). Eurasian Collared-Dove (*Streptopelia decaocto*), version 1.0. In S. M. Billerman (Ed.), *Birds of the World*. Cornell Lab of Ornithology.
- Román-Palacios, C., & Wiens, J. J. (2020). Recent responses to climate change reveal the drivers of species extinction and survival. *Proceedings of the National Academy of Sciences*, *117*(8), 4211–4217.
- Rose, M. D., & Polis, G. A. (2000). On the insularity of islands. *Ecography*, *23*, 693–701.

- Smith Jr., R. P., Rand, P. W., Lacombe, E. H., Morris, S. R., Holmes, D. W., & Caporale, D. A. (1996). Role of bird migration in the long-distance dispersal of *Ixodes dammini*, the vector of Lyme disease. *Journal of Infectious Diseases*, *174*(1), 221–224.
- Southwood, T. R. E., May, R. M., Hassell, M. P., & Conway, G. R. (1974). Ecological strategies and population parameters. *The American Naturalist*, *108*(964), 791–804.
- Thorup, K. (1998). Vagrancy of yellow-browed warbler *Phylloscopus inornatus* and pallas's warbler *Ph. proregulus* in north-west Europe: misorientation on great circles? *Ringing and Migration*, *19*(1), 7–12.
- Thorup, K. (2004). Reverse migration as a cause of vagrancy. *Bird Study*, *51*(3), 228–238.
- Thorup, K., Ortvad, T. E., Holland, R. A., Rabøl, J., Kristensen, M. W., & Wikelski, M. (2012). Orientation of vagrant birds on the Faroe Islands in the Atlantic Ocean. *Journal of Ornithology*, *153*(4), 1261–1265.
- Thorup, K., Ortvad, T. E., Rabøl, J., Holland, R. A., Tøttrup, A. P., & Wikelski, M. (2011). Juvenile songbirds compensate for displacement to oceanic islands during autumn migration. *PLoS One*, *6*(3), 17903.
- Umegaki, Y. (2014). Testing the effect of migratory restlessness on the occurrence of vagrant continental passerines in Japan. *Ornithological Science*, *13*, 83–90.
- Urban, M. C. (2015). Accelerating extinction risk from climate change. *Science*, *348*(6234), 571–573.
- Van Impe, J., & Derasse, S. (1994). De recente toename van Bladkoninkje *Phylloscopus inornatus* en Pallas' Boszanger *P. proregulus* in Europa: zijn dwaalgasten werkelijk dwalende vogels. *Oriolus*, *60*, 3–17.
- Veit, R. R. (1989). Vagrant birds: Passive or active dispersal? *Bird Observer*, *17*(1), 25–29.
- Veit, R. R. (1990). Do vagrant birds in Massachusetts reflect population growth and dispersal rather than weather patterns? *Bird Observer*, *18*(2), 86–91.
- Veit, R. R. (1997). Long-distance dispersal and population growth of the Yellow-headed Blackbird *Xanthocephalus xanthocephalus*. *Ardea*, *85*(1), 135–143.
- Veit, R. R. (2000). Vagrants as the expanding fringe of a growing population. *The Auk*, *117*(1), 242–246.
- Veit, R. R. (2008). Why expect clusters of vagrants? *Bird Observer*, *36*(4), 213–217.
- Veit, R. R., & Lewis, M. A. (1996). Dispersal, population growth, and the Allee effect: Dynamics of the house finch invasion of eastern North America. *The American Naturalist*, *148*(2), 255–274.
- Veit, R. R., Velarde, E., Horn, M. H., & Manne, L. L. (2021). Population growth and long-distance vagrancy leads to colonization of Europe by Elegant Terns *Thalasseus elegans*. *Frontiers in Ecology and Evolution*, *9*, 725614.

- Veit, R. R., Zawadzki, L. C., Manne, L. L., Cales, P., Fibikar, D., Curley, S., Dluhos, E., & Norton, R. L. (2016). Vagrancy and colonization of St. Thomas and St. John, U.S. Virgin Islands, by Adelaide's Warblers (*Setophaga adelaidae*). *The Journal of Caribbean Ornithology*, 29, 47–50.
- Vernimmen, T. (2017). Miracles on the wing. *New Scientist*, 233(3118), 36–39.
- Williamson, K. (1952). Migrational drift in Britain in autumn 1951. *Scottish Nature*, 64, 1–18.
- Williamson, K. (1955). Migrational drift.
- Williamson, K. (1959). The September drift-movements of 1956 and 1958. *British Birds*, 52, 334–377.
- Williamson, K. (1961). The concept of 'cyclonic approach'. *Bird Migration*, 1, 235–240.
- Williamson, K. (1963). Movements as an indicator of population changes. *Bird Migration*, 2, 207–223.
- Williamson, K. (1969). Weather systems and bird movements. *Quarterly Journal of the Royal Meteorological Society*, 95(404), 414–423.
- Wilson, W. H. (1988). Weather and long-distance vagrancy in Red-billed Tropicbirds. *Bird Observer*, 16, 139–144.
- Wiltschko, W., & Wiltschko, R. (2005). Magnetic orientation and magnetoreception in birds and other animals. *Journal of Comparative Physiology A*, 191(8), 675–693.
- Winkler, D. (2005). How do migration and dispersal interact? In R. Greenberg & P. P. Marra (Eds.), *Birds of two worlds*. The John Hopkins University Press.
- Winkler, D. W., Gandoy, F. A., Areta, J. I., Iliff, M. J., Rakhimberdiev, E., Kardynal, K. J., & Hobson, K. A. (2017). Long-distance range expansion and rapid adjustment of migration in a newly established population of barn swallows breeding in Argentina. *Current Biology*, 27(7), 1080–1084.
- Winkhofer, M., Dylida, E., Thalau, P., Wiltschko, W., & Wiltschko, R. (2013). Avian magnetic compass can be tuned to anomalously low magnetic intensities. *Proceedings of the Royal Society B: Biological Sciences*, 280(1763), 20130853.
- Zawadzki, L. C., Veit, R. R., & Manne, L. L. (2019). The influence of population growth and wind on vagrancy in a North American passerine. *Ardea*, 107(2), 131–147.
- Zhan, S., Zhang, W., Niitepöld, K., Hsu, J., Haeger, J. F., Zalucki, M. P., Altizer, S., Roode, J. C., Reppert, S. M., & Kronforst, M. (2014). The genetics of monarch butterfly migration and warning colouration. *Nature*, 514, 317–322.

# 2

## Preferred orientation of vagrant versus non-vagrant passerines during autumn migration

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## 2.1 Abstract

Vagrants are often thought to be aberrant, and it is theorised that they are either prone to navigational errors on migration, or displacement via wind-drift. To determine whether vagrants are capable of demonstrating a preferred orientation on migration, we tested the orientation of both vagrants and non-vagrants (Blackpoll Warblers (*Setophaga striata*)) on two islands off the southwest coast of Nova Scotia during autumn migration in 2018 and 2019. Vagrants and non-vagrants were tested on the day of capture in outdoor circular orientation cages for two hours around sunset. Only hatching-year birds, and birds with a fat score greater than zero, were tested. Results indicate that vagrants orient as effectively as non-vagrants, and are likely capable of directed migratory flights. Vagrants demonstrated a significant mean orientation of 348.37° or NNW, and Blackpoll Warblers demonstrated a significant mean orientation of 354.05° or N. Based on previous studies of Blackpoll Warblers in Nova Scotia, directional tendencies of both vagrants and Blackpoll Warblers were attributed to exploratory movements via post-fledging dispersal. Though we cannot rule out the possibility that vagrants may have been wind-drifted to Nova Scotia, oriented movements during experimentation suggest that vagrants are oriented to the coast, and likely oriented offshore to Nova Scotia as well.

## 2.2 Introduction

Vagrants are individuals that engage in long-distance movements outside of the known species' range (Grinnell 1922). Though vagrancy occurs across a variety of taxa, migratory birds are often the main focus of this behaviour due to repeated occurrence in avian species. Instead of travelling to the species' breeding or wintering grounds, vagrant birds engage in migratory flights that can take them up to thousands of kilometres from their range (e.g. Nearctic birds flying east across the Atlantic; Elkins 1979, 2008).

Genetic factors such as inheritance of an incorrect compass bearing (e.g. Rabøl 1969, DeSante 1973, Thorup 1998, Thorup 2004, Thorup et al. 2012), or external factors such as displacement by wind or weather systems (e.g. Williamson 1959; Elkins 1979, 2005, 2008; McLaren 1981) are the most cited reasons for these movements, implying that vagrants are aberrant (Clarke 1912), or that something is wrong with them or their migratory ability (Cottridge and Vinicombe 1996). They are often seen as distinctly different from non-vagrants, though quantitative evidence to confirm this is lacking.

The nature of vagrancy makes it difficult to study in the field directly. To date, most studies on vagrants have been qualitative or correlational (e.g. Williamson 1959, Baker 1977, Elkins 1979, McLaren 1981) and cannot definitively conclude whether or not their movements are aberrant. The few direct field studies on vagrant orientation imply that vagrancy results from individual mistakes (Able 1977; DeSante 1973, 1983b; Thorup 1998; Thorup et al. 2011, 2012), and that vagrants have been displaced from the normal migratory route. Orientation of immature vagrants in these experiments has been concluded to result from an inability to correct for displacement, either due to navigational misorientation (DeSante 1973, 1983b; Thorup 1998; Thorup et al. 2011, 2012), or displacement via wind drift (Able 1977). However, in these studies, some (DeSante 1973, 1983b; Able 1977; Thorup et al. 2012) or even all (Thorup 1998) of the individuals tested showed directed orientation in the “wrong” direction (i.e. the direction required to reach the vagrant site), indicating active movement in this direction. It is thus likely that these movements are actually the result of the bird’s preferred orientation (Ralph 1978), rather than a mistake, and vagrant flights are directed much like migratory flights of non-vagrants.

To study whether vagrants are aberrant, we tested hatch-year vagrant and non-vagrant (Blackpoll Warblers (*Setophaga striata*)) passerines in outdoor circular orientation cages during peak autumn migration on two islands off the southwest coast of Nova Scotia. If vagrants exhibited preferred orientation during testing, this indicated that they have the capacity for directed migratory flights, and are not simply “aberrant” as previous studies suggest. Further, if preferred orientations were similar to those of non-vagrants,

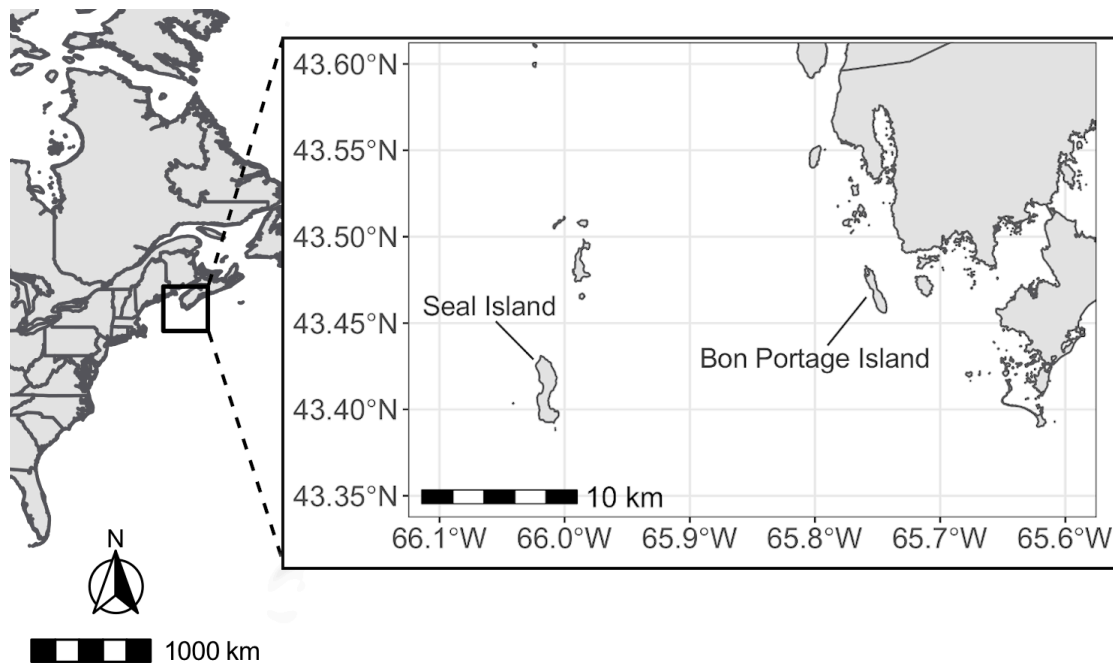
this suggests that vagrants are not behaviourally different from non-vagrants during migration, despite theorised disadvantages that vagrant movements pose to the individual. Orientation tests took advantage of *Zugunruhe* (Kramer 1949), or migratory restlessness, whereby individuals engage in directed movements in their preferred migratory direction before migratory flights, which is the basis for orientation experiments. Individuals were affixed with MOTUS nanotags after testing to analyse departure directions, and where possible, continued migratory flights.

## 2.3 Methods

### 2.3.1 Study site and study species

This study was conducted on two islands off the southwest coast of Nova Scotia, Canada (Figure 2.1) during autumn migration (August to October) – Bon Portage Island (hereafter, “BP”) (also known as Outer Island; 43°47’ N, 65°75’ W), which is 3 km offshore; and Seal Island (43°41’ N, 66°01’ W), which is 15 km west of BP. BP is the location of the Atlantic Bird Observatory (ABO), though banding operations for this observatory sometimes take place on Seal Island as well. Both islands are small ( $\sim 3.00 \text{ km}^2$ ) and low-lying, with a maximum elevation of approximately 15 m, and are characterised by inland coniferous forests (spruce and fir), and marshlands. The majority of the study was carried out on BP across two field seasons from 8 August – 3 September and 13 September – 29 October in 2018, and 3 August – 25 October in 2019, while nine days were spent on Seal Island during the 2018 field season from 4 to 12 September. These islands were chosen for this study due to their historically high incidence of vagrants in the autumn (McLaren 1981).

Vagrant passerines were targeted for our experiments. We defined vagrants as individuals of species that are not known to breed or winter on the two islands (DeSante 1973). Blackpoll Warblers (hereafter “blackpolls”), a non-vagrant species in Nova Scotia that breeds on both BP and Seal Island, were targeted and captured as our control species. Only hatch-year birds (i.e. recently fledged birds on their first autumn migration) were

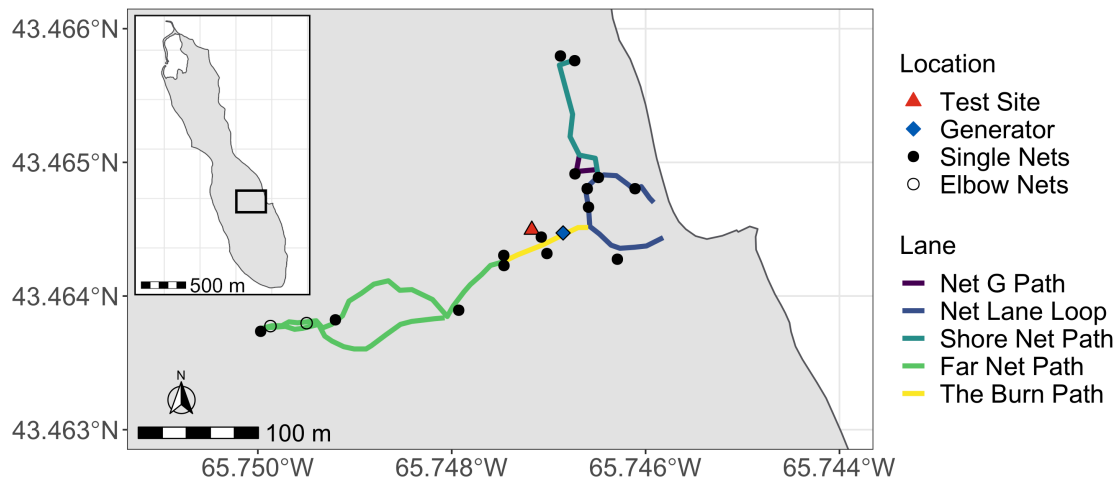


**Figure 2.1.** Location of the study site within eastern North America (main map), and off the southwest coast of Nova Scotia (inset). Birds were captured and tested on both Bon Portage Island and Seal Island.

included in this study under the premise that vagrant passerines are juveniles embarking on their first autumn migration.

### 2.3.2 Capture methods

Vagrants ( $n = 29$ ) and blackpolls ( $n = 166$ ) were captured using mist-nets. We mist-netted for birds daily, setting up 30 min before sunrise, and running nets for a total of 6 hours per day. Birds were captured via passive netting. 19 mist-nets, positioned along approximately 500 m of path, were used on BP (Figure 2.2), and 5 mist-nets were used on Seal Island. All nets were aimed to be used daily, however, we opened and closed nets at our discretion based on weather conditions, bird activity, and available help. Experimental birds were captured approximately 3 to 13 hours before experimentation. Upon capture, we banded experimental birds with Canadian Bird Banding Office (BBO) aluminium leg bands, took morphometric measurements (wing chord, fat score, body mass, tail length, tarsus, bill from nares to tip, head length and width, and body length from base of tail to tip of bill) according to Pyle (1997), and took photographs. The term “banding” rather



**Figure 2.2.** Location of the 19 mist-nets used daily on Bon Portage Island, Nova Scotia to capture birds. Mist-nets were positioned along approximately 500 m of path. 15 mist-nets were positioned by themselves (black circles), while 2 sets of 2 mist-nets were setup on the same poles to form elbow configurations (open circles). The orientation test site and generator used to power recording equipment were located off the Burn Path. Net lane paths used on Seal Island were not mapped.

than “ringing” is used in this chapter (and throughout this thesis), since this experiment was conducted in North America, which refers to “ringing” as “banding”. Blackpolls were also colour-banded for separate resighting studies on the two islands. One tail feather (rectrix R2) was collected for stable isotope analysis to determine the individual’s natal origin (see Chapter 3). Target individuals were only kept for orientation experiments if they had a fat score greater than 0 (from a scale of 0 to 7; Pyle 1997). All by-catch were banded and processed in accordance with BBO protocol.

### 2.3.3 Experimental birds

2452 unique individuals of 92 different species were captured in total across the two field seasons. 195 individuals of our target species were captured – 29 hatch-year vagrants of 15 different species, and 166 hatch-year blackpolls (Table 2.1; see Tables S2.1 and S2.2 for information on individual vagrants and blackpolls). Of the experimental birds captured, 120 birds were transferred to cages for testing. All 29 vagrants were transferred to orientation cages (Table 2.1), but only 91 out of 166 blackpolls were transferred. 75 blackpolls were not chosen for experimentation because they did not

**Table 2.1.** Sample sizes of target species captured and tested on Bon Portage Island and Seal Island in 2018 and 2019.

	Captured	Transferred to cage	Tested	Analysed	Tagged
<b>Vagrants</b>	<b>29</b>	<b>29</b>	<b>22</b>	<b>15</b>	<b>24</b>
<i>Bon Portage Island</i>	28	28	21	14	23
<i>Seal Island</i>	1	1	1	1	1
<b>Blackpoll Warblers</b>	<b>166</b>	<b>91</b>	<b>70</b>	<b>50</b>	<b>37</b>
<i>Bon Portage Island</i>	164	89	68	49	36
<i>Seal Island</i>	2	2	2	1	1
<b>Total</b>	<b>195</b>	<b>120</b>	<b>92</b>	<b>65</b>	<b>61</b>

**Table 2.2.** Sample sizes of target species that were tagged on Bon Portage Island and Seal Island in 2018 and 2019. Tags that were unregistered were not detectable within the MOTUS system. Tags without tracks were not picked up by antennas after deployment.

	Tagged	Unregistered	Found dead	No tracks	Tracks
<b>Vagrants</b>	<b>24</b>	<b>1</b>	<b>1</b>	<b>1</b>	<b>21</b>
<i>Bon Portage Island</i>	23	1	1	1	20
<i>Seal Island</i>	1	0	0	0	1
<b>Blackpoll Warblers</b>	<b>37</b>	<b>3</b>	<b>1</b>	<b>5</b>	<b>28</b>
<i>Bon Portage Island</i>	36	3	1	5	27
<i>Seal Island</i>	1	0	0	0	1
<b>Total</b>	<b>61</b>	<b>4</b>	<b>2</b>	<b>6</b>	<b>49</b>

meet testing criteria (i.e. fat score of 0 ( $n = 45$ ), or a physical deformity ( $n = 3$ ) such as a missing tail, or a foot abnormality that may have prevented the bird from perching properly), all of the orientation cages were already occupied by other birds ( $n = 16$ ), the weather (i.e. rain during banding;  $n = 1$ ), the cages were not yet setup for the season ( $n = 2$ ), or tests were not able to be conducted that day due to logistics or unforeseen circumstances ( $n = 8$ ) (Tables S2.1, S2.2).

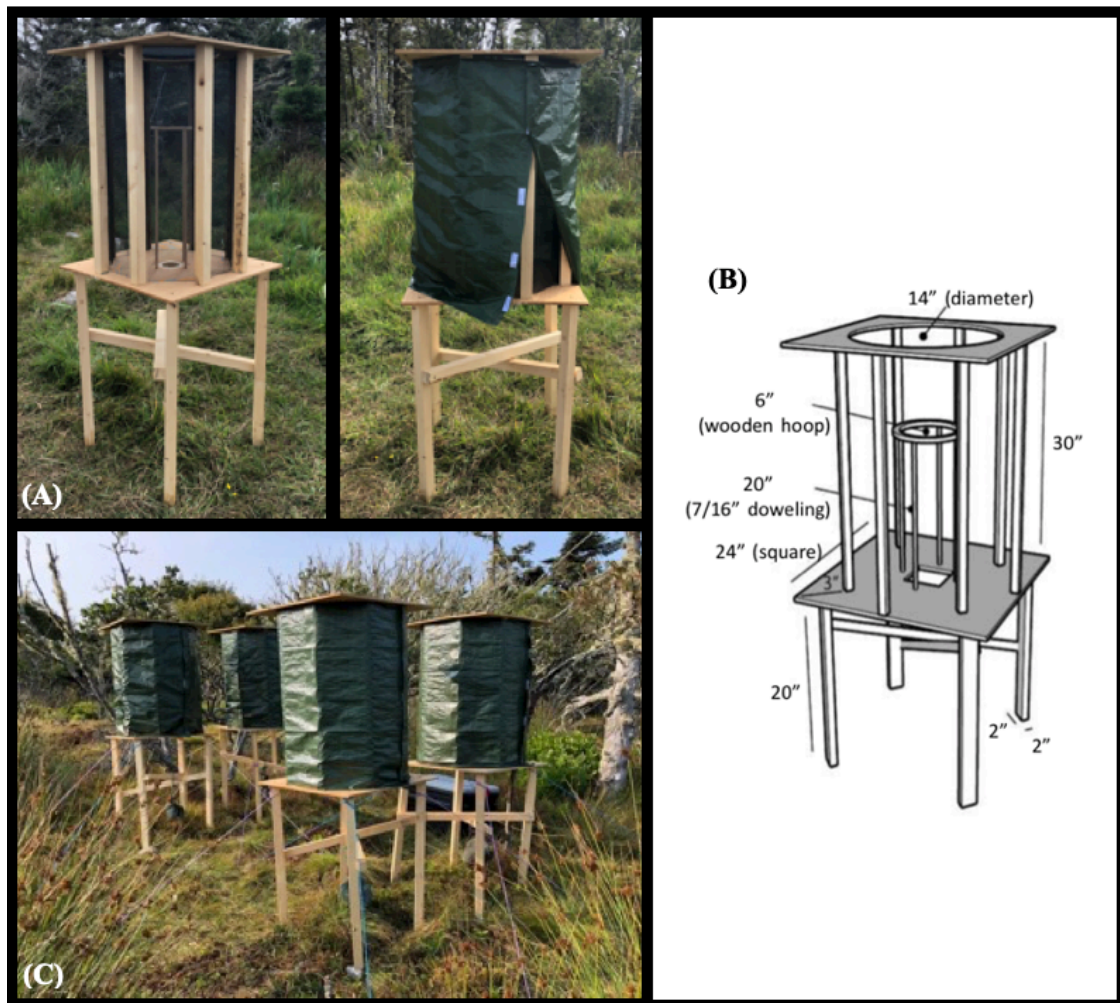
### 2.3.4 Orientation cage experiments

Experimental birds ( $n = 120$ ) were transferred to outdoor circular orientation cages (located at 43° 46' 45" N, 65° 74' 72" W on BP, and 43° 39' 90" N, 66° 01' 36" W on Seal Island) which were modified from Toews et al. (2017) based on available materials (Figure 2.3a, b). Cages were constructed from non-magnetic materials (wood, brass nails

and screws, and fiberglass mesh), to avoid the possibility of magnetic interference on orientation cues (Wiltschko and Wiltschko 1972). The cage structure was constructed out of pine boards, and the top and bottom of the cage were made from composite plywood. The perch was built from a 6” wooden embroidery hoop that was held up by four 7/16” wooden dowels. Brass screws were used to join the pieces of the cage together, and brass finishing nails were used to affix the fiberglass window screen mesh to the sides of the cage. The screen mesh for the top of the cage was held down with masking tape to enable easy access to the inside of the cage. The sides of the cage were covered with a green, opaque tarp, to provide shade during the day, with part of the tarp rolled up for airflow. Circular orientation cages were used over traditional Emlen funnels (Emlen and Emlen 1966) because they do not require the bird to be transferred between holding cages and orientation cages, which is likely to reduce stress of the individual (Toews et al. 2017). The chance of escape behaviour during testing is also likely to be reduced, since individuals had 3 to 13 hours to adjust to the cages before evening orientation trials.

Cages were set up in an open area (Figure 2.3c), approximately 1 m apart, with no visible artificial light. Birds had an unobstructed view of the sky. Cages were levelled, and oriented towards geographic (true) North (gN) (magnetic declination of BP is 16° 34’ W, and Seal Island is 16° 29’ W). Birds were given water, and mealworms mixed with insect pâté and a grated hard-boiled egg, *ad libitum*, throughout the day. Welfare of individuals in captivity was monitored carefully. If the birds did not adjust to the cages, i.e. did not immediately fly to the perch, showed visible signs of stress (e.g. panting), and/or were not eating or drinking, the individuals were released, and omitted from further experimental procedure (7 birds or 5.83% of experimental birds; see Tables S2.1 and S2.2). Weather was also monitored closely, and birds were released if it started to rain before experimentation (5 birds or 4.17% of experimental birds; see Tables S2.1 and S2.2). Four cages were used on BP, and two cages were used on Seal Island for a maximum of four tests and two tests in a single night, respectively.

Of those transferred to cages, 92 birds (22 vagrants and 70 controls) were able to be tested (76.7% of experimental birds). 28 individuals were not tested because they did



**Figure 2.3.** (A) Orientation cage on Bon Portage Island, Nova Scotia. (B) Outdoor video orientation cage design modified from Toews et al. (2017). Image taken with permission from Toews et al. (2017), and measurements have been adjusted based on available materials in Nova Scotia. (C) Cage setup on Bon Portage Island ( $43^{\circ} 46' 45''$  N,  $65^{\circ} 74' 72''$  W; magnetic declination  $16^{\circ}34'$  W).

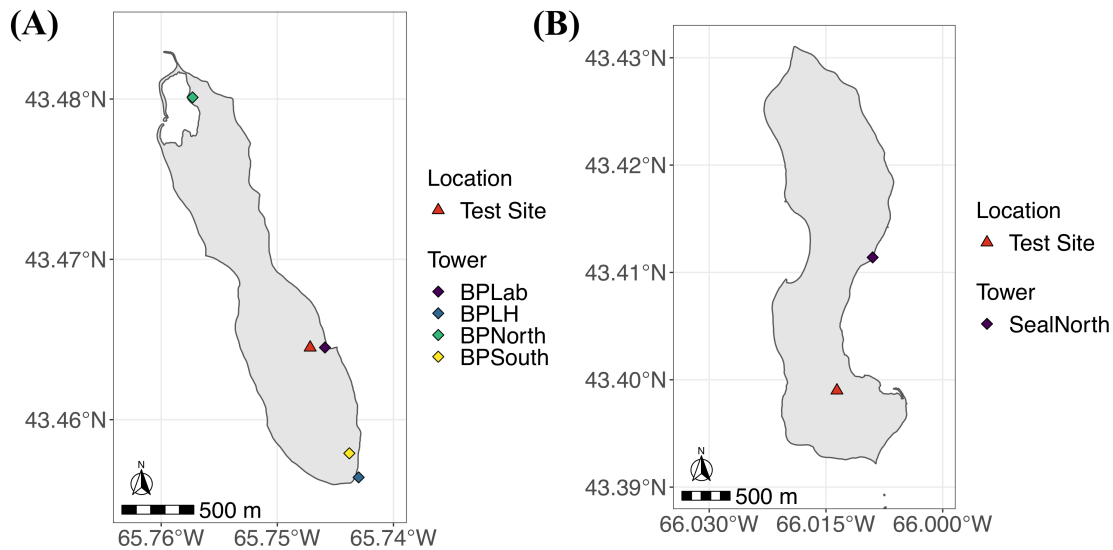
not adjust to the cages ( $n = 7$ ), they escaped before the experiment began ( $n = 6$ ), they were replaced with another individual ( $n = 3$ ), the birds were released due to technical issues ( $n = 3$ ), the species cannot be tested cages (i.e. flycatchers;  $n = 1$ ), the weather (i.e. rain started before the experiment;  $n = 5$ ), or they died before the experiment could begin ( $n = 3$ ) (Table S2.1, S2.2). A total of ten species of vagrants were tested.

Food and water were removed 0.5 – 1 hr before testing, and the tarps were shut so individuals could only see out of the top of the cage. Orientation experiments lasted for 2 hrs – tests began 1 hr before sunset, and ended 1 hr after sunset (Fitzgerald and Taylor

2008, Toews et al. 2017). Orientation of individuals was video-recorded from below through a hole in the bottom of the cage with bullet-style CCTV surveillance cameras (SANNCE, model no. SU-DN81BJ1-14DR-P#CA1) (Figure 2.4). Each camera was assigned a particular cage for the duration of the season, and cameras were assigned so that the channel number did not match the cage number to eliminate any bias during analysis. Cameras were positioned so that the top of the video was directed towards true North. All recordings occurred simultaneously, and were saved onto an external DVR in AVI format. Under low-light conditions, an infrared LED light on the cameras was activated. A gasoline-powered generator was used to power the cameras, and was positioned approximately 26 m east of the cages (Figure 2.2). Weather data (wind speed and direction, temperature, and cloud cover) and astronomical data (sun and moon visibility, and moon phase) were collected before each test was conducted. Because birds were only kept for one day, birds were tested regardless of astronomical conditions. Birds were tested once, and then released.



**Figure 2.4.** Recording setup for orientation cages. (A) CCTV cameras were placed at the bottom of the cage during testing, and videos were recorded onto a DVR. Cameras were positioned so the top of the video pointed towards true North. (B) The monitor and DVR were kept inside of a watertight plastic bin near the cages.



**Figure 2.5.** Location of the orientation cage setup (“Test Site”) and MOTUS radio towers on both (A) Bon Portage Island and (B) Seal Island. Four MOTUS towers were in operation in 2018 – BPLH, BPNorth, and BPSouth, and SealNorth, and three were in operation in 2019 – BPLab, BPNorth, and BPSouth.

### 2.3.5 Radio tag deployment

After testing, individuals were removed from cages and weighed. They were then affixed with digitally coded radio transmitters (either Avian NanoTag NTQB2-2 or NTQB2-5-1, Lotek Wireless; see Tables S2.1, S2.2), using a figure-8 leg loop harness (Mackenzie et al. in prep, Rappole and Tipton 1991, Brown and Taylor 2015), and tracked via telemetry towers in the Motus Wildlife Tracking System (MOTUS; Taylor et al. 2017) to observe vanishing direction (heading) and post-vagrant movements. Deployments of NTQB2-2 nanotags with a leg-loop harness weighed 0.37 g, and deployments of NTQB2-5-1 nanotags with a leg-loop harness weighed 0.49 g. Tags transmit a coded burst at 166.380 MHz every 11.2 s, and tag life is approximately 40 days. 37 blackpolls and 24 vagrants were tagged (Table 2.2). Three MOTUS towers were operational on BP in 2018 (BPLH, BPNorth, and BPSouth) and 2019 (BPLab, BPNorth, and BPSouth) (Figure 2.5a), and one MOTUS tower was operational on Seal Island throughout the 2018 season (SealNorth; Figure 2.5b). Due to minimal success of tagging for this study, results of radio tag analysis are reported as part of the Supplementary Material (Section 2.7; Figure S2.1).

### 2.3.6 Video analysis and processing

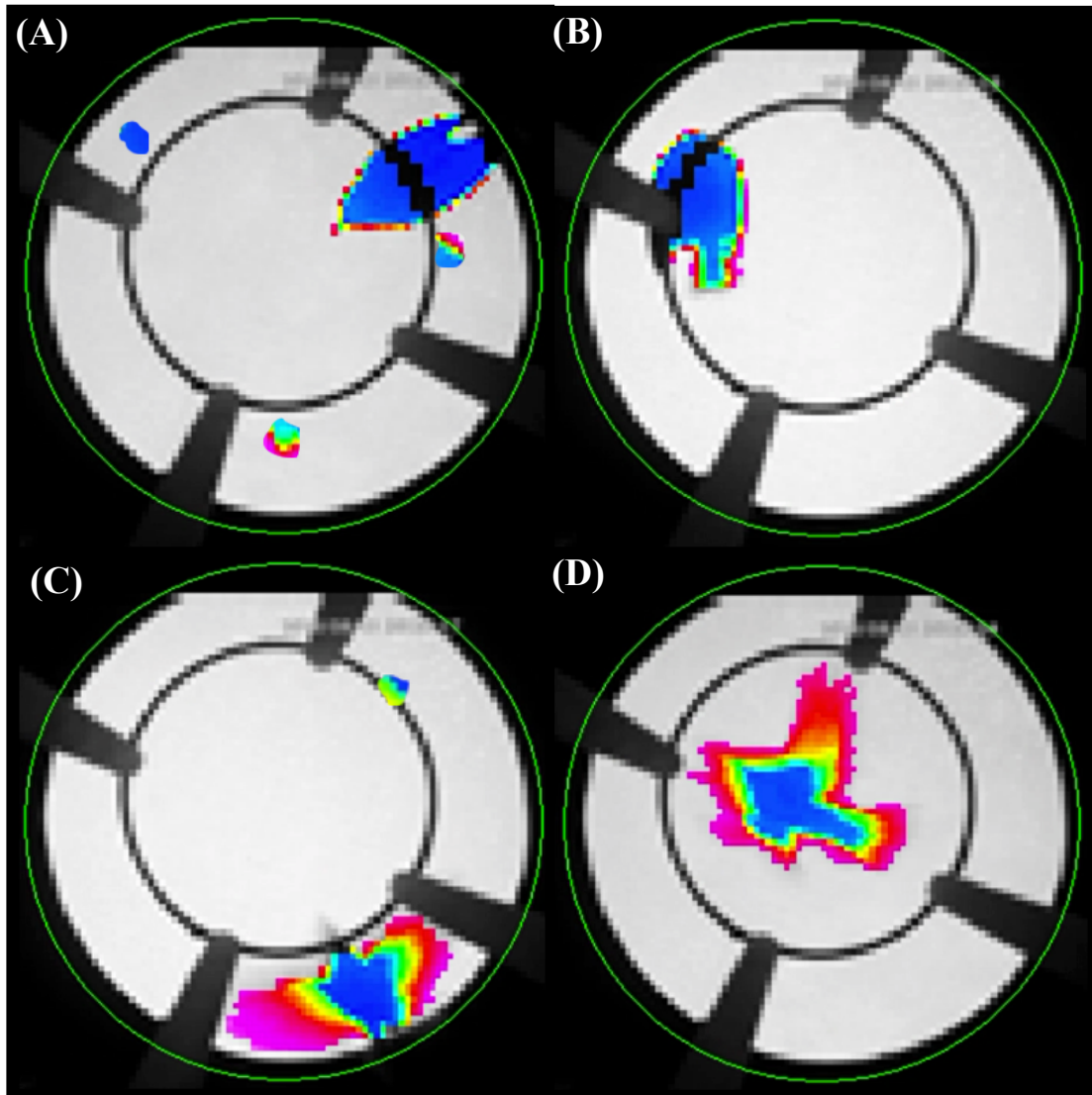
Videos were analysed similarly to Toews et al. (2017) using radR software (Taylor et al. 2010), an open-source program developed to analyse radar data, which has been adapted to analyse video files. radR works by detecting the contrast of pixels at each user-defined frame, and calculates which pixels constitute a single object, or “blip”, based on their relative intensity and proximity to pixels of similar intensity (see Figure S2.2 for radR interface). Blips that meet user-defined filtering parameters are retained (e.g. minimum area of a blip; see Figure S2.2 for radR parameters during processing). Each blip is assigned an (X, Y) coordinate based on their position in the video, and these coordinates are saved to an output file along with their corresponding timestamp. Our videos were sampled at a rate of five frames per second, and blips were assigned coordinates in relation to the centre of the circular perch. Researchers were unaware of the species in the video during radR processing. Though there is no visual evidence that infrared light affected orientation behaviour of individuals during experimentation, times after the infrared light turned on were excluded from analysis since the infrared light artificially increased the number of blips. Output for each video was saved for further processing in R (R Core Team 2019).

65 out of 92 videos were suitable for further analysis (15 vagrants and 50 controls; 70.7% of birds tested). 27 videos were excluded from radR analysis due to escape during the experiment ( $n = 1$ ), technical issues (i.e. camera didn't record, camera fell out of cage, DVR didn't start recording at set time;  $n = 12$ ), weather (i.e. rain in the middle of an experiment that required the birds to be released early;  $n = 3$ ), inactivity (i.e. bird was stationary for the entire test;  $n = 9$ ), or an obscured video (i.e. the bird defecated on the camera;  $n = 1$ ) (Tables S2.1, S2.2).

Orientation of the blips was first corrected in R by flipping the (X, Y) coordinates of each blip over the E-W axis, since cameras mirrored the image over the E-W axis during recording. Blips were then filtered to remove (1) noise, (2) times when the bird was stationary, and (3) blips within the centre of the perch (Figure 2.6). To remove

noise, we only saved timestamps where one blip was identified (Figure 2.6a), with one exception. Due to the positioning of the four dowels holding up the perch in the video, radR sometimes identified the bird as two separate blips, particularly if the bird was directly above them (Figure 2.6b). To correct for this, we averaged the (X, Y) coordinates for timestamps with two blips that were less than 50 pixels apart (i.e. likely to be the bird split into two), while two blips that were more than 50 pixels apart were removed (Figure 2.6c). We chose 50 pixels as our baseline because the dowels had a maximum width of 30 pixels in radR, and when a bird was positioned over them, the centres of the two blips were between 30 to 50 pixels apart. To remove timestamps when the bird was stationary, we removed consecutive timestamps whose coordinates were less than 20 pixels apart. This distance was based on manual observation of videos when the bird was stationary. To remove blips within the centre of the perch, blips recorded within a radius of 108 pixels from the centre of the video, known as the “perch exclusion zone”, were excluded (Figure 2.6d). These blips were removed because we were only interested in movements when the bird flew outwards from the perch, similar to studies with Emlen funnels where movements are only recorded if they occur on the walls of the funnel, and not in the centre (Emlen and Emlen 1966). All coordinates that passed the filtering process were converted into polar angles relative to North.

We processed five videos manually to assess the ability of radR to accurately detect the bird’s position in each frame. Videos were randomly selected using the *sample* function in R, and each video was split into 1/30 frames per second (i.e. 1 frame every 30 seconds) using the *splitVideo* function from the ‘pathtrackr’ package in R (Harmer and Thomas 2020). We manually analysed videos at a smaller framerate than the videos in radR to decrease processing times (Toews et al. 2017). The ‘pathtrackr’ package was used to select the bird in each frame and assign (X, Y) coordinates to the centre of the bird. Coordinates were filtered similarly to radR in that coordinates were only kept if the bird was outside of the perch exclusion zone.



**Figure 2.6.** Examples of blips that were filtered after radR processing. Since the camera is positioned on the bottom of the cage facing upwards, the video is always looking at the bird from below. The outer circle is the top of the cage, where the bird has an unobstructed view of the sky, and the inner circle is the perch, held up by four dowels. (A) If 3 or more blips were detected, the timestamp was removed. The bird is sitting on the perch as 2 blips, and 3 additional artefacts are present. (B) If the bird was split into 2 blips by the dowels (30-50 pixels wide), the (X, Y) coordinates were averaged to create one blip. (C) When 2 blips were greater than 50 pixels apart, the timestamps were removed. The bird can be seen as a blip on the lower right side, and an artefact is located on the upper right. (D) If blips were detected within the centre of the perch (i.e. the “perch exclusion zone”;  $r = 108$  pixels), timestamps were removed.

### 2.3.7 Statistical analysis

Circular statistics were calculated using the ‘circular’ package in R (Agostinelli and Lund 2017). To test whether individual vagrants and controls exhibited preferred orientation on migratory flights, a Rayleigh test of uniformity was conducted for each video. The mean circular orientation and rho (mean resultant vector) of each bird were also calculated (Batschelet 1981). Data were then analysed in two groups – vagrants and blackpolls – to test whether direction of vagrant flights differed from direction of non-vagrant flights. Mean circular directions within each group were compared using the non-parametric Mardia-Watson-Wheeler test. Mean circular directions for group analysis for each individual were taken from the above circular statistics which assumed a unimodal distribution.

Additionally, we tested for multimodality in each video using a model-selection approach based on maximum likelihood as outlined by Fitak and Johnsen (2017), which assesses the likelihood of ten models of animal orientation as described by Schnute and Groot (1992) using the *circ\_mle* function in the ‘CircMLE’ package in R (Fitak and Johnsen 2017). The ten models are M1 (uniform), M2A (unimodal), M2B (symmetric modified unimodal), M2C (modified unimodal), M3A (homogenous symmetric bimodal), M3B (symmetric bimodal), M4A (homogeneous axial bimodal), M4B (axial bimodal), M5A (homogenous bimodal), and M5B (bimodal). The model with the best fit was selected based on the lowest Akaike Information Criterion (AIC). Models with the smallest AIC value had the best fit, and those that have a difference of less than 2 AIC relative to the best model were well supported (Burnham and Anderson 2003).

To test whether wind direction influenced orientation during testing, we conducted a circular-circular correlation between wind direction on the night of each test and the mean preferred orientation of each individual.

### 2.3.8 Ethical note

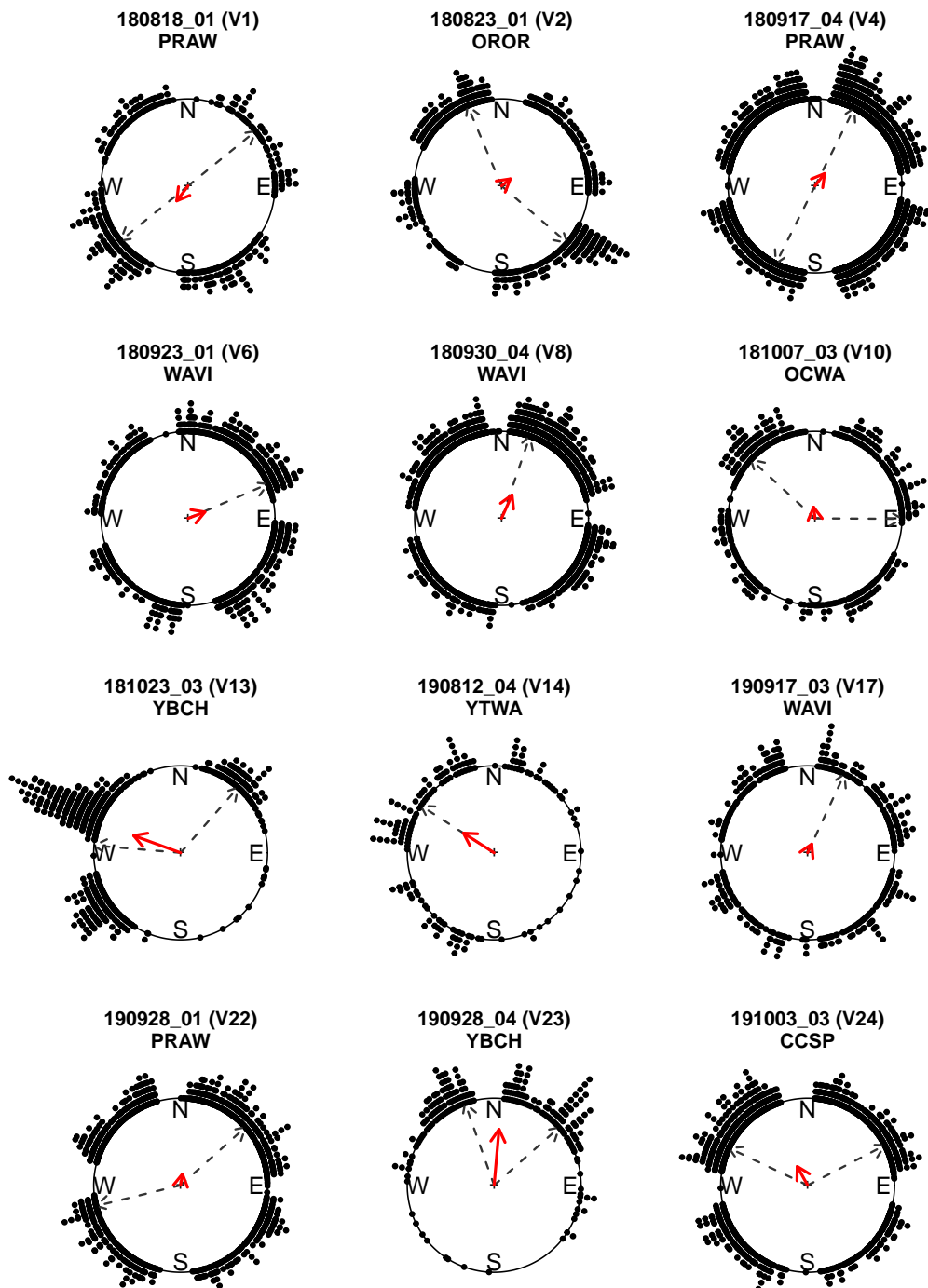
Ethical approval for this project was obtained through the Canadian Council for Animal Care as reviewed by the Acadia University Animal Care Committee (ACC) in Canada, as well as the local Zoology Animal Welfare and Ethical Review Board (AWERB) at the University of Oxford. The project was approved by the Canadian Wildlife Service (permit number SC4031) and Canadian Bird Banding Office. Permits to capture and band migratory birds, with special permissions to extract one tail feather and affix radio transmitters, were issued under a Bird Banding Office sub-permit (#10273 AP).

## 2.4 Results

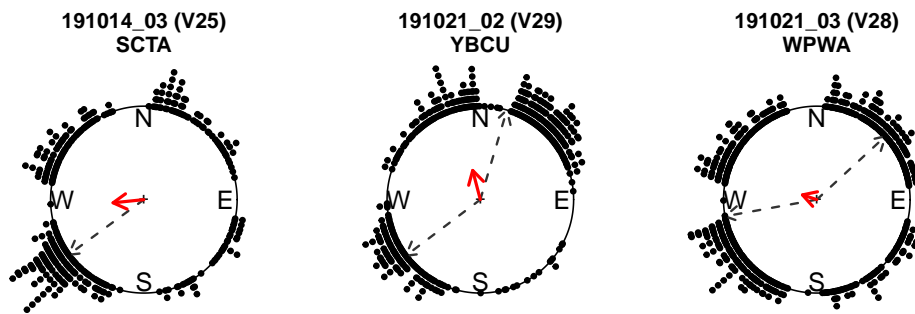
### 2.4.1 Orientation experiments

All individuals analysed ( $n = 62$ ) were significantly oriented (see Tables 2.3 and 2.4 for Rayleigh statistics and best orientation models; see Figures 2.7 and 2.8 for orientation plots). Vagrants had a mean orientation towards  $348.37^\circ$  or NNW ( $r = 0.59$ ,  $p = 0.004$ ,  $n = 15$ ; 95% CI =  $313.81^\circ - 22.92^\circ$ ; Figure 2.9). Blackpolls exhibited a mean orientation towards  $354.05^\circ$  or N ( $r = 0.56$ ,  $p < 0.001$ ,  $n = 50$ ; 95% CI =  $334.97^\circ - 13.12^\circ$ ; Figure 2.9). Mean orientation did not significantly differ between vagrants and blackpolls (Mardia-Watson-Wheeler test:  $W = 0.14$ ,  $p = 0.93$ ,  $n = 65$ ).

Out of the ten models of animal orientation, models with a bimodal distribution - M4B, M5A, and M5B - were selected for the majority of individuals. Orientation data from ten out of fifteen vagrants, and 30 out of 50 blackpolls, best fit either model M4B, model M5A, or model M5B (see Tables S2.3 and S2.4 for information on model selection).



**Figure 2.7.** Individual orientation plots of vagrants ( $n = 15$ ) tested in 2018 and 2019. All individuals were significantly oriented. Titles above each plot are the video ID for that test (Year-Month-Day\_DVR channel number), the bird ID, and the 4-letter code of the species tested (see Table 2.3 for species names). Dots represent flights off of the perch (blips in radR; similar to scratch marks in Emlen funnel tests) during one orientation test. Solid arrows depict the mean preferred orientation of the individual on the night of experimentation, and the length is the mean resultant vector length ( $r$ ). Dotted arrows depict the mean orientation(s) for the best orientation model chosen via maximum likelihood analysis. Directions are depicted relative to true North (gN). See Table 2.3 for Rayleigh statistics and best orientation models, and Table S2.3 for information on model selection.



**Figure 2.7 (cont.).** Individual orientation plots of vagrants ( $n = 15$ ) tested in 2018 and 2019. All individuals were significantly oriented. Titles above each plot are the video ID for that test (Year-Month-Day\_DVR channel number), the bird ID, and the 4-letter code of the species tested (see Table 2.3 for species names). Dots represent flights off of the perch (blips in radR; similar to scratch marks in Emlen funnel tests) during one orientation test. Solid arrows depict the mean preferred orientation of the individual on the night of experimentation, and the length is the mean resultant vector length ( $r$ ). Dotted arrows depict the mean orientation(s) for the best orientation model chosen via maximum likelihood analysis. Directions are depicted relative to true North (gN). See Table 2.3 for Rayleigh statistics and best orientation models, and Table S2.3 for information on model selection.

## 2.4.2 Manual tracking

Mean orientation of the birds in the five videos processed manually were consistent with orientations of videos processed in radR. Orientations were within  $+ 8.40^\circ$  of the radR output (Figure 2.10). The difference in orientations between manually processed and radR processed videos may have been smaller if videos were analysed at a frame rate closer to the frame rate used by radR.

## 2.4.3 Wind direction

Wind direction had no effect on the mean orientation of birds during testing. The circular-circular correlation of the mean orientation of each bird and the wind direction on the night of testing was non-significant ( $r = 0.07$ ,  $p = 0.58$ ). The correlation remained non-significant when vagrants ( $r = 0.05$ ,  $p = 0.84$ ) and blackpolls ( $r = 0.11$ ,  $p = 0.46$ ) were tested separately.

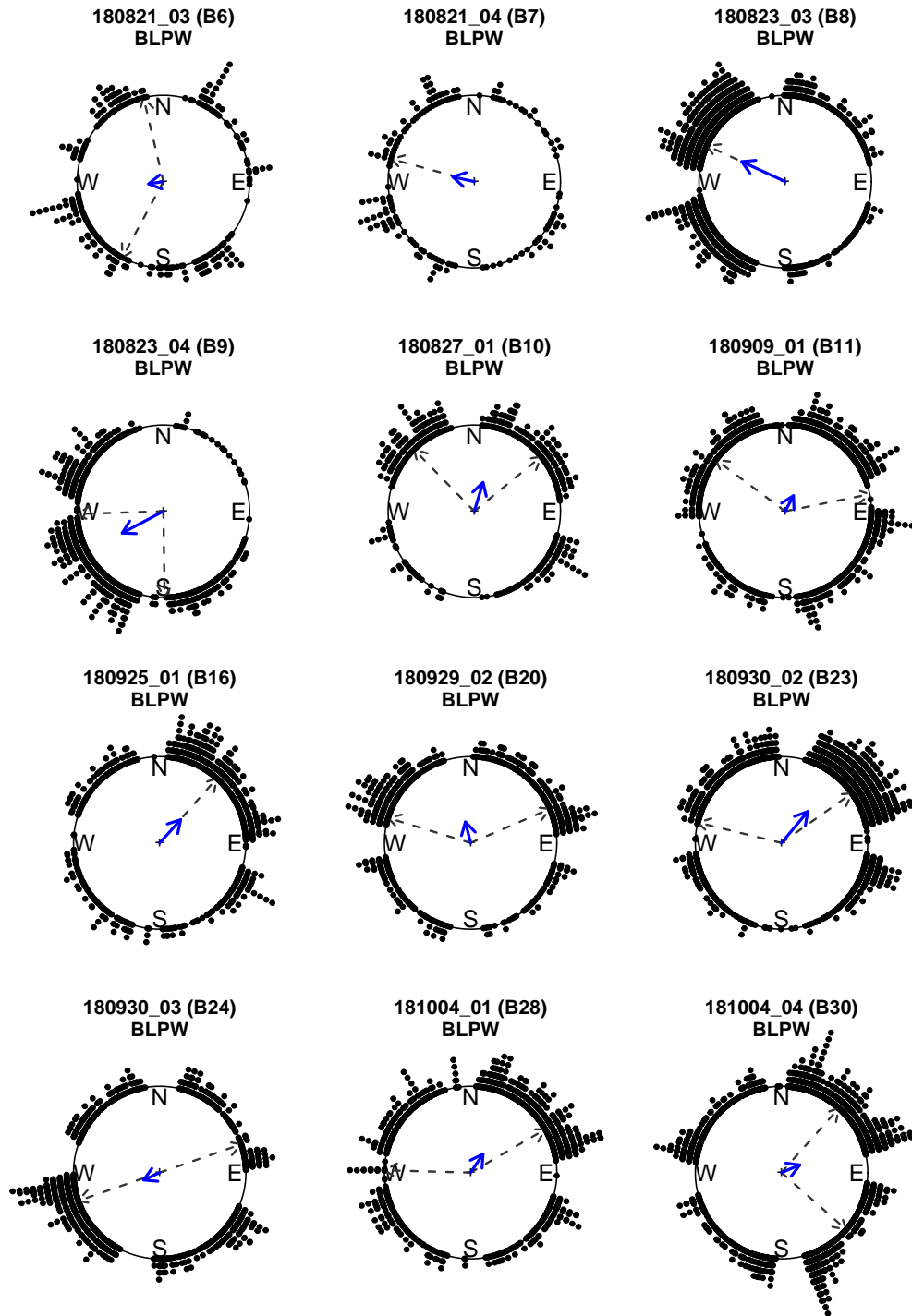
**Table 2.3.** Orientation results for vagrants tested in 2018 and 2019 ( $n = 15$ ). All orientation tests were conducted on Bon Portage Island. The mean preferred orientation and Rayleigh statistics for each test are provided, where  $n$  is the number of recorded flights off of the perch (activity),  $r$  is the mean resultant vector (or rho), and  $P$  is whether the individual is significantly oriented. The animal orientation model with the best fit, and mean modes from maximum likelihood analysis are also provided. See Figure 2.7 for individual orientation plots and Table S2.3 for information on model selection.

Bird ID <sup>1</sup>	Video ID (yymmdd_channel) <sup>2</sup>	Species	Alpha Code	Mean Orientation	Rayleigh statistics			Maximum likelihood analysis		
					$n$	$r$	$P$	Model <sup>3</sup>	Mean Orientation (1 <sup>st</sup> mode)	Mean Orientation (2 <sup>nd</sup> mode)
V1	180818_01	Prairie Warbler	PRAW	217.2	471	0.216	< 0.001	M4B	231.0	411.0
V2	180823_01	Orchard Oriole	OROR	51.4	707	0.130	< 0.001	M5B	130.9	337.0
V4	180917_04	Prairie Warbler	PRAW	37.8	3062	0.179	< 0.001	M4B	206.8	386.8
V6	180923_01	Warbling Vireo	WAVI	69.3	953	0.207	< 0.001	M2B	66.8	-
V8	180930_04	Warbling Vireo	WAVI	24.1	1624	0.295	< 0.001	M2C	19.1	-
V10	181007_03	Orange-crowned Warbler	OCWA	352.6	521	0.130	< 0.001	M5B	90.3	312.5
V13	181023_03	Yellow-breasted Chat	YBCH	290.1	658	0.575	< 0.001	M5B	41.4	274.8
V14	190812_04	Yellow-throated Warbler	YTWA	302.7	163	0.420	< 0.001	M2A	302.7	-
V17	190917_03	Warbling Vireo	WAVI	25.1	438	0.111	0.005	M2A	25.1	-
V22	190928_01	Prairie Warbler	PRAW	9.1	1112	0.131	< 0.001	M5B	256.2	48.2
V23	190928_04	Yellow-breasted Chat	YBCH	5.0	214	0.645	< 0.001	M5B	340.5	48.4
V24	191003_03	Clay-colored Sparrow	CCSP	331.0	1115	0.247	< 0.001	M5A	62.7	295.3
V25	191014_03	Scarlet Tanager	SCTA	264.1	383	0.332	< 0.001	M2C	233.8	-
V28	191021_02	Yellow-billed Cuckoo	YBCU	345.3	455	0.322	< 0.001	M5B	233.1	16.6
V29	191021_03	Western Palm Warbler	WPWA	288.2	651	0.162	< 0.001	M5B	259.7	47.3

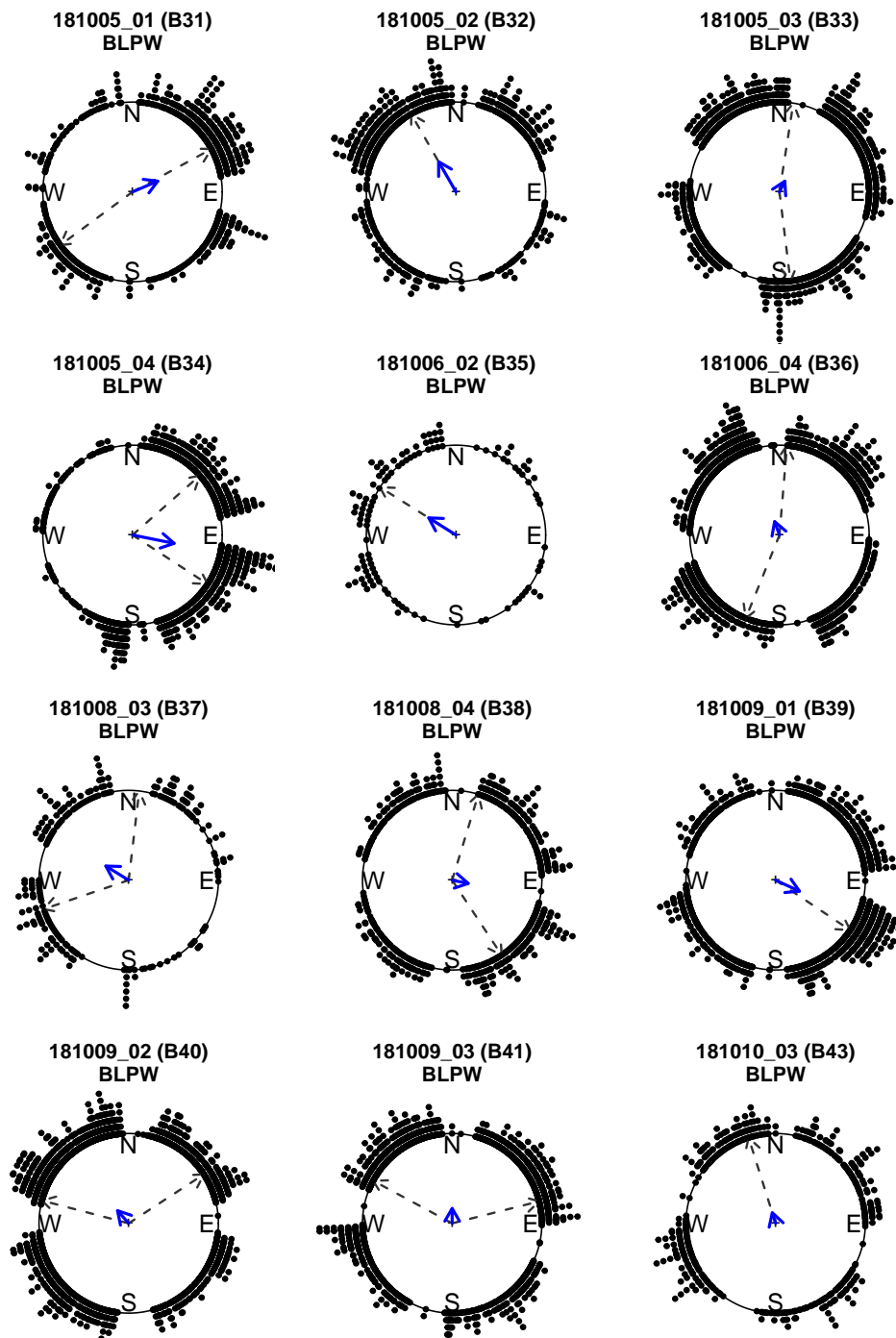
<sup>1</sup> Unique ID given to each individual for ease of interpretation of chapter figures and tables, and comparison between Chapters 2 and 3

<sup>2</sup> The video ID is the Year-Month-Day\_DVR channel number

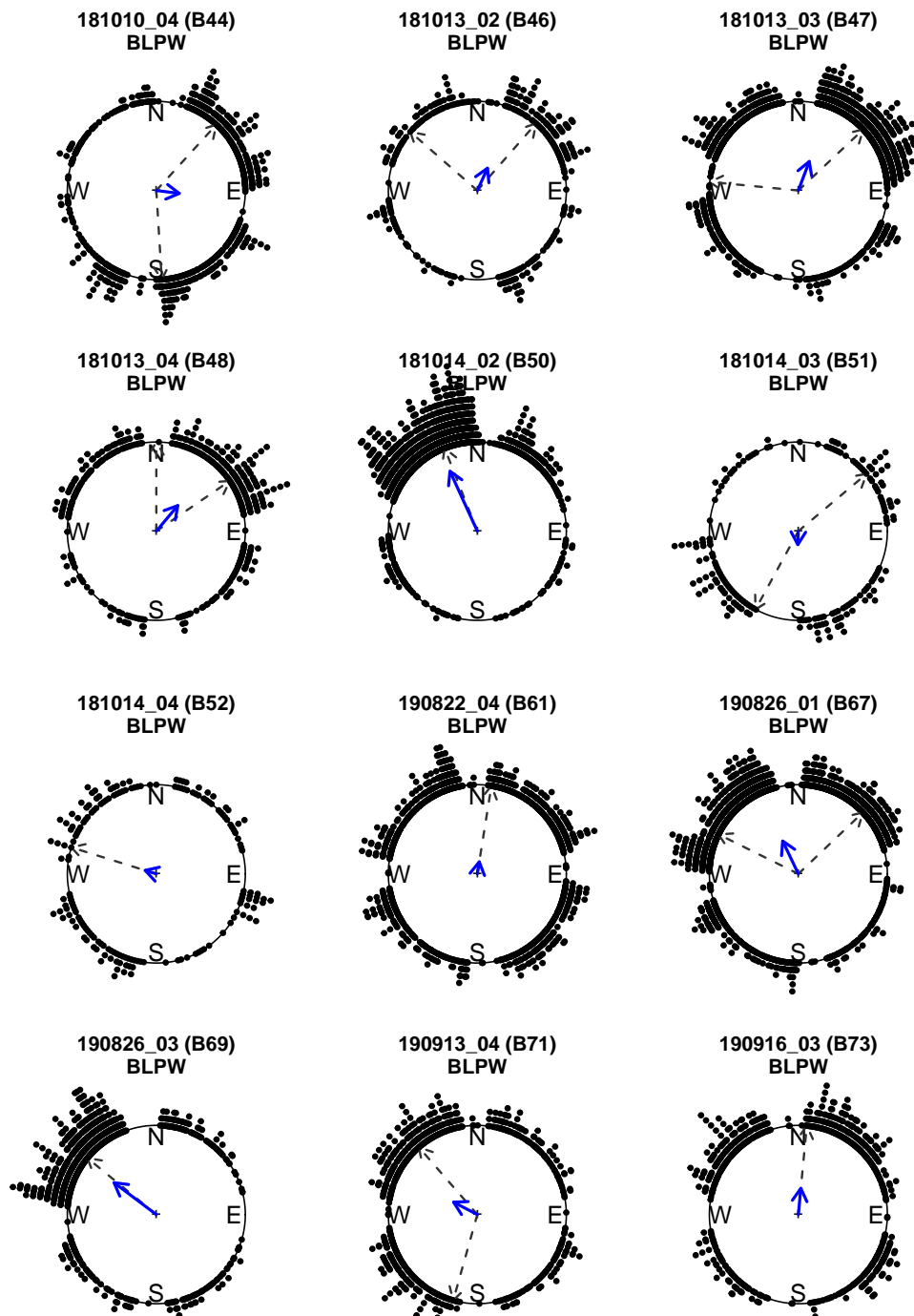
<sup>3</sup> Models of animal orientation as described by Schnute and Groot (1992). The models in this table are as follows: M2A (unimodal), M2B (symmetric modified unimodal), M2C (modified unimodal), M4B (axial bimodal), M5A (homogenous bimodal), M5B (bimodal).



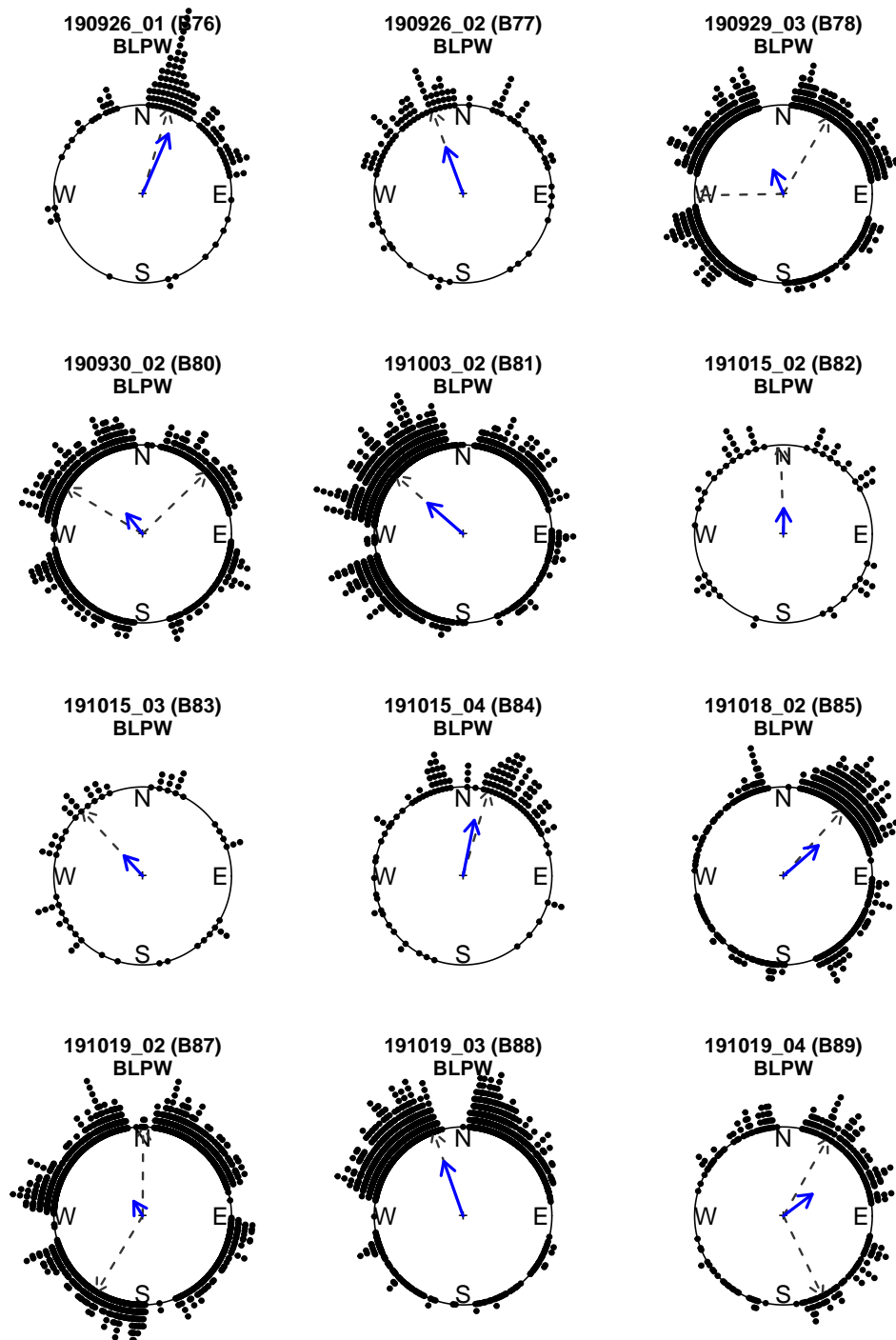
**Figure 2.8.** Individual orientation plots of Blackpoll Warblers ( $n = 50$ ) tested in 2018 and 2019. All individuals were significantly oriented. Titles above each plot are the video ID for that test (Year-Month-Day\_DVR channel number) and the bird ID. Dots represent flights off of the perch (blips in radR; similar to scratch marks in Emlen funnel tests). Solid arrows depict the mean preferred orientation of the individual on the night of experimentation, and the length is the mean resultant vector length ( $r$ ). Dotted arrows depict the mean orientation(s) for the best orientation model chosen via maximum likelihood analysis. Directions are depicted relative to true North (gN). See Table 2.4 for Rayleigh statistics and best orientation models, and Table S2.4 for information on model selection.



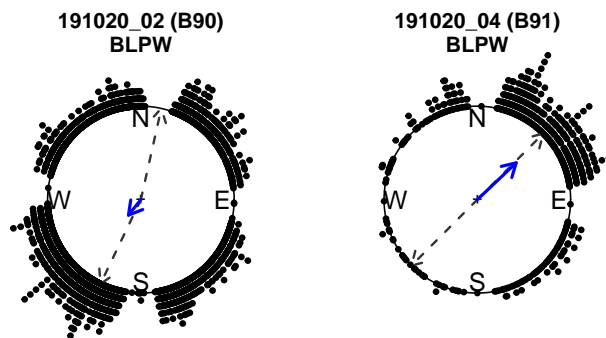
**Figure 2.8 (cont.).** Individual orientation plots of Blackpoll Warblers ( $n = 50$ ) tested in 2018 and 2019. All individuals were significantly oriented. Titles above each plot are the video ID for that test (Year-Month-Day\_DVR channel number) and the bird ID. Dots represent flights off of the perch (blips in radR; similar to scratch marks in Emlen funnel tests). Solid arrows depict the mean preferred orientation of the individual on the night of experimentation, and the length is the mean resultant vector length ( $r$ ). Dotted arrows depict the mean orientation(s) for the best orientation model chosen via maximum likelihood analysis. Directions are depicted relative to true North (gN). See Table 2.4 for Rayleigh statistics and best orientation models, and Table S2.4 for information on model selection.



**Figure 2.8 (cont.).** Individual orientation plots of Blackpoll Warblers ( $n = 50$ ) tested in 2018 and 2019. All individuals were significantly oriented. Titles above each plot are the video ID for that test (Year-Month-Day\_DVR channel number) and the bird ID. Dots represent flights off of the perch (blips in radR; similar to scratch marks in Emlen funnel tests). Solid arrows depict the mean preferred orientation of the individual on the night of experimentation, and the length is the mean resultant vector length ( $r$ ). Dotted arrows depict the mean orientation(s) for the best orientation model chosen via maximum likelihood analysis. Directions are depicted relative to true North (gN). See Table 2.4 for Rayleigh statistics and best orientation models, and Table S2.4 for information on model selection.



**Figure 2.8 (cont.).** Individual orientation plots of Blackpoll Warblers ( $n = 50$ ) tested in 2018 and 2019. All individuals were significantly oriented. Titles above each plot are the video ID for that test (Year-Month-Day\_DVR channel number) and the bird ID. Dots represent flights off of the perch (blips in radR; similar to scratch marks in Emlen funnel tests). Solid arrows depict the mean preferred orientation of the individual on the night of experimentation, and the length is the mean resultant vector length ( $r$ ). Dotted arrows depict the mean orientation(s) for the best orientation model chosen via maximum likelihood analysis. Directions are depicted relative to true North (gN). See Table 2.4 for Rayleigh statistics and best orientation models, and Table S2.4 for information on model selection.



**Figure 2.8 (cont.).** Individual orientation plots of Blackpoll Warblers ( $n = 50$ ) tested in 2018 and 2019. All individuals were significantly oriented. Titles above each plot are the video ID for that test (Year-Month-Day\_DVR channel number) and the bird ID. Dots represent flights off of the perch (blips in radR; similar to scratch marks in Emlen funnel tests). Solid arrows depict the mean preferred orientation of the individual on the night of experimentation, and the length is the mean resultant vector length ( $r$ ). Dotted arrows depict the mean orientation(s) for the best orientation model chosen via maximum likelihood analysis. Directions are depicted relative to true North (gN). See Table 2.4 for Rayleigh statistics and best orientation models, and Table S2.4 for information on model selection.

## 2.5 Discussion

Results of our orientation experiments demonstrate that vagrants do exhibit preferred migratory orientations during autumn migration, predominantly bimodally. Of the individuals tested, individuals that were active during testing (83.1% of birds tested, excluding tests halted due to technical issues or weather) were significantly oriented. Mean group preferred orientation of vagrants was similar to preferred orientations exhibited by our control species, the Blackpoll Warbler. Both vagrants and blackpolls oriented towards a mean northerly heading to the NNW and N, respectively (Figure 2.9). Furthermore, orientation exhibited by individuals in both groups was not influenced by the direction of the prevailing wind on the night of experimentation.

These results are in direct contrast to the prevailing assumption that vagrants are aberrant (Cottridge and Vinicombe 1996). Claims that vagrants are lost suggest that individuals are passively displaced to locations where they are found. However, it is clear that vagrants can orient as effectively as non-vagrants, which suggests that they may engage in directed flights to locations that are far from their normal migratory pathway. Vagrants captured demonstrated a capacity for directed migratory flights, and were capable of

**Table 2.4.** Orientation results for Blackpoll Warblers tested in 2018 and 2019 ( $n = 50$ ). All orientation tests were conducted on Bon Portage Island except for one individual (180909\_01, B11). The mean preferred orientation and Rayleigh statistics for each test are provided, where  $n$  is the number of recorded flights off of the perch (activity),  $r$  is the mean resultant vector (or rho), and  $P$  is whether the individual is significantly oriented. The animal orientation model with the best fit, and mean modes from maximum likelihood analysis are also provided. See Figure 2.8 for individual orientation plots and Table S2.4 for information on model selection.

Bird ID <sup>1</sup>	Video ID (yymmdd_channel) <sup>2</sup>	Mean Orientation	Rayleigh statistics			Maximum likelihood analysis		
			$n$	$r$	$P$	Model <sup>3</sup>	Mean Orientation (1 <sup>st</sup> mode)	Mean Orientation (2 <sup>nd</sup> mode)
B6	180821_03	261.1	265	0.173	< 0.001	M5A	346.6	208.4
B7	180821_04	282.3	156	0.256	< 0.001	M2B	285.2	-
B8	180823_03	294.6	1497	0.554	< 0.001	M2A	294.6	-
B9	180823_04	242.1	712	0.541	< 0.001	M5A	268.1	179.2
B10	180827_01	16.9	439	0.349	< 0.001	M5B	315.6	50.8
B11	180909_01*	28.0	1021	0.205	< 0.001	M5B	78.6	306.5
B16	180925_01	42.1	713	0.363	< 0.001	M2C	41.5	-
B20	180929_02	346.0	662	0.25	< 0.001	M5B	66.8	286.8
B23	180930_02	40.0	1942	0.474	< 0.001	M5A	283.7	54.8
B24	180930_03	245.3	966	0.205	< 0.001	M4B	250.9	430.9
B28	181004_01	33.7	939	0.259	< 0.001	M5A	271.5	59.9
B30	181004_04	67.4	1733	0.231	< 0.001	M5B	131.4	41.7
B31	181005_01	67.0	694	0.306	< 0.001	M5B	233.7	61.5
B32	181005_02	330.0	726	0.387	< 0.001	M2A	330.0	-
B33	181005_03	26.6	1323	0.133	< 0.001	M5A	173.0	8.9
B34	181005_04	101.4	1144	0.473	< 0.001	M5B	123.1	48.6
B35	181006_02	302.1	115	0.359	< 0.001	M2A	302.1	-
B36	181006_04	340.1	1743	0.159	< 0.001	M5A	4.8	202.1
B37	181008_03	301.7	215	0.3	< 0.001	M5A	251.2	6.8
B38	181008_04	101.3	686	0.182	< 0.001	M5A	146.5	17.0
B39	181009_01	114.8	1163	0.293	< 0.001	M2C	123.8	-
B40	181009_02	318.6	1921	0.188	< 0.001	M5B	284.7	57.0
B41	181009_03	0.0	1337	0.165	< 0.001	M5A	298.3	75.9
B43	181010_03	342.4	474	0.123	0.001	M2A	342.5	-
B44	181010_04	97.2	669	0.26	< 0.001	M5A	42.4	176.5
B46	181013_02	24.5	328	0.275	< 0.001	M5B	311.1	41.3
B47	181013_03	20.6	1352	0.348	< 0.001	M5A	275.5	46.8
B48	181013_04	40.0	430	0.375	< 0.001	M5B	360.0	55.7
B50	181014_02	335.4	1363	0.739	< 0.001	M2C	338.4	-
B51	181014_03	182.2	184	0.151	0.015	M5B	208.8	50.0
B52	181014_04	287.3	178	0.131	0.048	M2A	287.3	-
B61	190822_04	9.1	1189	0.137	< 0.001	M2A	9.1	-

<sup>1</sup> Unique ID given to each individual for ease of interpretation of chapter figures and tables

<sup>2</sup> The video ID is the Year-Month-Day\_DVR channel number

<sup>3</sup> Models of animal orientation as described by Schnute and Groot (1992); the models in this table are as follows: M2A (unimodal), M2B (symmetric modified unimodal), M2C (modified unimodal), M4B (axial bimodal), M5A (homogenous bimodal), M5B (bimodal)

\* Bird was captured and tested on Seal Island

**Table 2.4 (cont.).** Orientation results for Blackpoll Warblers tested in 2018 and 2019 ( $n = 50$ ). All orientation tests were conducted on Bon Portage Island except for one individual (180909\_01, B11). The mean preferred orientation and Rayleigh statistics for each test are provided, where  $n$  is the number of recorded flights off of the perch (activity),  $r$  is the mean resultant vector (or rho), and  $P$  is whether the individual is significantly oriented. The animal orientation model with the best fit, and mean modes from maximum likelihood analysis are also provided. See Figure 2.8 for individual orientation plots and Table S2.4 for information on model selection.

Bird ID	Video ID (yymmdd_channel)	Mean Orientation	Rayleigh statistics			Maximum likelihood analysis		
			$n$	$r$	$P$	Model	Mean Orientation (1 <sup>st</sup> mode)	Mean Orientation (2 <sup>nd</sup> mode)
B67	190826_01	334.4	1652	0.408	< 0.001	M5B	46.5	296.3
B69	190826_03	306.9	763	0.594	< 0.001	M2C	309.3	-
B71	190913_04	297.4	688	0.301	< 0.001	M5A	195.7	319.0
B73	190916_03	5.4	601	0.295	< 0.001	M2A	5.4	-
B76	190926_01	23.2	140	0.734	< 0.001	M2C	16.7	-
B77	190926_02	339.7	115	0.556	< 0.001	M2A	339.7	-
B78	190929_03	337.0	1076	0.29	< 0.001	M5A	30.4	269.0
B80	190930_02	321.3	916	0.288	< 0.001	M5A	46.0	301.1
B81	191003_02	310.9	2259	0.528	< 0.001	M2A	310.9	-
B82	191015_02	0.6	65	0.285	0.005	M2B	358.2	-
B83	191015_03	317.2	66	0.309	0.002	M2A	317.2	-
B84	191015_04	11.4	134	0.638	< 0.001	M2C	16.7	-
B85	191018_02	49.0	633	0.52	< 0.001	M2B	41.8	-
B87	191019_02	328.5	1960	0.193	< 0.001	M5B	211.2	0.3
B88	191019_03	340.5	1707	0.651	< 0.001	M2A	340.6	-
B89	191019_04	53.1	289	0.406	< 0.001	M5B	154.0	29.9
B90	191020_02	218.7	2811	0.213	< 0.001	M5A	205.6	12.7
B91	191020_04	46.6	566	0.573	< 0.001	M4B	45.0	225.0

<sup>1</sup> Unique ID given to each individual for ease of interpretation of chapter figures and tables

<sup>2</sup> The video ID is the Year-Month-Day\_DVR channel number

<sup>3</sup> Models of animal orientation as described by Schnute and Groot (1992); the models in this table are as follows: M2A (unimodal), M2B (symmetric modified unimodal), M2C (modified unimodal), M4B (axial bimodal), M5A (homogenous bimodal), M5B (bimodal)

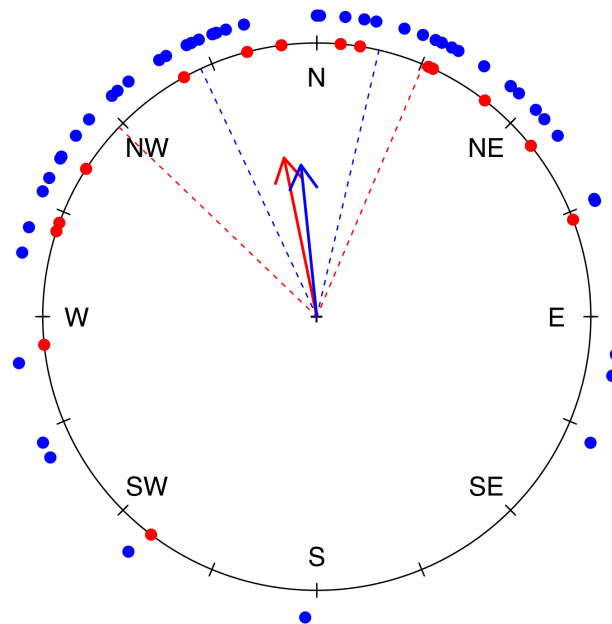
\* Bird was captured and tested on Seal Island

selecting a preferred orientation regardless of wind direction. Group preferred direction of vagrants was also similar to that of resident hatch-year blackpolls, suggesting that hatch-year vagrants may not differ behaviourally from non-vagrants during migration. Rather, young vagrants and non-vagrants share similarities in execution of migratory flights. This provides additional support for our hypothesis that vagrants are not aberrant, but instead part of the natural spectrum of migratory behaviour that occurs within populations (Phillips 2000).

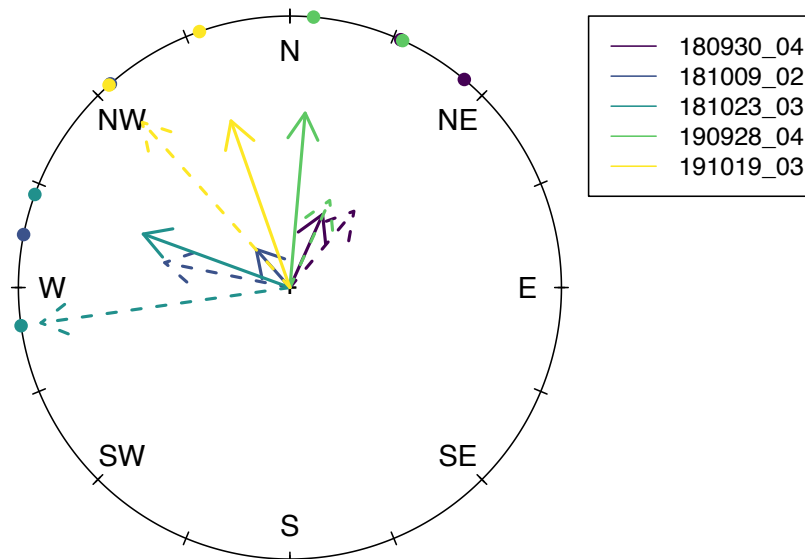
There are a few possible explanations as to why vagrants and blackpolls exhibited a mean

NNW and N heading, respectively. It is possible that their orientation was just a “default” response to orientation cages. Thorup (1998) found that both vagrants and common birds tested in cages on Christiansø, Denmark oriented northwest on the first night, but changed orientation on subsequent nights, suggesting an initial “default” orientation that is not the preferred migratory direction. Sandberg et al. (1991) previously demonstrated this in young migrant Wheatears (*Oenanthe oenanthe*), which oriented towards magnetic northwest when tested in both Sweden and Greenland. However, individuals in both of these tests were held in different cages prior to testing. Individuals in our study were kept in the same cage for both captivity and testing, and presumably would have already adjusted to the cage and exhibited a more natural migratory response, rather than “default” or escape behaviour. Fitzgerald and Taylor (2008) found that juvenile Yellow-rumped Warblers (*Setophaga coronata*) tested on the day of capture on BP in similar cages to our study, did not orient towards the northwest (i.e. the presumed “default” orientation), suggesting that our results are a real migratory response. Orientations were between 178° to 311°, with the majority orienting southwest. Still, since we were only able to test individuals on their first night, we cannot wholly dismiss the “default” response as a possibility.

Another exciting possibility is that the mean heading observed for both vagrants and blackpolls is a result of post-fledging dispersal. A tracking study by Brown and Taylor (2015) on the migratory movements of blackpolls on BP found that movements of hatch-year blackpolls were consistent with the exploration hypothesis of post-fledging dispersal outlined by Baker (1978, 1980, 1993). Baker’s hypothesis states that immediately after fledging, young birds engage in exploratory movements outside of the natal area to locate future breeding sites, and create a familiar area map of the region surrounding the natal site, including visual landmarks (e.g. shape of the coastline) and possibly the regional magnetic field (Brown and Taylor 2015). Dispersal in this context is not dispersal in the traditional sense, defined by movements ending in breeding (Matthysen 2012), but rather a period of exploratory movements far from the natal site. This exploratory period helps individuals navigate effectively on their return migration, since they will be familiar with important areas surrounding the breeding site. Baker also hypothesised



**Figure 2.9.** Mean preferred orientation of vagrants (in red) and Blackpoll Warblers (in blue). Vagrants oriented towards  $348.37^\circ$  or NNW ( $r = 0.59$ ,  $p = 0.004$ ,  $n = 15$ ; 95% CI =  $313.81^\circ - 22.92^\circ$ ), and Blackpoll Warblers oriented towards  $354.05^\circ$  or N ( $r = 0.56$ ,  $p < 0.001$ ,  $n = 50$ ; 95% CI =  $334.97^\circ - 13.12^\circ$ ). Orientation did not significantly differ between the two groups ( $W = 0.14$ ,  $p = 0.93$ ,  $n = 65$ ). Points around the circle represent the mean preferred orientation of each individual tested, and the arrows depict the group mean preferred orientation. The length of each arrow is the mean resultant vector length. Dotted lines represent the 95% confidence intervals of each group-specific mean. Directions are depicted relative to true North (gN).



**Figure 2.10.** Manual tracking of 5 randomly selected videos. Manually tracked mean orientations are represented by dotted lines, and mean orientations from videos processed in radR are represented by solid lines. The mean orientations using manual tracking were within  $\pm 8.40^\circ$  of the radR output. Directions are depicted relative to true North (gN).

that the first autumn migration serves as an extension of post-fledging dispersal to locate overwintering sites. Autumn migration combined with post-fledging dispersal is known as the “Exploratory Migration Model” (Baker 1978, 1980, 1993).

In Brown and Taylor’s (2015) study, while adults oriented southwest from Nova Scotia across the Gulf of Maine to reach wintering grounds in South America (Deluca et al. 2015), hatch-year birds departed in directions ranging from NW to NE, before returning south to begin their autumn migration. These NW to NE movements were explained as exploratory movements post-fledging, to create a familiar area map of Nova Scotia, and to extract information on local magnetic fields. The hatch-year birds in our study also oriented in a similar direction, and from the clear departure directions we were able to obtain from MOTUS tracks ( $n = 19$ ; Figure S2.1), departures ranged from NW to NE. For blackpolls, these movements are consistent with Brown and Taylor’s (2015) tracking data, and suggest the likelihood of post-fledging exploratory movements from their natal site. Since vagrants oriented similarly at our study site compared to blackpolls, they may also be engaging in exploratory movements, possibly along the coastline. This suggests that vagrancy fits the “Exploratory Migration Model”, whereby individuals orient in directed flights during post-fledging exploration, combined with an exploratory autumn migration in search of wintering grounds, in directions that differ from the natal population mean. When presented with a unique situation along their directed route (e.g. arrival at an offshore island such as our study site), vagrants may default to post-fledging exploratory behaviour possibly to familiarise themselves with the area, or to determine whether the location is suitable for overwintering.

How vagrants explore in directions that differ, sometimes drastically, from the normal migratory bearing may result from inheritance of a range of preferred migratory directions in juveniles (Phillips 2000), though it is still not known if vagrancy is an inherited behaviour. Nonetheless, juvenile passerines have been shown to demonstrate variation or scatter in their preferred migratory directions on their first autumn migration (Able 1977, Moore 1984), a bet-hedging strategy that can impart increased fitness benefits (Alerstam 1982, Reilly and Reilly 2009). According to Phillips (2000), vagrants inherit

directions that are different from the population mean, and they will travel directly in these directions to arrive at the vagrant location. Variation in innate directions are not selected against because it is highly advantageous for birds to have flexibility in their preferred migratory direction (Ralph 1978). Individuals can take advantage of newly available habitat, or avoid those that are no longer suitable (Grinnell 1922), which is important in unpredictable environments (Reilly and Reilly 2009). Additionally, birds on their first autumn migration do not need to have an accurate migratory bearing since they can winter anywhere within the wintering range (DeSante 1983a). Though some individuals may die (Able 1977, Ralph 1978, Thorup et al. 2012), the flexibility that this behaviour imparts onto the individual increases their survival enough for this trait to persist (Veit 2008).

Due to the design of our study, we cannot say with certainty whether vagrants meant to have an overseas crossing to Nova Scotia. We know from oriented movements in cages that vagrants are capable of directed flights, and were likely directed in their movements to the coast, but we cannot determine whether they intended to go offshore. Overseas crossings do occur during normal migration in all but one of the vagrant species captured (Clay-colored Sparrow (*Spizella pallida*)), to either the West Indies or across the Gulf of Mexico, so directed travel over open water is not implausible for these species. While we do not think that vagrants are displaced by wind, offshore vagrants are thought to result from displacement (McLaren 1981), and individuals have been hypothesised to react by either (1) reorienting to regain the normal migratory pathway, (2) orienting from the new location to the wintering grounds, (3) orienting in a direction to recover the mainland, or (4) failing to reorient and continuing in the normal migratory direction before displacement, likely resulting in death at sea (Able 1977, Ralph 1978, Fitzgerald and Taylor 2008). We refer to each of these scenarios as (1) pathway recovery, (2) winter flight, (3) mainland recovery, and (4) recovery failure. Phillips (2000) however suggests a much simpler hypothesis, that vagrants “have flown straight to these various places, following a range of innate orientations”. According to this hypothesis, vagrants that landed on BP or Seal Island arrived due to a directed migratory flight from the breeding grounds, rather than displacement. We refer to this scenario as (5) directed flight.

Out of the 15 vagrants tested, three individuals exhibited pathway recovery (hypothesis 1), seven exhibited mainland recovery (hypothesis 3), and five engaged in directed flight (hypothesis 5) (Table 2.5). None of the vagrants tested oriented towards the wintering grounds (hypothesis 2), or maintained the normal migratory pathway which would have resulted in death over the open ocean (hypothesis 4). That none of the vagrants significantly oriented S to SE towards the open ocean means that vagrants in this experiment, either (a) are not individuals programmed to orient along the normal migratory pathway that have been displaced across the open ocean, or (b) if they were wind-drifted to Nova Scotia, they are able to correct for displacement. The three individuals in our study that exhibited pathway recovery (hypothesis 1), oriented W or SW, which would recover them with the “normal” migratory pathway. While it is possible that these individuals may have been wind-drifted to Nova Scotia, it is also possible that their movements prior to their arrival in Nova Scotia were directed towards the east coast, but we cannot test if this is the case. The five individuals that oriented in the direction required to reach the study site (NE to ENE; hypothesis 5) were likely directed there. The majority of individuals that exhibited mainland recovery (hypothesis 3) oriented WNW to N, towards the mainland. WNW to N is the same direction that blackpolls that engage in post-fledging exploration orient. Mainland recovery may actually be exploration, and vagrants that oriented in this direction are likely engaging in exploratory movements (as outlined above; “Exploratory Migration Model”). It is possible that all vagrants tested were oriented overseas to Nova Scotia, and oriented in a different direction once they arrived at the study site to either leave (hypothesis 1), or explore the coast or region (hypothesis 3).

The individuals that oriented in the direction necessary to reach the study site during testing may have been captured the exact day that they arrived at the study site and were still orienting NE to ENE, while other individuals may have been on the island for a day or two prior to capture and had already determined where to go next. We know from oriented movements in cages that vagrants are capable of directed flights, so it is likely that vagrants are likely directed offshore as well, rather than being wind-drifted. A recent tracking study by Smetzer et al. (2017) suggests this to be true. They found that more than 70% of migrating blackpolls and Red-eyed Vireos (*Vireo olivaceus*)

**Table 2.5.** Comparison of preferred orientation of vagrants during experimentation (“Cage Orientation”), orientation required to reach Nova Scotia directly from the centre of breeding range (“Vagrant Orientation”), normal migratory direction during autumn migration from the breeding to the wintering range (“Migratory Direction”), the deviation from the normal migratory bearing required to reach Nova Scotia (“Angular Deviation”), and the wind direction on the night of testing (“Wind Direction”). Cage, vagrant, and migratory orientations are provided in both degrees (°) and cardinal directions. The scenario is the hypothesis that best matches the orientation demonstrated during testing when compared to both the vagrant direction and the normal migratory direction. The scenarios are: (1) pathway recovery, (2) winter flight, (3) mainland recovery/exploration, (4) recovery failure, and (5) directed flight.

Bird ID	Video ID	Species	Cage Orientation		Vagrant Direction		Migratory Direction		Angular Deviation		Wind Direction	
			Degrees (°)	Cardinal	Degrees (°)	Cardinal	Degrees (°)	Cardinal	Scenario	Deviation	Direction	Direction
V24	191003_03	Clay-colored Sparrow	331.0	NNW	103.3	ESE	176.4	S	3	73.2		300
V10	181007_03	Orange-crowned Warbler	352.6	N	106.1	ESE	154.4	SSE	3	48.3		0
V2	180823_01	Orchard Oriole	51.4	NE	69.1	ENE	165.1	SSE	5	96.0		260
V1	180818_01	Prairie Warbler	217.2	SW	58.9	ENE	158.4	SSE	1	99.5		287
V4	180917_04	Prairie Warbler	37.8	NE	58.9	ENE	158.4	SSE	5	99.5		190
V22	190928_01	Prairie Warbler	9.1	N	58.9	ENE	158.4	SSE	3	99.5		160
V25	191014_03	Scarlet Tanager	264.1	W	77.8	ENE	166.0	SSE	1	88.2		110
V6	180923_01	Warbling Vireo	69.3	ENE	100.9	E	151.4	SSE	5	50.5		300
V8	180930_04	Warbling Vireo	24.1	NNE	100.9	E	151.4	SSE	5	50.5		140
V17	190917_03	Warbling Vireo	25.1	NNE	100.9	E	151.4	SSE	5	50.5		350
V29	191021_03	Western Palm Warbler	288.2	WNW	112.1	ESE	156.1	SSE	1	44.0		0
V28	191021_02	Yellow-billed Cuckoo	345.3	NNW	66.5	ENE	146.1	SE	3	79.6		0
V13	181023_03	Yellow-breasted Chat	290.1	WNW	76.5	ENE	158.5	SSE	3	82.0		120
V23	190928_04	Yellow-breasted Chat	5.0	N	76.5	ENE	158.5	SSE	3	82.0		160
V14	190812_04	Yellow-throated Warbler	302.7	WNW	61.5	ENE	175.1	S	3	113.6		170

actively selected coastal and offshore migratory routes during autumn migration, and were not drifted or displaced offshore.

We had hoped to use radio-tracking of individuals on the MOTUS network to ground truth our orientation cage results, however, due to various complications, this was only minimally successful. We were only able to obtain 19 clear departures (31% of all deployments; Figure S2.1). Inability to resolve clear departure directions for all deployments may have resulted from an inability to triangulate from the MOTUS towers at our study site. For departures to be clear, tags need to be picked up by more than one antenna on a tower, and by multiple towers in the network to properly resolve the vanishing bearings (Crewe et al. 2020). Placement of our towers (Figure 2.3) combined with tower failure during both seasons led to poor results. In 2018, on BP, the three towers were on opposite ends of the island, so an individual needed to depart either from the north (BPNorth) or south end (BPLH and BPSouth) to have a clear bearing. In 2019, we were able to add one tower to the middle of the island (BPLab), however, BPNorth was not operational for the majority of the season due to two failed charge controllers, and was finally knocked over as a result of strong easterlies during a storm in mid-October. BPSouth was also damaged during Hurricane Dorian, and while it was still operational, the antennas and mast were bent for half of the season. On Seal Island, we had one operational tower on the northeast side of the island (SealNorth) in 2018, but this tower was not operational in 2019. This meant that if any individuals travelled westward across the Atlantic, they would not have been detected again until they reached the east coast of North America. It is also possible that some tags were taken off by the birds, or the leg-loop harnesses fell off during the study period as birds lost weight on migratory flights. Tracking for this study could be improved by setting towers up more evenly across both study sites, and anchoring tower structures more strongly to increase stability during storms. Different attachment techniques should also be explored to ensure tags stay on for longer periods.

Our study reveals exciting insights about the behaviour of vagrants. We found that vagrants demonstrate preferred orientations during migration, and are capable of executing

directed migratory flights. Their movements may result from a combination of post-fledging dispersal and exploratory migrations, in directions that differ from the normal migratory route. Vagrants are therefore not aberrant as has been often assumed, but rather part of the normal migratory spectrum. Though migration in different directions seems as though it should be selected against, vagrants continue to increase in number each year across a variety of species. This is highly important for our understanding of migration, and reveals that migratory routes and orientations are not as fixed as previously believed. While our study shows the capacity for directed flights in vagrants, we cannot discern how individuals select these orientations. Future studies could track vagrants to the breeding grounds to determine if vagrant offspring migrate along similar tracks to their parents, or if vagrant and control offspring of a single species inherit a range of migratory bearings regardless of lineage.

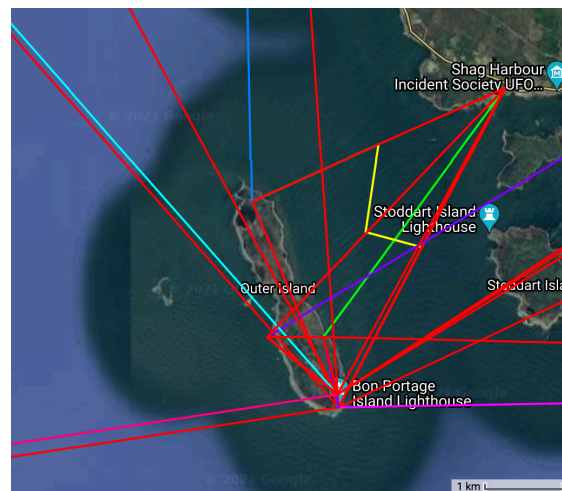
## **2.6 Acknowledgements**

Many thanks to all who helped make this project a reality. Thanks to my volunteers who helped with the fieldwork for this project – Bethany Darby, Shayla Nickerson, John Papajohn, Katy Dahl, Rebekah Persad, Kelly Chiang, and Jessy Wilson – and to Rielle Hoeg, Jessie McIntyre, and Richard R. Veit for field assistance during the season. Thanks to Lee and Carlene Adams, Gerry Cunningham, and Mike O’Brien for logistical support. Thanks also to Laura Achenbach, Lucas Berrigan, and Dominic Cormier for assistance with MOTUS tower setup and maintenance, and to David Bell for advice and input during initial project design. Support for this study was provided in part by the Oxford-Christ Church-NaturalMotion Graduate Scholarship, the Christ Church Graduate Travel and Research Grant, and funding from Phil Taylor. Permits were provided by the Canadian Wildlife Service and the Canadian Bird Banding Office.

## 2.7 Supplementary Material

### Radio tag analysis

Data from radio tags were processed in R (R Core Team 2019) following the Motus R Book (Crewe et al. 2020). Signal strength of devices was used to determine vanishing trajectory of individuals. Out of the 37 blackpolls and 24 vagrants tagged, 12 tags were excluded from analysis because they were not registered before deployment ( $n = 4$ ), tagged individuals were found dead, 1 to 14 days after deployment ( $n = 2$ ), or tags did not produce tracks in the MOTUS network despite being registered and deployed ( $n = 6$ ). 49 out of 61 deployments produced tracks, of which only 19 tags showed clear departure directions from the study site. The majority of vanishing bearings of clear departures were oriented between NW to NE (Figure S2.1).

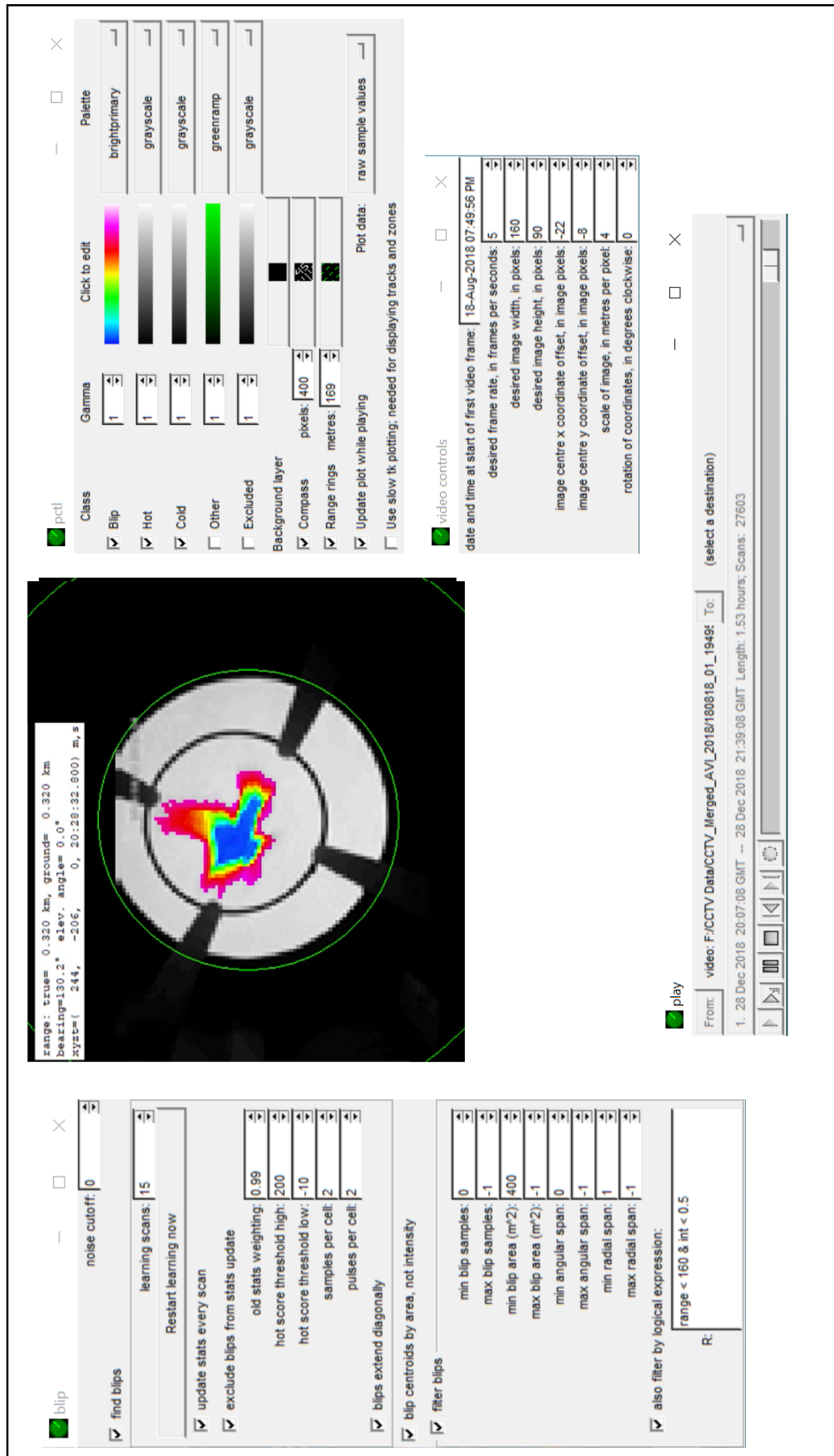


**Figure S2.1.** Departures of both vagrants (multi-coloured tracks) and blackpolls (red tracks) from Bon Portage Island, Nova Scotia in both 2018 and 2019 using the MOTUS network. Birds were affixed with either Lotek Wireless Avian NanoTag NTQB2-2s or NTQB2-5-1s after tests in orientation cages. A total of 61 individuals were tagged, but only 19 clear departures off island were detected. The majority of individuals went on a north/northwesterly heading, though easterly and westerly departures were also recorded.

However, since only 19 individuals had clear departures, these results do not show the entire picture. Clear departures were not detected for 30 tracks due to either low signal strength detected by antennas, or they were only detected by one antenna in the array.

It is also possible that some individuals departed southwards out over the open ocean from the island, but were not detected due to a lack of land masses directly south of BP (and therefore, a lack of MOTUS towers). Therefore, while it seems as though most individuals departed on orientations between NW to NE, this may not be the case since we are missing departures from 30 individuals. Mean orientation of both groups (Figure 2.9) suggests that the small sample size of tracks is representative of all of the individuals we tested, since both groups oriented towards the N/NNW in orientation cages, but we cannot say for certain in which direction the missing individuals would have left BP.

**Figure S2.2.** radR interface during video processing. The parameters used to analyse each video are shown below. When using radR, the video is loaded into the software, and the parameters are chosen from the ‘blip’ panel, and the ‘video controls panel’. Parameters in the ‘pctl’ panel can also be changed, but they were kept at their default for this study. When the parameters are set, play can be selected from the ‘play’ panel, and the video is processed automatically. The output is saved as an excel file.



**Table S2.1.** Vagrants ( $n = 29$ ) captured on Bon Portage (BP) and Seal Island (SL), Nova Scotia in 2018 and 2019. All vagrants captured were hatching-year birds. 7 vagrants were not tested. Of the 22 vagrants tested, 15 videos were able to be analysed for mean orientation. 24 vagrants were tagged with Lotek Wireless nanotags. The bird ID is a unique ID given to each individual for ease of interpretation of chapter figures and tables, and for comparison between Chapters 2 and 3. The Video ID is the Year-Month-Day\_DVR channel number. The dotted line in the table indicates where individuals from 2018 end and individuals from 2019 begin.

Bird ID	Species	Island	Date		Not Tested <sup>2</sup>	Video <sup>3</sup>	Analysed <sup>4</sup>	Not Analysed <sup>5</sup>	Video ID	Tagged <sup>6</sup>	Tag Type	Tag ID
			Captured	Tested <sup>1</sup>								
V1	Prairie Warbler	BP	18 Aug	Y	-	Y	Y	-	180818_01	N	-	-
V2	Orchard Oriole	BP	23 Aug	Y	-	Y	Y	-	180823_01	Y*	NTQB2-2	107
V3	Lark Sparrow	SL	07 Sep	Y	-	Y	N	inactive	-	Y	NTQB2-2	106
V4	Prairie Warbler	BP	17 Sep	Y	-	Y	Y	-	180917_04	Y	NTQB2-2	109
V5	Warbling Vireo	BP	20 Sep	Y	-	Y	N	inactive	-	Y	NTQB2-2	111
V6	Warbling Vireo	BP	23 Sep	Y	-	Y	Y	-	180923_01	Y	NTQB2-2	118
V7	Warbling Vireo	BP	28 Sep	Y	-	P	N	weather	-	Y**	NTQB2-2	112
V8	Warbling Vireo	BP	30 Sep	Y	-	Y	Y	-	180930_04	Y	NTQB2-2	122
V9	Yellow-billed Cuckoo	BP	01 Oct	Y	-	P	N	technical issues	-	Y	NTQB2-2	123
V10	Orange-crowned Warbler	BP	07 Oct	Y	-	Y	Y	-	181007_03	Y	NTQB2-2	130
V11	Yellow-billed Cuckoo	BP	15 Oct	Y	-	P	N	inactive	-	Y	NTQB2-2	133
V12	Warbling Vireo	BP	21 Oct	N	died	-	-	-	-	N	-	-
V13	Yellow-breasted Chat	BP	23 Oct	Y	-	Y	Y	-	181023_03	Y	NTQB2-2	134
V14	Yellow-throated Warbler	BP	12 Aug	Y	-	Y	Y	-	190812_04	Y	NTQB2-2	225
V15	Yellow-billed Cuckoo	BP	13 Aug	N	weather	-	-	-	-	Y	NTQB2-2	226

<sup>1</sup> Was the bird tested in an orientation cage? Y – yes, N – no

<sup>2</sup> Why was the bird not tested? “didn’t adjust” – bird was released because it did not immediately fly to the perch, showed visible signs of stress (e.g. panting), and/or was not eating or drinking; “died” – the bird died before being transferred to orientation cages; “released” – bird was released because species does not adjust well to cages; “weather” – bird was released due to rain before experimentation

<sup>3</sup> Was the test recorded? Y – the full experiment was recorded, P – part of the experiment was recorded

<sup>4</sup> Was the orientation video analysed? Y – yes, N – no

<sup>5</sup> Why was the video not analysed? “inactive” – the bird was stationary and/or was on the bottom of the cage during experimentation; “obscured” – the bird defecated on the camera, obscuring the footage; “technical issues” – video did not record due to equipment failure; “weather” – experiment was stopped due to rain during the experiment

<sup>6</sup> Was the bird tagged with a radio tag? Y – yes, N – no

\* Tag unregistered; no data available

\*\* Individual was killed by a Sharp-shinned Hawk (*Accipiter striatus*) in a mist-net on 29 Sep 2018; tag removed; no data available

**Table S2.1 (cont.).** Vagrants ( $n = 29$ ) captured on Bon Portage (BP) and Seal Island (SL), Nova Scotia in 2018 and 2019. All vagrants captured were hatching-year birds. 7 vagrants were not tested. Of the 22 vagrants tested, 15 videos were able to be analysed for mean orientation. 24 vagrants were tagged with Lotek Wireless nanotags. The bird ID is a unique ID given to each individual for ease of interpretation of chapter figures and tables, and for comparison between Chapters 2 and 3. The Video ID is the Year-Month-Day\_DVR channel number. The dotted line in the table indicates where individuals from 2018 end and individuals from 2019 begin.

Bird ID	Species	Island	Date		Tested <sup>1</sup>	Not Tested <sup>2</sup>	Video <sup>3</sup>	Analysed <sup>4</sup>	Not Analysed <sup>5</sup>	Video ID	Tagged <sup>6</sup>	Tag Type	Tag ID
			Captured	Released									
V16	Hammond's Flycatcher	BP	12 Sep	N	released	-	-	-	-	-	Y	NTQB2-2	227
V17	Warbling Vireo	BP	17 Sep	Y	-	Y	Y	-	-	190917_03	Y	NTQB2-2	229
V18	Indigo Bunting	BP	20 Sep	Y	-	Y	N	inactive	-	-	Y	NTQB2-2	230
V19	Warbling Vireo	BP	21 Sep	N	didn't adjust	-	-	-	-	-	N	-	-
V20	Yellow-breasted Chat	BP	24 Sep	N	weather	-	-	-	-	-	Y	NTQB2-2	232
V21	Blue Grosbeak	BP	26 Sep	N	didn't adjust	-	-	-	-	-	N	-	-
V22	Prairie Warbler	BP	28 Sep	Y	-	Y	Y	-	-	190928_01	Y	NTQB2-2	235
V23	Yellow-breasted Chat	BP	28 Sep	Y	-	Y	Y	-	-	190928_04	Y	NTQB2-2	233
V24	Clay-colored Sparrow	BP	03 Oct	Y	-	Y	Y	-	-	191003_03	Y	NTQB2-2	236
V25	Scarlet Tanager	BP	14 Oct	Y	-	Y	Y	-	-	191014_03	Y	NTQB2-2	238
V26	Yellow-billed Cuckoo	BP	15 Oct	Y	-	P	N	obscured	-	-	Y	NTQB2-2	239
V27	Pine Warbler	BP	19 Oct	N	didn't adjust	-	-	-	-	-	N	-	-
V28	Yellow-billed Cuckoo	BP	21 Oct	Y	-	Y	Y	-	-	191021_02	Y	NTQB2-2	240
V29	Western Palm Warbler	BP	21 Oct	Y	-	Y	Y	-	-	191021_03	Y	NTQB2-2	241

<sup>1</sup> Was the bird tested in an orientation cage? Y – yes, N – no

<sup>2</sup> Why was the bird not tested? “didn't adjust” – bird was released because it did not immediately fly to the perch, showed visible signs of stress (e.g. panting), and/or was not eating or drinking; “died” – the bird died before being transferred to orientation cages; “released” – bird was released because species does not adjust well to cages; “weather” – bird was released due to rain before experimentation

<sup>3</sup> Was the test recorded? Y – the full experiment was recorded, P – part of the experiment was recorded

<sup>4</sup> Was the orientation video analysed? Y – yes, N – no

<sup>5</sup> Why was the video not analysed? “inactive” – the bird was stationary and/or was on the bottom of the cage during experimentation; “obscured” – the bird defecated on the camera, obscuring the footage; “technical issues” – video did not record due to equipment failure; “weather” – experiment was stopped due to rain during the experiment

<sup>6</sup> Was the bird tagged with a radio tag? Y – yes, N – no

\* Tag unregistered; no data available

\*\* Individual was killed by a Sharp-shinned Hawk (*Accipiter striatus*) in a mist-net on 29 Sep 2018; tag removed; no data available

**Table S2.2.** Blackpoll Warblers ( $n = 91$ ) transferred to cages on Bon Portage (BP) and Seal Island (SL), Nova Scotia in 2018 and 2019. All blackpolls transferred to cages were hatching-year birds. 21 blackpolls were not tested. Of the 70 blackpolls tested, 50 videos were able to be analysed for mean orientation. 37 blackpolls were tagged with Lotek Wireless nanotags. The bird ID is a unique ID given to each individual for ease of interpretation of chapter figures and tables, and the Video ID is the Year-Month-Day\_DVR channel number. The dotted line in the table indicates where individuals from 2018 end and individuals from 2019 begin.

Bird ID	Island	Date Captured	Tested <sup>1</sup>	Not Tested <sup>2</sup>	Video <sup>3</sup>	Analysed <sup>4</sup>	Not Analysed <sup>5</sup>	Video ID	Tagged <sup>6</sup>	Tag Type	Tag ID
B1	BP	18 Aug	Y	-	Y	N	inactive	-	N	-	-
B2	BP	20 Aug	N	escaped	N	N	-	-	N	-	-
B3	BP	20 Aug	N	escaped	N	N	-	-	N	-	-
B4	BP	21 Aug	N	escaped	N	N	-	-	N	-	-
B5	BP	21 Aug	Y	-	P	N	technical issues	-	N	-	-
B6	BP	21 Aug	Y	-	Y	Y	-	180821_03	N	-	-
B7	BP	21 Aug	Y	-	Y	Y	-	180821_04	N	-	-
B8	BP	23 Aug	Y	-	Y	Y	-	180823_03	Y*	NTQB2-2	108
B9	BP	23 Aug	Y	-	Y	Y	-	180823_04	Y*	NTQB2-2	105
B10	BP	27 Aug	Y	-	Y	Y	-	180827_01	Y*	NTQB2-2	117
B11	SL	09 Sep	Y	-	Y	Y	-	180909_01	Y	NTQB2-2	110
B12	SL	10 Sep	Y	-	Y	N	inactive	-	N	-	-
B13	BP	20 Sep	N	escaped	N	N	-	-	N	-	-
B14	BP	23 Sep	Y	-	P	N	technical issues	-	Y	NTQB2-2	115
B15	BP	25 Sep	Y	-	N	N	escaped	-	N	-	-
B16	BP	25 Sep	Y	-	Y	Y	-	180925_01	Y	NTQB2-2	121

<sup>1</sup> Was the bird tested in an orientation cage? Y – yes, N – no

<sup>2</sup> Why was the bird not tested? “didn’t adjust” – bird was released because it did not immediately fly to the perch, showed visible signs of stress (e.g. panting), and/or was not eating or drinking; “died” – the bird died before being transferred to orientation cages; “escaped” – the bird escaped from the cage before experimentation; “released” – bird was released and due to technical issues; “replaced” – the bird was replaced with another individual; “weather” – bird was released due to rain before experimentation

<sup>3</sup> Was the test recorded? Y – the full experiment was recorded, P – part of the experiment was recorded, N – no

<sup>4</sup> Was the orientation video analysed? Y – yes, N – no

<sup>5</sup> Why was the video not analysed? “inactive” – the bird was stationary and/or was on the bottom of the cage during experimentation; “escaped” – the bird escaped during the experiment; “technical issues” – video did not record due to equipment failure; “weather” – experiment was stopped due to rain during the experiment

<sup>6</sup> Was the bird tagged with a radio tag? Y – yes, N – no

\* Tag unregistered; no data available

\*\* Individual was found dead on the island on 13 Oct 2019; tag removed; no data available

**Table S2.2 (cont.).** Blackpoll Warblers ( $n = 91$ ) transferred to cages on Bon Portage (BP) and Seal Island (SL), Nova Scotia in 2018 and 2019. All blackpolls transferred to cages were hatching-year birds. 21 blackpolls were not tested. Of the 70 blackpolls tested, 50 videos were able to be analysed for mean orientation. 37 blackpolls were tagged with Lotek Wireless nanotags. The bird ID is a unique ID given to each individual for ease of interpretation of chapter figures and tables, and the Video ID is the Year-Month-Day\_DVR channel number. The dotted line in the table indicates where individuals from 2018 end and individuals from 2019 begin.

Bird ID	Island	Date Captured	Tested <sup>1</sup>	Not Tested <sup>2</sup>	Video <sup>3</sup>	Analysed <sup>4</sup>	Not Analysed <sup>5</sup>	Video ID	Tagged <sup>6</sup>	Tag Type	Tag ID
B17	BP	25 Sep	Y	-	P	N	technical issues	-	N	-	-
B18	BP	28 Sep	Y	-	P	N	weather	-	Y	NTQB2-2	114
B19	BP	28 Sep	Y	-	P	N	weather	-	Y	NTQB2-2	113
B20	BP	29 Sep	Y	-	Y	Y	-	180929_02	Y	NTQB2-2	112
B21	BP	30 Sep	N	replaced	N	N	-	-	N	-	-
B22	BP	30 Sep	Y	-	P	N	technical issues	-	Y	NTQB2-2	120
B23	BP	30 Sep	Y	-	Y	Y	-	180930_02	Y	NTQB2-2	116
B24	BP	30 Sep	Y	-	Y	Y	-	180930_03	Y	NTQB2-2	119
B25	BP	01 Oct	Y	-	P	N	technical issues	-	Y	NTQB2-2	124
B26	BP	01 Oct	Y	-	P	N	technical issues	-	Y	NTQB2-2	125
B27	BP	01 Oct	Y	-	P	N	technical issues	-	Y	NTQB2-2	126
B28	BP	04 Oct	Y	-	Y	Y	-	181004_01	Y	NTQB2-2	127
B29	BP	04 Oct	Y	-	Y	N	inactive	-	Y	NTQB2-2	128
B30	BP	04 Oct	Y	-	Y	Y	-	181004_04	Y	NTQB2-2	129
B31	BP	05 Oct	Y	-	Y	Y	-	181005_01	Y	NTQB2-2	131
B32	BP	05 Oct	Y	-	Y	Y	-	181005_02	Y	NTQB2-2	132

<sup>1</sup> Was the bird tested in an orientation cage? Y – yes, N – no

<sup>2</sup> Why was the bird not tested? “didn’t adjust” – bird was released because it did not immediately fly to the perch, showed visible signs of stress (e.g. panting), and/or was not eating or drinking; “died” – the bird died before being transferred to orientation cages; “escaped” – the bird escaped from the cage before experimentation; “released” – bird was released and due to technical issues; “replaced” – the bird was replaced with another individual; “weather” – bird was released due to rain before experimentation

<sup>3</sup> Was the test recorded? Y – the full experiment was recorded, P – part of the experiment was recorded, N – no

<sup>4</sup> Was the orientation video analysed? Y – yes, N – no

<sup>5</sup> Why was the video not analysed? “inactive” – the bird was stationary and/or was on the bottom of the cage during experimentation; “escaped” – the bird escaped during the experiment; “technical issues” – video did not record due to equipment failure; “weather” – experiment was stopped due to rain during the experiment

<sup>6</sup> Was the bird tagged with a radio tag? Y – yes, N – no

\* Tag unregistered; no data available

\*\* Individual was found dead on the island on 13 Oct 2019; tag removed; no data available

**Table S2.2 (cont.).** Blackpoll Warblers ( $n = 91$ ) transferred to cages on Bon Portage (BP) and Seal Island (SL), Nova Scotia in 2018 and 2019. All blackpolls transferred to cages were hatching-year birds. 21 blackpolls were not tested. Of the 70 blackpolls tested, 50 videos were able to be analysed for mean orientation. 37 blackpolls were tagged with Lotek Wireless nanotags. The bird ID is a unique ID given to each individual for ease of interpretation of chapter figures and tables, and the Video ID is the Year-Month-Day\_DVR channel number. The dotted line in the table indicates where individuals from 2018 end and individuals from 2019 begin.

Bird ID	Island	Date Captured	Tested <sup>1</sup>	Not Tested <sup>2</sup>	Video <sup>3</sup>	Analysed <sup>4</sup>	Not Analysed <sup>5</sup>	Video ID	Tagged <sup>6</sup>	Tag Type	Tag ID
B33	BP	05 Oct	Y	-	Y	Y	-	181005_03	N	-	-
B34	BP	05 Oct	Y	-	Y	Y	-	181005_04	N	-	-
B35	BP	06 Oct	Y	-	Y	Y	-	181006_02	N	-	-
B36	BP	06 Oct	Y	-	Y	Y	-	181006_04	N	-	-
B37	BP	08 Oct	Y	-	Y	Y	-	181008_03	N	-	-
B38	BP	08 Oct	Y	-	Y	Y	-	181008_04	N	-	-
B39	BP	09 Oct	Y	-	Y	Y	-	181009_01	N	-	-
B40	BP	09 Oct	Y	-	Y	Y	-	181009_02	N	-	-
B41	BP	09 Oct	Y	-	Y	Y	-	181009_03	N	-	-
B42	BP	09 Oct	Y	-	Y	N	inactive	-	N	-	-
B43	BP	10 Oct	Y	-	Y	Y	-	181010_03	N	-	-
B44	BP	10 Oct	Y	-	Y	Y	-	181010_04	N	-	-
B45	BP	13 Oct	Y	-	N	N	technical issues	-	N	-	-
B46	BP	13 Oct	Y	-	P	Y	-	181013_02	N	-	-
B47	BP	13 Oct	Y	-	P	Y	-	181013_03	N	-	-
B48	BP	13 Oct	Y	-	P	Y	-	181013_04	N	-	-

<sup>1</sup> Was the bird tested in an orientation cage? Y – yes, N – no

<sup>2</sup> Why was the bird not tested? “didn’t adjust” – bird was released because it did not immediately fly to the perch, showed visible signs of stress (e.g. panting), and/or was not eating or drinking; “died” – the bird died before being transferred to orientation cages; “escaped” – the bird escaped from the cage before experimentation; “released” – bird was released and due to technical issues; “replaced” – the bird was replaced with another individual; “weather” – bird was released due to rain before experimentation

<sup>3</sup> Was the test recorded? Y – the full experiment was recorded, P – part of the experiment was recorded, N – no

<sup>4</sup> Was the orientation video analysed? Y – yes, N – no

<sup>5</sup> Why was the video not analysed? “inactive” – the bird was stationary and/or was on the bottom of the cage during experimentation; “escaped” – the bird escaped during the experiment; “technical issues” – video did not record due to equipment failure; “weather” – experiment was stopped due to rain during the experiment

<sup>6</sup> Was the bird tagged with a radio tag? Y – yes, N – no

\* Tag unregistered; no data available

\*\* Individual was found dead on the island on 13 Oct 2019; tag removed; no data available

**Table S2.2 (cont.).** Blackpoll Warblers ( $n = 91$ ) transferred to cages on Bon Portage (BP) and Seal Island (SL), Nova Scotia in 2018 and 2019. All blackpolls transferred to cages were hatching-year birds. 21 blackpolls were not tested. Of the 70 blackpolls tested, 50 videos were able to be analysed for mean orientation. 37 blackpolls were tagged with Lotek Wireless nanotags. The bird ID is a unique ID given to each individual for ease of interpretation of chapter figures and tables, and the Video ID is the Year-Month-Day\_DVR channel number. The dotted line in the table indicates where individuals from 2018 end and individuals from 2019 begin.

Bird ID	Island	Date Captured	Tested <sup>1</sup>	Not Tested <sup>2</sup>	Video <sup>3</sup>	Analysed <sup>4</sup>	Not Analysed <sup>5</sup>	Video ID	Tagged <sup>6</sup>	Tag Type	Tag ID
B49	BP	14 Oct	N	released	N	N	-	-	N	-	-
B50	BP	14 Oct	Y	-	Y	Y	-	181014_02	N	-	-
B51	BP	14 Oct	Y	-	Y	Y	-	181014_03	N	-	-
B52	BP	14 Oct	Y	-	Y	Y	-	181014_04	N	-	-
B53	BP	15 Oct	N	weather	N	N	-	-	N	-	-
B54	BP	21 Oct	N	released	N	N	-	-	N	-	-
B55	BP	21 Oct	N	released	N	N	-	-	N	-	-
B56	BP	12 Aug	N	died	N	N	-	-	N	-	-
B57	BP	13 Aug	N	died	N	N	-	-	N	-	-
B58	BP	13 Aug	N	weather	N	N	-	-	Y	NTQB2-5-1	165
B59	BP	13 Aug	N	weather	N	N	-	-	Y	NTQB2-5-1	166
B60	BP	22 Aug	N	didn't adjust	N	N	-	-	N	-	-
B61	BP	22 Aug	Y	-	Y	Y	-	190822_04	Y	NTQB2-5-1	168
B62	BP	25 Aug	Y	-	N	N	technical issues	-	N	-	-
B63	BP	25 Aug	Y	-	N	N	technical issues	-	N	-	-
B64	BP	25 Aug	N	didn't adjust	N	N	-	-	N	-	-

<sup>1</sup> Was the bird tested in an orientation cage? Y – yes, N – no

<sup>2</sup> Why was the bird not tested? “didn't adjust” – bird was released because it did not immediately fly to the perch, showed visible signs of stress (e.g. panting), and/or was not eating or drinking; “died” – the bird died before being transferred to orientation cages; “escaped” – the bird escaped from the cage before experimentation; “released” – bird was released and due to technical issues; “replaced” – the bird was replaced with another individual; “weather” – bird was released due to rain before experimentation

<sup>3</sup> Was the test recorded? Y – the full experiment was recorded, P – part of the experiment was recorded, N – no

<sup>4</sup> Was the orientation video analysed? Y – yes, N – no

<sup>5</sup> Why was the video not analysed? “inactive” – the bird was stationary and/or was on the bottom of the cage during experimentation; “escaped” – the bird escaped during the experiment; “technical issues” – video did not record due to equipment failure; “weather” – experiment was stopped due to rain during the experiment

<sup>6</sup> Was the bird tagged with a radio tag? Y – yes, N – no

\* Tag unregistered; no data available

\*\* Individual was found dead on the island on 13 Oct 2019; tag removed; no data available

**Table S2.2 (cont.).** Blackpoll Warblers ( $n = 91$ ) transferred to cages on Bon Portage (BP) and Seal Island (SL), Nova Scotia in 2018 and 2019. All blackpolls transferred to cages were hatching-year birds. 21 blackpolls were not tested. Of the 70 blackpolls tested, 50 videos were able to be analysed for mean orientation. 37 blackpolls were tagged with Lotek Wireless nanotags. The bird ID is a unique ID given to each individual for ease of interpretation of chapter figures and tables, and the Video ID is the Year-Month-Day\_DVR channel number. The dotted line in the table indicates where individuals from 2018 end and individuals from 2019 begin.

Bird ID	Island	Date Captured	Tested <sup>1</sup>	Not Tested <sup>2</sup>	Video <sup>3</sup>	Analysed <sup>4</sup>	Not Analysed <sup>5</sup>	Video ID	Tagged <sup>6</sup>	Tag Type	Tag ID
B65	BP	25 Aug	N	released	N	N	-	-	N	-	-
B66	BP	25 Aug	Y	-	N	N	technical issues	-	N	-	-
B67	BP	26 Aug	Y	-	Y	Y	-	190826_01	Y	NTQB2-5-1	171
B68	BP	26 Aug	Y	-	Y	N	inactive	-	Y	NTQB2-5-1	169
B69	BP	26 Aug	Y	-	Y	Y	-	190826_03	Y	NTQB2-5-1	167
B70	BP	30 Aug	N	didn't adjust	N	N	-	-	N	-	-
B71	BP	13 Sep	Y	-	Y	Y	-	190913_04	Y	NTQB2-2	228
B72	BP	16 Sep	N	didn't adjust	N	N	-	-	N	-	-
B73	BP	16 Sep	Y	-	Y	Y	-	190916_03	Y	NTQB2-5-1	170
B74	BP	19 Sep	N	escaped	N	N	-	-	N	-	-
B75	BP	26 Sep	N	escaped	N	N	-	-	N	-	-
B76	BP	26 Sep	Y	-	Y	Y	-	190926_01	Y	NTQB2-5-1	172
B77	BP	26 Sep	Y	-	Y	Y	-	190926_02	Y	NTQB2-5-1	173
B78	BP	29 Sep	Y	-	Y	Y	-	190929_03	Y**	NTQB2-5-1	174
B79	BP	30 Sep	Y	-	N	N	technical issues	-	Y	NTQB2-5-1	176
B80	BP	30 Sep	Y	-	Y	Y	-	190930_02	Y	NTQB2-5-1	175

<sup>1</sup> Was the bird tested in an orientation cage? Y – yes, N – no

<sup>2</sup> Why was the bird not tested? “didn't adjust” – bird was released because it did not immediately fly to the perch, showed visible signs of stress (e.g. panting), and/or was not eating or drinking; “died” – the bird died before being transferred to orientation cages; “escaped” – the bird escaped from the cage before experimentation; “released” – bird was released and due to technical issues; “replaced” – the bird was replaced with another individual; “weather” – bird was released due to rain before experimentation

<sup>3</sup> Was the test recorded? Y – the full experiment was recorded, P – part of the experiment was recorded, N – no

<sup>4</sup> Was the orientation video analysed? Y – yes, N – no

<sup>5</sup> Why was the video not analysed? “inactive” – the bird was stationary and/or was on the bottom of the cage during experimentation; “escaped” – the bird escaped during the experiment; “technical issues” – video did not record due to equipment failure; “weather” – experiment was stopped due to rain during the experiment

<sup>6</sup> Was the bird tagged with a radio tag? Y – yes, N – no

\* Tag unregistered; no data available

\*\* Individual was found dead on the island on 13 Oct 2019; tag removed; no data available

**Table S2.2 (cont.).** Blackpoll Warblers ( $n = 91$ ) transferred to cages on Bon Portage (BP) and Seal Island (SL), Nova Scotia in 2018 and 2019. All blackpolls transferred to cages were hatching-year birds. 21 blackpolls were not tested. Of the 70 blackpolls tested, 50 videos were able to be analysed for mean orientation. 37 blackpolls were tagged with Lotek Wireless nanotags. The bird ID is a unique ID given to each individual for ease of interpretation of chapter figures and tables, and the Video ID is the Year-Month-Day\_DVR channel number. The dotted line in the table indicates where individuals from 2018 end and individuals from 2019 begin.

Bird ID	Island	Date Captured	Tested <sup>1</sup>	Not Tested <sup>2</sup>	Video <sup>3</sup>	Analysed <sup>4</sup>	Not Analysed <sup>5</sup>	Video ID	Tagged <sup>6</sup>	Tag Type	Tag ID
B81	BP	03 Oct	Y	-	Y	Y	-	191003_02	Y	NTQB2-5-1	177
B82	BP	15 Oct	Y	-	Y	Y	-	191015_02	Y	NTQB2-2	249
B83	BP	15 Oct	Y	-	Y	Y	-	191015_03	Y	NTQB2-5-1	179
B84	BP	15 Oct	Y	-	Y	Y	-	191015_04	Y	NTQB2-5-1	178
B85	BP	18 Oct	Y	-	Y	Y	-	191018_02	N	-	-
B86	BP	19 Oct	N	replaced	N	N	-	-	N	-	-
B87	BP	19 Oct	Y	-	Y	Y	-	191019_02	N	-	-
B88	BP	19 Oct	Y	-	Y	Y	-	191019_03	N	-	-
B89	BP	19 Oct	Y	-	Y	Y	-	191019_04	N	-	-
B90	BP	20 Oct	Y	-	Y	Y	-	191020_02	N	-	-
B91	BP	20 Oct	Y	-	Y	Y	-	191020_04	N	-	-

<sup>1</sup> Was the bird tested in an orientation cage? Y – yes, N – no

<sup>2</sup> Why was the bird not tested? “didn’t adjust” – bird was released because it did not immediately fly to the perch, showed visible signs of stress (e.g. panting), and/or was not eating or drinking; “died” – the bird died before being transferred to orientation cages; “escaped” – the bird escaped from the cage before experimentation; “released” – bird was released and due to technical issues; “replaced” – the bird was replaced with another individual; “weather” – bird was released due to rain before experimentation

<sup>3</sup> Was the test recorded? Y – the full experiment was recorded, P – part of the experiment was recorded, N – no

<sup>4</sup> Was the orientation video analysed? Y – yes, N – no

<sup>5</sup> Why was the video not analysed? “inactive” – the bird was stationary and/or was on the bottom of the cage during experimentation; “escaped” – the bird escaped during the experiment; “technical issues” – video did not record due to equipment failure; “weather” – experiment was stopped due to rain during the experiment

<sup>6</sup> Was the bird tagged with a radio tag? Y – yes, N – no

\* Tag unregistered; no data available

\*\* Individual was found dead on the island on 13 Oct 2019; tag removed; no data available

**Table S2.3.** Model selection results for vagrants from the 10 orientation models described by Schnute and Groot (1992). The difference in Akaike Information Criterion relative to the best model ( $\Delta$ AIC) and the AIC model weights ( $w$ ) are shown. Models with  $\Delta$ AIC  $<$  2 are shown in **bold**, and the best model is indicated by an asterisk. See Table S2.3 for mean orientation of the best model.

Model	180818_01 (V1)		180823_01 (V2)		180917_04 (V4)		180923_01 (V6)		180930_04 (V8)	
	$\Delta$ AIC	$w$	$\Delta$ AIC	$w$	$\Delta$ AIC	$w$	$\Delta$ AIC	$w$	$\Delta$ AIC	$w$
M1 (uniform)	45.59	0.00	154.21	0.00	285.43	0.00	81.88	0.00	301.34	0.00
M2A (unimodal)	5.00	0.03	134.39	0.00	90.89	0.00	2.93	0.08	16.08	0.00
M2B (symmetric modified unimodal)	2.42	0.11	140.08	0.00	68.95	0.00	<b>0.00*</b>	<b>0.33*</b>	<b>0.16</b>	<b>0.35</b>
M2C (modified unimodal)	<b>0.13</b>	<b>0.34</b>	111.34	0.00	18.95	0.00	1.21	0.18	<b>0.00*</b>	<b>0.38*</b>
M3A (homogenous symmetric bimodal)	42.02	0.00	37.81	0.00	186.63	0.00	75.90	0.00	258.77	0.00
M3B (symmetric bimodal)	3.13	0.08	39.02	0.00	19.63	0.00	<b>1.19</b>	<b>0.18</b>	<b>1.49</b>	<b>0.18</b>
M4A (homogenous axial bimodal)	4.48	0.04	39.72	0.00	30.04	0.00	2.05	0.12	19.24	0.00
M4B (axial bimodal)	<b>0.00*</b>	<b>0.37*</b>	28.52	0.00	<b>0.00*</b>	<b>1.00*</b>	24.89	0.00	3.01	0.08
M5A (homogenous bimodal)	5.92	0.02	8.82	0.01	17.49	0.00	2.09	0.12	10.47	0.00
M5B (bimodal)	6.39	0.02	<b>0.00*</b>	<b>0.99*</b>	98.98	0.00	32.19	0.00	22.29	0.00

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Model	181007_03 (V10)		181023_03 (V13)		190812_04 (V14)		190917_03 (V17)		190928_01 (V22)	
	$\Delta$ AIC	$w$	$\Delta$ AIC	$w$	$\Delta$ AIC	$w$	$\Delta$ AIC	$w$	$\Delta$ AIC	$w$
M1 (uniform)	15.74	0.00	738.11	0.00	56.19	0.00	6.83	0.01	35.70	0.00
M2A (unimodal)	2.09	0.14	261.60	0.00	<b>0.00*</b>	<b>0.72*</b>	<b>0.00*</b>	<b>0.31*</b>	<b>1.27</b>	<b>0.28</b>
M2B (symmetric modified unimodal)	<b>1.86</b>	<b>0.15</b>	247.82	0.00	9.14	0.01	<b>0.12</b>	<b>0.29</b>	2.91	0.12
M2C (modified unimodal)	61.22	0.00	223.34	0.00	5.35	0.05	2.03	0.11	51.57	0.00
M3A (homogenous symmetric bimodal)	15.00	0.00	522.29	0.00	58.68	0.00	10.49	0.00	31.26	0.00
M3B (symmetric bimodal)	3.43	0.07	251.42	0.00	11.51	0.00	2.14	0.10	4.93	0.05
M4A (homogenous axial bimodal)	3.08	0.08	287.65	0.00	21.97	0.00	2.46	0.09	7.95	0.01
M4B (axial bimodal)	5.07	0.03	225.04	0.00	13.83	0.00	5.47	0.02	10.29	0.00
M5A (homogenous bimodal)	<b>1.99</b>	<b>0.14</b>	52.30	0.00	5.37	0.05	3.66	0.05	88.93	0.00
M5B (bimodal)	<b>0.00*</b>	<b>0.39*</b>	<b>0.00*</b>	<b>1.00*</b>	2.93	0.17	5.33	0.02	<b>0.00*</b>	<b>0.53*</b>

**Table S2.3 (cont.).** Model selection results for vagrants from the 10 orientation models described by Schnute and Groot (1992). The difference in Akaike Information Criterion relative to the best model ( $\Delta$ AIC) and the AIC model weights ( $w$ ) are shown. Models with  $\Delta$ AIC < 2 are shown in **bold**, and the best model is indicated by an asterisk. See Table S2.3 for mean orientation of the best model.

Model	190928_04 (V23)		191003_03 (V24)		191014_03 (V25)		191021_02 (V28)		191021_03 (V29)	
	$\Delta$ AIC	$w$	$\Delta$ AIC	$w$	$\Delta$ AIC	$w$	$\Delta$ AIC	$w$	$\Delta$ AIC	$w$
M1 (uniform)	200.02	0.00	149.17	0.00	165.21	0.00	318.90	0.00	91.22	0.00
M2A (unimodal)	<b>1.13</b>	<b>0.36</b>	15.53	0.00	82.46	0.00	225.65	0.00	61.03	0.00
M2B (symmetric modified unimodal)	53.82	0.00	22.90	0.00	52.95	0.00	204.24	0.00	61.65	0.00
M2C (modified unimodal)	52.06	0.00	19.85	0.00	<b>0.00*</b>	<b>0.93*</b>	240.33	0.00	59.86	0.00
M3A (homogenous symmetric bimodal)	187.67	0.00	140.22	0.00	131.52	0.00	169.91	0.00	54.42	0.00
M3B (symmetric bimodal)	56.33	0.00	25.04	0.00	65.78	0.00	156.26	0.00	41.94	0.00
M4A (homogenous axial bimodal)	72.16	0.00	41.71	0.00	72.96	0.00	134.64	0.00	40.47	0.00
M4B (axial bimodal)	64.63	0.00	22.35	0.00	5.11	0.07	124.75	0.00	28.24	0.00
M5A (homogenous bimodal)	39.18	0.00	<b>0.00*</b>	<b>1.00*</b>	60.98	0.00	44.28	0.00	21.35	0.00
M5B (bimodal)	<b>0.00*</b>	<b>0.64*</b>	43.50	0.00	46.80	0.00	<b>0.00*</b>	<b>1.00*</b>	<b>0.00*</b>	<b>1.00*</b>

**Table S2.4.** Model selection results for Blackpoll Warblers from the 10 orientation models described by Schmutte and Groot (1992). The difference in Akaike Information Criterion relative to the best model ( $\Delta$ AIC) and the AIC model weights ( $w$ ) are shown. Models with  $\Delta$ AIC  $<$  2 are shown in **bold**, and the best model is indicated by an asterisk. See Table S2.3 for mean orientation of the best model.

Model	180821_03 (B6)		180821_04 (B7)		180823_03 (B8)		180823_04 (B9)		180827_01 (B10)	
	$\Delta$ AIC	$w$	$\Delta$ AIC	$w$	$\Delta$ AIC	$w$	$\Delta$ AIC	$w$	$\Delta$ AIC	$w$
M1 (uniform)	12.80	0.00	17.27	0.00	1002.83	0.00	485.95	0.00	150.13	0.00
M2A (unimodal)	<b>0.74</b>	<b>0.30</b>	<b>0.43</b>	<b>0.25</b>	<b>0.00*</b>	<b>1.00*</b>	35.92	0.00	43.58	0.00
M2B (symmetric modified unimodal)	2.00	0.16	<b>0.00*</b>	<b>0.31*</b>	92.38	0.00	138.56	0.00	61.40	0.00
M2C (modified unimodal)	35.56	0.00	<b>1.94</b>	<b>0.12</b>	16.73	0.00	76.21	0.00	51.84	0.00
M3A (homogenous symmetric bimodal)	13.56	0.00	18.96	0.00	883.02	0.00	474.47	0.00	145.90	0.00
M3B (symmetric bimodal)	4.02	0.06	2.00	0.12	111.75	0.00	149.29	0.00	63.56	0.00
M4A (homogenous axial bimodal)	6.42	0.02	<b>1.70</b>	<b>0.13</b>	317.64	0.00	306.72	0.00	81.85	0.00
M4B (axial bimodal)	5.46	0.03	11.97	0.00	503.10	0.00	180.57	0.00	56.85	0.00
M5A (homogenous bimodal)	<b>0.00*</b>	<b>0.43*</b>	3.34	0.06	259.24	0.00	<b>0.00*</b>	<b>0.74*</b>	26.45	0.00
M5B (bimodal)	16.14	0.00	10.92	0.00	425.59	0.00	2.12	0.26	<b>0.00*</b>	<b>1.00*</b>

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Model	180909_01 (B11)		180925_01 (B16)		180929_02 (B20)		180930_02 (B23)		180930_03 (B24)	
	$\Delta$ AIC	$w$	$\Delta$ AIC	$w$	$\Delta$ AIC	$w$	$\Delta$ AIC	$w$	$\Delta$ AIC	$w$
M1 (uniform)	98.23	0.00	233.49	0.00	197.23	0.00	1158.91	0.00	257.80	0.00
M2A (unimodal)	15.90	0.00	43.40	0.00	117.16	0.00	234.94	0.00	180.03	0.00
M2B (symmetric modified unimodal)	24.15	0.00	4.92	0.06	135.79	0.00	136.82	0.00	155.94	0.00
M2C (modified unimodal)	20.93	0.00	<b>0.00*</b>	<b>0.75*</b>	127.87	0.00	99.52	0.00	7.04	0.02
M3A (homogenous symmetric bimodal)	90.61	0.00	168.93	0.00	114.78	0.00	846.89	0.00	158.90	0.00
M3B (symmetric bimodal)	41.85	0.00	4.49	0.08	115.19	0.00	139.78	0.00	74.38	0.00
M4A (homogenous axial bimodal)	38.70	0.00	15.42	0.00	113.59	0.00	274.27	0.00	110.33	0.00
M4B (axial bimodal)	24.42	0.00	4.12	0.10	112.36	0.00	148.22	0.00	<b>0.00*</b>	<b>0.65*</b>
M5A (homogenous bimodal)	<b>1.99</b>	<b>0.27</b>	16.95	0.00	<b>1.14</b>	<b>0.36</b>	<b>0.00*</b>	<b>1.00*</b>	103.99	0.00
M5B (bimodal)	<b>0.00*</b>	<b>0.73*</b>	8.60	0.01	<b>0.00*</b>	<b>0.64*</b>	152.79	0.00	<b>1.33</b>	<b>0.33</b>

**Table S2.4 (cont.).** Model selection results for Blackpoll Warblers from the 10 orientation models described by Schnute and Groot (1992). The difference in Akaike Information Criterion relative to the best model ( $\Delta$ AIC) and the AIC model weights ( $w$ ) are shown. Models with  $\Delta$ AIC < 2 are shown in **bold**, and the best model is indicated by an asterisk. See Table S2.3 for mean orientation of the best model.

Model	181004_01 (B28)		181004_04 (B30)		181005_01 (B31)		181005_02 (B32)		181005_03 (B33)	
	$\Delta$ AIC	$w$	$\Delta$ AIC	$w$	$\Delta$ AIC	$w$	$\Delta$ AIC	$w$	$\Delta$ AIC	$w$
M1 (uniform)	199.18	0.00	258.17	0.00	271.13	0.00	222.46	0.00	56.91	0.00
M2A (unimodal)	75.49	0.00	75.49	0.00	142.13	0.00	<b>0.00*</b>	<b>0.68*</b>	13.84	0.00
M2B (symmetric modified unimodal)	63.26	0.00	76.61	0.00	58.55	0.00	12.15	0.00	11.95	0.00
M2C (modified unimodal)	24.00	0.00	36.10	0.00	21.11	0.00	3.87	0.10	11.64	0.00
M3A (homogenous symmetric bimodal)	123.03	0.00	229.12	0.00	107.94	0.00	216.39	0.00	42.43	0.00
M3B (symmetric bimodal)	40.98	0.00	78.63	0.00	28.54	0.00	17.49	0.00	6.64	0.03
M4A (homogenous axial bimodal)	50.51	0.00	98.68	0.00	5.50	0.04	47.37	0.00	4.32	0.10
M4B (axial bimodal)	26.28	0.00	37.33	0.00	2.66	0.17	24.17	0.00	16.37	0.00
M5A (homogenous bimodal)	<b>0.00*</b>	<b>0.73*</b>	47.36	0.00	3.04	0.14	2.22	0.22	<b>0.00*</b>	<b>0.86*</b>
M5B (bimodal)	<b>1.98</b>	<b>0.27</b>	<b>0.00*</b>	<b>1.00*</b>	<b>0.00*</b>	<b>0.65*</b>	12.79	0.00	98.70	0.00

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Model	181005_04 (B34)		181006_02 (B35)		181006_04 (B36)		181008_03 (B37)		181008_04 (B38)	
	$\Delta$ AIC	$w$	$\Delta$ AIC	$w$	$\Delta$ AIC	$w$	$\Delta$ AIC	$w$	$\Delta$ AIC	$w$
M1 (uniform)	575.08	0.00	26.62	0.00	177.47	0.00	39.11	0.00	43.72	0.00
M2A (unimodal)	34.70	0.00	<b>0.00*</b>	<b>0.33*</b>	93.25	0.00	3.54	0.11	<b>1.79</b>	<b>0.24</b>
M2B (symmetric modified unimodal)	141.83	0.00	<b>0.57</b>	<b>0.25</b>	87.06	0.00	9.27	0.01	4.09	0.08
M2C (modified unimodal)	70.83	0.00	<b>1.69</b>	<b>0.14</b>	67.98	0.00	7.73	0.01	4.57	0.06
M3A (homogenous symmetric bimodal)	571.57	0.00	26.96	0.00	76.57	0.00	39.96	0.00	44.37	0.00
M3B (symmetric bimodal)	152.89	0.00	2.58	0.09	22.61	0.00	11.72	0.00	6.22	0.03
M4A (homogenous axial bimodal)	230.47	0.00	6.17	0.02	26.50	0.00	18.75	0.00	11.53	0.00
M4B (axial bimodal)	197.52	0.00	3.91	0.05	23.66	0.00	30.87	0.00	18.80	0.00
M5A (homogenous bimodal)	3.67	0.14	3.01	0.07	<b>0.00*</b>	<b>1.00*</b>	<b>0.00*</b>	<b>0.63*</b>	<b>0.00*</b>	<b>0.59*</b>
M5B (bimodal)	<b>0.00*</b>	<b>0.86*</b>	4.24	0.04	15.67	0.00	1.92	0.24	14.39	0.00

**Table S2.4 (cont.).** Model selection results for Blackpoll Warblers from the 10 orientation models described by Schnute and Groot (1992). The difference in Akaike Information Criterion relative to the best model ( $\Delta$ AIC) and the AIC model weights ( $w$ ) are shown. Models with  $\Delta$ AIC < 2 are shown in **bold**, and the best model is indicated by an asterisk. See Table S2.3 for mean orientation of the best model.

Model	181009_01 (B39)		181009_02 (B40)		181009_03 (B41)		181010_03 (B43)		181010_04 (B44)	
	$\Delta$ AIC	$w$	$\Delta$ AIC	$w$	$\Delta$ AIC	$w$	$\Delta$ AIC	$w$	$\Delta$ AIC	$w$
M1 (uniform)	229.02	0.00	147.44	0.00	86.92	0.00	10.32	0.00	147.79	0.00
M2A (unimodal)	29.37	0.00	15.11	0.00	17.32	0.00	<b>0.00*</b>	<b>0.41*</b>	59.92	0.00
M2B (symmetric modified unimodal)	10.96	0.00	23.73	0.00	23.46	0.00	<b>0.58</b>	<b>0.31</b>	75.73	0.00
M2C (modified unimodal)	<b>0.00*</b>	<b>0.96*</b>	355.72	0.00	22.26	0.00	8.90	0.00	87.59	0.00
M3A (homogenous symmetric bimodal)	185.70	0.00	141.30	0.00	76.37	0.00	13.63	0.00	108.72	0.00
M3B (symmetric bimodal)	9.25	0.01	25.78	0.00	25.77	0.00	2.69	0.11	80.66	0.00
M4A (homogenous axial bimodal)	19.37	0.00	47.43	0.00	34.75	0.00	3.79	0.06	93.17	0.00
M4B (axial bimodal)	9.51	0.01	28.45	0.00	42.74	0.00	7.45	0.01	74.81	0.00
M5A (homogenous bimodal)	7.45	0.02	<b>1.33</b>	<b>0.34</b>	<b>0.00*</b>	<b>0.62*</b>	2.91	0.10	<b>0.00*</b>	<b>1.00*</b>
M5B (bimodal)	30.48	0.00	<b>0.00*</b>	<b>0.66*</b>	<b>0.96</b>	<b>0.38</b>	13.04	0.00	231.85	0.00

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Model	181013_02 (B46)		181013_03 (B47)		181013_04 (B48)		181014_02 (B50)		181014_03 (B51)	
	$\Delta$ AIC	$w$	$\Delta$ AIC	$w$	$\Delta$ AIC	$w$	$\Delta$ AIC	$w$	$\Delta$ AIC	$w$
M1 (uniform)	51.43	0.00	431.84	0.00	137.15	0.00	1825.46	0.00	12.94	0.00
M2A (unimodal)	4.96	0.06	98.50	0.00	15.58	0.00	31.76	0.00	8.53	0.01
M2B (symmetric modified unimodal)	2.77	0.17	86.56	0.00	15.66	0.00	182.29	0.00	8.63	0.01
M2C (modified unimodal)	21.07	0.00	27.33	0.00	17.09	0.00	<b>0.00*</b>	<b>1.00*</b>	19.36	0.00
M3A (homogenous symmetric bimodal)	49.71	0.00	328.96	0.00	125.01	0.00	1258.45	0.00	8.06	0.01
M3B (symmetric bimodal)	4.59	0.07	83.25	0.00	17.67	0.00	295.01	0.00	6.54	0.03
M4A (homogenous axial bimodal)	8.56	0.01	116.47	0.00	36.83	0.00	560.80	0.00	5.33	0.05
M4B (axial bimodal)	5.82	0.04	38.35	0.00	30.23	0.00	183.11	0.00	7.24	0.02
M5A (homogenous bimodal)	10.53	0.00	<b>0.00*</b>	<b>1.00*</b>	38.80	0.00	792.84	0.00	2.91	0.17
M5B (bimodal)	<b>0.00*</b>	<b>0.66*</b>	64.30	0.00	<b>0.00*</b>	<b>1.00*</b>	73.24	0.00	<b>0.00*</b>	<b>0.71*</b>

**Table S2.4 (cont.).** Model selection results for Blackpoll Warblers from the 10 orientation models described by Schnute and Groot (1992). The difference in Akaike Information Criterion relative to the best model ( $\Delta$ AIC) and the AIC model weights ( $w$ ) are shown. Models with  $\Delta$ AIC < 2 are shown in **bold**, and the best model is indicated by an asterisk. See Table S2.3 for mean orientation of the best model.

Model	181014_04 (B52)		190822_04 (B61)		190826_01 (B67)		190826_03 (B69)		190913_04 (B71)	
	$\Delta$ AIC	$w$	$\Delta$ AIC	$w$	$\Delta$ AIC	$w$	$\Delta$ AIC	$w$	$\Delta$ AIC	$w$
M1 (uniform)	2.12	0.10	40.62	0.00	592.57	0.00	738.96	0.00	127.55	0.00
M2A (unimodal)	<b>0.00*</b>	<b>0.29*</b>	<b>0.00*</b>	<b>0.36*</b>	21.54	0.00	145.04	0.00	4.22	0.09
M2B (symmetric modified unimodal)	<b>0.32</b>	<b>0.25</b>	<b>0.35</b>	<b>0.30</b>	88.53	0.00	10.14	0.01	5.66	0.05
M2C (modified unimodal)	9.53	0.00	32.97	0.00	38.49	0.00	<b>0.00*</b>	<b>0.99*</b>	5.64	0.05
M3A (homogenous symmetric bimodal)	4.94	0.02	42.30	0.00	588.25	0.00	476.64	0.00	117.70	0.00
M3B (symmetric bimodal)	2.45	0.08	2.36	0.11	150.83	0.00	27.72	0.00	8.06	0.01
M4A (homogenous axial bimodal)	2.76	0.07	4.59	0.04	163.19	0.00	127.41	0.00	18.44	0.00
M4B (axial bimodal)	4.31	0.03	47.61	0.00	65.50	0.00	15.00	0.00	7.58	0.02
M5A (homogenous bimodal)	2.73	0.07	<b>1.16</b>	<b>0.20</b>	27.93	0.00	85.86	0.00	<b>0.00*</b>	<b>0.78*</b>
M5B (bimodal)	2.73	0.07	14.00	0.00	<b>0.00*</b>	<b>1.00*</b>	50.90	0.00	39.05	0.00

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Model	190916_03 (B73)		190926_01 (B76)		190926_02 (B77)		190929_03 (B78)		190930_02 (B80)	
	$\Delta$ AIC	$w$	$\Delta$ AIC	$w$	$\Delta$ AIC	$w$	$\Delta$ AIC	$w$	$\Delta$ AIC	$w$
M1 (uniform)	102.98	0.00	181.62	0.00	73.79	0.00	232.69	0.00	153.86	0.00
M2A (unimodal)	<b>0.00*</b>	<b>0.54*</b>	4.39	0.10	<b>0.00*</b>	<b>0.75*</b>	51.52	0.00	2.18	0.22
M2B (symmetric modified unimodal)	2.71	0.14	16.21	0.00	7.09	0.02	81.87	0.00	5.43	0.04
M2C (modified unimodal)	2.41	0.16	<b>0.00*</b>	<b>0.86*</b>	2.42	0.22	65.91	0.00	4.55	0.07
M3A (homogenous symmetric bimodal)	102.34	0.00	117.53	0.00	67.63	0.00	207.78	0.00	147.40	0.00
M3B (symmetric bimodal)	5.77	0.03	20.81	0.00	9.90	0.01	86.78	0.00	8.87	0.01
M4A (homogenous axial bimodal)	16.68	0.00	33.31	0.00	37.09	0.00	119.44	0.00	25.19	0.00
M4B (axial bimodal)	9.06	0.01	31.70	0.00	11.14	0.00	111.43	0.00	8.75	0.01
M5A (homogenous bimodal)	3.15	0.11	18.69	0.00	16.59	0.00	<b>0.00*</b>	<b>1.00*</b>	<b>0.00*</b>	<b>0.65*</b>
M5B (bimodal)	8.47	0.01	5.79	0.05	13.01	0.00	42.12	0.00	173.30	0.00

**Table S2.4 (cont.).** Model selection results for Blackpoll Warblers from the 10 orientation models described by Schnute and Groot (1992). The difference in Akaike Information Criterion relative to the best model ( $\Delta$ AIC) and the AIC model weights ( $w$ ) are shown. Models with  $\Delta$ AIC < 2 are shown in **bold**, and the best model is indicated by an asterisk. See Table S2.3 for mean orientation of the best model.

Model	191003_02 (B81)		191015_02 (B82)		191015_03 (B83)		191015_04 (B84)		191018_02 (B85)	
	$\Delta$ AIC	$w$	$\Delta$ AIC	$w$	$\Delta$ AIC	$w$	$\Delta$ AIC	$w$	$\Delta$ AIC	$w$
M1 (uniform)	1361.29	0.00	7.02	0.01	8.91	0.00	131.30	0.00	549.85	0.00
M2A (unimodal)	<b>0.00*</b>	<b>1.00*</b>	<b>0.25</b>	<b>0.28</b>	<b>0.00*</b>	<b>0.32*</b>	11.53	0.00	184.07	0.00
M2B (symmetric modified unimodal)	182.18	0.00	<b>0.00*</b>	<b>0.32*</b>	<b>0.19</b>	<b>0.29</b>	9.82	0.01	<b>0.00*</b>	<b>0.70*</b>
M2C (modified unimodal)	51.30	0.00	2.04	0.11	<b>1.90</b>	<b>0.12</b>	<b>0.00*</b>	<b>0.83*</b>	<b>1.89</b>	<b>0.27</b>
M3A (homogenous symmetric bimodal)	1276.19	0.00	9.89	0.00	12.29	0.00	88.32	0.00	387.98	0.00
M3B (symmetric bimodal)	211.22	0.00	2.00	0.12	2.22	0.11	16.74	0.00	6.06	0.03
M4A (homogenous axial bimodal)	416.89	0.00	3.39	0.06	3.28	0.06	22.79	0.00	370.24	0.00
M4B (axial bimodal)	209.42	0.00	4.00	0.04	3.89	0.05	3.26	0.16	49.13	0.00
M5A (homogenous bimodal)	644.77	0.00	3.99	0.04	4.80	0.03	12.39	0.00	107.79	0.00
M5B (bimodal)	118.11	0.00	5.85	0.02	6.35	0.01	12.72	0.00	242.96	0.00

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Model	191019_02 (B87)		191019_03 (B88)		191019_04 (B89)		191020_02 (B90)		191020_04 (B91)	
	$\Delta$ AIC	$w$	$\Delta$ AIC	$w$	$\Delta$ AIC	$w$	$\Delta$ AIC	$w$	$\Delta$ AIC	$w$
M1 (uniform)	193.02	0.00	1649.16	0.00	109.12	0.00	504.78	0.00	414.44	0.00
M2A (unimodal)	50.37	0.00	<b>0.00*</b>	<b>0.84*</b>	13.70	0.00	251.68	0.00	9.24	0.01
M2B (symmetric modified unimodal)	56.93	0.00	348.51	0.00	17.83	0.00	184.82	0.00	6.65	0.03
M2C (modified unimodal)	54.80	0.00	75.65	0.00	16.80	0.00	20.24	0.00	39.89	0.00
M3A (homogenous symmetric bimodal)	152.18	0.00	1400.32	0.00	95.13	0.00	222.34	0.00	327.48	0.00
M3B (symmetric bimodal)	58.99	0.00	361.72	0.00	19.86	0.00	38.66	0.00	19.80	0.00
M4A (homogenous axial bimodal)	64.27	0.00	465.88	0.00	32.99	0.00	26.41	0.00	89.46	0.00
M4B (axial bimodal)	59.12	0.00	280.03	0.00	22.36	0.00	28.32	0.00	<b>0.00*</b>	<b>0.96*</b>
M5A (homogenous bimodal)	187.74	0.00	3.36	0.16	25.05	0.00	<b>0.00*</b>	<b>1.00*</b>	23.26	0.00
M5B (bimodal)	<b>0.00*</b>	<b>1.00*</b>	408.83	0.00	<b>0.00*</b>	<b>1.00*</b>	233.32	0.00	22.52	0.00

**Table S2.4 (cont.).** Model selection results for Blackpoll Warblers from the 10 orientation models described by Schnute and Groot (1992). The difference in Akaike Information Criterion relative to the best model ( $\Delta$ AIC) and the AIC model weights ( $w$ ) are shown. Models with  $\Delta$ AIC < 2 are shown in **bold**, and the best model is indicated by an asterisk. See Table S2.3 for mean orientation of the best model.

Model	191003_02 (B81)		191015_02 (B82)		191015_03 (B83)		191015_04 (B84)		191018_02 (B85)	
	$\Delta$ AIC	$w$	$\Delta$ AIC	$w$	$\Delta$ AIC	$w$	$\Delta$ AIC	$w$	$\Delta$ AIC	$w$
M1 (uniform)	1361.29	0.00	7.02	0.01	8.91	0.00	131.30	0.00	549.85	0.00
M2A (unimodal)	<b>0.00*</b>	<b>1.00*</b>	<b>0.25</b>	<b>0.28</b>	<b>0.00*</b>	<b>0.32*</b>	11.53	0.00	184.07	0.00
M2B (symmetric modified unimodal)	182.18	0.00	<b>0.00*</b>	<b>0.32*</b>	<b>0.19</b>	<b>0.29</b>	9.82	0.01	<b>0.00*</b>	<b>0.70*</b>
M2C (modified unimodal)	51.30	0.00	2.04	0.11	<b>1.90</b>	<b>0.12</b>	<b>0.00*</b>	<b>0.83*</b>	<b>1.89</b>	<b>0.27</b>
M3A (homogenous symmetric bimodal)	1276.19	0.00	9.89	0.00	12.29	0.00	88.32	0.00	387.98	0.00
M3B (symmetric bimodal)	211.22	0.00	2.00	0.12	2.22	0.11	16.74	0.00	6.06	0.03
M4A (homogenous axial bimodal)	416.89	0.00	3.39	0.06	3.28	0.06	22.79	0.00	370.24	0.00
M4B (axial bimodal)	209.42	0.00	4.00	0.04	3.89	0.05	3.26	0.16	49.13	0.00
M5A (homogenous bimodal)	644.77	0.00	3.99	0.04	4.80	0.03	12.39	0.00	107.79	0.00
M5B (bimodal)	118.11	0.00	5.85	0.02	6.35	0.01	12.72	0.00	242.96	0.00

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Model	191019_02 (B87)		191019_03 (B88)		191019_04 (B89)		191020_02 (B90)		191020_04 (B91)	
	$\Delta$ AIC	$w$	$\Delta$ AIC	$w$	$\Delta$ AIC	$w$	$\Delta$ AIC	$w$	$\Delta$ AIC	$w$
M1 (uniform)	193.02	0.00	1649.16	0.00	109.12	0.00	504.78	0.00	414.44	0.00
M2A (unimodal)	50.37	0.00	<b>0.00*</b>	<b>0.84*</b>	13.70	0.00	251.68	0.00	9.24	0.01
M2B (symmetric modified unimodal)	56.93	0.00	348.51	0.00	17.83	0.00	184.82	0.00	6.65	0.03
M2C (modified unimodal)	54.80	0.00	75.65	0.00	16.80	0.00	20.24	0.00	39.89	0.00
M3A (homogenous symmetric bimodal)	152.18	0.00	1400.32	0.00	95.13	0.00	222.34	0.00	327.48	0.00
M3B (symmetric bimodal)	58.99	0.00	361.72	0.00	19.86	0.00	38.66	0.00	19.80	0.00
M4A (homogenous axial bimodal)	64.27	0.00	465.88	0.00	32.99	0.00	26.41	0.00	89.46	0.00
M4B (axial bimodal)	59.12	0.00	280.03	0.00	22.36	0.00	28.32	0.00	<b>0.00*</b>	<b>0.96*</b>
M5A (homogenous bimodal)	187.74	0.00	3.36	0.16	25.05	0.00	<b>0.00*</b>	<b>1.00*</b>	23.26	0.00
M5B (bimodal)	<b>0.00*</b>	<b>1.00*</b>	408.83	0.00	<b>0.00*</b>	<b>1.00*</b>	233.32	0.00	22.52	0.00

## References

- Able, K. P. (1977). The orientation of passerine nocturnal migrants following offshore drift. *The Auk*, *94*(2), 320–330.
- Agostinelli, C., & Lund, U. (2017). R package ‘circular’: Circular statistics. <https://r-forge.r-project.org/projects/circular/>
- Alerstam, T. (1982). *Figelflyttning*. Signum.
- Baker, K. (1977). Westward vagrancy of Siberian passerines in autumn 1975. *Bird Study*, *24*(4), 233–242.
- Baker, R. R. (1978). *The evolutionary ecology of animal migration*. Holmes; Meier Publishers.
- Baker, R. R. (1980). The significance of the Lesser Black-backed Gull to models of bird migration. *Bird Study*, *27*(1), 41–50.
- Baker, R. R. (1993). The function of post-fledging exploration: A pilot study of three species of passerines ringed in Britain. *Ornis Scandinavica*, *24*, 71–79.
- Batschelet, E. (1981). *Circular statistics in biology*. Academic Press.
- Bowen, G. J., Wassenaar, L. I., & Hobson, K. A. (2005). Global application of stable hydrogen and oxygen isotopes to wildlife forensics. *Oecologia*, *143*, 337–348.
- Brown, J. M., & Taylor, P. D. (2015). Adult and hatch-year blackpoll warblers exhibit radically different regional-scale movements during post-fledging dispersal. *Biology Letters*, *11*, 20150593.
- Burnham, K. P., & Anderson, D. R. (2003). *Model selection and multimodel inference: A practical information-theoretic approach* (Second). Springer-Verlag.
- Clarke, W. E. (1912). *Studies in bird migration*. Gurney; Jackson.
- Cottridge, D., & Vinicombe, K. (1996). *Rare birds in Britain and Ireland - a photographic record*. Harper Collins.
- Crewe, T. L., Crysler, Z., & Taylor, P. (2020). Motus R book: A walk through the use of R for motus automated radio-telemetry data. <https://beta.motus.org/MotusRBook/>

- Deluca, W. V., Woodworth, B. K., Rimmer, C. C., Marra, P. P., Taylor, P. D., McFarland, K. P., Mackenzie, S. A., & Norris, D. R. (2015). Transoceanic migration by a 12 g songbird. *Biology Letters*, *11*(4), 20141045.
- DeSante, D. F. (1973). *An analysis of the fall occurrences and nocturnal orientations of vagrant wood warblers (Parulidae) in California* (Doctoral dissertation). Stanford University. Stanford, California.
- DeSante, D. F. (1983a). Annual variability in the abundance of migrant landbirds on Southeast Farallon Island, California. *The Auk*, *100*(4), 826–852.
- DeSante, D. F. (1983b). Vagrants: when orientation or navigation goes wrong. *Point Reyes Bird Observatory Newsletter*, *61*, 12–16.
- Elkins, N. (1979). Nearctic landbirds in Britain and Ireland: A meteorological analysis. *British Birds*, *72*(9), 417–433.
- Elkins, N. (2005). Weather and bird migration. *British Birds*, *98*, 238–256.
- Elkins, N. (2008). Further thoughts on transatlantic vagrancy of landbirds to Britain & Ireland. *British Birds*, *101*, 458–477.
- Emlen, S. T., & Emlen, J. T. (1966). A technique for recording migratory orientation of captive birds. *The Auk*, *83*, 361–367.
- Fitak, R. R., & Johnsen, S. (2017). Bringing the analysis of animal orientation data full circle: Model-based approaches with maximum likelihood. *Journal of Experimental Biology*, *220*(Pt 21), 3878–3882.
- Fitzgerald, T. M., & Taylor, P. D. (2008). Migratory orientation of juvenile yellow-rumped warblers (*Dendroica coronata*) following stopover: Sources of variation and the importance of geographic origins. *Behavioral Ecology and Sociobiology*, *62*(9), 1499–1508.
- Grinnell, J. (1922). The role of the “accidental”. *The Auk*, *39*(3), 373–380.
- Harmer, A., & Thomas, D. (2020). pathtrackr: Video tracking and analysis of animal movement. R package version 1.2.3.
- Hobson, K. A. (1999). Tracing origins and migration of wildlife using stable isotopes: A review. *Oecologia*, *120*, 314–326.
- Hobson, K. A., Bowen, G. J., Wassenaar, L. I., Ferrand, Y., & Lormee, H. (2004). Using stable hydrogen and oxygen isotope measurements of feathers to infer geographical origins of migrating European birds. *Oecologia*, *141*, 477–488.
- Kramer, G. (1949). Über Richtungstendenzen bei der nächtlichen Zugunruhe gekäfigter Vögel. *Ornithologie als biologische Wissenschaft* (pp. 269–283).

- Matthysen, E. (2012). Multicausality of dispersal: A review. In M. Baguette, T. G. Benton, & J. M. Bullock (Eds.), *Dispersal ecology and evolution* (pp. 3–18). Oxford University Press.
- McLaren, I. A. (1981). The incidence of vagrant landbirds on Nova Scotian islands. *The Auk*, *98*(2), 243–257.
- McLaren, I. A., Lees, A. C., Field, C., & Collins, K. J. (2006). Origins and characteristics of Nearctic landbirds in Britain and Ireland in autumn: A statistical analysis. *Ibis*, *148*(4), 1–20.
- Moore, F. R. (1984). Age-dependent variability in the migratory orientation of the Savannah Sparrow (*Passerculus sandwichensis*). *The Auk*, *101*, 875–880.
- Phillips, J. (2000). Autumn vagrancy: “reverse migration” and migratory orientation. *Ringing & Migration*, *20*, 35–38.
- R Core Team. (2019). R: A language and environment for statistical computing. <https://www.R-project.org/>.
- Rabøl, J. (1969). Reversed migration as a cause of westward vagrancy by four Phylloscopus warblers. *British Birds*, *62*(3), 89–92.
- Ralph, C. J. (1978). Disorientation and possible fate of young passerine coastal migrants. *Bird-banding*, *49*(3), 237–247.
- Reilly, J. R., & Reilly, R. J. (2009). Bet-hedging and the orientation of juvenile passerines in fall migration. *Journal of Animal Ecology*, *78*, 990–1001.
- Sandberg, R., Ottoson, U., & Pettersson, J. (1991). Magnetic orientation of migratory wheatears (*Oenanthe oenanthe*) in Sweden and Greenland. *Journal of Experimental Biology*, *155*, 51–64.
- Schnute, J. T., & Groot, K. (1992). Statistical analysis of animal orientation data. *Animal Behaviour*, *43*(1), 15–33.
- Smetzer, J. R., King, D. I., & Taylor, P. D. (2017). Fall migratory departure decision and routes of blackpoll warblers *Setophaga striata* and red-eyed vireos *Vireo olivaceus* at a coastal barrier in the gulf of maine. *Journal of Avian Biology*, *48*(11), 1451–1461.
- Taylor, P. D., Brzustowski, J. M., Matkovich, C., Peckford, M. L., & Wilson, D. (2010). radR: An open-source platform for acquiring and analysing data on biological targets observed by surveillance radar. *BMC Ecology*, *10*(22).
- Taylor, P. D., Crewe, T. L., Mackenzie, S. A., Lepage, D., Aubry, Y., Crysler, Z., Finney, G., Francis, C. M., Guglielmo, C. G., Hamilton, D. J., Holberton, R. L., Loring, P. H., Mitchell, G. W., Norris, D., Paquet, J., Ronconi, R. A., Smetzer, J., Smith, P. A., Welch, L. J., & Woodworth, B. K. (2017). The Motus Wildlife Tracking System: A collaborative research network to enhance the understanding of wildlife movement. *Avian Conservation and Ecology*, *12*(1).

- Thorup, K. (1998). Vagrancy of yellow-browed warbler *Phylloscopus inornatus* and pallas's warbler *Ph. proregulus* in north-west Europe: misorientation on great circles? *Ringing and Migration*, 19(1), 7–12.
- Thorup, K. (2004). Reverse migration as a cause of vagrancy. *Bird Study*, 51(3), 228–238.
- Thorup, K., Ortvad, T. E., Holland, R. A., Rabøl, J., Kristensen, M. W., & Wikelski, M. (2012). Orientation of vagrant birds on the Faroe Islands in the Atlantic Ocean. *Journal of Ornithology*, 153(4), 1261–1265.
- Thorup, K., Ortvad, T. E., Rabøl, J., Holland, R. A., Tøttrup, A. P., & Wikelski, M. (2011). Juvenile songbirds compensate for displacement to oceanic islands during autumn migration. *PLoS One*, 6(3), 17903.
- Toews, D. P. L., Delmore, K. E., Osmond, M. M., Taylor, P. D., & Irwin, D. E. (2017). Migratory orientation in a narrow avian hybrid zone. *PeerJ*, 5, 3201.
- Veit, R. R. (2008). Why expect clusters of vagrants? *Bird Observer*, 36(4), 213–217.
- Williamson, K. (1959). The September drift-movements of 1956 and 1958. *British Birds*, 52, 334–377.
- Wiltschko, W., & Wiltschko, R. (1972). Magnetic compass of European robins. *Science*, 176, 62–64.

# 3

## Determining natal origin of vagrants with stable isotope analysis: an exploratory study

### Contents

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### **3.1 Abstract**

Vagrancy remains poorly understood, and few techniques exist to effectively study vagrancy in the field. We tested whether stable isotope analysis would be a suitable method to determine the natal origin of vagrants. Vagrants were captured on two islands off the southwest coast of Nova Scotia during autumn migration in 2018 and 2019. Feather samples (rectrix R2) were collected for 29 individual vagrants from 15 different species. The ratio of stable-hydrogen isotope (deuterium;  $\delta^2H$ ) was measured from each feather, and assigned to a calibrated isoscape of amount-weighted growing-season  $\delta^2H$  in precipitation in North America. Samples were assigned using likelihood-based assignment methods with Bayesian inversion. We found that the majority of vagrants ( $n = 21$ , 75.0% of the 28 samples analysed) had a high probability of originating from the edge of their range, while the remaining vagrants were assigned origins somewhere within the centre of their range. This is likely due to increased propensity for dispersal and exploratory behaviour for individuals located at a range edge. Our results show that stable isotope analysis is an effective method to determine natal origin of vagrants in North America, and this technique should be used in future studies to elucidate the origin of vagrants.

### **3.2 Introduction**

Vagrancy, long-distance dispersal movement in which individuals travel far outside of their known species' range (Grinnell 1922), has garnered much attention in avian taxa due to repeated occurrence of this behaviour across years and species (e.g. Patten and Marantz 1996, White and Kehoe 2014, Zawadzki et al. 2019). Sightings of vagrants bring up many unanswered questions in regards to how and why vagrants appear in the locations they are discovered, as well as speculations of their origin. However, the overall rarity of cases has made it difficult to study vagrancy directly using conventional techniques, such as mark-recapture or GPS-tracking (predominantly for larger species). Vagrancy

thus remains poorly understood, though insights could provide important context to the migration ecology of species and conservation efforts.

Stable isotope analysis, a technique that has been used over the past three decades to determine geographic origin of migratory birds, as well as migratory connectivity, (see reviews by Hobson 1999, 2003, 2005a, 2005b; Rubenstein and Hobson 2004), may be the best technique to help elucidate origin of vagrants. Stable isotope analysis is unique in that, unlike mark-recapture or current GPS-tracking methodologies, it does not require recapture of the individual, but rather the single capture of an individual to infer breeding origin. For vagrants, this technique is ideal since vagrants are likely to never be captured again, and individuals are often too small for tracking devices. While this does require intensive mist-netting at locations where vagrants are known to occur, feather collection for analysis can easily coincide with seasonal mist-netting efforts at operational bird banding stations and bird observatories. A large number of bird observatories are set up along flyways and/or coastal regions, areas which are historically known to have large numbers of vagrants during autumn migration (Ralph 1978; DeSante 1983a, 1983b; McLaren 1981).

Use of stable isotope analysis in migratory studies is possible due to the discovery of a strong correlation between well-known and predictable patterns in amount-weighted growing-season stable-hydrogen isotope ratios in precipitation (deuterium; hereafter " $\delta^2H$ " for deuterium, and " $\delta^2H_p$ " for deuterium in precipitation) across North America (Bowen et al. 2005), and stable-hydrogen isotopes in feathers (hereafter  $\delta^2H_f$ ) (Chamberlain et al. 1997, Hobson and Wassenaar 1997). Since feathers are metabolically inert, they retain an isotopic signature of  $\delta^2H$  for the geographic location in which they were formed, which can later be related to  $\delta^2H_p$  isoscapes to assess the origin where these tissues were grown. For many migrant songbirds, feathers are grown on or close to the breeding grounds prior to migration, so feathers collected on autumn migration can be used to trace breeding origin.

Analysing  $\delta^2H_f$  also has many other advantages over other techniques. It is inexpensive, has quick processing times, and is not taxon or species specific (Hobson and Norris 2008). However,  $\delta^2H_p$  isoscapes have poor longitudinal resolution.  $\delta^2H_p$  isoscapes show strong latitudinal gradients with decreasing  $\delta^2H_p$  values across North America, from the southeast to the northwest (Bowen et al. 2005). Inference of breeding origin is thus much better suited for species with narrow longitudinal distributions (e.g. Kelly et al. 2002, Rubenstein et al. 2002, Hobson et al. 2004a).

In this study, we used stable isotope analysis of  $\delta^2H$  to determine the natal origin of vagrant songbird species in North America. This serves as an exploratory study to determine the suitability of this technique in ascertaining natal origin of young vagrants caught during autumn migration, and whether stable isotope analysis should be explored further in future studies. Only two studies to date have attempted to discern natal origin of vagrants with stable isotope analysis of  $\delta^2H_f$  (Fox et al. 2007, De Jong et al. 2019). Fox et al. (2007) used stable isotope analysis to determine if an immature Baikal Teal (*Anas formosa*) in Denmark was an escaped cage bird or a genuine vagrant. They found that the bird grew its feathers in locations consistent with the range of the Baikal Teal, concluding that it was a wild bird. De Jong et al. (2019) later used  $\delta^2H_f$  of tail feathers of vagrant Yellow-browed Warblers (*Phylloscopus inornatus*) captured in Fennoscandia to try and link vagrants with their natal sites in Central Siberia. While they were able to detect areas of high probability across the breeding range with this technique, they could not resolve a precise region of origin due to the Yellow-browed Warbler's wide longitudinal breeding distribution across eastern Europe. The majority of North American songbirds that occur as vagrants in North America, however, have relatively narrow longitudinal distributions (i.e.  $\leq$  the width of half of North America along the east-west axis), so natal origin may be able to be assigned with greater precision with this technique. Further, relationships between  $\delta^2H_p$  and  $\delta^2H_f$  are much stronger in North America. Hobson et al. (2004) found that the relationship between  $\delta^2H_p$  and  $\delta^2H_f$  was weaker in Europe ( $r^2 = 0.66$ ), while Hobson and Wassenaar (1997) and Hobson et al. (2012) found a much stronger relationship in North America ( $r^2 = 0.91$  and  $r^2 = 0.83$ , respectively). Stable isotope analysis may prove to be remarkably useful for determining natal origin of vagrants in

North America, which will vastly improve our ability to study vagrancy in the field and answer questions pertaining to vagrant movements and migratory ecology.

### **3.3 Methods**

#### **3.3.1 Study site and species**

Our study was carried out on two islands off the southwest coast of Nova Scotia, Canada (see Figure 2.1), collectively the Atlantic Bird Observatory (ABO), during autumn migration in 2018 and 2019. 155 days were spent on Bon Portage Island (hereafter “BP”; 43°47’ N, 65°75’ W) and 9 days were spent on Seal Island (43°41’ N, 66°01’ W). Both islands are relatively small ( $\sim 3.00 \text{ km}^2$ ) and low-lying (maximum elevation of  $\sim 15 \text{ m}$  above sea level), and are part of the Atlantic Maritime ecozone, consisting of inland coniferous forests (mainly spruce and fir), and marshland. We chose this location for our study since these islands are known for their high occurrence of vagrants during autumn migration (McLaren 1981). Vagrants are species that are not known to breed, winter, or migrate through a particular region, and are commonly hatch-year birds on their first autumn migration (DeSante 1973).

Both vagrants and Blackpoll Warblers (*Setophaga striata*; hereafter “blackpolls”) were captured for this study. Blackpolls are a non-vagrant species in Nova Scotia that are known to breed on within our study area. They were selected as a control species to assess the validity of our stable isotope analysis. Only hatch-year birds (i.e. recently fledged individuals) were included in this study.

#### **3.3.2 Sampling methods**

In order to collect feather samples, vagrants and blackpolls were captured in mist-nets (see Figure 2.2) that were operational for a total of six hours per day on BP and Seal Island. Captured birds were banded with Canadian Bird Banding Office (BBO) aluminium leg

bands, and morphometric measurements (wing chord, fat score, body mass, tail length, tarsus, bill from nares to tip, head length and width, and body length from base of tail to tip of bill) were taken following methods in Pyle (1997). After banding, one outer tail feather (rectrix R2) was collected from each individual. The shape of the feather was checked to ensure that only hatch-year feathers (i.e. those grown on the nest) were collected (Pyle 1997). Feathers were stored dry at room temperature. We collected 86 blackpoll feathers, and 29 feathers from 15 different species of vagrants (though a feather from one vagrant failed to be processed during stable isotope analysis). Photographs of each individual were taken after processing, and hatch-year vagrants were moved to orientation cages for orientation testing (see Chapter 2 for orientation experiments). Any by-catch were banded and processed in accordance with BBO standards.

### **3.3.3 Stable isotope analysis**

Stable isotope analysis was conducted at the Laboratory for Stable Isotope Science (LSIS) at the University of Western Ontario. Feathers were cleaned in a 2:1 chloroform/methanol solvent to remove surface oils. Samples of feather vane weighing  $0.35 \pm 0.01$  mg were cut from each feather and placed in silver capsules.

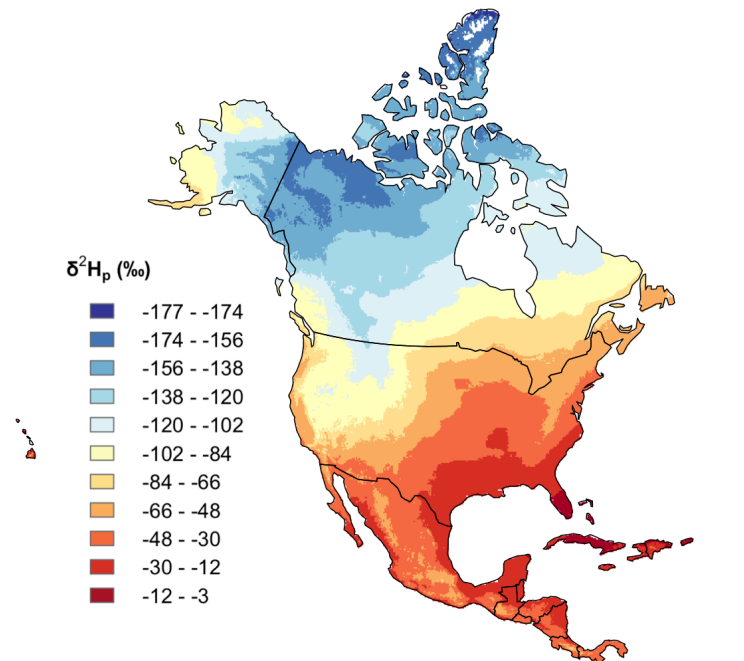
Samples were processed using a comparative equilibrium approach described by Wassenaar and Hobson (2003) to account for the isotopic exchange that occurs between hydrogen atoms in the sample and hydrogen atoms in ambient water vapour (Wassenaar 2008). For this approach, both samples and working standards are air equilibrated with lab air moisture prior to analysis, and then analysed together in a single session. The two working standards used in our analysis were KHS (Kudu Horn Standard) and CBS (Caribou Hoof Standard), with mean  $\delta^2H \pm$  SD values of  $-54.1 \pm 0.83\text{‰}$  ( $n = 7$ ) and  $-197.0 \pm 0.95\text{‰}$  ( $n = 7$ ) respectively. Samples and working standards were left to air equilibrate with ambient lab moisture at room temperature for a minimum of five days prior to analysis.

Stable isotope ratios were measured using a Thermo Electron DELTA V Plus CF-IRMS coupled with a Thermo Scientific TC-EA Elemental Analyser. Capsules were loaded into an auto sampler, and working standards and feather samples were pyrolysed to a single pulse of  $H_2$  gas with the TC-EA elemental analyser. The pyrolysis column consisted of a newly packed chromium reactor held at  $1120^\circ\text{C}$  with a column flow rate of 100 ml/min, followed by a molecular sieve GC oven at  $90^\circ\text{C}$  to resolve the sample  $H_2$  from  $N_2$  and CO produced during pyrolysis. The  $H_2$  gas was introduced to the isotope ratio mass spectrometer (Thermo Electron DELTA V Plus CF-IRMS), and the ratio of isotopic hydrogen was measured. Standards were analysed in triplicate at the beginning of every autorun, and then once every 10 samples to build a calibration curve for the correction formula. An internal keratin standard was also analysed to correct for drift in the  $\delta^2H$  of lab moisture during the analytical session.

A correction formula was derived from least squares regression between the uncorrected isotope values of the working standards and the Vienna Standard Mean Ocean Water – Standard Light Antarctic Precipitation (VSMOW-SLAP) standard scale. This correction formula was applied to both the standards and the unknown feather samples to obtain isotopic ratios for non-exchangeable  $\delta^2H$ . All measurements are reported for non-exchangeable  $\delta^2H$  in units of per mil (‰) relative to the VSMOW-SLAP standard scale.

### 3.3.4 Assigning natal origin

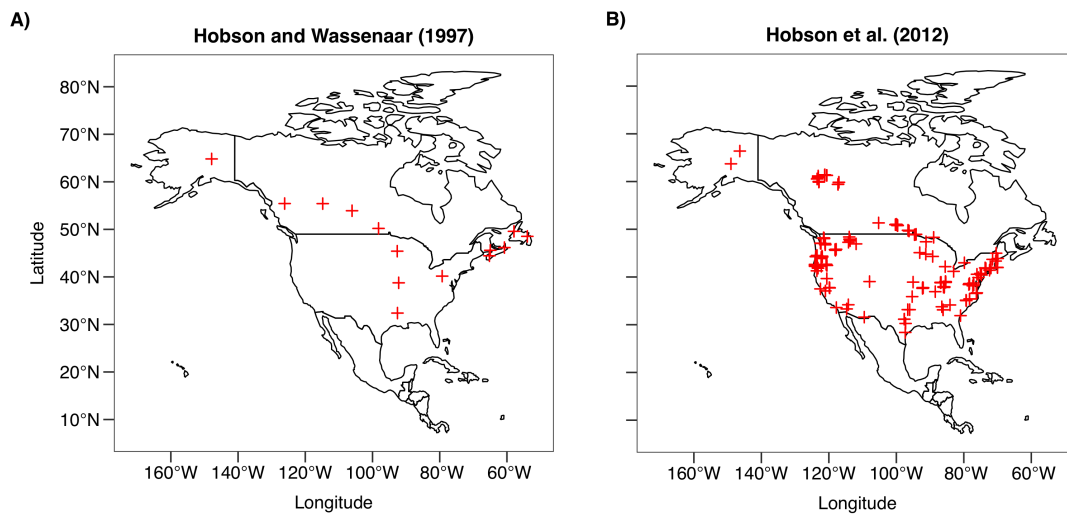
We assigned natal origin of vagrants based on likelihood-based assignment methods with Bayesian inversion as described by Wunder (2010). Methods were carried out using the ‘assignR’ package (Ma et al. 2020) in R (R Core Team 2020). To do this, we first had to calibrate our assignment isoscape by relating  $\delta^2H_f$  of known-origin samples to the isoscape of amount-weighted mean growing-season  $\delta^2H_p$  (Figure 3.1; Bowen et al. 2005). Known-origin samples were taken from Hobson and Wassenaar (1997) and Hobson et al. (2012). We decided to include samples from both studies because, while Hobson et al. (2012) covers the majority of North America (Figure 3.2b), there are



**Figure 3.1.** Isoscape of amount-weighted mean growing-season  $\delta^2H_p$  across North America, adapted from data in Bowen et al. (2005).

sampling gaps in Nova Scotia and Newfoundland that Hobson and Wassenaar (1997) fill (Figure 3.2a). To create as accurate an isoscape as possible for our study, only known-origin samples from Neotropical migrants were used for calibration since our captured vagrants are Neotropical migrants. Known-origin feather values were regressed against predicted growing-season  $\delta^2H_p$  from Bowen et al. (2005), and the resulting linear equation ( $\delta^2H_f = -27.47 + 0.85\delta^2H_p$ ) was applied to the  $\delta^2H_p$  isoscape to produce a calibrated  $\delta^2H_f$  isoscape (Figure 3.3). We tested the validity of our calibrated isoscape by assigning natal origin of blackpoll feather samples collected during the study period, using the *unionP* function in the ‘assignR’ package in R (Ma et al. 2020). If the calibrated isoscape was accurate, natal origin of our samples should be assigned to Nova Scotia.

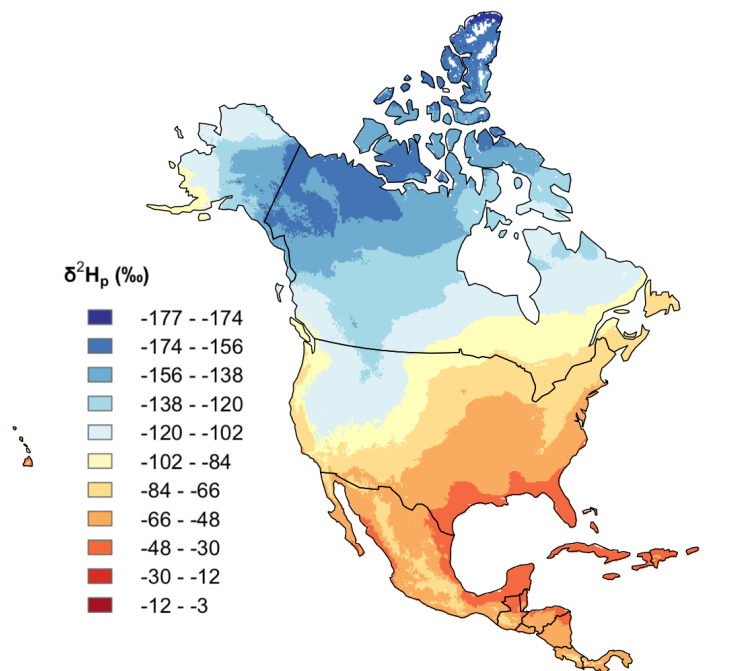
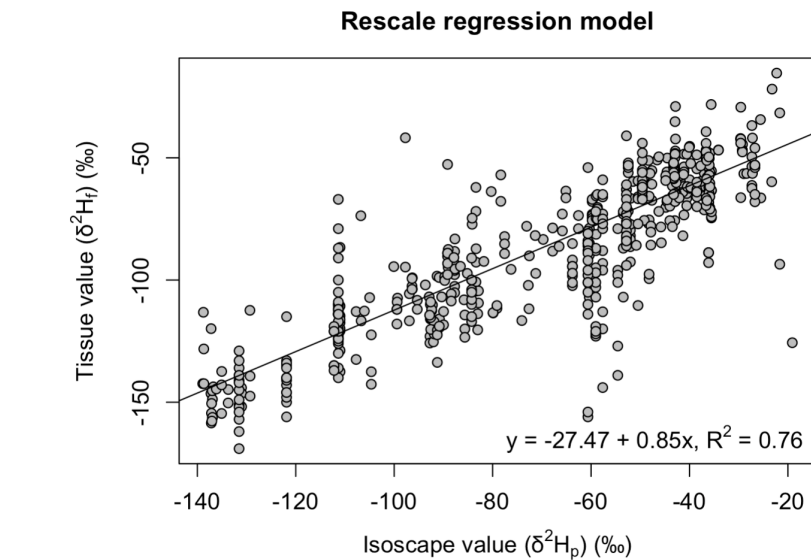
Unknown samples were assigned to the calibrated isoscape by producing posterior probability density maps (Wunder 2010) using the *pdRaster* function in ‘assignR’ (Ma et al. 2020). Posterior probability density maps use Bayes’ Rule (see Supplementary Material for explanation of Bayes’ Rule, Section 3.7) to determine the probability that any given cell (pixel) within the  $\delta^2H_f$  isoscape is the origin of the unknown sample.



**Figure 3.2.** Study sites of Neotropical migrant feathers collected in (A) Hobson and Wassenaar (1997), and (B) Hobson et al. (2012).  $\delta^2H_f$  from these samples was used to calibrate the amount-weighted mean growing-season  $\delta^2H_p$  isoscape for assignment of natal origin.

Isoscapes were constrained to known breeding areas for each particular species (BirdLife International and Handbook of the Birds of the World 2020) using the ‘mask’ argument in *pdRaster*, to more accurately assign probable origin under the assumption that individuals will most likely originate from somewhere within the known breeding range (Hobson et al. 2015). This method assumes a uniform distribution, whereby a multiplier of zero is assigned to locations (pixels) outside of the breeding range, and a multiplier of 1 to locations (pixels) inside of the breeding range. Probability values were rescaled relative to the largest observed density value to improve interpretation of plots (Wunder 2010). Posterior probability density maps that were not constrained to the breeding range were also calculated and are included in the Supplementary Material (Figures S3.3 – S3.7). Probability values were not rescaled for these plots.

Non-isotopic values can be applied as prior probabilities, such as relative abundance of populations across the isoscape (Royle and Rubenstein 2004), to provide more information about any one location as a possible origin (Wunder 2010). Use of non-isotopic priors does not assume a uniform distribution, but rather, each location (pixel) is assigned a multiplier depending on the prior chosen (e.g. relative abundance at a particular pixel), decreasing the ambiguity of natal origin assignment. However, due to data availability,



**Figure 3.3.** (A) Linear regression of  $\delta^2H_f$  of known-origin feather samples from Neotropical migrants in Hobson and Wassenaar (1997) and Hobson et al. (2012) against amount-weighted mean growing-season  $\delta^2H_p$  from Bowen et al. (2005). (B) Calibrated isoscape of  $\delta^2H_f$  derived from the regression equation in (A) that was used to assign origin of unknown feather samples.

we were not able to add relative abundance as a prior in our likelihood-based assignments for all species. A preliminary analysis using North American Breeding Bird Survey (BBS) relative abundance data (Sauer et al. 2017; relative abundance maps available at [https://www.mbr-pwrc.usgs.gov/bbs/ra2015/ra2015\\_red\\_v3.shtml](https://www.mbr-pwrc.usgs.gov/bbs/ra2015/ra2015_red_v3.shtml)) as a prior is included in this chapter for the Orange-crowned Warbler (*Leiothlypis celata*). Results calculated with and without a prior are compared.

### **3.3.5 Ethical note**

Methods were approved by the Canadian Council for Animal Care as reviewed by Acadia University's Animal Care Committee (ACC), as well as the Animal Welfare and Ethical Review Board (AWERB) at the University of Oxford. Federal permits to capture and use feather material were obtained through the Canadian Wildlife Service (permit number SC4031) and the Canadian Bird Banding Office (sub-permit 10273 AP).

## **3.4 Results**

### **3.4.1 Feather samples**

15 different species of vagrants were captured during the study (Table 3.1; see Table S2.1 for further information on orientation experiments and tagging for each vagrant). For 4 species of vagrants, 18 separate individuals were captured (5, 7, 3, and 3, respectively), and for 11 species of vagrants, one individual of each species was captured. In total, 29 rectrix feathers (R2) from 29 individual vagrants were collected. A sample from one species failed to be analysed during stable isotope analysis.

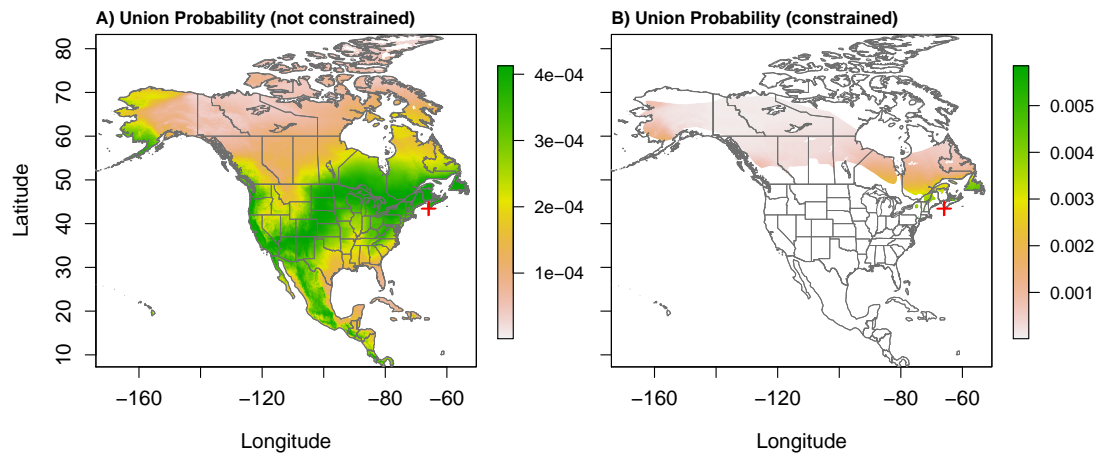
**Table 3.1.** Values of deuterium in feathers ( $\delta^2H_f$ ) from vagrants captured on Bon Portage and Seal Island, Nova Scotia. 29 vagrants from 15 different species were captured. One sample (Yellow-throated Warbler (*Setophaga dominica*); V14) failed to be processed during stable isotope analysis.  $\delta^2H_f$  were used to predict probable natal origin of each individual. The Bird ID is a unique ID given to each individual for ease of comparison between Chapters 2 and 3.

Year	Site	Bird ID	Species	Date Captured	Sample #	$\delta^2H_f$ (‰)
2018	BP	V1	Prairie Warbler ( <i>Setophaga discolor</i> )	18 Aug	267	-148.4
	BP	V2	Orchard Oriole ( <i>Icterus spurius</i> )	23 Aug	258	-82.9
	SL	V3	Lark Sparrow ( <i>Chondestes grammacus</i> )	07 Sep	255	-72.3
	BP	V4	Prairie Warbler ( <i>Setophaga discolor</i> )	17 Sep	252	-77.8
	BP	V5	Western Warbling Vireo ( <i>Vireo g. swainsoni</i> )	20 Sep	250	-77.0
	BP	V6	Western Warbling Vireo ( <i>Vireo g. swainsoni</i> )	23 Sep	248	-68.1
	BP	V7	Western Warbling Vireo ( <i>Vireo g. swainsoni</i> )	28 Sep	242	-82.3
	BP	V8	Western Warbling Vireo ( <i>Vireo g. swainsoni</i> )	30 Sep	236	-78.8
	BP	V9	Yellow-billed Cuckoo ( <i>Coccyzus americanus</i> )	01 Oct	234	-93.4
	BP	V10	Orange-crowned Warbler ( <i>Leiothlypis celata</i> )	07 Oct	222	-89.2
	BP	V11	Yellow-billed Cuckoo ( <i>Coccyzus americanus</i> )	15 Oct	205	-84.0
	BP	V12	Western Warbling Vireo ( <i>Vireo g. swainsoni</i> )	21 Oct	203	-88.9
	BP	V13	Yellow-breasted Chat ( <i>Icteria virens</i> )	23 Oct	200	-85.6
2019	BP	V14	Yellow-throated Warbler ( <i>Setophaga dominica</i> )*	12 Aug	--	--
	BP	V15	Yellow-billed Cuckoo ( <i>Coccyzus americanus</i> )	13 Aug	304	-76.6
	BP	V16	Hammond's Flycatcher ( <i>Empidonax hammondi</i> )	12 Sep	313	-57.6
	BP	V17	Western Warbling Vireo ( <i>Vireo g. swainsoni</i> )	17 Sep	309	-72.2
	BP	V18	Indigo Bunting ( <i>Passerina cyanea</i> )	20 Sep	307	-151.5
	BP	V19	Western Warbling Vireo ( <i>Vireo g. swainsoni</i> )	21 Sep	300	-67.9
	BP	V20	Yellow-breasted Chat ( <i>Icteria virens</i> )	24 Sep	299	-71.1
	BP	V21	Blue Grosbeak ( <i>Passerina caerulea</i> )	26 Sep	297	-59.8
	BP	V22	Prairie Warbler ( <i>Setophaga discolor</i> )	28 Sep	293	-46.2
	BP	V23	Yellow-breasted Chat ( <i>Icteria virens</i> )	28 Sep	292	-41.4
	BP	V24	Clay-colored Sparrow ( <i>Spizella pallida</i> )	03 Oct	286	-43.3
	BP	V25	Scarlet Tanager ( <i>Piranga olivacea</i> )	14 Oct	285	-89.7
	BP	V26	Yellow-billed Cuckoo ( <i>Coccyzus americanus</i> )	15 Oct	281	-122.8
	BP	V27	Pine Warbler ( <i>Setophaga pinus</i> )	19 Oct	275	-65.9
	BP	V28	Yellow-billed Cuckoo ( <i>Coccyzus americanus</i> )	21 Oct	272	-99.5
	BP	V29	Western Palm Warbler ( <i>Setophaga p. palmarum</i> )	21 Oct	271	-89.7

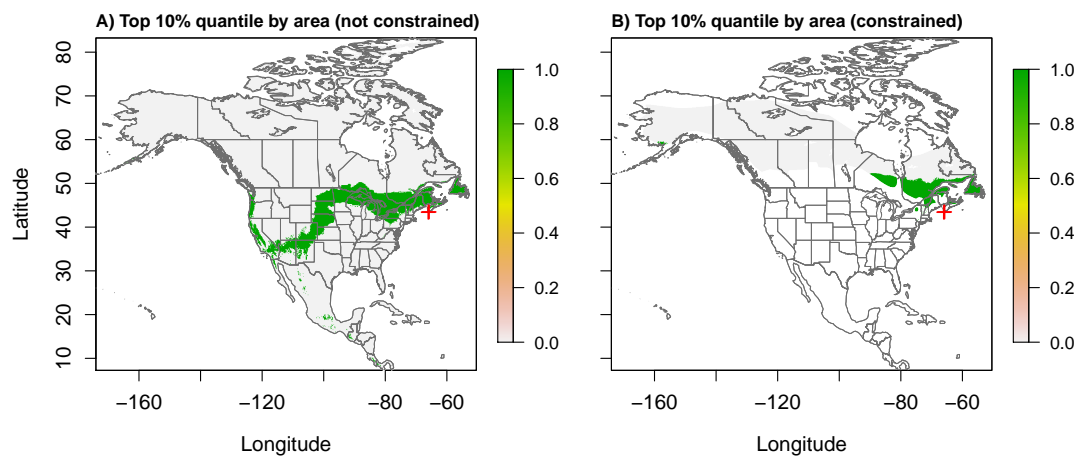
\* Feather sample failed to be processed during stable isotope analysis

### 3.4.2 Natal origins

Blackpolls were highly predicted to originate from Nova Scotia (Figure 3.4). Nova Scotia fell within the top 10% of the study area that was the most likely to be the origin of one or more samples (Figure 3.5). For vagrants, 10 out of 14 species captured had at least one individual that was predicted to originate from a range edge (71.4% of species), rather than from somewhere within the centre of the breeding range. In total, 21 out of 28 individuals originated from a range edge (75.0%), while the other 8 individuals were predicted to originate from within the centre of their range.



**Figure 3.4.** Union probability plots for the 86 Blackpoll Warbler (*Setophaga striata*) feather samples collected on both BP and Seal Island in 2018 and 2019. The density value of each pixel in the probability surface represents the probability that that pixel is the origin of any sample within the dataset, with green being the most probable, and white being the least. Geographic assignments were either (A) not constrained by the breeding area, or (B) constrained by the breeding area. Red crosses depict the study site at which birds were captured. Nova Scotia falls within the area of highest probable natal origin for both plots.

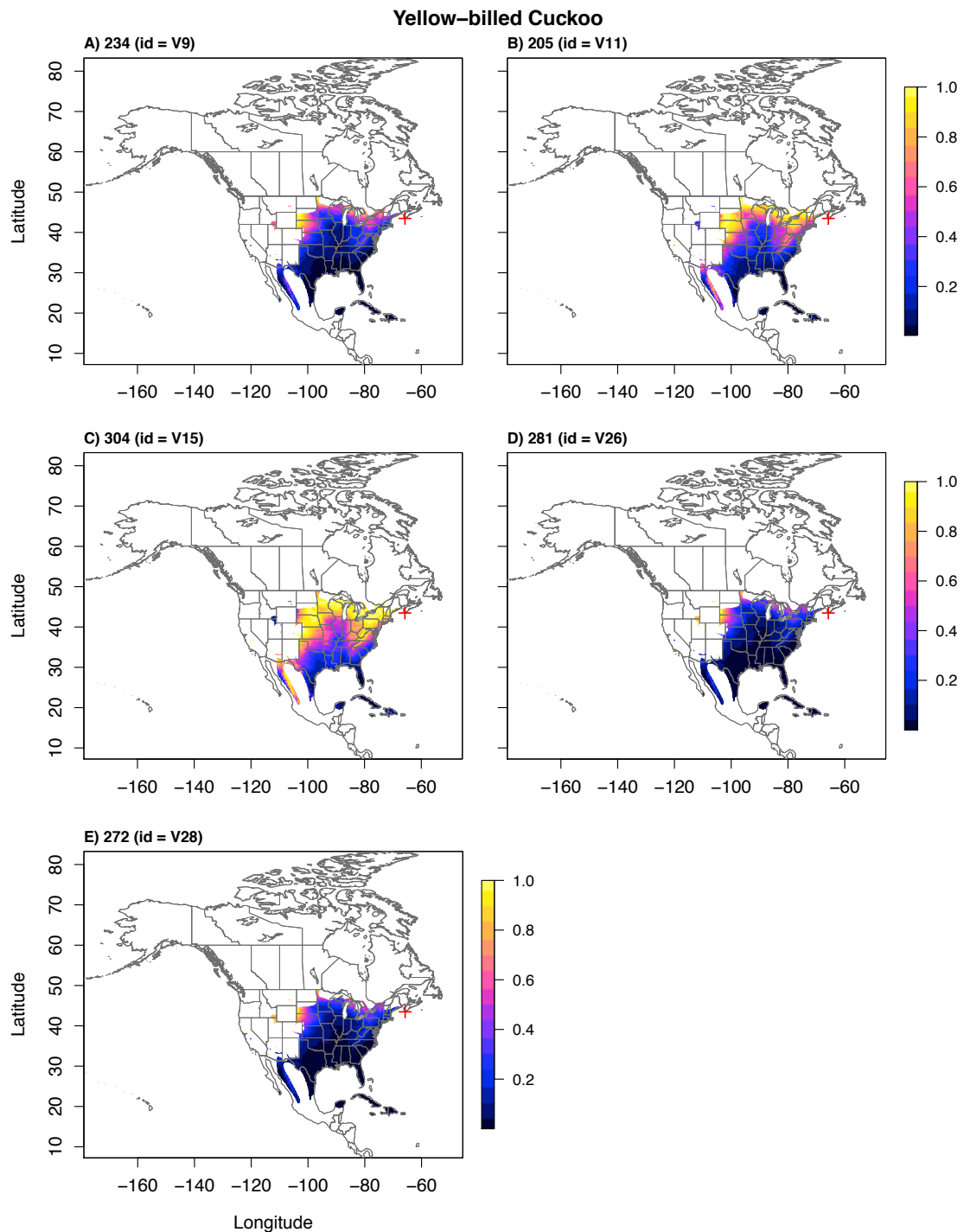


**Figure 3.5.** 10% quantile plots for the 86 Blackpoll Warbler (*Setophaga striata*) feather samples collected on both BP and Seal Island in 2018 and 2019. Using the union probabilities calculated in Figure 3.4, the top 10% quantile by area (i.e. the area within the top 10% of the study area that was the most likely to be the origin of one or more samples) was calculated. Geographic assignments were either (A) not constrained by the breeding area, or (B) constrained by the breeding area. Red crosses depict the study site at which birds were captured. Nova Scotia falls within the top 10% quantile by area for both plots.

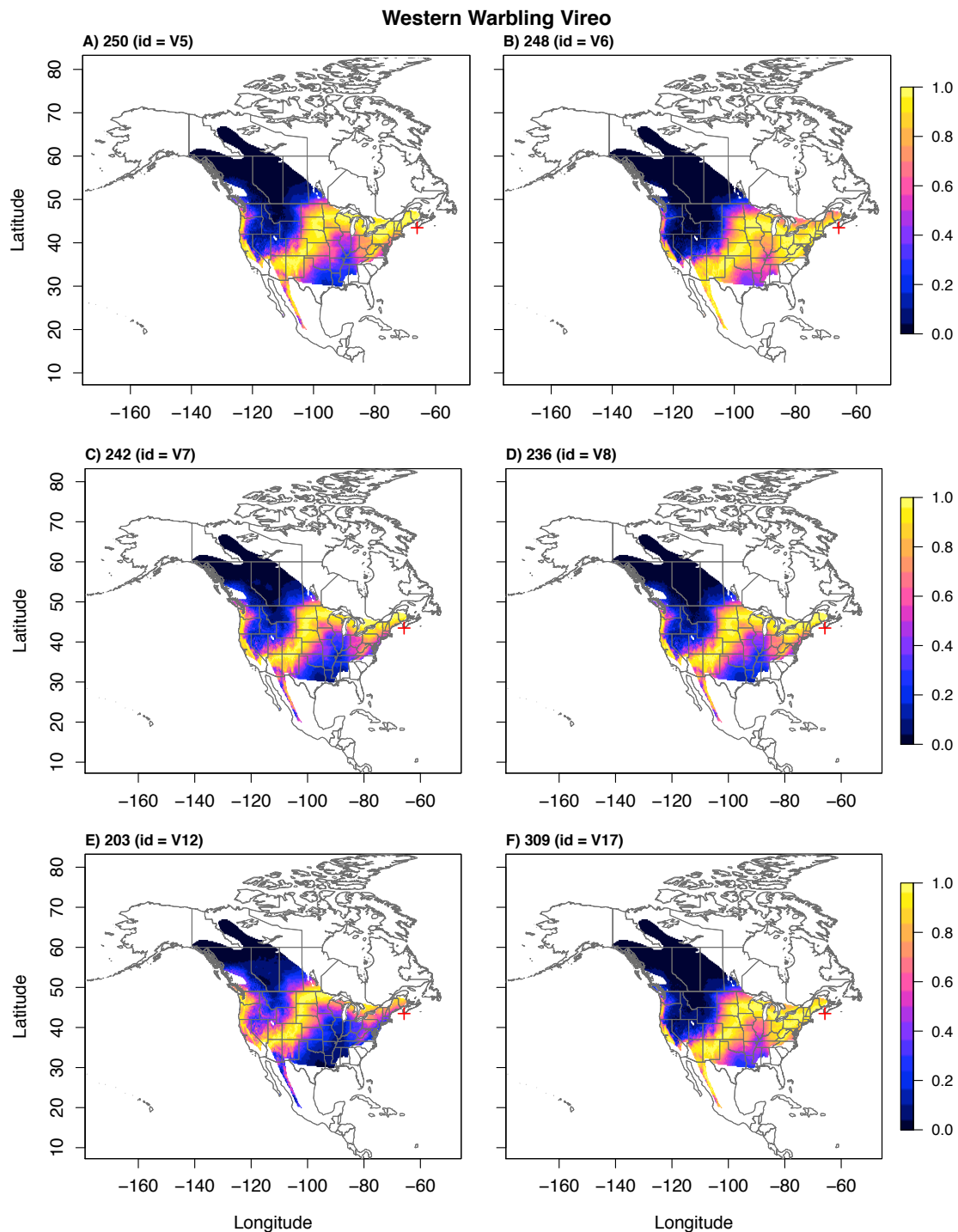
All Yellow-billed Cuckoos (*Coccyzus americanus*) captured ( $n = 5$ ) likely originated from the northern part of their breeding range (Figure 3.6). Four individuals were assigned to one edge of their range, with one individual (Sample 205 (V11)) originating broadly along the northernmost edge (Figure 3.6b), and three assigned to narrow areas on the northwesterly edge of their range in either South Dakota and Nebraska (Samples 234 (V9) and 272 (V28), respectively; Figures 3.6a, e), or a small region in Iowa and Utah (Sample 281 (V26); Figure 3.6d). Sample 304 (V15) was not precisely assigned along the range edge, though it was still mainly within the northern half of the breeding range (Figure 3.6c). All of the Western Warbling Vireos (*Vireo gilvus swainsoni*) captured ( $n = 7$ ) originated from the westernmost edge of their breeding range, along the coast of California up through Washington (Figure 3.7).

Prairie Warblers (*Setophaga discolor*) ( $n = 3$ ) varied in their assigned origin among individuals (Figure 3.8). Sample 252 (V4) derived from the northern extent of the breeding range in parts of Ontario through New York and Pennsylvania (Figure 3.8b), while sample 267 (V1) was assigned a very small area at the northernmost tip of the breeding range in southern Ontario (Figure 3.8a). Sample 293 (V22) differed from the other individuals, originating instead from a broad region within the southern portion of the breeding range, with the most probable area spanning eight states (Figure 3.8c). Yellow-breasted Chats (*Icteria virens*) ( $n = 3$ ) also varied in their assigned origin, though assignments within this species were not as precise (Figure 3.9). The probable origin of sample 200 (V13) was not clearly defined, and the individual most likely originated from somewhere along the midwestern portion of the breeding range (Figure 3.9a). Sample 292 (V23) was mainly restricted to the southeasterly part of the range (Figure 3.9c), and assignment for this individual was broad. Sample 299 (V20) was the least well-defined, and likely originated from either the midwestern portion of their range or a large portion of the northeast (Figure 3.9b).

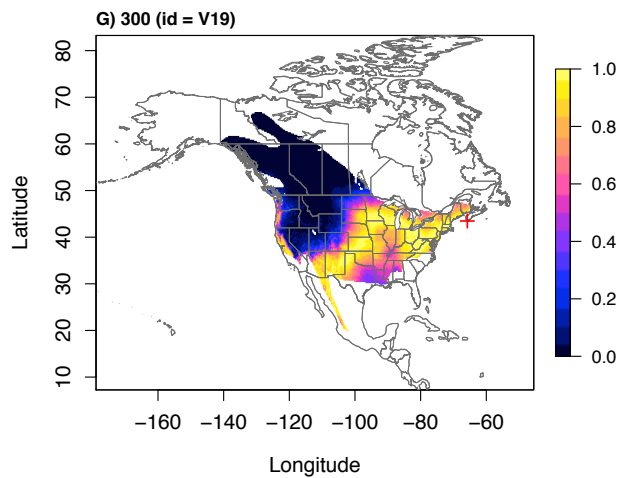
Of the ten individuals captured from ten distinct species, seven were assigned origins along the edge of their breeding range, while the other three were assigned origins from the centre of their breeding range (Figure 3.10). Those predicted to originate along one edge



**Figure 3.6.** Posterior probability density maps (i.e. probable geographic origin) of Yellow-billed Cuckoos (*Coccyzus americanus*) ( $n = 5$ ) captured in Nova Scotia during autumn migration. Each map represents a different individual, with the number representing the feather sample number followed by the bird ID. Geographic assignments were constrained to the species' known breeding range. The density value of each pixel in the probability surface represents the probability that that pixel is the origin of the sample, with 1.0 (yellow) being the most probable, and 0.0 (dark blue) being the least. All values have been rescaled by the largest observed density value for ease of interpretation. Red crosses depict the study site at which birds were captured.



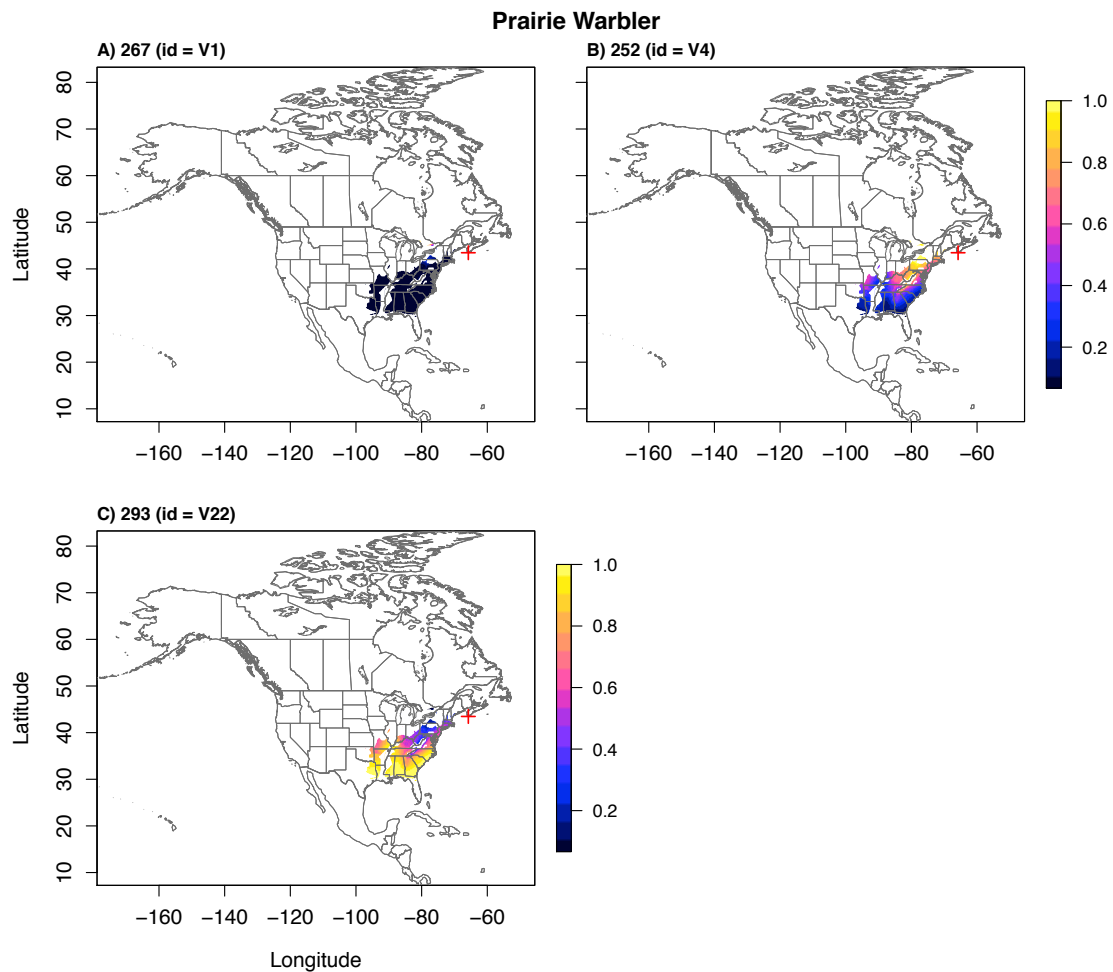
**Figure 3.7.** Posterior probability density maps of Western Warbling Vireos (*Vireo gilvus swainsoni*) ( $n = 7$ ) captured in Nova Scotia during autumn migration. Each map represents a different individual, with the number representing the feather sample number followed by the bird ID. Geographic assignments were constrained to the species' known breeding range. The density value of each pixel in the probability surface represents the probability that that pixel is the origin of the sample, with 1.0 (yellow) being the most probable, and 0.0 (dark blue) being the least. All values have been rescaled by the largest observed density value for ease of interpretation. Red crosses depict the study site at which birds were captured.



**Figure 3.7 (cont.).** Posterior probability density maps of Western Warbling Vireos (*Vireo gilvus swainsoni*) ( $n = 7$ ) captured in Nova Scotia during autumn migration. Each map represents a different individual, with the number representing the feather sample number followed by the bird ID. Geographic assignments were constrained to the species' known breeding range. The density value of each pixel in the probability surface represents the probability that that pixel is the origin of the sample, with 1.0 (yellow) being the most probable, and 0.0 (dark blue) being the least. All values have been rescaled by the largest observed density value for ease of interpretation. Red crosses depict the study site at which birds were captured.

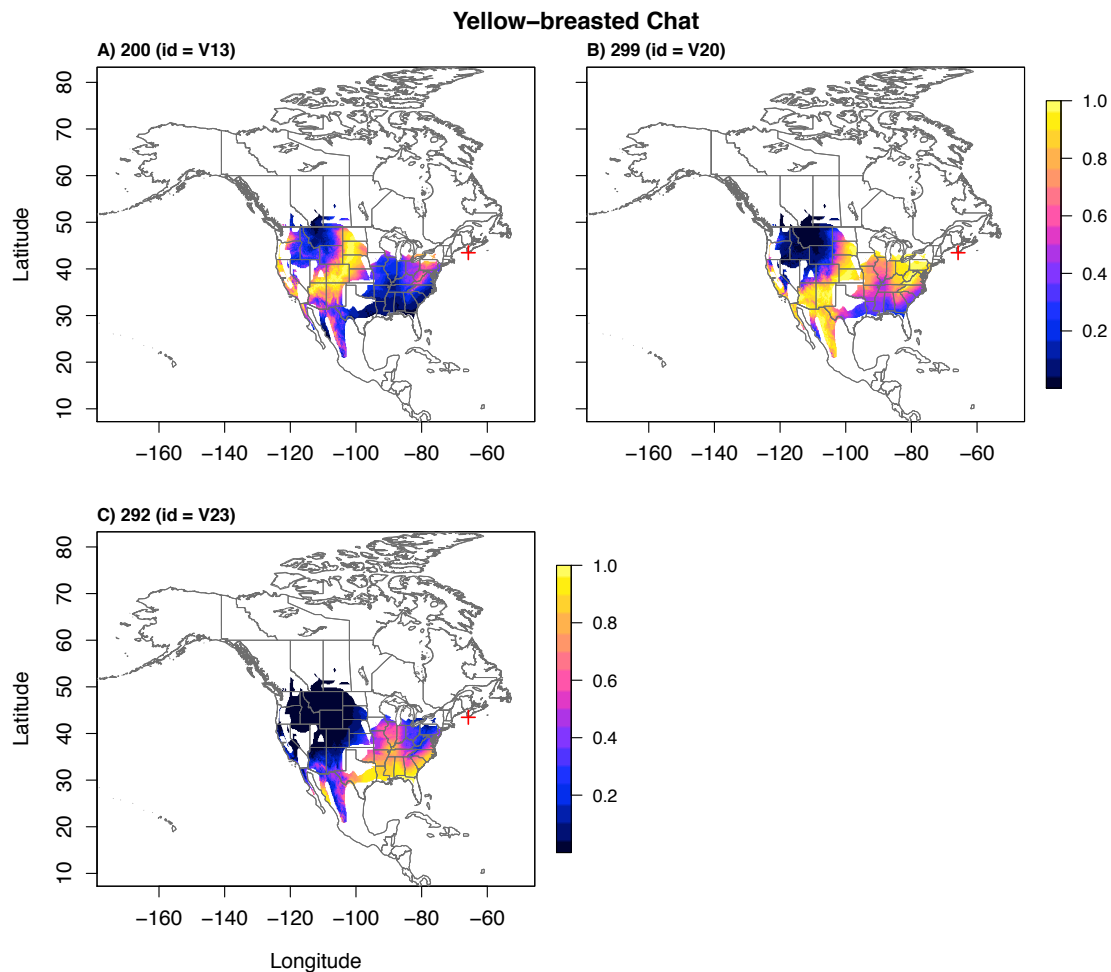
of their range were the Hammond's Flycatcher (*Empidonax hammondii*), Orange-crowned Warbler (*Leiothlypis celata*), Western Palm Warbler (*Setophaga palmarum palmarum*), Clay-colored Sparrow (*Spizella pallida*), Scarlet Tanager (*Piranga olivacea*), Indigo Bunting (*Passerina cyanea*), and Orchard Oriole (*Icterus spurius*). Those predicted to originate from within the centre of their breeding range were the Pine Warbler (*Setophaga pinus*), Lark Sparrow (*Chondestes grammacus*), and Blue Grosbeak (*Passerina caerulea*).

Of those predicted to occur along one edge of their range, three individuals were assigned a very restricted probable origin. The Hammond's Flycatcher was assigned a small region on the south-westernmost edge of its range in California (Figure 3.10a), the Clay-colored Sparrow was assigned the southernmost edge of its range in Minnesota and Wisconsin (Figure 3.10e), and the Indigo Bunting was assigned the most northernmost tip of its range in Saskatchewan and Manitoba (Figure 3.10i). The other four species were more broadly defined, but were still constrained to one or more range edges. The Western Palm Warbler was consolidated to the southeastern edge of its breeding range that passes through Ontario, southern Manitoba, and Minnesota (Figure 3.10d). The



**Figure 3.8.** Posterior probability density maps of Prairie Warblers (*Setophaga discolor*) ( $n = 3$ ) captured in Nova Scotia during autumn migration. Each map represents a different individual, with the number representing the feather sample number followed by the bird ID. Geographic assignments were constrained to the species' known breeding range. The density value of each pixel in the probability surface represents the probability that that pixel is the origin of the sample, with 1.0 (yellow) being the most probable, and 0.0 (dark blue) being the least. All values have been rescaled by the largest observed density value for ease of interpretation. Red crosses depict the study site at which birds were captured.

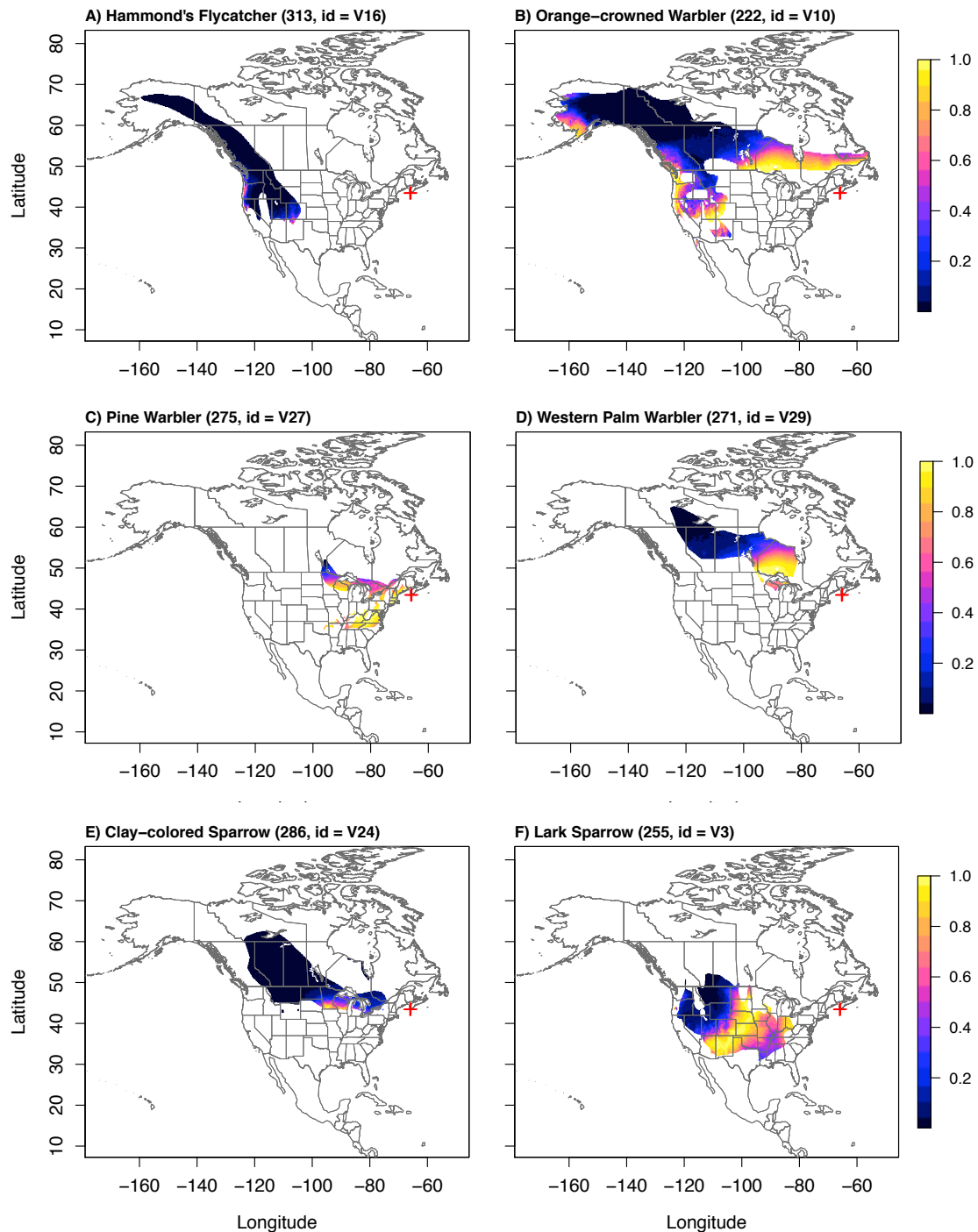
Scarlet Tanager (Figure 3.10g) and the Orchard Oriole (Figure 3.10j) were both assigned to the northern edge of their range, though they were likely to originate from either the northwest edge (Minnesota and part of Manitoba and Ontario for the Scarlet Tanager, and North Dakota through Nebraska for the Orchard Oriole), or the northeast edge (Quebec and New Brunswick for the Scarlet Tanager, and New York, Pennsylvania, and southern Ontario for the Orchard Oriole). The Orange-crowned Warbler likely originated from a range edge, however, that edge was not clearly defined (Figure 3.10b). This individual



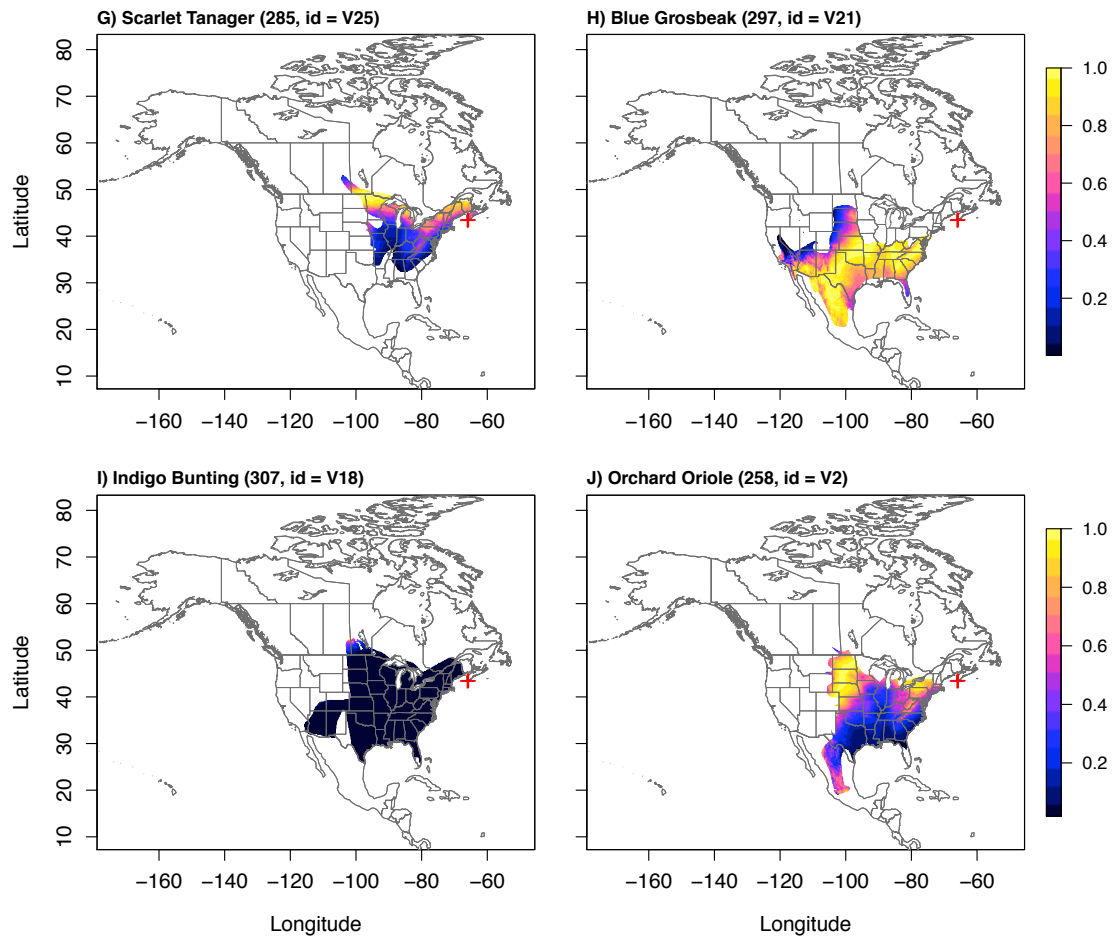
**Figure 3.9.** Posterior probability density maps of Yellow-breasted Chats (*Icteria virens*) ( $n = 3$ ) captured in Nova Scotia during autumn migration. Each map represents a different individual, with the number representing the feather sample number followed by the bird ID. Geographic assignments were constrained to the species' known breeding range. The density value of each pixel in the probability surface represents the probability that that pixel is the origin of the sample, with 1.0 (yellow) being the most probable, and 0.0 (dark blue) being the least. All values have been rescaled by the largest observed density value for ease of interpretation. Red crosses depict the study site at which birds were captured.

either originated from the eastern edge of the breeding range spanning half of North America along its east-west axis, the southwestern edge of the range from California to Washington, part of the southeastern edge that passes through Utah and Colorado, or the northwestern edge of its range in Alaska.

Of those that were assigned origins within the centre of their range, the Lark Sparrow had a narrower predicted origin (Figure 3.10f) than the Pine Warbler (Figure 3.10c) or the Blue Grosbeak (Figure 3.10h), which were much more broadly defined.



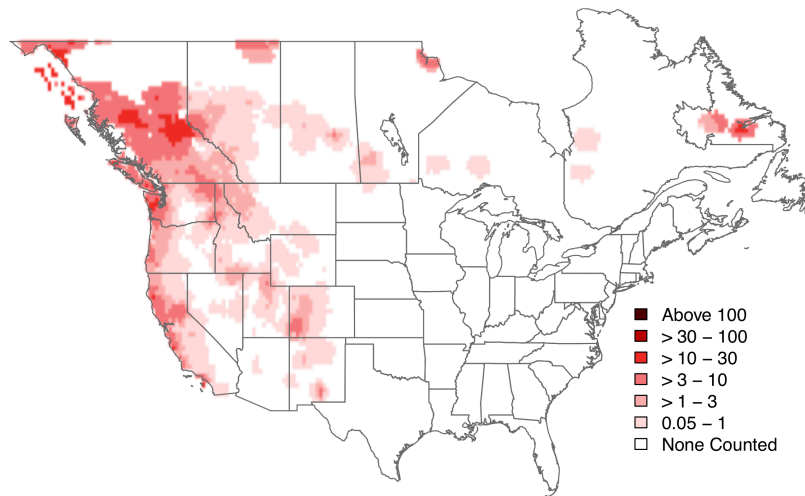
**Figure 3.10.** Posterior probability density maps (i.e. probable geographic origin) of species captured once ( $n = 10$ ) in Nova Scotia during autumn migration. Each map represents a different individual, with the number representing the feather sample number followed by the bird ID. Geographic assignments were constrained to the species' known breeding range. The density value of each pixel in the probability surface represents the probability that that pixel is the origin of the sample, with 1.0 (yellow) being the most probable, and 0.0 (dark blue) being the least. All values have been rescaled by the largest observed density value for ease of interpretation. Red crosses depict the study site at which birds were captured.



**Figure 3.10 (cont.).** Posterior probability density maps (i.e. probable geographic origin) of species captured once ( $n = 10$ ) in Nova Scotia during autumn migration. Each map represents a different individual, with the number representing the feather sample number followed by the bird ID. Geographic assignments were constrained to the species' known breeding range. The density value of each pixel in the probability surface represents the probability that that pixel is the origin of the sample, with 1.0 (yellow) being the most probable, and 0.0 (dark blue) being the least. All values have been rescaled by the largest observed density value for ease of interpretation. Red crosses depict the study site at which birds were captured.

### 3.4.3 Preliminary prior probability analysis

Analysis of the natal origin of the Orange-crowned Warbler with use of a prior demonstrated that more precise natal origins can be predicted when prior information such as relative abundance across the breeding range are used (Figure 3.11). Compared to maps that were only restricted to the breeding range itself (Figure 3.10b), the probability map generated with priors predicted that the individual Orange-crowned

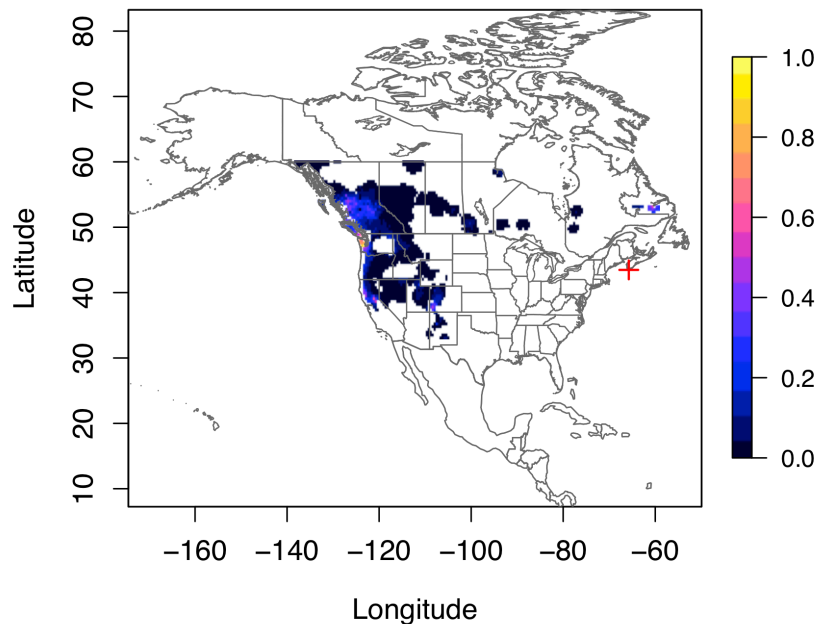


**Figure 3.11.** Breeding Bird Survey (BBS) map of relative abundance for the Orange-crowned Warbler (*Leiothlypis celata*) adapted from Sauer et al. (2017). Relative abundance maps are produced by estimating average counts from surveys conducted between 2011 – 2015, via inverse distancing to estimate the abundance at each location as a distance-weighted average of counts from nearby survey routes. Maps were only created using data within the “Core” survey area of the BBS, as shown here. The “Core” survey area encompasses the contiguous United States and southern Canada (Link et al. 2020).

Warbler was most likely to originate from western Washington (Figure 3.12). However, data used from BBS relative abundance maps (Figure 3.11) did not include population information along survey routes in Alaska and northern Canada, making it impossible to determine whether the Orange-crowned Warbler could have originated from Alaska instead. For further analysis, raw BBS route counts from the expanded survey area (Link et al. 2020), converted into relative abundance maps via Kriging (e.g. Royle and Rubenstein 2004), should be used to definitively determine prior probabilities of occurrence in across the whole of the breeding range.

### 3.5 Discussion

Our results show that it is possible to infer natal origin of vagrant songbirds in North America with stable isotope analysis of hydrogen isotopes. By comparing hydrogen isotopes in feathers to that of growing-season precipitation, we were able to determine probable regions of natal origin for 14 different species of vagrants that occurred in Nova



**Figure 3.12.** Posterior probability density map for the Orange-crowned Warbler (*Leiothlypis celata*) captured in Nova Scotia during autumn migration. This geographic assignment was derived with the addition of prior information about the relative abundance of the species across its breeding range (BBS data) to calculate probability of origin. Assignments were constrained to the species' known breeding range, though the data from BBS was not available across the entire breeding range. The density value of each pixel in the probability surface represents the probability that that pixel is the origin of the sample, with 1.0 (yellow) being the most probable, and 0.0 (dark blue) being the least. All values have been rescaled by the largest observed density value for ease of interpretation. Red crosses depict the study site at which birds were captured.

Scotia during autumn migration. Our results demonstrate that stable isotope analysis is a viable method for determining the natal origin of vagrants. Given that vagrants are difficult to capture and are highly unlikely to be recaptured in the same places that they are seen, use of intrinsic markers such as stable isotopes in feathers provides an opportunity to be able to study vagrancy directly through only single and chance encounters of vagrant individuals. Previously, most studies on vagrants have been limited to observational and correlative studies (e.g. Williamson 1959, DeBenedictis 1971, McLaren et al. 2006, Ralph and Wolfe 2018), and, consequently, our understanding of how and why vagrancy occurs is lacking. By implementing this easy and cost-effective technique, we can begin to examine vagrants directly with biological markers, and piece together migratory connectivity of vagrant species across North America.

It is expected that the majority of vagrants would originate from the edge of their range, rather than from the centre of their range. Long-distance dispersers are often described as those that disperse the furthest, and are therefore found along range edges (Veit and Lewis 1996, Phillips et al. 2010), though this would not be the case for the vagrants in our study since they were born on the range edge. However, individuals may also be more likely to disperse if they are already at a range edge (Liebl and Martin 2012). Studies have found that House Sparrows (*Passer domesticus*) that occur along range edges are more likely to display exploratory behaviour (Liebl and Martin 2012), and will interact with novel food much faster, than individuals located within the centre of the range (Liebl and Martin 2014). This suggests that the vagrants in our study that originated from the edge of their range may be more likely to disperse and/or engage in exploratory movements than regular migrants. Individuals at the range edge may therefore have a higher propensity to disperse and occur as vagrants, than those that originate from the centre of their range.

As with most effective methodologies, there are some limitations and challenges when using stable isotope analysis. Firstly, the isoscape of amount-weighted mean growing-season  $\delta^2H_p$  has a strong latitudinal gradient across North America, but a weak longitudinal gradient (Figure 3.1; Bowen et al. 2005). Consequently, precise natal origins cannot be assigned to species with broad longitudinal breeding ranges. Low precision should only affect a small number of vagrant species, however, since the ranges of a large number of migrant songbirds that occur as vagrants in North America are largely limited to either the eastern or western half of the continent (Sibley 2014). Species whose breeding ranges extend into Alaska also pose challenges for isotopic assignment. Since isotopic patterns in Alaska are similar to those within the southern boreal forest regions of Canada and the northwest region of the United States (see Figure 3.1), species can be incorrectly assigned to Alaska if analyses are not limited to their known breeding range (Hobson et al. 2015). Further, species that do breed within these regions can be difficult to assign.

The effect of these limitations can be reduced by constraining natal origins with prior information within a Bayesian framework. Prior information can include limiting

assignments to the known breeding area (e.g. Hobson et al. 2015), incorporation of relative abundance of the species across the breeding range (Royle and Rubenstein 2004), or use of band recovery data to define prior probabilities of the likelihood of a bird being captured in the flyway that it bred in (Hobson et al. 2009), or the likelihood of a bird being captured in a particular catchment area given its predicted migratory trajectory (Van Wilgenburg and Hobson 2011, Hobson et al. 2015). Addition of these priors, however, may be counterproductive since we do not know precisely how these factors affect or are affected by vagrancy, and it may be better to assign stable isotopes with just the breeding range as a prior.

For our study, we limited assignments to the known breeding range to increase the resolution of assigned origins. However, this was not sufficient to counter limitations across all species studied. Three species had broad breeding ranges that extended across North America along the east-west axis – the Yellow-breasted Chat (Figure 3.9), Orange-crowned Warbler (Figure 3.10b), and the Blue Grosbeak (Figure 3.10h) – resulting in ambiguous assignment of natal origin either across broad sections of their range (Figure 3.9c, Figure 3.10h), or in multiple regions within the breeding range (Figure 3.9a, b; Figure 3.10b). The breeding range of one of these species, the Orange-crowned Warbler, also extends from the boreal forest region of Canada and the northwest United States into Alaska, which made assignment for this individual highly ambiguous. This individual likely originated from either western Alaska, eastern Canada spanning Labrador, Quebec, Ontario, and Manitoba, the west coast from California through Washington, or the southeastern edge of their range within Utah and Colorado.

We conducted a preliminary analysis to determine whether addition of relative abundance across the breeding range (Sauer et al. 2017) could improve assignments of vagrants, using the Orange-crowned Warbler as our example species since it was strongly affected by both limitations of stable isotope analysis. As previous studies have shown (e.g. Royle and Rubenstein 2004, Hobson et al. 2015), it was evident that inclusion of prior information into our assignments decreased ambiguity of probable natal origins, limiting selection to one probable natal site (Figure 3.12). However, the BBS data used only consisted of

relative abundance estimates within the core BBS survey area region, which excludes Alaska and parts of northern Canada (see Figure 3.11; Link et al. 2020). Additionally, several regions in Alaska and northern Canada were not consistently surveyed by the BBS prior to 1993, and less precise smoothing methods (inverse distancing instead of Kriging) were used to create relative abundance maps (Sauer et al. 1995). In the future, using Kriging to calculate relative abundance maps from raw count data within the Expanded region, rather than using shapefiles provided by the BBS, can create a more accurate surface of breeding population data as a prior for each species.

Although limitations are present when using stable isotope analysis, the benefits of this methodology in studying vagrants outweigh the challenges it poses. Incorporation of stable isotope analysis into vagrant studies will improve our understanding of migratory connectivity and movement of these species, such as possible connections between the natal origin and orientation behaviour of vagrants (see Supplementary Material, Section 3.7), and elucidate the natal origin of these individuals. Improving this analysis through inclusion of prior information for natal assignment, and addition of other intrinsic markers, such as trace elements (e.g. iron, mercury; Asante et al. 2017), additional stable isotopes (e.g. Hobson et al. 2004 ( $\delta^{13}C$ ), Wunder et al. 2005 ( $\delta^{15}N$ ), Hobson et al. 2004b ( $\delta^{18}O$ )), or genetic markers (e.g. Kelly et al. 2005), can further improve assignment, and reduce the effects that limitations and individual variation in  $\delta^2H_f$  have on results (Langin et al. 2007). Reiterating the words of De Jong et al. (2019), we hope that this study demonstrates that vagrancy is a “genuine research topic”, and through use of direct methodologies such as stable isotope analysis, and collaboration between bird observatories and scientists, we can begin to unpack and evaluate vagrant theories.

### **3.6 Acknowledgements**

We thank Fred Longstaffe, J. Walker, K. Law and all the laboratory staff at LSIS for stable isotope analysis of our feather samples, and for help interpreting the data. Thanks also to G. Bowen and K. Hobson for answering questions about processing data and

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### 3.7 Supplementary Material

#### Bayes' Rule

Inverse conditional probabilities state that the probability of events A and B occurring are equal to the probability of event A times the probability of event B happening, given that event A has occurred.

$$P(A \text{ and } B) = P(A) * P(B|A) \quad (3.1)$$

Bayes' Rule finds the probability of the conditional event, as a condition of the probability of A happening, given that B has occurred, times the probability of B occurring over the probability of A.

For feather analysis, we seek to determine the probability of J given Y and X, where J is the possible natal origin, Y is the  $\delta^2H_f$  value of the feather, and X is the  $\delta^2H_p$  value of location J. The probability that a feather will be assigned a particular natal origin is equal to the probability of Y given X, divided by the integral of Y given X. That is, the probability is equal to the probability of the  $\delta^2H_f$  value of the feather (Y) occurring, given the  $\delta^2H_p$  value of the location (X), times the probability of any location being the origin (J) (i.e. the distribution of the population being sampled), divided by integral of this probability.

$$f_{(J|Y,X)}(J = j|Y = y_{ij}, X = x_j) = \frac{f_{Y|X}(Y = y_{ij}|X = x_i) * f_j(J = j)}{\int (f_{Y|X}(Y = y_{ij}|X = x_\xi) f_j(J = \xi) d\xi)} \quad (3.2)$$

In our study, the probability of J was the same for all locations, since we did not add additional prior probabilities in our analysis. For the preliminary analysis with BBS data, the probability of J was reflected by the BBS abundance.

### Orientation versus origin

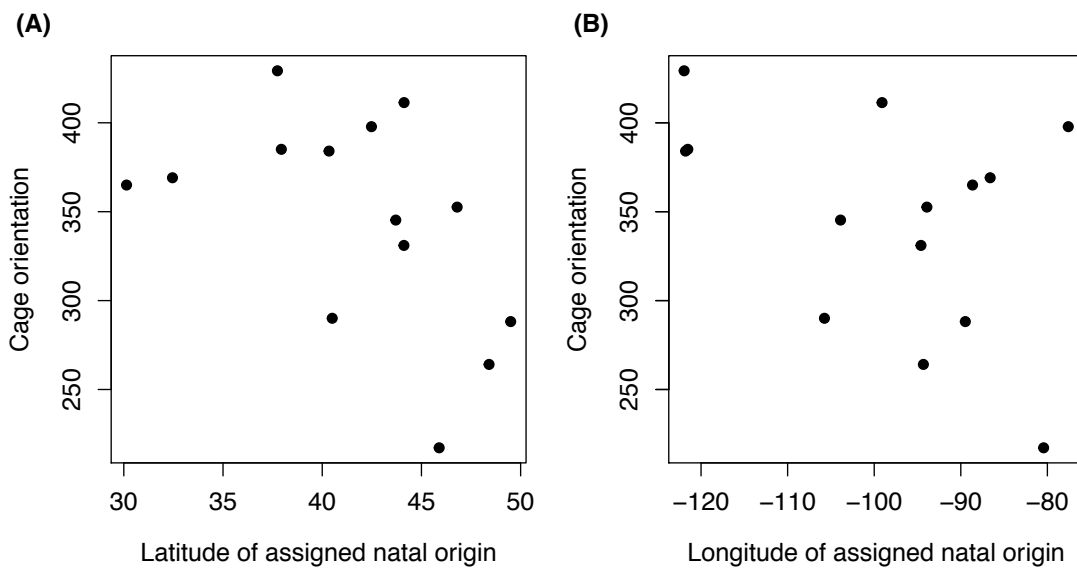
We used a circular-linear regression analysis (Fisher and Lee 1992, Agostinelli and Lund 2017) to determine whether there was a relationship between the assigned natal origin and the orientation chosen during orientation experiments (see Chapter 2 for information on orientation tests and results). We defined the assigned natal origin as the centrepoint of the region of most probable natal origin from posterior probability density maps, where the probability of assignment was greater than 95% (the yellow region of the maps; see Figures 3.6 to 3.10). Only 15 out of the 29 vagrants with feather samples were included in this analysis, since only 15 vagrants had orientation results from orientation experiments (see Table 2.3 for orientation results of each vagrant).

When latitude and longitude were included in the same model, the location of the most probable natal origin was not significantly correlated with orientation chosen during orientation experiments in Chapter 2 (Table S3.1). However, a significant relationship was found when separate models were evaluated for both latitude ( $\beta = 0.023 + 0.006$ ,  $t = 3.71$ ,  $p < 0.001$ ) and longitude ( $\beta = 0.009 + 0.002$ ,  $t = 3.58$ ,  $p < 0.001$ ). That is, the further north or east the natal origin was, respectively, the more likely an individual was to orient along a westerly bearing, and the further south or west the assigned natal origin, respectively, the more likely an individual was to orient along a north/northeasterly bearing (Figure S3.1). The  $\delta^2H_f$ , which is itself an estimate of the natal origin, was also significantly correlated with orientation ( $\beta = -0.008 + 0.002$ ,  $t = 3.38$ ,  $p < 0.001$ ). The smaller the  $\delta^2H_f$  of an individual feather, the more likely an individual was to orient along a westerly bearing, and the larger the  $\delta^2H_f$  of an individual feather, the more likely an individual was to orient along a north/northeasterly bearing (Figure S3.2).

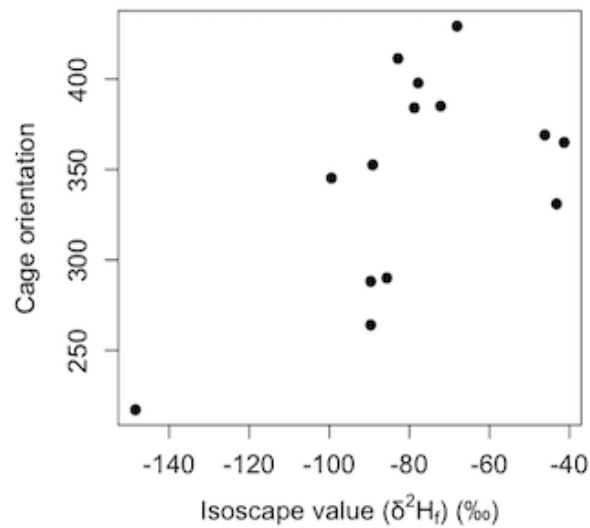
We expect that the orientation of a vagrant at the study site would be correlated with their natal origin, since the direction required to reach Nova Scotia from the breeding grounds, and subsequently their migratory behaviour and movements, is likely related to the location of their natal site (Fitzgerald and Taylor 2008). Possible explanations for the orientation exhibited by each vagrant are outlined in Chapter 2 (see Section 2.5).

**Table S3.1.** Parameter estimates ( $\beta$  coefficient  $\pm$  SE,  $t$ -statistic, and  $p$ -value) for the circular-linear regression of orientation of vagrants (see Chapter 2) versus the latitude and longitude of the assigned natal origin from stable isotope analysis of deuterium in feathers ( $\delta^2 H_f$ ). Data from 15 out of the 29 vagrants were used, since only 15 vagrants had orientation data.

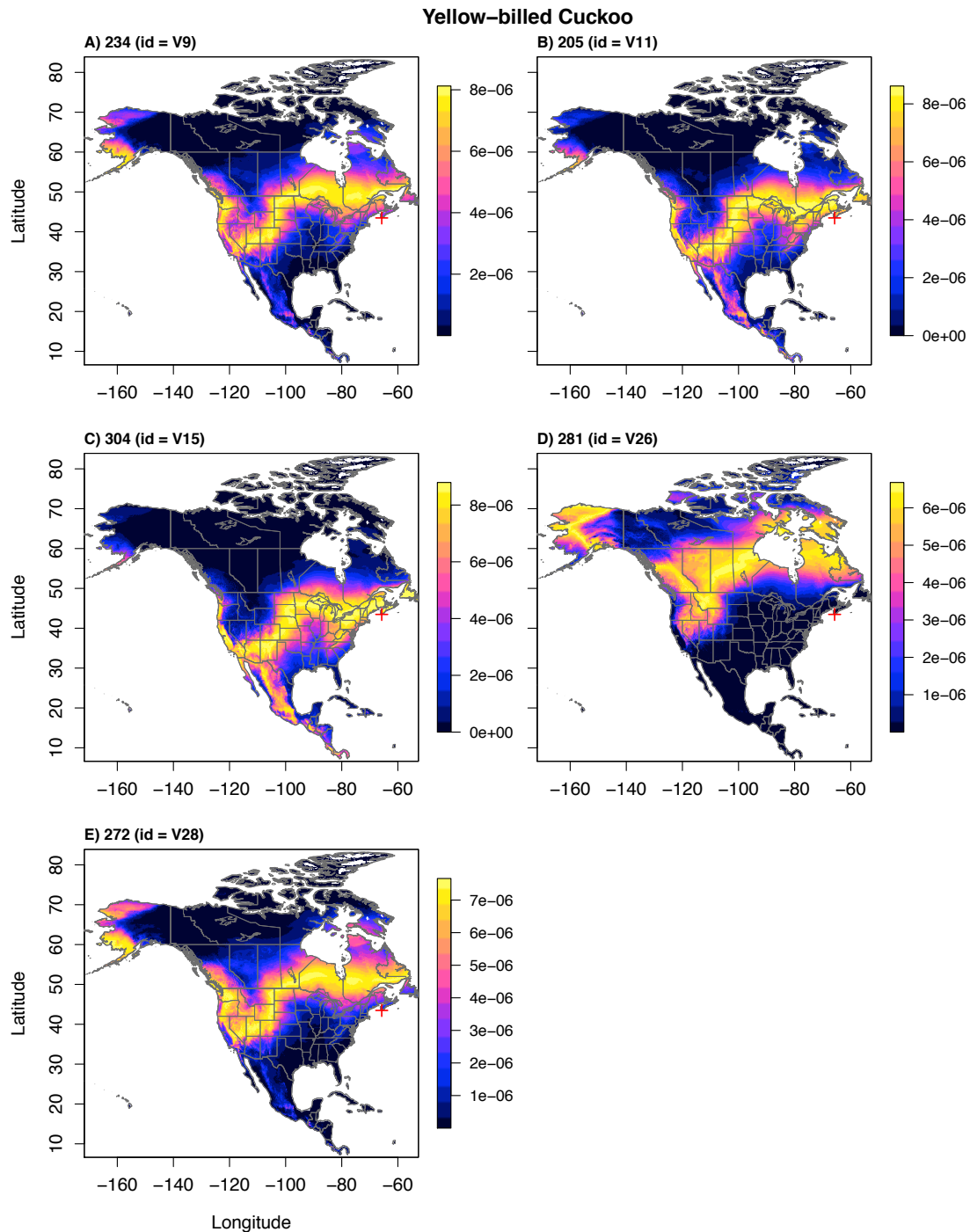
Parameter	$\beta \pm$ SE	$t$	$p$	Log-likelihood
Latitude	$1.119 \pm 0.848$	1.32	0.094	9.02
Longitude	$0.641 \pm 0.483$	1.33	0.092	



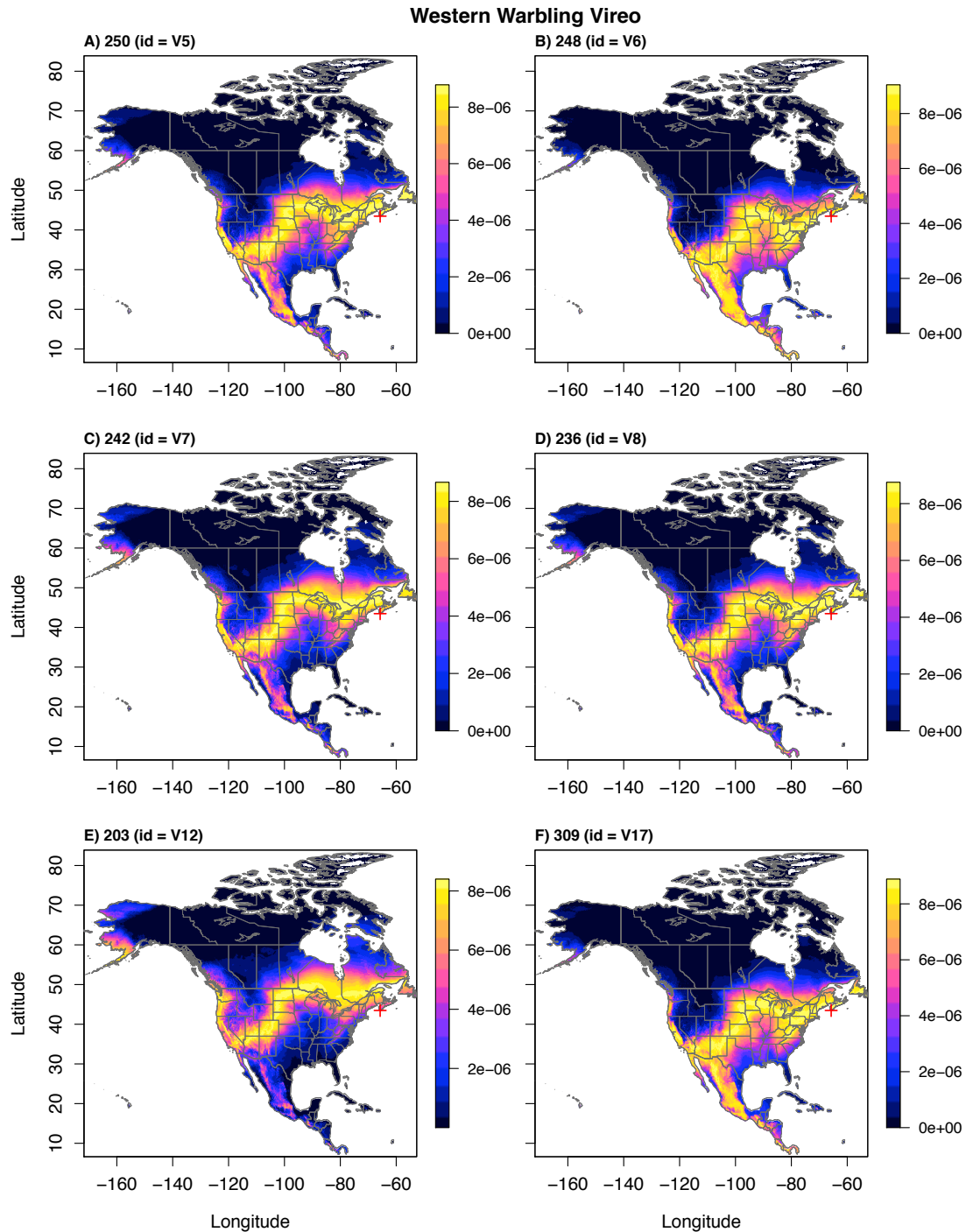
**Figure S3.1.** (A) Latitude and (B) longitude of assigned origin of vagrants plotted against the cage orientation (see Table 2.3 for orientation results). Since vagrants did not exhibit preferred orientations between the directions  $70^\circ$  to  $216^\circ$ , we added  $360^\circ$  to any orientation less than  $70^\circ$  for ease of interpretation of results. (A) As the latitude of the natal origin increases (i.e. the further north an individual is assigned), the more likely an individual will orient along a more westerly bearing. (B) As the longitude of the natal origin increases (i.e. the further east an individual is assigned), the more likely an individual will orient along a more westerly bearing. These plots are for visual interpretation only, since the circular-linear regression codes the circular variables as different values.



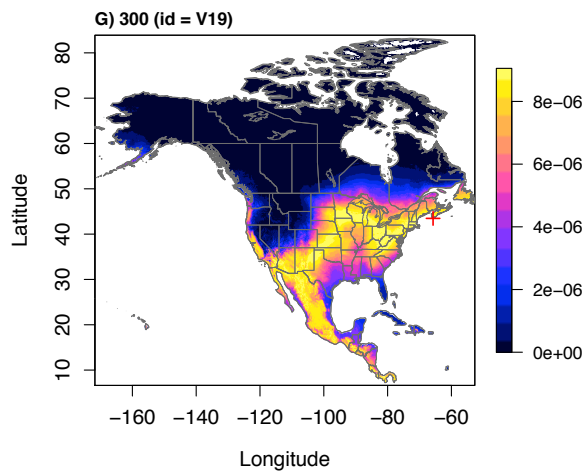
**Figure S3.2.** The ratio of deuterium in each feather ( $\delta^2H_f$ ) vagrants plotted against the cage orientation (see Table 2.3 for orientation results). Since vagrants did not exhibit preferred orientations between the directions  $70^\circ$  to  $216^\circ$ , we added  $360^\circ$  to any orientation less than  $70^\circ$  for ease of interpretation of results. As  $\delta^2H_f$  increases, the more likely an individual will orient along a north/northeasterly bearing. These plots are for visual interpretation only, since the circular-linear regression codes the circular variables as different values.



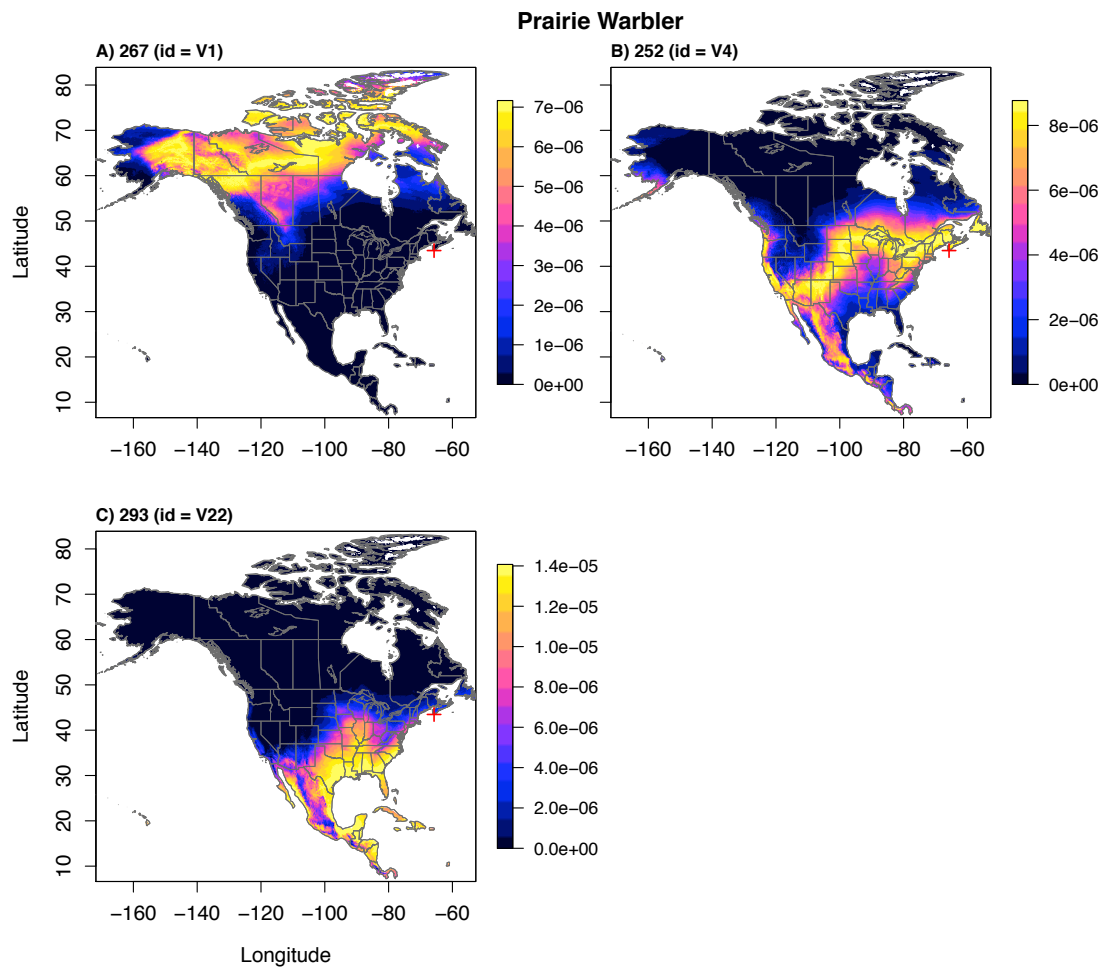
**Figure S3.3.** Posterior probability density maps (i.e. probable geographic origin) of Yellow-billed Cuckoos (*Coccyzus americanus*) ( $n = 5$ ) captured in Nova Scotia during autumn migration. Each map represents a different individual, with the number representing the feather sample number followed by the bird ID. Geographic assignments were not constrained to the breeding range for these plots, and probabilities were not rescaled. The density value of each pixel in the probability surface represents the probability that that pixel is the origin of the sample, with yellow being the most probable, and dark blue being the least. Red crosses depict the study site at which birds were captured.



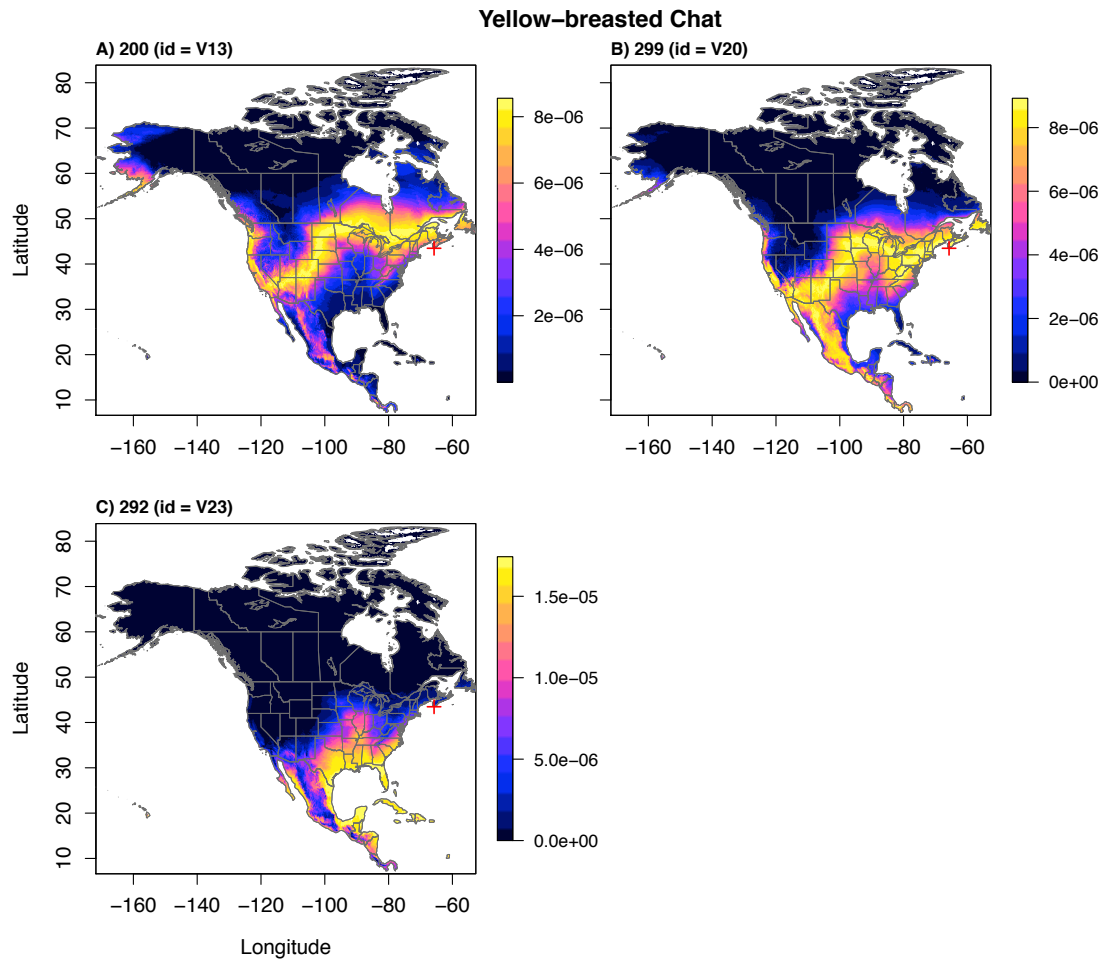
**Figure S3.4.** Posterior probability density maps of Western Warbling Vireos (*Vireo gilvus swainsoni*) ( $n = 7$ ) captured in Nova Scotia during autumn migration. Each map represents a different individual, with the number representing the feather sample number followed by the bird ID. Geographic assignments were not constrained to the breeding range for these plots, and probabilities were not rescaled. The density value of each pixel in the probability surface represents the probability that that pixel is the origin of the sample, with yellow being the most probable, and dark blue being the least. Red crosses depict the study site at which birds were captured.



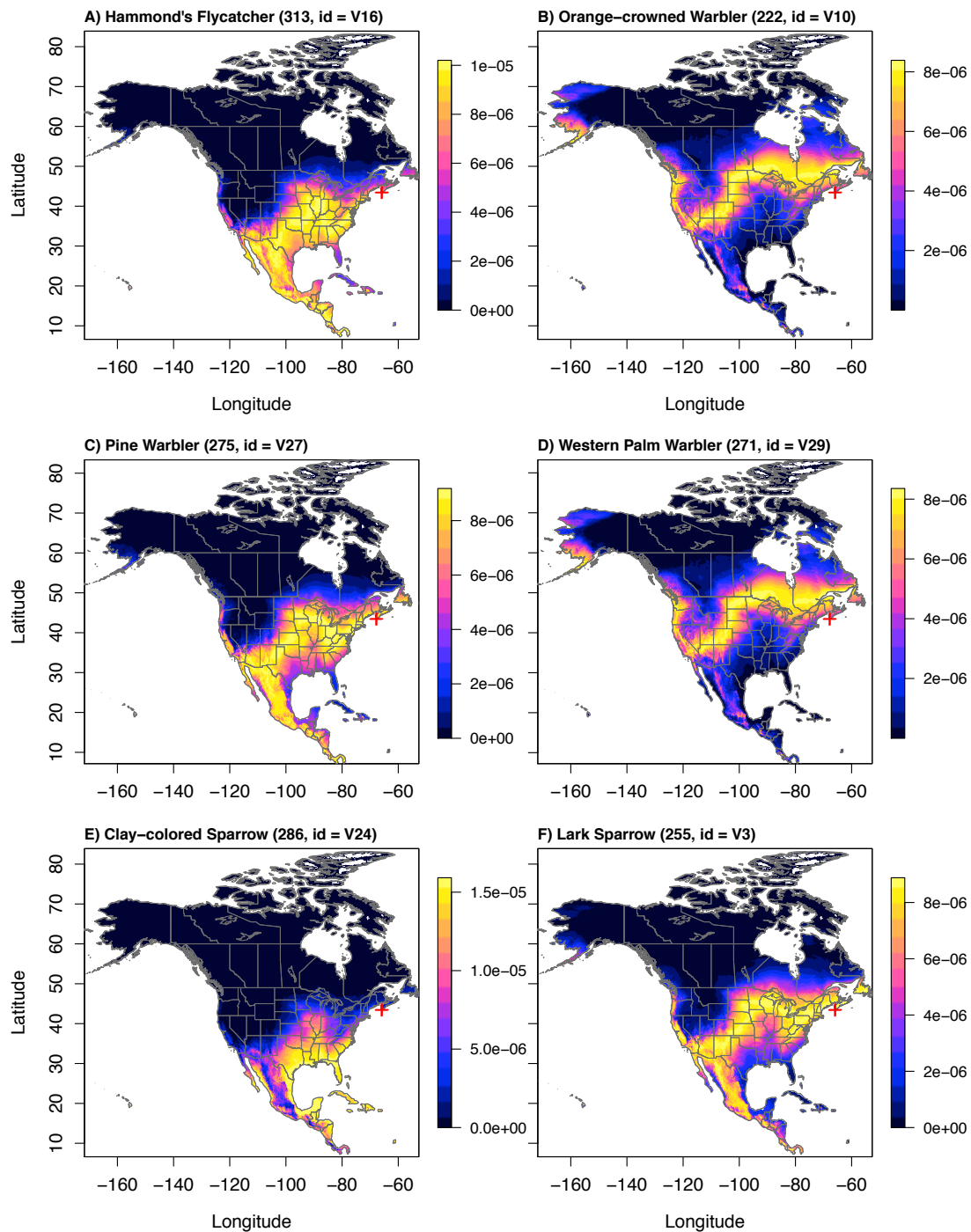
**Figure S3.4 (cont.).** Posterior probability density maps of Western Warbling Vireos (*Vireo gilvus swainsoni*) ( $n = 7$ ) captured in Nova Scotia during autumn migration. Each map represents a different individual, with the number representing the feather sample number followed by the bird ID. Geographic assignments were not constrained to the breeding range for these plots, and probabilities were not rescaled. The density value of each pixel in the probability surface represents the probability that that pixel is the origin of the sample, with yellow being the most probable, and dark blue being the least. Red crosses depict the study site at which birds were captured.



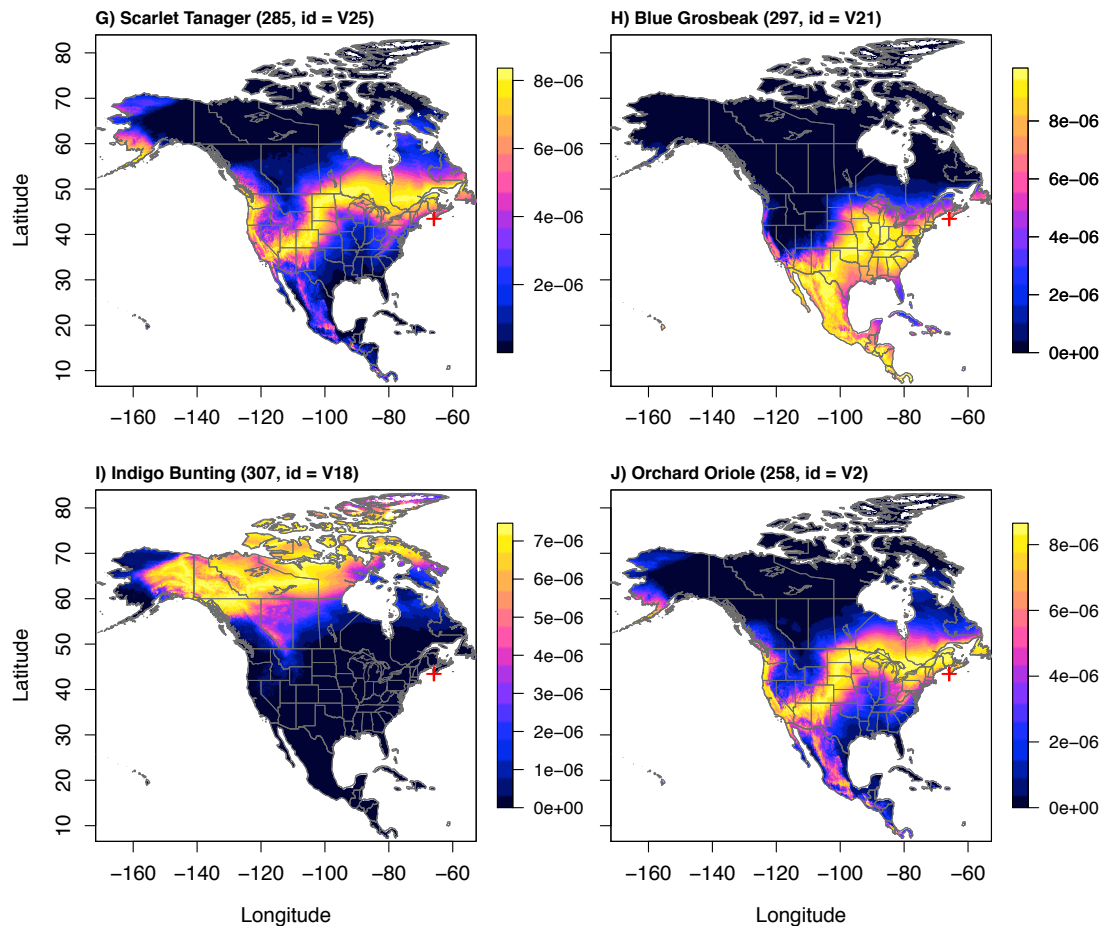
**Figure S3.5.** Posterior probability density maps of Prairie Warblers (*Setophaga discolor*) ( $n = 3$ ) captured in Nova Scotia during autumn migration. Each map represents a different individual, with the number representing the feather sample number followed by the bird ID. Geographic assignments were not constrained to the breeding range for these plots, and probabilities were not rescaled. The density value of each pixel in the probability surface represents the probability that that pixel is the origin of the sample, with yellow being the most probable, and dark blue being the least. Red crosses depict the study site at which birds were captured.



**Figure S3.6.** Posterior probability density maps of Yellow-breasted Chats (*Icteria virens*) ( $n = 3$ ) captured in Nova Scotia during autumn migration. Each map represents a different individual, with the number representing the feather sample number followed by the bird ID. Geographic assignments were not constrained to the breeding range for these plots, and probabilities were not rescaled. The density value of each pixel in the probability surface represents the probability that that pixel is the origin of the sample, with yellow being the most probable, and dark blue being the least. Red crosses depict the study site at which birds were captured.



**Figure S3.7.** Posterior probability density maps (i.e. probable geographic origin) of species captured once ( $n = 10$ ) in Nova Scotia during autumn migration. Each map represents a different individual, with the number representing the feather sample number followed by the bird ID. Geographic assignments were not constrained to the breeding range for these plots, and probabilities were not rescaled. The density value of each pixel in the probability surface represents the probability that that pixel is the origin of the sample, with yellow being the most probable, and dark blue being the least. Red crosses depict the study site at which birds were captured.



**Figure S3.7 (cont.).** Posterior probability density maps (i.e. probable geographic origin) of species captured once ( $n = 10$ ) in Nova Scotia during autumn migration. Each map represents a different individual, with the number representing the feather sample number followed by the bird ID. Geographic assignments were not constrained to the breeding range for these plots, and probabilities were not rescaled. The density value of each pixel in the probability surface represents the probability that that pixel is the origin of the sample, with yellow being the most probable, and dark blue being the least. Red crosses depict the study site at which birds were captured.

## References

- Asante, C. K., Hobson, K. A., Bond, A. L., & Jardine, T. D. (2017). Resource partitioning among five species of waterfowl (*Anas* spp.) at an autumn migratory stopover: Combining stable isotope and mercury biomarkers. *Canadian Journal of Zoology*, *95*(4), 279–286.
- BirdLife International and Handbook of the Birds of the World. (2020). Bird species distribution maps of the world. <http://datazone.birdlife.org/species/requestdis>
- Bowen, G. J., Wassenaar, L. I., & Hobson, K. A. (2005). Global application of stable hydrogen and oxygen isotopes to wildlife forensics. *Oecologia*, *143*, 337–348.
- Chamberlain, C. P., Blum, J. D., Holmes, R. T., Feng, X., Sherry, T. W., & Graves, G. R. (1997). The use of isotope tracers for identifying populations of migratory birds. *Oecologia*, *109*, 132–141.
- De Jong, A., Torniainen, J., Bourski, O. V., Heim, W., & Edenius, L. (2019). Tracing the origin of vagrant Siberian songbirds with stable isotopes: the case of Yellow-browed Warbler (*Abroornis inornatus*) in Fennoscandia. *Ornis Fennica*, *96*, 90–99.
- DeBenedictis, P. (1971). Wood warblers and vireos in California: The nature of the accidental. *California Birds*, *2*(4), 111–128.
- DeSante, D. F. (1973). *An analysis of the fall occurrences and nocturnal orientations of vagrant wood warblers (Parulidae) in California* (Doctoral dissertation). Stanford University. Stanford, California.
- DeSante, D. F. (1983a). Annual variability in the abundance of migrant landbirds on Southeast Farallon Island, California. *The Auk*, *100*(4), 826–852.
- DeSante, D. F. (1983b). Vagrants: when orientation or navigation goes wrong. *Point Reyes Bird Observatory Newsletter*, *61*, 12–16.
- Fisher, N., & Lee, A. (1992). Regression models for an angular response. *Biometrics*, *48*, 665–677.
- Fox, T. A. D., Christensen, T. K., Bearhop, S., & Newton, J. (2007). Using stable isotope analysis of multiple feather tracts to identify moulting provenance of vagrant birds: A case study of the Baikal Teal *Anas formosa* in Denmark. *Ibis*, *149*, 622–625.
- Grinnell, J. (1922). The role of the “accidental”. *The Auk*, *39*(3), 373–380.

- Hobson, K. A. (1999). Tracing origins and migration of wildlife using stable isotopes: A review. *Oecologia*, *120*, 314–326.
- Hobson, K. A. (2003). Making migratory connections with stable isotopes. In P. Berthold, E. Gwinner, & E. Sonnenschein (Eds.), *Avian migration* (pp. 379–391). Springer-Verlag.
- Hobson, K. A. (2005a). Stable isotopes and the determination of avian migratory connectivity and seasonal interactions. *The Auk*, *122*(4), 1037–1048.
- Hobson, K. A. (2005b). Using stable isotopes to trace long-distance dispersal in birds and other taxa. *Diversity and Distributions*, *11*, 157–164.
- Hobson, K. A., Aubry, Y., & Wassenaar, L. I. (2004a). Migratory connectivity in Bicknell's Thrush: Locating missing populations with hydrogen isotopes. *The Condor*, *106*, 905–909.
- Hobson, K. A., Bowen, G. J., Wassenaar, L. I., Ferrand, Y., & Lormee, H. (2004b). Using stable hydrogen and oxygen isotope measurements of feathers to infer geographical origins of migrating European birds. *Oecologia*, *141*, 477–488.
- Hobson, K. A., & Norris, D. R. (2008). Animal migration: A context for using new techniques and approaches. In K. A. Hobson & L. I. Wassenaar (Eds.), *Tracking animal migration with stable isotopes* (pp. 1–19). Academic Press.
- Hobson, K. A., Van Wilgenburg, S. L., Dunn, E. H., Hussell, D. J. T., Taylor, P. D., & Collister, D. M. (2015). Predicting origins of passerines migrating through Canadian migration monitoring stations using stable-hydrogen isotope analyses of feathers: A new tool for bird conservation. *Avian Conservation & Ecology*, *10*(1), 3.
- Hobson, K. A., Van Wilgenburg, S. L., Wassenaar, L. I., & Larson, K. (2012). Linking hydrogen ( $\delta^2H$ ) isotopes in feathers and precipitation: Sources of variance and consequences for assignment to isoscapes. *PLoS ONE*, *7*(4), 35137.
- Hobson, K. A., & Wassenaar, L. I. (1997). Linking breeding and wintering grounds of neotropical migrant songbirds using stable hydrogen isotopic analysis of feathers. *Oecologia*, *109*, 142–148.
- Hobson, K. A., Wassenaar, L. I., & Bayne, E. (2004c). Using isotopic variance to detect long-distance dispersal and philopatry in birds: An example with Ovenbirds and American Redstarts. *The Condor*, *106*, 732–743.
- Hobson, K. A., Wunder, M. B., Van Wilgenburg, S. L., Clark, R. G., & Wassenaar, L. I. (2009). A method for investigating population declines of migratory birds using stable isotopes: Origins of harvested Lesser Scaup in North America. *PLoS ONE*, *4*(11), 7915.
- Kelly, J. F., Atudorei, V., Sharp, Z. D., & Finch, D. M. (2002). Insights into Wilson's Warbler migration from analyses of hydrogen stable-isotope ratios. *Oecologia*, *130*, 216–221.
- Kelly, J. F., Ruegg, K. C., & Smith, T. B. (2005). Combining isotopic and genetic markers to identify breeding origins of migrant birds. *Ecological Applications*, *15*(5), 1487–1494.

- Liebl, A. L., & Martin, L. B. (2012). Exploratory behaviour and stressor hyper-responsiveness facilitate range expansion of an introduced songbird. *Proceedings of The Royal Society B*, 279(1746), 4375–4381.
- Link, W. A., Sauer, J. R., & Niven, D. K. (2020). Model selection for the North American Breeding Bird Survey. *Ecological Applications*, 30(6), 02137.
- Ma, C., Vander Zanden, H. B., Wunder, M. B., & Bowen, G. J. (2020). assignr: An R package for isotope-based geographic assignment.
- McLaren, I. A. (1981). The incidence of vagrant landbirds on Nova Scotian islands. *The Auk*, 98(2), 243–257.
- McLaren, I. A., Lees, A. C., Field, C., & Collins, K. J. (2006). Origins and characteristics of Nearctic landbirds in Britain and Ireland in autumn: A statistical analysis. *Ibis*, 148(4), 1–20.
- Patten, M. A., & Marantz, C. A. (1996). Implications of vagrant southeastern vireos and warblers in California. *The Auk*, 113(4), 911–923.
- Phillips, B. L., Brown, G. P., & Shine, R. (2010). Evolutionarily accelerated invasions: The rate of dispersal evolves upwards during the range advance of cane toads. *Journal of Evolutionary Biology*, 23(12), 2595–2601.
- Pyle, P. (1997). *Identification guide to North American birds, Part i: Columbidae to Ploceidae*. Slate Creek Press.
- R Core Team. (2020). R: A language and environment for statistical computing. <https://www.R-project.org/>.
- Ralph, C. J. (1978). Disorientation and possible fate of young passerine coastal migrants. *Bird-banding*, 49(3), 237–247.
- Ralph, C. J., & Wolfe, J. D. (2018). Factors affecting the distribution and abundance of autumn vagrant New World warblers in northwestern California and southern Oregon. *PeerJ*, 6, 5881.
- Royle, J. A., & Rubenstein, D. R. (2004). The role of species abundance in determining breeding origins of migratory birds with stable isotopes. *Ecological Applications*, 14, 1780–1788.
- Rubenstein, D. R., Chamberlain, C. P., Holmes, R. T., Ayres, M. P., Waldbauer, J. R., Graves, G. R., & Tuross, N. C. (2002). Linking breeding and wintering ranges of a migratory songbird using stable isotopes. *Science*, 295, 1062–1065.
- Rubenstein, D. R., & Hobson, K. A. (2004). From birds to butterflies: Animal movement patterns and stable isotopes. *Trends in Ecology and Evolution*, 19, 256–263.
- Sauer, J. R., Niven, D. K., Hines, J. E., Ziolkowski, D. J., Jr., Pardieck, K. L., Fallon, J. E., & Link, W. A. (2017). *The North American Breeding Bird Survey, results and analysis 1966 – 2015* (Version 2.07.2017). USGS Patuxent Wildlife Research Center.

- Sauer, J. R., Pendleton, G. W., & Orsillo, S. (1995). Mapping of bird distributions from point count surveys [General Technical Report PSW-GTR-149.]. In C. J. Ralph, J. R. Sauer, & S. Droege (Eds.), *Monitoring bird populations by point counts* (pp. 151–160). U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station.
- Sibley, D. A. (2014). *The Sibley Guide to Birds* (Second). Alfred A. Knopf.
- Van Wilgenburg, S. L., & Hobson, K. A. (2011). Combining stable-isotope ( $\delta D$ ) and band recovery data to improve probabilistic assignment of migratory birds to origin. *Ecological Applications*, *21*(4), 1340–1351.
- Veit, R. R., & Lewis, M. A. (1996). Dispersal, population growth, and the Allee effect: Dynamics of the house finch invasion of eastern North America. *The American Naturalist*, *148*(2), 255–274.
- Wassenaar, L. I. (2008). An introduction to light stable isotopes for use in terrestrial animal migration studies. In K. A. Hobson & L. I. Wassenaar (Eds.), *Tracking animal migration with stable isotopes* (pp. 21–44). Academic Press.
- Wassenaar, L., & Hobson, K. (2003). Comparative equilibrium and online technique for determination of non-exchangeable hydrogen of keratins for use in animal migration studies. *Isotopes in Environmental and Health Studies*, *39*(3), 211–217.
- White, S., & Kehoe, C. (2014). Report on scarce migrant birds in Britain in 2008–10, Part 2: Passerines. *British Birds*, *107*(3), 251–281.
- Williamson, K. (1959). The September drift-movements of 1956 and 1958. *British Birds*, *52*, 334–377.
- Wunder, M. B. (2010). Using isoscapes to model probability surfaces for determining geographic origins. In J. B. West, G. J. Bowen, T. E. Dawson, & K. P. Tu (Eds.), *Isoscapes: Understanding movement, pattern, and process on earth through isotope mapping* (pp. 251–270). Springer.
- Zawadzki, L. C., Veit, R. R., & Manne, L. L. (2019). The influence of population growth and wind on vagrancy in a North American passerine. *Ardea*, *107*(2), 131–147.

# 4

## Factors influencing occurrence of vagrant New World warblers in the eastern United States during autumn migration

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## 4.1 Abstract

Though vagrancy occurs in most migratory bird species, it is unknown what factors influence their occurrence and abundance. Previous studies have found that, among a series of factors, population size and population growth explain most of the variation in vagrant occurrence. In this study, we expanded upon previous models, to determine which factors influence vagrancy of New World warblers to New England. Our models included factors such as population size, population growth – i.e. number of young produced in previous spring, vagrant distance – i.e. the distance from the centre of the breeding range to the centre of the study area, and angular deviation from the normal migratory bearing, and breeding location – i.e. the region of North America where the breeding range is located. We also constructed models for each species separately to determine how population size and growth within distinct regions of their breeding range influence vagrant patterns. We found that vagrancy is strongly correlated with population size, vagrant distance, and breeding location. As the size of the population increases, and the length of the vagrant distance decreases, vagrant occurrence increases. Additionally, vagrant occurrence increases if the species has a northeasterly breeding range. For our separate species models, population size and growth were negatively correlated with vagrancy, and the breeding region that best predicted vagrancy for the majority of species was located on the edge of the breeding range. It is likely that vagrancy is a density-dependent phenomenon, in which vagrants respond to changing conditions in a quadratic fashion. Numbers of vagrants increase as population growth increases, since more vagrants are produced (i.e. an irruption), but vagrants will also increase when the population growth slows or decreases, since individuals will emigrate out of areas that can no longer support the entire population (i.e. an eruption).

## 4.2 Introduction

Vagrancy is a process in which individual birds travel far outside of their known species' range (Grinnell 1922), often juveniles on their first autumn migration (Baker 1978). While vagrancy occurs in a multitude of migratory species, the factors that influence vagrant occurrence are not well understood. Theories on vagrancy hypothesise that vagrancy occurs as a result of inheritance of an incorrect compass orientation (Rabøl 1969, DeSante 1973, Cottridge and Vinicombe 1996), or an error during migration due to strong winds or weather patterns (Williamson 1959, 1961; Elkins 1979, 2005, 2008; McLaren 1981), that result in seemingly misoriented flights in inexperienced individuals. However, these theories are difficult to test quantitatively, and they do not explain why vagrants occur each year, or why there is interannual variation in vagrant abundance across species (Hengeveld 1989, Veit 1990). Other factors, such as population variables or migratory characteristics, may better explain vagrant occurrence.

Previous studies have attempted to analyse possible factors that influence numbers of vagrants. Population factors (e.g. population size (DeBenedictis 1971; DeSante 1983; Hampton 1997; Veit 1990, 1997, 2000; Elkins 1999; Thorup 2004; Jiguet et al. 2008; De Juana and Garcia 2010; Farnsworth et al. 2015; Ralph and Wolfe 2018; Zawadzki et al. 2019), growth (Veit 1997, McLaren et al. 2006, Zawadzki et al. 2019), and range size (Pfeifer et al. 2007, Umegaki 2014)), migratory factors (e.g. migratory distance (DeBenedictis 1971, Hampton 1997, Robbins 1980, McLaren et al. 2006, Pfeifer et al. 2007, Umegaki 2014, Ralph and Wolfe 2018), direction (Thorup 2004, Umegaki 2014), and angular deviation from the migratory route (DeBenedictis 1971, Ralph and Wolfe 2018)), and morphological factors (e.g. body mass (Robbins 1980, McLaren et al. 2006, Pfeifer et al. 2007) and wing length (McLaren et al. 2006, Pfeifer et al. 2007)), have all been analysed for their influence on vagrancy for both North American and European species.

Among these factors, the majority of models have shown that population size has a strong influence over vagrant occurrence (DeBenedictis 1971; DeSante 1983; Veit 1990, 1997,

2000; Thorup 2004; Pfeifer et al. 2007 (by proxy of range size); Jiguet et al. 2008; De Juana and Garcia 2010; Ralph and Wolfe 2018; Zawadzki et al. 2019), followed by migratory distance in some models (DeBenedictis 1971, Ralph and Wolfe 2018). This link between population size and vagrant abundance has been hypothesised before in numerous studies on patterns of vagrant abundance (e.g. Grinnell 1922; Williamson 1963, 1969; Holt 1978; Veit 1990, 2005, 2008; Phillips 2000), and is well-cited in the literature as a possible driver of vagrancy. More recently, population growth has also been shown to be strongly correlated with numbers of vagrants (Veit 1997, McLaren et al. 2006, Zawadzki et al. 2019), suggesting that vagrancy may be a density-dependent phenomenon.

In this study, we aimed to test which factors most influenced vagrant occurrence of sixteen New World warblers to New England on the east coast of North America. Previous studies have mainly focused on occurrence of vagrants to western North America (primarily California), or Europe. Factors were chosen based on those found to be the most influential in previous studies (DeBenedictis 1971; Robbins 1980; DeSante 1983; Veit 1990, 1997, 2000; Thorup 2004; McLaren et al. 2006; Pfeifer et al. 2007; Jiguet et al. 2008; De Juana and Garcia 2010; Ralph and Wolfe 2018; Zawadzki et al. 2019), including population size, population growth, vagrant distance (i.e. the distance required to travel from the centre of the breeding range to the centre of the vagrant site), angular deviation from the historical migratory bearing, and breeding location. We hypothesised that population size and growth would have the greatest influence on vagrant occurrence based on strong correlations in previous studies. We also used the output of our model to predict how many individuals of unrecorded vagrant New World warblers to New England should have arrived based on their population and migratory factors during the study period (Robbins 1980, Ralph and Wolfe 2018).

This study additionally expanded upon analyses by Zawadzki et al. (2019), who found that population size and growth in the core of the species' breeding range strongly influenced occurrence of vagrant Ash-throated Flycatchers (*Myiarchus cinerascens*) to the east coast of North America, where the 'core' is defined as the region of highest abundance. By incorporating data on population size and growth, we constructed separate

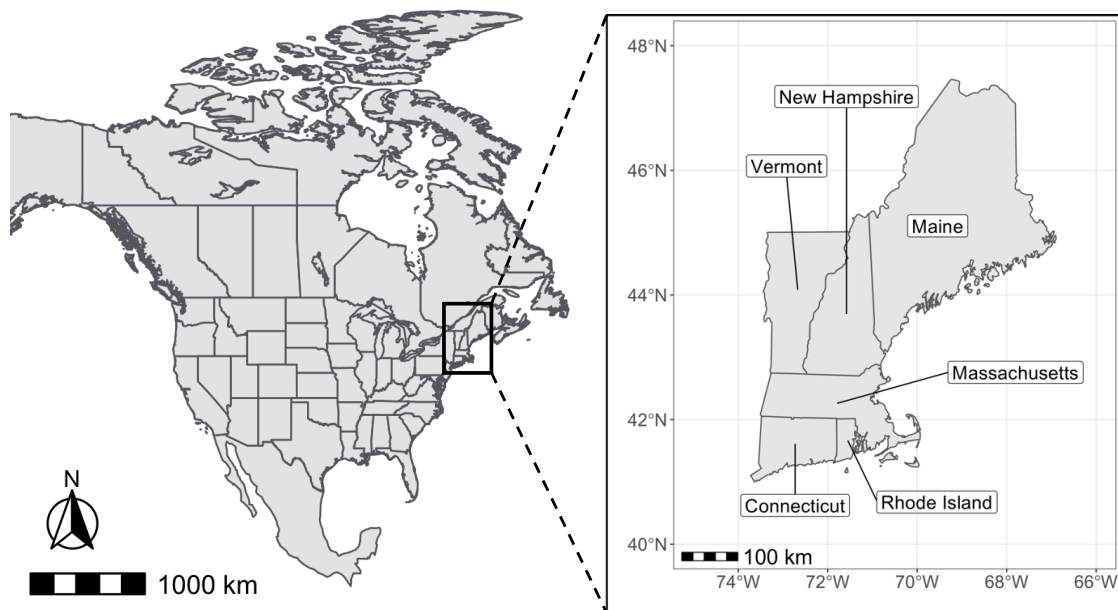
models for each species to determine whether population factors in separate regions of the species' breeding range, particularly in the core of the breeding range, influenced abundance of vagrants. We hypothesised that regions that produced the highest numbers of young (i.e. regions with the highest population growth) would produce high numbers of vagrants, resulting in a strong correlation between population size and growth, and numbers of observed vagrants to New England.

## 4.3 Methods

### 4.3.1 Vagrant records

The study area was confined to the region of New England in the northeastern United States, which comprises the states of Maine, New Hampshire, Vermont, Massachusetts, Rhode Island, and Connecticut (Figure 4.1). Species of migratory New World Warblers that occur as vagrants in New England during autumn migration were selected for analysis. Vagrants were defined as individuals of species that do not historically breed, migrate, or winter in the region (DeSante 1973), and were chosen for further analysis if they had at least one record in New England during autumn migration between 1966 – 2019. Twenty-two species were classified as vagrants in this region, of which 18 had at least one sighting during the study period (Table 4.1). However, only 16 of these species were chosen for further study due to the availability of breeding population data from the Breeding Bird Survey (BBS; Pardieck et al. 2020). Both Audubon's Warbler (*Setophaga coronata auduboni*) and Western Palm Warbler (*Setophaga palmarum palmarum*) were excluded since they are western subspecies of the Yellow-rumped Warbler (*Setophaga coronata*) and Palm Warbler (*Setophaga palmarum*), respectively, and are not differentiated from their eastern subspecies during BBS counts.

Vagrant sightings were extracted from seasonal bird reports in state bird journals, as well as rarities committee reports, across New England. Seasonal bird reports aim to report every bird seen across the state during each seasonal period (e.g. "Fall Season: Aug



**Figure 4.1.** Map portraying the study area of New England (inset map) and its location within North America (main map).

through Nov”; *Bird Observer*), including any rarities, whereas committee reports only report accepted records of rare birds for the state. Journals from which seasonal reports were extracted included *Maine Bird Notes*, *New Hampshire Bird Records*, *Records of Vermont Birds*, *Bird Observer* (for Massachusetts), and *The Connecticut Warbler*. Committee reports included the Maine Bird Records Committee Reports, Vermont Bird Records Committee Annual Reports, the Avian Records Committee of Connecticut (ARCC) Reports, and the Rhode Island Avian Records Committee (RIARC) Year Summaries, and predecessor Rhode Island Ornithological Club (RIOCI) Year Summaries. Records were extracted from the period of autumn migration from August to February, between 1966 – 2019.

Not all states had records available across the entire study period since some journals did not begin publication until over a decade later (Table 4.2). Despite this, journals sometimes mentioned sighting records that occurred prior to publication which we were able to include in our analysis. The earliest year of available vagrant sightings for any of the 16 species studied was 1975 for Maine, 1975 for Vermont, 1972 for New Hampshire, 1970 for Massachusetts, 1967 for Connecticut, and 1994 for Rhode Island.

**Table 4.1.** 22 different species of New World warblers that are classified as vagrants in New England. Vagrants are species that do not breed, winter, or migrate through a particular region. Species 1 to 16 were analysed in the ‘All Species Model’, while species 17 and 18 were excluded due to lack of BBS data. Species 19 to 22 were also excluded from the ‘All Species Model’ since they were unrecorded in New England during the study period. Numbers of vagrants for species 20 to 22 were predicted using the resulting ‘All Species Model’. We could not predict numbers for species 19 due to lack of BBS data.

#	Species	AOU code	Breeding Location	Vagrants	North American population	BBS Trend	Vagrant distance (km) <sup>1</sup>	Angular deviation (°)
1	Black-throated Gray Warbler ( <i>Setophaga nigrescens</i> )	BTGW	NW	39	3,100,000	-0.63	3673.64	67.70
2	Cerulean Warbler ( <i>Setophaga cerulea</i> )	CERW	NE	53	530,000	-1.85	1309.33	93.18
3	Golden-winged Warbler ( <i>Vermivora chrysoptera</i> )	GWWA	NE	211	390,000	-1.83	968.96	88.94
4	Hermit Warbler ( <i>Setophaga occidentalis</i> )	HEWA	NW	6	2,500,000	0.09	4093.51	52.97
5	Hooded Warbler ( <i>Setophaga citrina</i> )	HOWA	SE	249	5,200,000	1.09	1531.75	126.52
6	Kentucky Warbler ( <i>Geothlypis formosa</i> )	KEWA	SE	93	2,600,000	-0.67	1611.42	111.31
7	Kirtland's Warbler ( <i>Setophaga kirtlandii</i> )	KIWA	NE	1	4,800	8.59	1340.64	61.96
8	Lucy's Warbler ( <i>Leiothlypis luciae</i> )	LUWA	SW	1	3,000,000	0.53	3723.65	78.99
9	MacGillivray's Warbler ( <i>Geothlypis tolmiei</i> )	MGWA	NW	32	11,000,000	-0.55	3707.31	54.07
10	Painted Redstart ( <i>Myioborus pictus</i> )	PARE	SW	1	130,000	0.38	3627.63	91.77
11	Prothonotary Warbler ( <i>Protonotaria citrea</i> )	PROW	SE	110	2,100,000	-0.71	1723.39	107.18
12	Swainson's Warbler ( <i>Limnothlypis swainsonii</i> )	SWWA	SE	2	160,000	2.11	1902.71	111.01
13	Townsend's Warbler ( <i>Setophaga townsendi</i> )	TOWA	NW	27	21,000,000	-0.14	4209.15	42.77
14	Virginia's Warbler ( <i>Leiothlypis virginiae</i> )	VIWA	SW	3	900,000	-1.11	3343.51	78.79
15	Worm-eating Warbler ( <i>Helminthos vermivorum</i> )	WEWA	SE	92	780,000	0.12	1545.08	123.98
16	Yellow-throated Warbler ( <i>Setophaga dominica</i> )	YTWA	SE	101	2,000,000	0.91	1711.41	120.45
17	Audubon's Warbler ( <i>Setophaga c. auduboni</i> ) <sup>2</sup>	AUWA	NW	28	-	-	3613.98	60.96
18	Western Palm Warbler ( <i>Setophaga p. palmarum</i> ) <sup>2</sup>	WPWA	NE	174	-	-	1948.74	45.31
19	Colima Warbler ( <i>Leiothlypis crissalis</i> ) <sup>3</sup>	COLW	SW	0	25,000	-	3440.98	142.71
20	Golden-cheeked Warbler ( <i>Setophaga chrysoparia</i> ) <sup>4,5</sup>	GCWA	SW	0	110,000	0.00	2859.89	93.66
21	Grace's Warbler ( <i>Setophaga graciae</i> ) <sup>4,5</sup>	GRWA	SW	0	1,500,000	-1.20	3475.50	87.56
22	Red-faced Warbler ( <i>Cardellina rubrifrons</i> ) <sup>4,5</sup>	RFWA	SW	0	250,000	-2.08	3667.60	78.81

<sup>1</sup>The vagrant distance is the distance in km between the centre of the breeding range and the centre of the study area (New England)

<sup>2</sup>Species were excluded from ‘All Species Model’ since BBS data and North American population estimates were unavailable for these species

<sup>3</sup>Species were excluded from ‘All Species Model’ since BBS data was unavailable for these species

<sup>4</sup>Species were excluded from ‘All Species Model’ and annual models because they were not recorded in New England during the study period

<sup>5</sup>Numbers of individuals that could have showed up in New England were predicted for these species using the ‘All Species Model’ (see Section 4.4.2)

**Table 4.2.** Years of publication for state journals and rarities committee reports in New England that were used to extract vagrant records. The earliest vagrant record documented in publications was often earlier than the first date of publication because past records were occasionally mentioned in context of other sightings, or they were just accepted as a record.

State	Publication/Report	Years of publication	Earliest vagrant record
Maine	<i>Maine Bird Notes</i>	1987 – 1999	1975
	Maine Bird Records Committee Reports	2006 – 2020*	
New Hampshire	<i>New Hampshire Bird Records</i>	1982 – 2017	1972
Vermont	<i>Records of Vermont Birds</i>	1973 – 2001	1975
	Vermont Bird Records Committee Annual Reports	1988 – 2019	
Massachusetts	<i>Bird Observer</i>	1973 – 2019	1970
Connecticut	<i>The Connecticut Warbler</i>	1982 – 2019	1967
	Avian Records Committee of Connecticut Reports	1986 – 2019*	
Rhode Island	Rhode Island Avian Records Committee Yearly Summaries	1960 – 2002*	1994

\*Reports were not published annually.

### 4.3.2 All species model

We first constructed a generalised linear model that included 16 study species to analyse which factors most influenced occurrence of autumn vagrancy to New England during our study period. The response variable was a log transformation of the total number of individual vagrants recorded for each species between 1966 – 2019 (see Table 4.1). That is, if two species were recorded 10 and 20 times respectively during the study period, each of those values would be inputted as a single y-value into the model. Explanatory variables were chosen to reflect factors that have been found to most likely influence vagrancy – population size and growth, and migratory distance and direction. Five explanatory variables that matched these factors were selected, and included the size of the North American breeding population ('North American population') (e.g. DeBenedictis 1971), population change during the study period ('BBS trend') (e.g. McLaren et al. 2006, Zawadzki et al. 2019), distance between the centre of the breeding area and the centre of the study area ('vagrant distance') (e.g. Thorup 2004), the angular deviation required to reach the study area ('angular deviation') (e.g. DeSante 1983), and the region of North America where the breeding area is located ("breeding location") (e.g. Robbins

1980, McLaren et al. 2006). We decided to choose vagrant distance over the migratory distance because all of our study species are long-distance migrants. Models of the form:  $\log(\text{Vagrants}) \sim \log(\text{North American Population}) + \text{BBS trend} + \log(\text{Vagrant distance}) + \text{Angular deviation} + \text{Breeding location}$  were constructed.

North American breeding population size was taken from the Partners in Flight population estimates database (Partners in Flight 2020), and was log-transformed for analysis. Data on population change during the study period was taken from the North American Breeding Bird Survey (BBS) trend estimates (Sauer et al. 2017). The BBS is a long-term monitoring program that conducts roadside surveys during the peak breeding season, typically June, to estimate population abundance of avian breeding populations across North America (Pardieck et al. 2020). Raw count data from survey routes are analysed using hierarchical models to calculate an index of abundance for each species in a given survey area (Sauer and Link 2011). BBS trends are then calculated from the ratio of endpoints of the annual indices using Bayesian methods to create interval-specific estimates of population change for a given survey area (Link and Sauer 2002). BBS trends were calculated for the entire ‘Core’ area, which includes the contiguous United States (Link et al. 2020), and has been surveyed for most species from 1966, 1967, or 1968 to 2019. This ‘Core’ area is different from the core of the breeding range that we defined above, and encompasses the main survey area of the BBS. We hypothesised that vagrant occurrence would increase with increasing population size and population growth.

Vagrant distance, the distance between the centre of the breeding area and the centre of the study area, was calculated by measuring the great-circle distance in kilometres between the centroid of the breeding range of each species (BirdLife International and Handbook of Birds of the World 2020) and the centroid of the study area, using the *distHaversine* function from the ‘geosphere’ package in R (Hijmans 2019). This variable was log-transformed for analysis. Angular deviation was calculated by measuring the difference between the angle required to reach the centroid of the wintering range from the centroid of the breeding range, and the angle required to reach the centroid of the study area from the centroid of the breeding range. We hypothesised that vagrant occurrence

would increase the closer the study area was to the breeding range; i.e. individuals that need to travel a shorter distance to a particular region are more likely to arrive at that location than those that are much further away. We further hypothesised that the smaller the angular deviation from the historical migratory route required to reach the study area, the more likely a vagrant was to occur in that region (DeBenedictis 1971, DeSante 1983), under the same logic. Inclusion of angular deviation as a factor does not imply that vagrants are misoriented, as has been often speculated (e.g. DeSante 1973), but rather that the closer a new region is to a species' breeding range, the more likely that species may occur there as a vagrant. How vagrants orient is outside of the scope of this chapter. For a discussion on the orientation of vagrants, see Chapter 2.

Breeding location, the region of North America where the breeding area is located, was defined as a categorical variable with four categories – northeastern North America (“NE”), northwestern North America (“NW”), southeastern North America (“SE”), and southwestern North America (“SW”). Breeding locations were classified for each species based on known breeding areas (BirdLife International and Handbook of Birds of the World 2020). We hypothesised that vagrant occurrence would be influenced by the breeding location, and that species that breed closer to New England (i.e. within NE and SE), would be more likely to occur as vagrants.

### 4.3.3 Predicting vagrants

Using estimates from the ‘All Species Model’, we predicted how many individuals might have been observed as vagrants in New England for three species that do not historically breed, migrate, or winter in New England, but have never been recorded in the region (see Ralph and Wolfe 2018 for a similar analysis). These species include the Golden-cheeked Warbler (*Setophaga chrysoparia*), Grace’s Warbler (*Setophaga graciae*), and the Red-faced Warbler (*Cardellina rubrifrons*) (see Table 4.1). Though the Colima Warbler (*Leiothlypis crissalis*) was also unrecorded in New England, we

were not able to predict the number of possible vagrants with our model due to a lack of BBS records for this species.

#### 4.3.4 Annual models

Annual generalised negative binomial models were constructed separately for each of the study species to determine how population trends influence each vagrant species across the study period. These models were based on findings outlined in Zawadzki et al. (2019) that occurrence of vagrants is linked to greater population growth in the core of the species' range. Separate models were formulated for each breeding region within the BBS 'Core' area based on spatial scales outlined by the U.S North American Bird Conservation Initiative (Bird Studies Canada and NABCI) Committee, known as Bird Conservation Regions (BCRs; Bird Studies Canada and NABCI 2014). BCRs were chosen as spatial scales over states for this study because BCRs are designated based on similar biotic and abiotic characteristics of the habitat, rather than arbitrary state boundaries that were historically designated. Reproductive trends of a breeding population are much more likely to be affected by the abiotic and biotic characteristics of the region, and thus models divided by BCRs will better highlight areas of importance for breeding species and vagrant occurrence.

Only 13 of the 16 study species were included in this analysis. Models could not be constructed for three of our study species – Kirtland's Warbler (*Setophaga kirtlandii*), Lucy's Warbler (*Leiothlypis luciae*), and the Painted Redstart (*Myioborus pictus*) – because they each had only one vagrant sighting across the entire study period. In total, we created 13 sets of models (1 for each species), with 1 to 14 models within each set based on the amount of BCRs each species occupies during the breeding season. One additional model for each species encompassed the whole breeding range within the BBS core area ("SU1").

The response variable for annual models was the number of individual vagrants recorded in the study area for a single species in each season year. A season year was defined

as the time period of autumn migration from August of year  $t$  to February of year  $t + 1$ . Two explanatory variables were extracted from BBS data to represent population size and growth across the study period – BBS index, and BBS difference. BBS index served as a proxy for breeding population size, and was taken as the annual index of abundance from BBS data in year  $t$ . Indices of abundance were extracted for each BCR separately, while one model for each species used the BBS index of abundance for the entire core area. BBS difference served as a proxy for population growth, and was calculated as the difference between the BBS index in year  $t + 1$  and the BBS index in year  $t$ , under the premise outlined in Zawadzki et al. (2019) and Veit (1997, 2000) that the number of young produced in the summer of year  $t$  is represented by the difference in index between year  $t + 1$  and year  $t$ . Models for each species and BCR were built from the following equation: *Vagrants*  $\sim$  *BBS Index* + *BBS Difference*.

Annual models were run using negative binomial errors to account for overdispersion in the dataset (Lindén and Mäntyniemi 2011). Models for each species were ranked using Akaike Information Criterion (AIC) comparison with the function *aictab* from the ‘AICcmodavg’ package in R (Mazerolle 2020) to determine which BCR breeding population influenced vagrancy the most. Corrected AIC values (AICc) were used to account for small sample sizes in the models (Hurvich and Tsai 1989). A model was selected as the best supported model if it had the lowest AICc value, and was at least two AICc values lower than the next best supported model (Burnham and Anderson 2003). Pseudo- $R^2$  values were calculated for each model using the *export\_summs* function from the ‘jtools’ package in R (Long 2020). All analyses were conducted in R (R Core Team 2020).

## 4.4 Results

### 4.4.1 All species model

Out of the five explanatory variables in our model, North American population (Effect size = 0.55,  $p < 0.05$ ), vagrant distance (Effect size = -7.03,  $p < 0.05$ ), and breeding location (Effect size (of NE) = 44.95,  $p < 0.05$ ) were significantly correlated with the number of vagrants detected in the study area during our study period, while BBS trend (Effect size = -0.07,  $p = 0.61$ ) and angular deviation (Effect size = 0.02,  $p = 0.38$ ) did not significantly influence the number of vagrants to our study area (see Table 4.3 for regression estimates).

This model explained 96.0% of the variation in vagrant occurrence (Table 4.4). While vagrant numbers were positively correlated with the size of the North American population, vagrants were negatively correlated with vagrant distance. That is, if the distance between the centre of the breeding range and the centre of the study area decreased, the number of vagrants increased. BBS trends in the breeding range were not significantly correlated with numbers of vagrants, but the negative relationship suggests that as the population growth in the region decreases, numbers of vagrants will increase, which is in direct contrast to previous trends (Veit 1997, McLaren et al. 2006, Zawadzki et al. 2019).

**Table 4.3.** Parameter estimates for the ‘All Species Model’. The model was constructed using the form  $\log(\text{Vagrants}) \sim \log(\text{North American Population}) + \text{BBS trend} + \log(\text{Vagrant distance}) + \text{Angular deviation} + \text{Breeding location}$ . Significant  $p$ -values ( $p < 0.05$ ) are in **bold**. Data from 16 study species were inputted into the model (see Table 4.1).

Predictor	Category	Effect size	$t$ statistic	$p$ -value
North American population	-	0.55	3.06	<b>&lt;0.05</b>
BBS trend	-	-0.07	-0.53	0.61
Vagrant distance	-	-7.03	-3.06	<b>&lt;0.05</b>
Angular deviation	-	0.02	0.93	0.38
Breeding location	NE	44.95	2.58	<b>&lt;0.05</b>
	NW	6.48	2.30	0.05
	SE	1.03	0.68	0.51
	SW	3.72	1.40	0.20

**Table 4.4.** Analysis of variance (ANOVA) values for the ‘All Species Model’. The model was constructed using the form  $\log(\text{Vagrants}) \sim \log(\text{North American Population}) + \text{BBS trend} + \log(\text{Vagrant distance}) + \text{Angular deviation} + \text{Breeding location}$ . Significant  $p$ -values ( $p < 0.05$ ) are in **bold**. Data from 16 study species were inputted into the model (see Table 4.1).

Predictor	Sum of Squares	$F$ statistic	$p$ -value	Deviance (%)	AICc	Pseudo- $R^2$
North American population	3.89	9.34	< <b>0.05</b>	14.73		
BBS trend	0.12	0.28	0.61	2.80		
Vagrant distance	3.91	9.38	< <b>0.05</b>	34.4	68.32	0.96
Angular deviation	0.36	0.87	0.38	0.27		
Breeding location	5.31	4.24	< <b>0.05</b>	5.31		

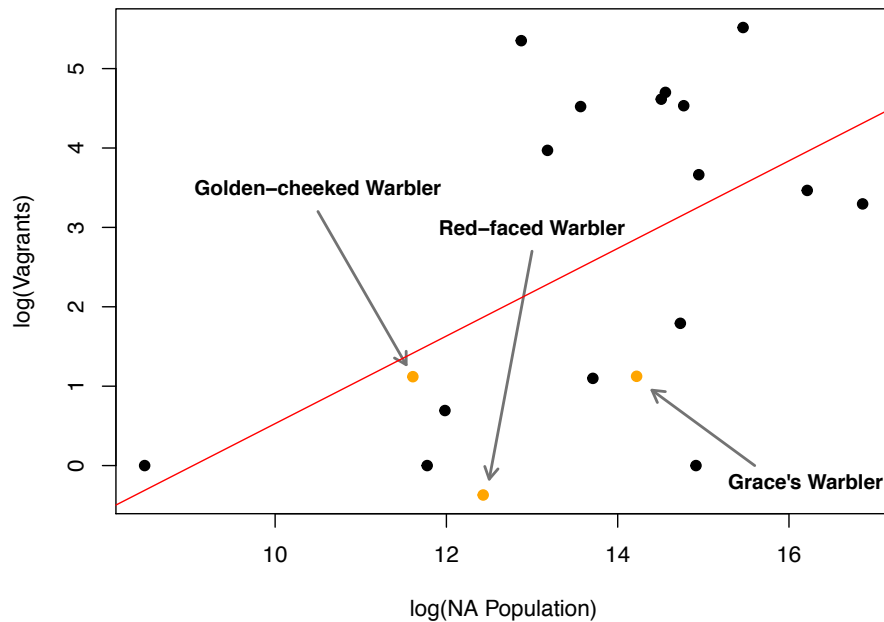
#### 4.4.2 Predicting vagrants

The number of predicted records for the Golden-cheeked Warbler and Grace’s Warbler to New England between 1966 and 2019 was approximately three individuals, and for Red-faced Warbler was approximately one individual (Figure 4.3), based on their population size, population change across the study period, distance to reach New England from the breeding range, angular deviation required to reach New England, and breeding location.

#### 4.4.3 Annual models

The annual models did not indicate clear trends between population size and growth, and the number of vagrant sightings in New England (Table S4.1). Ten out of the thirteen species modelled had at least one model with a significant predictor. For eight species, BBS index was significantly correlated with vagrancy in at least one model; for ten species, BBS difference was significantly correlated with vagrancy in at least one model; and for six species, both BBS index and BBS difference were significantly correlated with vagrancy in at least one model. For three species, none of the predictors were significantly correlated with vagrant occurrence in any of the models.

In the best supported model for each species, five species had BBS index as the sole significant parameter, one species had BBS difference as the sole significant parameter, two species had both BBS index and BBS difference as significant parameters, and for five species, neither predictor was significant. Either BBS index, BBS difference, or



**Figure 4.2.** The log of the North American population versus the log of the number of vagrants for each species studied (see Table 4.1 for details). The 16 study species are in black, and the three species that we predicted values for are in orange. Values were predicted by inputting the size of the North American population, the BBS trend, Vagrant distance, Angular deviation, and Breeding location into the resulting equation derived for the ‘All Species Model’. Golden-cheeked (*Setophaga chrysoparia*) and Grace’s Warbler (*Setophaga graciae*) were predicted to have occurred three times in New England, while Red-faced Warblers (*Cardellina rubrifrons*) was predicted to have occurred once.

both were negatively correlated with vagrancy in all of the best supported models but one (i.e. five models had one negative predictor, and both predictors were negative in seven models). That is, for all but the Swainson’s Warbler (*Limnothlypis swainsonii*), as population size and/or growth declined in the breeding range, numbers of vagrants of that species in New England increased.

For 12 out of 13 species, the region selected as the best supported model was located along the edge of the species’ breeding range. The region selected as the best supported model for the Kentucky Warbler (*Geothlypis formosa*), was close the eastern edge of the range, but not directly along it. The core of the breeding range (i.e. the region of highest abundance according to BBS relative abundance maps; Sauer et al. 2017; maps available at: [https://www.mbr-pwrc.usgs.gov/bbs/ra2015/ra2015\\_red\\_v3.shtml](https://www.mbr-pwrc.usgs.gov/bbs/ra2015/ra2015_red_v3.shtml)), was the best supported ( $n = 3$ ), or the next best supported model ( $n = 2$ ), for 5 out of 13 species

– Cerulean Warbler (*Setophaga cerulea*), Prothonotary Warbler (*Protonotaria citrea*), Townsend’s Warbler (*Setophaga townsendi*), Virginia’s Warbler (*Leiothlypis virginiae*), and Yellow-throated Warbler (*Setophaga dominica*).

## 4.5 Discussion

Our study highlighted two key points about the occurrence of vagrant New World warblers to New England. Overall, vagrant New World warblers were significantly influenced by the size of their North American breeding population, the distance required to reach the vagrant site, and their breeding location within North America, but they were not significantly influenced by the BBS trend or angular deviation to the vagrant site (Table 4.3). This finding is in line with previous studies that have shown a strong effect of population size on vagrant abundance (e.g. DeBenedictis 1971; DeSante 1983; Veit 1990, 1997, 2000; Thorup 2004; Pfeifer et al. 2007 (by proxy of range size); Jiguet et al. 2008; De Juana and Garcia 2010; Ralph and Wolfe 2018; Zawadzki et al. 2019), and a subsequent effect of distance (DeBenedictis 1971, Thorup 2004, Pfeifer et al. 2007). At the species level, there was an effect of population size and growth on vagrancy, and regions located along the edge of the species’ range best predicted vagrancy to New England. The range edge was the core of the species’ range for five species. This finding supports those found in previous studies, which found clear, positive trends between population size and growth along the edge (Veit 1997, 2000) or core (Zawadzki et al. 2019) of the breeding range and vagrant abundance. However, unlike previous studies, both population size and growth were negatively correlated with vagrancy in the majority of models.

For our ‘All Species Model’, the size of the source population was positively correlated with species’ abundance, and explained approximately 14.7% variation in abundance in our model (Table 4.4). The majority of studies have found that the size of the source population was the (or one of the) most influential factors in determining vagrant occurrence (e.g. DeBenedictis 1971 (60%), Thorup 2004, Ralph and Wolfe 2018), while

a few have shown little (30%; DeSante 1983), to no effect (Hampton 1997, Umegaki 2014) of population size on vagrant abundance. The small influence that population size had on abundance of New World warblers to New England could be due to the small amount of variation present in the size of the population across the study species (Table 4.1). This does not detract from the importance of population size as a factor in determining vagrant occurrence. It is still highly significant in the model, and the larger the population size of a species, the more vagrants are likely to be present within the population (Figure 4.2).

Vagrant distance, (i.e. the distance from the centre of the breeding range to the centre of the study area), explained the majority of variation in our model, at 34.4% (Table 4.4). It is intuitively logical that a species whose range lies closer to sites of potentially suitable habitat, will occur more often as vagrants at those sites during autumn migration. Though vagrants can, and do, travel over extraordinary distances (e.g. Yellow-nosed Albatross (*Thalassarche chlororhynchos*) (Veit 2005), Cattle Egret (*Bubulcus ibis*) (Hengeveld 1989), Eurasian Collared Dove (*Streptopelia decaocto*) (Romagosa 2020), Lesser Black-backed Gull (*Larus fuscus*) (see Chapter 5), and Ross's Gull (*Rhodostethia rosea*) (Bledsoe and Sibley 1985)), our analysis shows that, at least for New World warblers in North America, they may be more likely to travel to new areas closer to their breeding range, than to those much farther away. This result was further emphasised by the significance of breeding location in the model. Though the breeding location only explained a small amount of the variation in our models at 5.31% (Table 4.4), species which had breeding ranges in the northeastern region of North America were more likely to occur as vagrants, which is the region closest to our study area. Our result contradicts with results found in other studies. Hampton (1997), Pfeifer et al. (2007), and Umegaki (2014) did not find any relationship between vagrant distance and vagrant occurrence. However, Pfeifer et al. (2007) and Umegaki (2014) studied the occurrence of Palearctic vagrants to Europe and Japan, respectively, while Hampton (1997) studied the occurrence of vagrants to California. It is possible that the geographical scope of each study has influenced the results.

The three unrecorded species to New England, the Golden-cheeked Warbler, Grace's Warbler, and Red-faced Warbler, were predicted to have occurred three times, three times, and once, respectively. The low numbers of possible occurrence for these three species may result from their relatively small ranges, within the southern United States and Central America. Pfeifer et al. (2007) found a strong correlation between the size of a vagrant species' breeding range and the occurrence of vagrants. A smaller range lends itself to a smaller population, and smaller populations will produce fewer vagrants. Additionally, Golden-cheeked Warblers are currently an endangered species, and their population is already threatened (IUCN 2020), and both Grace's Warbler and Red-faced Warbler are short-distance migrants and are resident in some parts of their range (Martin and Barber 2020, Stacier and Guzy 2020). It is therefore possible that both vagrants have never occurred in New England as a result of their small range and short migratory routes, rather than having been missed by birders.

From our annual models, we have found that the BBS index and BBS difference in specific BCRs of each species (often more than one) are significantly related to vagrancy. That is, population size and/or growth did have an effect on vagrant occurrence in ten of the best supported models. The regions that best predicted vagrant occurrence to New England for all of the species studied were located on the edge of the breeding range, though for the Kentucky Warbler, while the region was not located on the exact range edge, it was close to it. These results are in line with our analyses on the origin of vagrants in Chapter 3. In Chapter 3, we found that vagrants were more likely to originate from the edge of their range rather than the centre. Since the vagrants in our study are better predicted by populations on the range edge, it is possible that they originated from these regions as well. It has also been shown that birds that occupy range edges are more likely to engage in exploratory behaviour and interact with novel objects (Liebl and Martin 2012, 2014). This would explain why the vagrant species in our study are predicted by regions along the edge of their range, rather than the centre – birds that are more prone to dispersal and vagrant movements, may be those that occupy range edges.

For some species ( $n = 3$ ), such as the Prothonotary Warbler, the best model was also within the core of the species range (Table S4.1). As stated previously, the 'core' of the species range is the region of highest abundance in the breeding range. This finding was discovered by Zawadzki et al. (2019) for vagrant Ash-throated Flycatchers to the east coast of the United States. The model that best explained vagrant occurrence of Ash-throated Flycatchers was the core of the species range in Arizona, and included BBS index and BBS difference as significant parameters in the model. However, even this result is seemingly confusing as Prothonotary Warbler populations have been significantly declining across the whole of their range, including within the core of their range, whereas Ash-throated Flycatcher populations are increasing in Arizona, and across their range.

From the best supported models chosen (except for the Swainson's Warbler), BBS index, BBS difference, or both were negatively correlated with vagrancy. That is, if the population size, or the population growth decreases, the number of vagrants seen in New England will increase. This trend was also evident in our 'All Species Model', where BBS trend was negatively correlated with vagrancy (albeit non-significantly; Table 4.3). Why numbers of vagrants would increase in relation to decreasing populations is not immediately clear. It could be that as populations decrease, individuals are more likely to escape poor conditions, resulting in an increased number of vagrants that year. This seems to directly counter previous findings that vagrants will increase in response to increasing populations (e.g. Veit 1990, 1997, 2000; Zawadzki et al. 2019), but they may in fact be two sides of the same coin.

The core of the premise that vagrancy is related to population growth is that vagrancy is a density-dependent phenomenon. During times of prosperity, populations will increase in response to an abundance of resources (Patten and Burger 1998, Lees and Gilroy 2009), consequently, resulting in the production of more vagrants (Veit 2008). However, after this initial population boom, the size of the current population may exceed the amount of available resources (Newton 2006). Consequently, dispersal and vagrancy will increase, resulting in emigration away from the population to find new resources (Newton 2006, Veit 2008, Lees and Gilroy 2009). Thus, when populations increase, we see an increase

in vagrants, first due to the initial increase in the population itself, and then in response to the ratio of population density to resource availability (Veit 2008). When the population is no longer increasing, and populations begin to decline, this is a signal to individuals that resources and conditions are poor. Individuals will die if they remain in areas of poor resources, and may be more inclined to disperse outwards to find areas with much more suitable habitat (Southwood et al. 1974, Newton 2006, Lees and Gilroy 2009). In this case, when populations are decreasing, we will also see an increase in vagrants out of these poor areas. Vagrancy may thus be related to population differently than previously thought. It is possible that vagrancy is related to population growth in a quadratic fashion, where vagrants are high when populations are well above or below the carrying capacity of the population, but vagrant numbers remain low when populations are stable.

Vagrancy, as a density-dependent phenomenon, may be related to changing conditions within regions of the breeding area, either due to food availability or habitat change. Patten and Burger (1998) found that vagrant New World warblers respond to changes in spruce budworm (*Chorisonneura fumiferana*) populations the previous spring. In years of high food availability, reproductive success may increase, resulting in an increase in the number of vagrants in that population. However, when food availability is low, vagrants will increase in search of suitable resources. This response is similar to irruptions that occur in boreal owl species (Cheveau et al. 2004, Newton 2006, Cote et al. 2007, Bowman et al. 2010), where populations will increase when prey is abundant, but movements outside of the area will increase when prey densities are low, resulting in a large emigration of individuals to new regions. In relation to habitat, DeBenedictis (1971) found that vagrancy is positively correlated with seral stage of the breeding habitat, in which species that breed in early seral stages are more likely to occur as vagrants, while species in mature stages are less likely to occur as vagrants. This results from the rate of change of the habitat – early seral stage habitat will become unsuitable for breeding much faster than mature seral stage habitat, resulting in increased dispersal outside of breeding areas. DeSante (1983) later hypothesised that proportions of vagrants will increase with increasing rates of habitat change in both the breeding and wintering range, since dispersers are selected for when habitats change (Southwood et al. 1974).

Patten and Marantz (1996) also hypothesised in their study on patterns of vagrancy of vireos and warblers to California, that loss of habitat may have resulted in increased dispersal of individuals outside of their range. Therefore, if population growth slows in the breeding range, due to habitat loss and deterioration of habitat, vagrants may increase to escape poor conditions and find more suitable habitat.

Our study highlights the hypothesis that vagrancy is density-dependent and relies heavily on, not only the population dynamics of the region, but where that region is situated in relation to the rest of the range. Future studies should include habitat change across the breeding range of each species to better understand how population size and growth, as well as distance, influence vagrancy in the context of their habitat. Suitability of the surrounding area, including the study area, may also be an important factor in where and when vagrants occur.

## **4.6 Acknowledgements**

Thanks to the thousands of dedicated participants and compilers for the annual North American Breeding Bird Survey (BBS), without which this study would not have been possible. The utmost thanks are also given to the enthusiastic birdwatchers and observers throughout New England, and North America, who continue to document vagrancy in action. Data collected by these observers are invaluable to continued efforts to study vagrancy. We also thank the hardworking editors and compilers of seasonal reports of *Maine Bird Notes*, *New Hampshire Bird Records*, *Records of Vermont Birds*, *Bird Observer*, and *The Connecticut Warbler*, as well as the committee members that collected and evaluated records for regional rarities committee reports. Lastly, we thank Ollie Padget for comments and suggestions on the model analysis in this study, and Richard Veit for stimulating discussions on this topic.

## **4.7 Supplementary Material**

See next page for supplementary material.

**Table S4.1.** Outputs from the annual models for 13 species. Models for each species and BCR were constructed using the form:  $Vagrants \sim BBS\ Index + BBS\ Difference$ . For each species, models were ranked using the Akaike Information Criterion for small sample sizes (AICc). The best supported model for each species is in **bold**. Values listed for each predictor in the model are effect sizes and their corresponding  $p$ -values. Pseudo- $R^2$  was calculated for each model.

AOU code	BCR	BCR name	BBS Trend	BBS Index	BBS $p$ -value	BBS Difference	$p$ -value	AICc	$\Delta$ AICc	Log-likelihood	Pseudo $R^2$
BTGW	<b>S34</b>	<b>Sierra Madre Occidental</b>	<b>-0.54</b>	<b>-0.62</b>	<b>&lt; 0.001</b>	<b>-0.36</b>	<b>0.668</b>	<b>115.31</b>	<b>0.00</b>	<b>-53.22</b>	<b>0.28</b>
	S05*	Northern Pacific Rainforest	-0.75	-0.37	< 0.01	-1.14	< 0.05	118.06	2.75	-54.6	0.24
	SU1	Survey-wide (core only)	-0.63	-1.29	< 0.01	-2.98	0.159	119.11	3.80	-55.12	0.22
	S15	Sierra Nevada	-0.72	-0.34	< 0.01		0.777	122.19	6.88	-56.66	0.16
	S10	Northern Rockies	0.06	198.05	< 0.05	237.56	0.291	124.51	9.20	-57.82	0.12
	S32	Coastal California	-0.21	-10.35	0.058	-22.96	0.189	126.26	10.96	-58.7	0.08
	S16	Southern Rockies/colorado Plateau	-0.41	-0.28	0.867	4.69	0.349	129.33	14.03	-60.23	0.02
	S09	Great Basin	0.33	-1.07	0.428	2.26	0.557	129.46	14.16	-60.3	0.02
CERW	<b>S25</b>	<b>West Gulf Coastal Plain/Ouachitas</b>	<b>-2.36</b>	<b>-15.55</b>	<b>0.134</b>	<b>-42.95</b>	<b>0.471</b>	<b>147.05</b>	<b>0.00</b>	<b>-69.1</b>	<b>0.08</b>
	SU1	Survey-wide (core only)	-1.85	-2.73	0.092	-21.85	0.055	147.7	<b>0.65**</b>	-69.43	0.10
	S28*	Appalachian Mountains	-1.95	-0.58	0.131	-4.67	< 0.05	147.77	<b>0.73**</b>	-69.47	0.09
	S24	Central Hardwoods	-1.73	-4.84	0.126	-16.17	0.659	149.08	2.03	-70.12	0.07
	S23	Prairie Hardwood Transition	-1.26	-10.36	0.221	83.35	0.332	149.73	2.69	-70.45	0.06
	S29	Piedmont	-0.12	-51.25	0.178	-162.39	0.213	149.92	2.88	-70.55	0.05
	S22	Eastern Tallgrass Prairie	-2.31	-24.90	0.257	182.79	0.601	150.95	3.91	-71.06	0.03
	S13	Lower Great Lakes/ St. Lawrence Plain	-1.61	-4.76	0.376	-31.69	0.495	151.45	4.40	-71.31	0.02

\*BCR is located in the core of the species' breeding range. The core was determined from BBS relative abundance maps ([https://www.mbr-pwrc.usgs.gov/bbs/ra2015/ra2015\\_red\\_v3.shtml](https://www.mbr-pwrc.usgs.gov/bbs/ra2015/ra2015_red_v3.shtml)) as the location with the highest relative abundance within the breeding range.

**Table S4.1 (cont.).** Outputs from the annual models for 13 species. Models for each species and BCR were constructed using the form: *Vagrants* ~ *BBS Index* + *BBS Difference*. For each species, models were ranked using the Akaike Information Criterion for small sample sizes (AICc). The best supported model for each species is in **bold**. Values listed for each predictor in the model are effect sizes and their corresponding *p*-values. Pseudo-*R*<sup>2</sup> was calculated for each model.

AOU code	BCR	BCR name	BBS Trend	BBS Index	<i>p</i> -value	BBS Difference	<i>p</i> -value	AICc	ΔAICc	Log-likelihood	Pseudo <i>R</i> <sup>2</sup>	
CERW	S12	Boreal Hardwood Transition	-0.24	132.97	0.352	-294.58	0.666	151.48	4.44	-71.32	0.02	
	S30	New England/mid-atlantic Coast	2.75	13.78	0.365	-33.83	0.834	151.77	4.72	-71.47	0.02	
	S27	Southeastern Coastal Plain	-0.07	24.92	0.881	102.33	0.86	152.56	5.52	-71.86	0.00	
GWWA	<b>S06</b>	<b>Boreal Taiga Plains</b>	<b>3.37</b>	<b>-6.52</b>	<b>0.05</b>	<b>-18.94</b>	<b>0.554</b>	<b>259.25</b>	<b>0.00</b>	<b>-125.19</b>	<b>0.07</b>	
	S28	Appalachian Mountains	-6.26	-1.69	<0.01	-9.91	<0.01	260.09	<b>0.85**</b>	-125.63	0.19	
	S23	Prairie Hardwood Transition	-3.71	-2.61	<0.01	-3.26	0.544	264.46	5.21	-127.81	0.12	
	S30	New England/mid-atlantic Coast	-3.83	-23.47	<0.05	-117.35	0.375	266.03	6.78	-128.6	0.09	
	SU1	Survey-wide (core only)	-1.83	-2.07	<0.05	-6.39	0.204	267.92	8.68	-129.54	0.06	
	S14	Atlantic Northern Forest	-3.3	-3.92	0.313	-50.35	0.133	268.23	8.99	-129.7	0.06	
	S13	Lower Great Lakes/ St. Lawrence Plain	-1.23	7.29	0.174	3.57	0.83	269.44	10.20	-130.31	0.03	
	S12*	Boreal Hardwood Transition	-0.69	1.01	0.382	-0.64	0.808	270.07	10.82	-130.62	0.02	
	HEWA	<b>S09</b>	<b>Great Basin</b>	<b>0.72</b>	<b>1.41</b>	<b>0.446</b>	<b>-8.93</b>	<b>0.194</b>	<b>43.37</b>	<b>0.00</b>	<b>-17.25</b>	<b>0.12</b>
	S15	Sierra Nevada	-0.69	-0.20	0.229	-0.55	0.438	44.5	<b>1.13**</b>	-17.82	0.08	
	S32	Coastal California	0.66	19.91	0.323	-27.03	0.701	44.99	<b>1.62**</b>	-18.06	0.06	
	SU1	Survey-wide (core only)	0.09	-0.37	0.538	-1.90	0.281	45.3	<b>1.92**</b>	-18.21	0.05	
S05*	Northern Pacific Rainforest	0.22	-0.11	0.63	-0.41	0.475	45.97	2.60	-18.55	0.02		

\*BCR is located in the core of the species' breeding range. The core was determined from BBS relative abundance maps ([https://www.mbr-pwrc.usgs.gov/bbs/ra2015/ra2015\\_red\\_v3.shtml](https://www.mbr-pwrc.usgs.gov/bbs/ra2015/ra2015_red_v3.shtml)) as the location with the highest relative abundance within the breeding range.

**Table S4.1 (cont.).** Outputs from the annual models for 13 species. Models for each species and BCR were constructed using the form: *Vagrants* ~ *BBS Index* + *BBS Difference*. For each species, models were ranked using the Akaike Information Criterion for small sample sizes (AICc). The best supported model for each species is in **bold**. Values listed for each predictor in the model are effect sizes and their corresponding *p*-values. Pseudo-*R*<sup>2</sup> was calculated for each model.

AOU code	BCR	BCR name	BBS Trend	BBS Index	<i>p</i> -value	BBS Difference	<i>p</i> -value	AICc	ΔAICc	Log-likelihood	Pseudo <i>R</i> <sup>2</sup>
HOWA	<b>S37</b>	<b>Gulf Coastal Prairie</b>	<b>-0.54</b>	<b>-11.63</b>	<b>&lt; 0.01</b>	<b>35.19</b>	<b>0.055</b>	<b>257.09</b>	<b>0.00</b>	<b>-124.12</b>	<b>0.38</b>
	S31	Peninsular Florida	-1.67	-277.18	< 0.001	-1125.35	< 0.05	259.03	<b>1.94**</b>	-125.1	0.40
	S21	Oaks and Prairies	2.36	61.33	< 0.001	211.86	0.346	261.15	4.06	-126.15	0.32
	S13	Lower Great Lakes/ St. Lawrence Plain	3.22	1.71	< 0.001	-0.89	0.771	263.2	6.11	-127.18	0.35
	S14	Atlantic Northern Forest	0.65	300.57	< 0.001	509.64	0.416	264.38	7.29	-127.77	0.34
	S23	Prairie Hardwood Transition	1.9	54.47	< 0.001	-78.42	0.507	266.38	9.30	-128.78	0.31
	S29	Piedmont	1.43	0.91	< 0.001	3.36	0.071	266.57	9.48	-128.87	0.31
	SU1	Survey-wide (core only)	1.09	0.89	< 0.001	-0.37	0.747	266.94	9.85	-129.05	0.30
	S28*	Appalachian Mountains	1.14	0.45	< 0.001	0.02	0.984	267.16	10.07	-129.16	0.30
	S27	Southeastern Coastal Plain	1.05	0.82	< 0.001	0.14	0.811	269.16	12.08	-130.16	0.27
	S25*	West Gulf Coastal Plain/Ouachitas	1.18	0.14	< 0.01	-0.04	0.817	271.26	14.18	-131.21	0.18
	S24	Central Hardwoods	0.74	2.32	< 0.05	20.32	< 0.05	272.55	15.46	-131.86	0.23
	S26*	Mississippi Alluvial Valley	0.47	3.78	< 0.05	-15.72	0.053	276.14	19.05	-133.65	0.17
	S22	Eastern Tallgrass Prairie	0.09	1370.40	< 0.05	-3310.37	0.287	278.78	21.70	-134.97	0.13
	S30	New England/mid-atlantic Coast	-0.16	3.62	< 0.01	4.14	0.496	279.48	22.39	-135.32	0.12

\*BCR is located in the core of the species' breeding range. The core was determined from BBS relative abundance maps ([https://www.mbr-pwrc.usgs.gov/bbs/ra2015\\_red\\_v3.shtml](https://www.mbr-pwrc.usgs.gov/bbs/ra2015_red_v3.shtml)) as the location with the highest relative abundance within the breeding range.

**Table S4.1 (cont.).** Outputs from the annual models for 13 species. Models for each species and BCR were constructed using the form:  $Vagrants \sim BBS\ Index + BBS\ Difference$ . For each species, models were ranked using the Akaike Information Criterion for small sample sizes (AICc). The best supported model for each species is in **bold**. Values listed for each predictor in the model are effect sizes and their corresponding  $p$ -values. Pseudo- $R^2$  was calculated for each model.

AOU code	BCR	BCR name	BBS Trend	BBS Index	$p$ -value	BBS Difference	$p$ -value	AICc	$\Delta$ AICc	Log-likelihood	Pseudo $R^2$
KEWA	<b>S29</b>	<b>Piedmont</b>	<b>-0.11</b>	<b>-18.79</b>	<b>&lt; 0.001</b>	<b>-28.24</b>	<b>&lt; 0.05</b>	<b>180.04</b>	<b>0.00</b>	<b>-85.6</b>	<b>0.29</b>
	S24*	Central Hardwoods	0.04	-2.55	< 0.05	2.75	0.113	186.9	6.86	-89.04	0.19
	S26	Mississippi Alluvial Valley	-0.48	8.65	< 0.01	3.83	0.779	189.25	9.21	-90.21	0.15
	S13	Lower Great Lakes/ St. Lawrence Plain	-0.36	158.21	0.082	480.55	0.239	193.49	13.45	-92.33	0.08
	S22	Eastern Tallgrass Prairie	0.68	-3.63	0.275	28.99	0.115	193.92	13.88	-92.54	0.07
	S25	West Gulf Coastal Plain/Ouachitas	-1.51	-0.17	0.229	-0.48	0.609	194.45	14.41	-92.8	0.02
	S27	Southeastern Coastal Plain	0.73	2.60	0.066	0.41	0.914	195.1	15.06	-93.13	0.05
	S21	Oaks and Prairies	-0.43	10.92	0.579	9.21	0.954	195.35	15.31	-93.25	0.01
	SU1	Survey-wide (core only)	-0.67	-0.83	0.354	4.95	0.373	196.11	16.07	-93.64	0.03
	S28	Appalachian Mountains	-1.42	-0.07	0.842	1.13	0.637	197.54	17.49	-94.35	0.01
	S30	New England/mid-atlantic Coast	-2.56	-0.13	0.75	-2.08	0.639	197.56	17.51	-94.36	0.01
MGWA	<b>S09</b>	<b>Great Basin</b>	<b>-0.75</b>	<b>-3.18</b>	<b>&lt; 0.01</b>	<b>1.02</b>	<b>0.813</b>	<b>101.56</b>	<b>0.00</b>	<b>-46.34</b>	<b>0.33</b>
	S05	Northern Pacific Rainforest	-1.34	-0.20	< 0.001	0.08	0.869	102.63	<b>1.08**</b>	-46.88	0.31
	S06	Boreal Taiga Plains	-0.72	-19.75	< 0.05	6.83	0.932	102.67	<b>1.11**</b>	-46.9	0.31
	SU1	Survey-wide (core only)	-0.55	-0.95	< 0.001	1.64	0.394	107.94	6.39	-49.55	0.24
	S32	Coastal California	0.38	43.20	< 0.01	60.33	0.343	109.55	8.00	-50.34	0.19

\*BCR is located in the core of the species' breeding range. The core was determined from BBS relative abundance maps ([https://www.mbr-pwrc.usgs.gov/bbs/ra2015/ra2015\\_red\\_v3.shtml](https://www.mbr-pwrc.usgs.gov/bbs/ra2015/ra2015_red_v3.shtml)) as the location with the highest relative abundance within the breeding range.

**Table S4.1 (cont.).** Outputs from the annual models for 13 species. Models for each species and BCR were constructed using the form:  $Vagrants \sim BBS\ Index + BBS\ Difference$ . For each species, models were ranked using the Akaike Information Criterion for small sample sizes (AICc). The best supported model for each species is in **bold**. Values listed for each predictor in the model are effect sizes and their corresponding  $p$ -values. Pseudo- $R^2$  was calculated for each model.

AOU code	BCR	BCR name	BBS Trend	BBS Index	$p$ -value	BBS Difference	$p$ -value	AICc	$\Delta$ AICc	Log-likelihood	Pseudo $R^2$
MGWA	S17	Badlands and Prairies	-0.04	2.19	0.726	-49.32	< 0.05	115.81	14.25	-53.48	0.09
	S15	Sierra Nevada	0.75	0.57	0.145	-0.18	0.858	116.54	14.99	-53.84	0.05
	S16	Southern Rockies/colorado Plateau	-0.21	1.86	0.283	-2.21	0.556	117.11	15.56	-54.12	0.04
	S10*	Northern Rockies	-0.09	-0.06	0.693	0.15	0.823	118.76	17.20	-54.94	0.01
PROW	<b>S26*</b>	<b>Mississippi Alluvial Valley</b>	<b>-1.02</b>	<b>-0.22</b>	<b>&lt; 0.05</b>	<b>-1.08</b>	<b>&lt; 0.05</b>	<b>204.66</b>	<b>0.00</b>	<b>-97.91</b>	<b>0.14</b>
	SU1	Survey-wide (core only)	-0.71	-1.11	0.19	-15.66	< 0.05	205.97	<b>1.31**</b>	-98.57	0.12
	S25	West Gulf Coastal Plain/Ouachitas	-2.52	-0.64	0.152	-5.65	0.145	207.28	2.62	-99.21	0.05
	S28	Appalachian Mountains	-2.04	-23.68	0.068	-13.96	0.912	207.54	2.88	-99.35	0.09
	S37	Gulf Coastal Prairie	-0.38	2.21	0.183	-2.72	0.734	208.08	3.42	-99.61	0.04
	S23	Prairie Hardwood Transition	0.84	45.39	0.124	305.93	0.116	208.83	4.17	-100	0.07
	S31	Peninsular Florida	-2.24	-11.89	0.148	37.56	0.748	209.15	4.49	-100.16	0.07
	S22	Eastern Tallgrass Prairie	0.96	11.65	0.226	205.19	0.082	209.64	4.98	-100.4	0.06
	S21	Oaks and Prairies	1	4.65	0.639	-1.98	0.984	209.67	5.01	-100.41	0.00
	S27	Southeastern Coastal Plain	-0.32	0.07	0.851	-3.21	0.082	209.83	5.17	-100.5	0.05
	S29	Piedmont	0.63	-6.26	0.299	45.06	0.257	210.64	5.98	-100.9	0.04
	S30	New England/mid-atlantic Coast	-0.23	1.21	0.804	6.80	0.433	212.05	7.39	-101.61	0.01

\*BCR is located in the core of the species' breeding range. The core was determined from BBS relative abundance maps ([https://www.mbr-pwrc.usgs.gov/bbs/ra2015\\_red\\_v3.shtml](https://www.mbr-pwrc.usgs.gov/bbs/ra2015_red_v3.shtml)) as the location with the highest relative abundance within the breeding range.

**Table S4.1 (cont.).** Outputs from the annual models for 13 species. Models for each species and BCR were constructed using the form:  $Vagrants \sim BBS\ Index + BBS\ Difference$ . For each species, models were ranked using the Akaike Information Criterion for small sample sizes (AICc). The best supported model for each species is in **bold**. Values listed for each predictor in the model are effect sizes and their corresponding  $p$ -values. Pseudo- $R^2$  was calculated for each model.

AOU code	BCR	BCR name	BBS Trend	BBS Index	$p$ -value	BBS Difference	$p$ -value	AICc	$\Delta$ AICc	Log-likelihood	Pseudo $R^2$
PROW	S24	Central Hardwoods	0.62	2.12	0.715	0.38	0.989	212.49	7.83	-101.83	0.00
SWWA	<b>S21</b>	<b>Oaks and Prairies</b>	<b>1.24</b>	<b>278.73</b>	<b>0.331</b>	<b>1857.95</b>	<b>0.284</b>	<b>23.58</b>	<b>0.00</b>	<b>-7.36</b>	<b>0.16</b>
	S37	Gulf Coastal Prairie	0.03	-520.24	0.304	-2622.83	0.321	23.84	<b>0.27**</b>	-7.5	0.14
	S26	Mississippi Alluvial Valley	0.55	43.16	0.227	24.87	0.784	24.24	<b>0.67**</b>	-7.7	0.11
	S29	Piedmont	2.41	84.83	0.23	-803.89	0.362	24.61	<b>1.03**</b>	-7.89	0.09
	S25	West Gulf Coastal Plain/Ouachitas	2.77	4.73	0.347	5.07	0.813	24.89	<b>1.31**</b>	-8.02	0.07
	S28	Appalachian Mountains	1.96	-19.11	0.7	94.34	0.622	25.62	2.05	-8.39	0.02
	SU1	Survey-wide (core only)	2.11	7.38	0.618	-7.22	0.951	25.68	2.11	-8.42	0.02
	S27*	Southeastern Coastal Plain	2.12	5.30	0.747	-41.43	0.736	25.81	2.23	-8.49	0.01
TOWA	<b>S10*</b>	<b>Northern Rockies</b>	<b>0.21</b>	<b>0.42</b>	<b>&lt;0.05</b>	<b>-0.71</b>	<b>0.288</b>	<b>98.3</b>	<b>0.00</b>	<b>-44.72</b>	<b>0.19</b>
	S04	Northwestern Interior Forest	-0.57	1.17	<0.05	-1.46	0.298	99.6	<b>1.30**</b>	-45.37	0.17
	S09	Great Basin	-1.71	-0.18	0.328	-3.54	<0.05	99.82	<b>1.52**</b>	-45.47	0.16
	SU1	Survey-wide (core only)	-0.14	0.41	<0.05	-0.51	0.388	102.16	3.86	-46.65	0.12
	S05	Northern Pacific Rainforest	-0.15	0.21	0.062	0.10	0.668	104.09	5.79	-47.61	0.07
VIWA	<b>S34*</b>	<b>Sierra Madre Occidental</b>	<b>-1.08</b>	<b>-8.70</b>	<b>0.213</b>	<b>-39.11</b>	<b>0.201</b>	<b>23.95</b>	<b>0.00</b>	<b>-7.54</b>	<b>0.32</b>
	SU1	Survey-wide (core only)	-1.11	-3.99	0.279	-72.08	0.108	25.68	<b>1.73**</b>	-8.41	0.23

\*BCR is located in the core of the species' breeding range. The core was determined from BBS relative abundance maps ([https://www.mbr-pwrc.usgs.gov/bbs/ra2015/ra2015\\_red\\_v3.shtm](https://www.mbr-pwrc.usgs.gov/bbs/ra2015/ra2015_red_v3.shtm)) as the location with the highest relative abundance within the breeding range.

**Table S4.1 (cont.).** Outputs from the annual models for 13 species. Models for each species and BCR were constructed using the form: *Vagrants* ~ *BBS Index* + *BBS Difference*. For each species, models were ranked using the Akaike Information Criterion for small sample sizes (AICc). The best supported model for each species is in **bold**. Values listed for each predictor in the model are effect sizes and their corresponding *p*-values. Pseudo-*R*<sup>2</sup> was calculated for each model.

AOU code	BCR	BCR name	BBS Trend	BBS Index	<i>p</i> -value	BBS Difference	<i>p</i> -value	AICc	ΔAICc	Log-likelihood	Pseudo <i>R</i> <sup>2</sup>
VIWA	S35	Chihuahuan Desert	-0.5	-29.86	0.142	-1.07	0.994	26.5	2.55	-8.82	0.19
	S16	Southern Rockies/colorado Plateau	-1.08	-1.77	0.577	-36.30	0.239	28	4.05	-9.57	0.10
	S09	Great Basin	0.91	71.67	0.138	39.67	0.927	28.47	4.52	-9.8	0.08
WEWA	<b>S25</b>	<b>West Gulf Coastal Plain/Ouachitas</b>	<b>-1.05</b>	<b>-1.78</b>	<b>0.622</b>	<b>23.27</b>	<b>&lt; 0.05</b>	<b>186.79</b>	<b>0.00</b>	<b>-88.97</b>	<b>0.13</b>
	S29	Piedmont	1.58	-3.44	0.492	144.57	< 0.01	189.54	2.75	-90.35	0.12
	S27	Southeastern Coastal Plain	2.23	4.21	0.184	-26.50	0.139	192.23	5.44	-91.7	0.08
	S28*	Appalachian Mountains	-0.18	-6.17	0.063	-10.79	0.289	192.56	5.76	-91.86	0.07
	S30	New England/mid-atlantic Coast	1.29	0.99	0.454	16.25	0.117	193.48	6.69	-92.33	0.05
	S22	Eastern Tallgrass Prairie	0.63	58.11	0.179	100.37	0.81	194.65	7.85	-92.91	0.03
	S14	Atlantic Northern Forest	-0.36	34.21	0.37	-285.52	0.406	195	8.20	-93.08	0.03
	S24	Central Hardwoods	0.48	2.58	0.25	5.30	0.663	195.15	8.35	-93.16	0.02
	S13	Lower Great Lakes/ St. Lawrence Plain	-1.34	-2.29	0.817	-26.00	0.703	196.13	9.33	-93.65	0.00
	SU1	Survey-wide (core only)	0.12	0.32	0.965	4.79	0.871	196.29	9.49	-93.73	0.00
YTWA	<b>S25</b>	<b>West Gulf Coastal Plain/Ouachitas</b>	<b>-0.6</b>	<b>-5.58</b>	<b>&lt; 0.001</b>	<b>-2.70</b>	<b>0.659</b>	<b>187.05</b>	<b>0.00</b>	<b>-89.1</b>	<b>0.24</b>
	S28*	Appalachian Mountains	0.97	1.23	< 0.01	6.10	< 0.05	188.2	<b>1.15**</b>	-89.68	0.26

\*BCR is located in the core of the species' breeding range. The core was determined from BBS relative abundance maps ([https://www.mbr-pwrc.usgs.gov/bbs/ra2015/ra2015\\_red\\_v3.shtml](https://www.mbr-pwrc.usgs.gov/bbs/ra2015/ra2015_red_v3.shtml)) as the location with the highest relative abundance within the breeding range.

**Table S4.1 (cont.).** Outputs from the annual models for 13 species. Models for each species and BCR were constructed using the form:  $Vagrants \sim BBS\ Index + BBS\ Difference$ . For each species, models were ranked using the Akaike Information Criterion for small sample sizes (AICc). The best supported model for each species is in **bold**. Values listed for each predictor in the model are effect sizes and their corresponding  $p$ -values. Pseudo- $R^2$  was calculated for each model.

AOU code	BCR	BCR name	BBS Trend	BBS Index	$p$ -value	BBS Difference	$p$ -value	AICc	$\Delta$ AICc	Log-likelihood	Pseudo $R^2$
YTWA	S37	Gulf Coastal Prairie	-0.29	203.22	< 0.01	-292.16	0.603	192.64	5.60	-91.9	0.15
	S26	Mississippi Alluvial Valley	1.14	14.95	< 0.01	-57.29	0.261	193.06	6.02	-92.11	0.18
	S20	Edwards Plateau	4.26	-0.06	0.959	12.46	0.057	193.08	6.03	-92.11	0.14
	S31	Peninsular Florida	-1.81	-4.51	< 0.01	1.00	0.877	194.24	7.19	-92.7	0.16
	S21	Oaks and Prairies	2.41	17.12	< 0.01	-104.75	0.135	194.39	7.34	-92.77	0.12
	S13	Lower Great Lakes/ St. Lawrence Plain	0.94	142.18	< 0.01	122.96	0.689	194.83	7.79	-93	0.15
	S22	Eastern Tallgrass Prairie	1.61	21.08	< 0.01	-82.82	0.354	195.08	8.04	-93.12	0.15
	S23	Prairie Hardwood Transition	2.01	10.08	< 0.01	-25.95	0.535	195.87	8.83	-93.52	0.14
	S24	Central Hardwoods	1.9	1.21	< 0.01	0.57	0.922	197.09	10.04	-94.13	0.12
	SU1	Survey-wide (core only)	0.91	2.75	< 0.01	-1.41	0.879	197.17	10.12	-94.17	0.12
	S29	Piedmont	2.21	1.37	< 0.05	-0.08	0.988	197.33	10.29	-94.25	0.11
	S27	Southeastern Coastal Plain	0.77	0.41	0.622	-4.55	0.059	199.43	12.38	-95.3	0.08
	S30	New England/mid-atlantic Coast	0.52	0.37	0.601	0.36	0.904	203.09	16.04	-97.13	0.01

\*BCR is located in the core of the species' breeding range. The core was determined from BBS relative abundance maps ([https://www.mbr-pwrc.usgs.gov/bbs/ra2015/ra2015\\_red\\_v3.shtml](https://www.mbr-pwrc.usgs.gov/bbs/ra2015/ra2015_red_v3.shtml)) as the location with the highest relative abundance within the breeding range.

## References

- Baker, R. R. (1978). *The evolutionary ecology of animal migration*. Holmes; Meier Publishers.
- Bird Observer. Arlington, Massachusetts. <https://www.birdobserver.org/Issues/Complete-Archive>
- Bird Studies and NABCI. (2014). Bird conservation regions. <https://www.birdscanada.org/bird-science/nabci-bird-conservation-regions>.
- BirdLife International and Handbook of the Birds of the World. (2020). Bird species distribution maps of the world. <http://datazone.birdlife.org/species/requestdis>
- Bledsoe, A. H., & Sibley, D. (1985). Patterns of vagrancy of Ross' Gull. *American Birds*, 39(2), 219–227.
- Bowman, J., Badzinski, D. S., & Brooks, R. J. (2010). The numerical response of breeding Northern Saw-whet Owls *Aegolius acadicus* suggests nomadism. *Journal of Ornithology*, 151, 499–506.
- Burnham, K. P., & Anderson, D. R. (2003). *Model selection and multimodel inference: A practical information-theoretic approach* (Second). Springer-Verlag.
- Cheveau, M., Drapeau, P., Imbeau, I., & Bergeron, Y. (2004). Owl winter irruptions as an indicator of small mammal population cycles in the boreal forest of eastern North America. *Oikos*, 107, 190–198.
- Cote, M., Ibarzabal, J., St-Laurent, M.-H., Ferron, J., & Gagnon, R. (2007). Age-dependent response of migrant and resident *Aegolius* owl species to small rodent population fluctuations in the eastern Canadian boreal forest. *Journal of Raptor Research*, 41(1), 16–25.
- Cottridge, D., & Vinicombe, K. (1996). *Rare birds in Britain and Ireland - a photographic record*. Harper Collins.
- De Juana, E., & Garcia, E. F. J. (2010). Vagrancy or migration: Why do American Teals cross the Atlantic? *Ardeola*, 57(2), 417–430.
- DeSante, D. F. (1973). *An analysis of the fall occurrences and nocturnal orientations of vagrant wood warblers (Parulidae) in California* (Doctoral dissertation). Stanford University. Stanford, California.

- DeSante, D. F. (1983). Annual variability in the abundance of migrant landbirds on Southeast Farallon Island, California. *The Auk*, 100(4), 826–852.
- Elkins, N. (1979). Nearctic landbirds in Britain and Ireland: A meteorological analysis. *British Birds*, 72(9), 417–433.
- Elkins, N. (1999). Recent records of Nearctic landbirds in Britain and Ireland. *British Birds*, 92, 83–95.
- Elkins, N. (2005). Weather and bird migration. *British Birds*, 98, 238–256.
- Elkins, N. (2008). Further thoughts on transatlantic vagrancy of landbirds to Britain & Ireland. *British Birds*, 101, 458–477.
- Ellison, W. G. (1991). *The mechanism and ecology of range expansion by the Blue-gray Gnatcatcher* (M.Sc. thesis.). University of Connecticut. Storrs, Connecticut.
- Ellison, W. G. (1993). Historical patterns of vagrancy by Blue-gray Gnatcatchers in New England. *Journal of Field Ornithology*, 64(3), 358–366.
- Grinnell, J. (1922). The role of the “accidental”. *The Auk*, 39(3), 373–380.
- Hampton, S. (1997). Rare migrants in California: The determinants of their frequency. *Western Birds*, 28, 30–42.
- Hengeveld, R. (1989). *Dynamics of biological invasions*. Kluwer Academic Publishers. Chapman; Hall.
- Hijmans, R. J. (2019). geosphere: Spherical trigonometry. R package version 1.5-10. <https://CRAN.R-project.org/package=geosphere>
- Holt, C. W. (1978). Westward vagrancy of Siberian passerines [Letters]. *Bird Study*, 25(2), 123–124.
- Hurvich, C. M., & Tsai, C. L. (1989). Regression and times series model selection in small samples. *Biometrika*, 76(2), 297–307.
- IUCN. (2020). The IUCN Red List of Threatened Species. *Version*. <https://www.iucnredlist.org>.
- Jiguet, F., Doxa, A., & Robert, A. (2008). The origin of out-of-range pelicans in Europe: Wild bird dispersal or zoo escapes? *Ibis*, 150, 606–618.
- Lees, A. C., & Gilroy, J. J. (2009). Vagrancy mechanisms in passerines and near-passerines. In R. Slack (Ed.), *Where and When: An analysis of status and distribution in Britain and Ireland. Volume 1: Sandgrouse to New World orioles*. Rare Bird Books.
- Liebl, A. L., & Martin, L. B. (2012). Exploratory behaviour and stressor hyper-responsiveness facilitate range expansion of an introduced songbird. *Proceedings of The Royal Society B*, 279(1746), 4375–4381.
- Liebl, A. L., & Martin, L. B. (2014). Living on the edge: Range edge birds consume novel foods sooner than established ones. *Behavioral Ecology*, 25(5), 1089–1096.

- Lindén, A., & Mäntyniemi, S. (2011). Using the negative binomial distribution to model overdispersion in ecological count data. *Ecology*, *92*(7), 1414–1421.
- Link, W. A., & Sauer, J. R. (2002). A hierarchical analysis of population change with application to Cerulean Warblers. *Ecology*, *83*(10), 2832–2840.
- Link, W. A., Sauer, J. R., & Niven, D. K. (2020). Model selection for the North American Breeding Bird Survey. *Ecological Applications*, *30*(6), 02137.
- Long, J. A. (2020). jtools: Analysis and presentation of social scientific data. R package version 2.1.0 [R package version 2.1.0]. <https://cran.r-project.org/package=jtools>
- Martin, T. E., & Barber, P. M. (2020). Red-faced Warbler (*Cardellina rubrifrons*), version 1.0. In A. F. Poole & F. B. Gill (Eds.), *Birds of the World*. Cornell Lab of Ornithology.
- Mazerolle, M. J. (2020). AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). R package version 2.3-1. <https://cran.r-project.org/package=AICcmodavg>.
- McLaren, I. A. (1981). The incidence of vagrant landbirds on Nova Scotian islands. *The Auk*, *98*(2), 243–257.
- McLaren, I. A., Lees, A. C., Field, C., & Collins, K. J. (2006). Origins and characteristics of Nearctic landbirds in Britain and Ireland in autumn: A statistical analysis. *Ibis*, *148*(4), 1–20.
- Newton, I. (2006). Advances in the study of irruptive migration. *Ardea*, *94*(3), 433–460.
- North American Breeding Bird Survey Dataset 1966 - 2019: U.S. (2020). *Geological Survey data release*.
- Partners in Flight. (2020). Population Estimates Database, version 3.1. <http://pif.birdconservancy.org/PopEstimates>.
- Patten, M. A., & Burger, J. C. (1998). Spruce budworm outbreaks and the incidence of vagrancy in eastern North American wood-warblers. *Canadian Journal of Zoology*, *76*, 433–439.
- Patten, M. A., & Marantz, C. A. (1996). Implications of vagrant southeastern vireos and warblers in California. *The Auk*, *113*(4), 911–923.
- Pfeifer, R., Stadler, J., & Brandl, R. (2007). Birds from the Far East in Central Europe: A test of the reverse migration hypothesis. *Journal of Ornithology*, *148*, 379–385.
- Phillips, J. (2000). Autumn vagrancy: “reverse migration” and migratory orientation. *Ringing & Migration*, *20*, 35–38.
- R Core Team. (2020). R: A language and environment for statistical computing. <https://www.R-project.org/>.
- Rabøl, J. (1969). Reversed migration as a cause of westward vagrancy by four Phylloscopus warblers. *British Birds*, *62*(3), 89–92.

- Ralph, C. J., & Wolfe, J. D. (2018). Factors affecting the distribution and abundance of autumn vagrant New World warblers in northwestern California and southern Oregon. *PeerJ*, 6, 5881.
- Robbins, C. S. (1980). Predictions of future Nearctic landbird vagrants to Europe. *British Birds*, 73, 448–457.
- Romagosa, C. M. (2020). Eurasian Collared-Dove (*Streptopelia decaocto*), version 1.0. In S. M. Billerman (Ed.), *Birds of the World*. Cornell Lab of Ornithology.
- Sauer, J. R., & Link, W. A. (2011). Analysis of The North American Breeding Bird Survey using hierarchical models. *The Auk*, 128(1), 87–98.
- Sauer, J. R., Niven, D. K., Hines, J. E., Ziolkowski, D. J., Jr., Pardieck, K. L., Fallon, J. E., & Link, W. A. (2017). *The North American Breeding Bird Survey, results and analysis 1966 – 2015* (Version 2.07.2017). USGS Patuxent Wildlife Research Center.
- Southwood, T. R. E., May, R. M., Hassell, M. P., & Conway, G. R. (1974). Ecological strategies and population parameters. *The American Naturalist*, 108(964), 791–804.
- Staicer, C. A., & Guzy, M. J. (2020). Grace's Warbler (*Setophaga graciae*), version 1.0. In A. F. Poole & F. B. Gill (Eds.), *Birds of the World*. Cornell Lab of Ornithology.
- Thorup, K. (2004). Reverse migration as a cause of vagrancy. *Bird Study*, 51(3), 228–238.
- Umegaki, Y. (2014). Testing the effect of migratory restlessness on the occurrence of vagrant continental passerines in Japan. *Ornithological Science*, 13, 83–90.
- Veit, R. R. (1990). Do vagrant birds in Massachusetts reflect population growth and dispersal rather than weather patterns? *Bird Observer*, 18(2), 86–91.
- Veit, R. R. (1997). Long-distance dispersal and population growth of the Yellow-headed Blackbird *Xanthocephalus xanthocephalus*. *Ardea*, 85(1), 135–143.
- Veit, R. R. (2000). Vagrants as the expanding fringe of a growing population. *The Auk*, 117(1), 242–246.
- Veit, R. R. (2005). Yellow-nosed Albatross at Tuckernuck Island, Massachusetts. *Bird Observer*, 33(5), 284–288.
- Veit, R. R. (2008). Why expect clusters of vagrants? *Bird Observer*, 36(4), 213–217.
- Williamson, K. (1959). The September drift-movements of 1956 and 1958. *British Birds*, 52, 334–377.
- Williamson, K. (1961). The concept of 'cyclonic approach'. *Bird Migration*, 1, 235–240.
- Williamson, K. (1963). Movements as an indicator of population changes. *Bird Migration*, 2, 207–223.
- Williamson, K. (1969). Weather systems and bird movements. *Quarterly Journal of the Royal Meteorological Society*, 95(404), 414–423.

- Zawadzki, L. C., Veit, R. R., & Manne, L. L. (2019). The influence of population growth and wind on vagrancy in a North American passerine. *Ardea*, *107*(2), 131–147.

# 5

## Predicting source populations of vagrants using breeding population data: a case study of the Lesser Black-backed Gull (*Larus fuscus*)

Adapted from: Lucinda C. Zawadzki, Gunnar T. Hallgrímsson, Richard R. Veit, Lars M. Rasmussen, David Boertmann, Natasha Gillies, Tim Guilford. ‘Predicting source populations of vagrants using breeding population data: a case study of the Lesser Black-backed Gull (*Larus fuscus*).’ *Frontiers in Ecology and Evolution*, **9**, (2021).

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## 5.1 Abstract

A critical consequence of vagrancy is range expansion and colonisation through exploration and occupation of potentially suitable habitat. Uncovering origins of vagrants will help us better understand not only species-specific vagrant movements, but how the dynamics of a naturally-growing population influence vagrancy, and potentially lead to range expansion. Under the premise that occurrence of vagrants is linked to increasing population growth in the core of the breeding range, we assessed the utility of breeding population survey data to predict source populations of vagrants. Lesser Black-backed Gulls (*Larus fuscus*) served as our focal species due to their dramatic and well-documented history of vagrancy to North America in the last 30 years. We related annual occurrence of vagrants to indices of breeding population size and growth rate of breeding populations. We propose that the fastest growing population is the most likely source of recent vagrants to North America. Our study shows that it is possible to predict potential source populations of vagrants with breeding population data, but breeding surveys require increased standardization across years to improve models. For the Lesser Black-backed Gull, Iceland's breeding population probably influenced vagrancy during the early years of colonisation, but the major increase in vagrants occurred during a period of growth of Greenland's population, suggesting that Greenland is the source population of the most recent pulse of vagrant Lesser Black-backed Gulls to North America.

## 5.2 Introduction

Anthropogenic climate change continues to threaten species' persistence (Román-Palacios and Wiens 2020), and species must remain flexible if they are to escape extinction driven by climate change. Occupation of potentially suitable habitat through range expansion

and colonisation is one way in which species can survive climatic effects. Vagrancy, a process by which organisms engage in long-distance dispersal movements outside of their known species range (Grinnell 1922, Baker 1978), may provide the mechanism through which individuals can explore and occupy potentially suitable habitat. Though these movements have often been attributed to internal errors in navigation (Rabøl 1969, DeSante 1973, Cottridge and Vinicombe 1996), or passive displacement by wind or weather systems (Williamson 1959, Elkins 1979, McLaren 1981, McLaren et al. 2006), vagrancy is a natural part of mobile populations (Baker 1978, Hengeveld 1989), and can result in range expansion (e.g. Veit and Lewis 1996, Massa et al. 2014) and colonisation of new habitat (e.g. Veit and Lewis 1996, Veit et al. 2016). Vagrants, however, are often difficult to study directly due to their inherent rarity and unpredictable occurrence. In order to investigate the role that vagrancy plays in range expansion and colonisation, we therefore need to study variability in this behaviour through a variety of methods.

It has been suggested that in order to naturally colonise new habitat, a species must have a growing source population (Hengeveld 1989, Szűcs et al. 2014). Of the studies that have examined factors that influence vagrancy (DeBenedictis 1971; DeSante 1983; Hampton 1997; Veit 1990, 1997, 2000; Elkins 1999; Thorup 2004; McLaren et al. 2006; Pfeifer et al. 2007; Jiguet et al. 2008; De Juana and Garcia 2010; Farnsworth et al. 2015; Ralph and Wolfe 2018; Zawadzki et al. 2019), the majority have found that vagrancy is strongly correlated with either overall population size (DeBenedictis 1971, DeSante 1983, Thorup 2004, Pfeifer et al. 2007, Ralph and Wolfe 2018), or its annual variation (Veit 1990, 1997, 2000; McLaren et al. 2006; Jiguet et al. 2008; De Juana and Garcia 2010; Zawadzki et al. 2019). It has also been found that increased incidence of vagrancy is linked to annual population growth in the core of a species' breeding range (Veit 1997, McLaren et al. 2006, Zawadzki et al. 2019). Population size and growth are therefore highly influential predictors when estimating vagrant occurrence. Vagrancy is likely a density-dependent phenomenon whereby increased productivity in a given year leads to the production of more individuals than the current habitat can support, and therefore, increased dispersal (Southwood et al. 1974) and vagrancy (DeBenedictis 1971, DeSante 1983, Patten and Marantz 1996) to find suitable, or even newly suitable, habitat. Data on

species' population size and growth will be important in understanding range expansions, as colonisers may be coming from regions that have experienced the most rapid population growth, and may therefore be predisposed to vagrancy (Phillips et al. 2010).

Using this information, we may be able to track colonisation of species undergoing range expansion, to determine where vagrants are coming from, and may even be able to predict which species are likely to occur as vagrants in the future. Though tagging of individuals at known breeding sites through either field-readable bands or GPS devices may provide more direct evidence on individual movement, the likelihood that any one bird tagged or banded will occur as a vagrant is low. Recovery rates of banded birds within their normal range are already as low as 1.5% for passerines (North 2020) and approximately 2.0% for gulls (specifically, 2.2% for LBBG in Britain; Robinson et al. 2009). Modelling with long-term population data is thus vital in understanding range expansion and colonisation of vagrants.

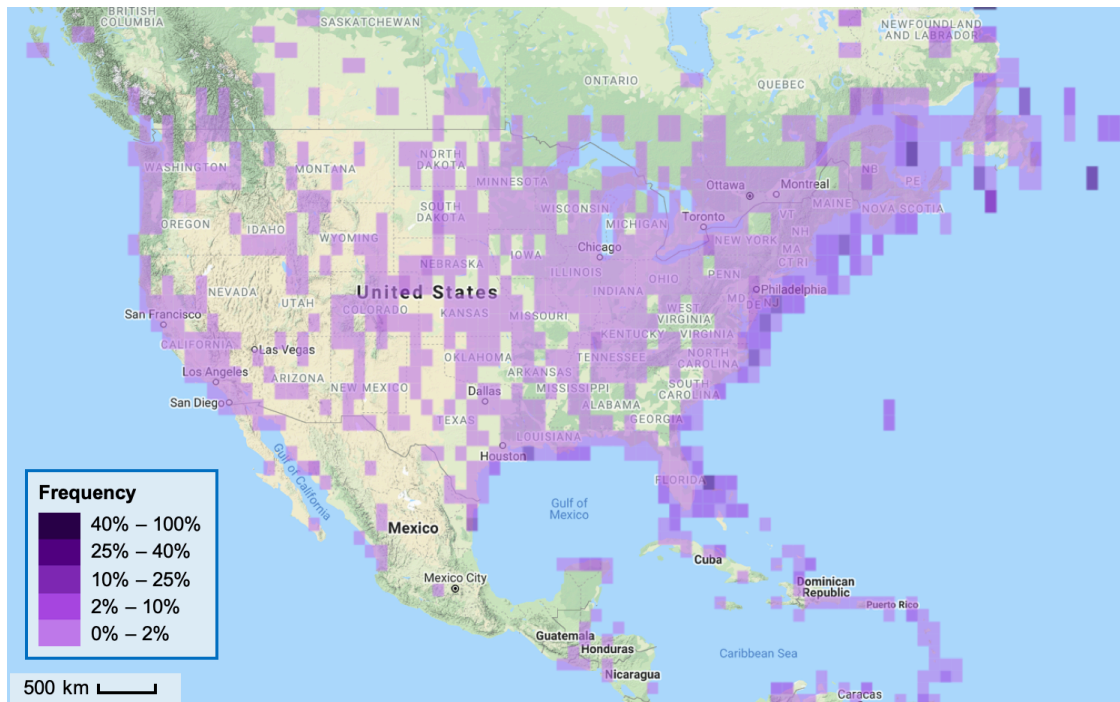
Breeding population surveys of birds provide information on annual breeding pairs at colonies or nesting-sites where species are known to breed. Though protocols often vary by country, data from these surveys provide long-term estimates of population size and growth that may be useful for studying how population dynamics in the breeding range influence vagrancy. To examine the potential use of breeding population survey data in determining source populations of vagrants, we investigated the relationship between annual breeding population size and growth rate of three known breeding populations of Lesser Black-backed Gulls (*Larus fuscus*; hereafter "LBBG") in western Europe, and the occurrence of vagrant LBBG in North America during the years 1986 to 2018. LBBG are a unique case since they have a well-documented history of vagrancy to North America, yet, as with most vagrants, it is unknown where they are arriving from. We predict that Greenland is the source population of vagrant LBBGs to North America based on Greenland's increasing population after colonisation, and proximity to North America.

## 5.3 Methods

### 5.3.1 Study species

LBBG are a polytypic species whose breeding range extends from Greenland to western Asia (Olsen and Larsson 2004). During the mid- to late-twentieth century, LBBGs experienced a rapid increase in global population (Liebers and Helbig 2002, Olsen and Larsson 2004), mainly attributed to an increase in population growth of the Atlantic subspecies (1) *intermedius*, whose breeding range extends from Belgium and the Netherlands, to Norway, and (2) *graellsii*, which breeds in Greenland and Iceland, along western Europe, south to the Iberian Peninsula (Olsen and Larsson 2004, Wetlands International 2020). As their populations increased, LBBGs expanded their range westward across the Atlantic (Post and Lewis 1995), moving from breeding grounds in western Europe to Iceland in the 1920s (Olsen and Larsson 2004), and subsequently colonising Greenland between 1985 and 1990 (Boertmann 2008). Iceland's breeding population increased from 1,250 breeding pairs in 1974 to over 40,000 breeding pairs in 2004 (Hallgrímsson et al. 2011). The colonisation of Greenland also rose rapidly, increasing from 13 records of non-breeding individuals by 1984 (Boertmann 2008), to an estimated 2,060 breeding pairs in 2016, the majority of which nest in southwestern Greenland (Boertmann and Frederiksen 2016, Boertmann et al. 2020).

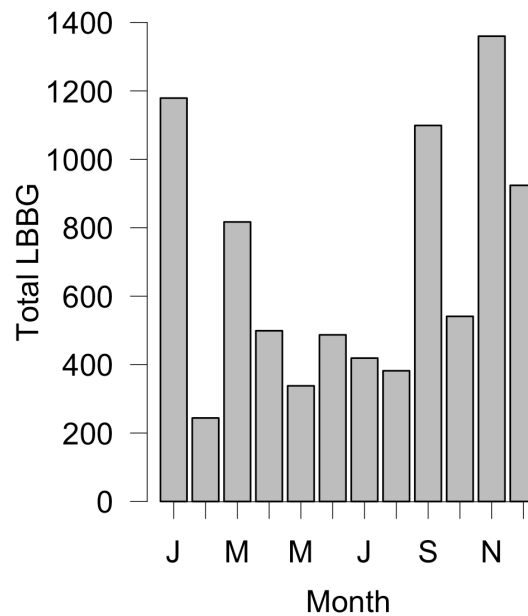
This rapid expansion shifted the LBBG breeding range closer to North America, and was accompanied by increased numbers of vagrant LBBGs on the continent. The first LBBG was recorded in North America in 1934 (Edwards 1935), and LBBG have now been seen in every state and Canadian province (Figure 5.1; eBird 2017), with over 1000 individuals recorded annually since 2005 (National Audubon Society 2020). LBBGs are mainly seen in North America from September to March (Figure 5.2), though sightings do occur year-round. Despite increasing occurrence of LBBGs each year, they have yet to breed in North America (with the exception of two hybrid pairs with Herring Gulls (*Larus argentatus*); vanVliet et al. 1993, Ellis et al. 2007, Ellis et al. 2014). This



**Figure 5.1.** eBird map of Lesser Black-backed Gulls (*Larus fuscus*) sightings in part of North America. The frequency is the percentage of submitted checklists from that region in which a LBBG was recorded. Image provided by eBird ([www.ebird.org](http://www.ebird.org)) and created November 10, 2020.

means that colonisation of North America by LBBGs is a result of repeated vagrancy by gulls arriving from outside the continent.

Our study focuses on the Atlantic subspecies *graellsii*, which is predominantly responsible for the westward range expansion of LBBG across the Atlantic that coincided with the rapid increase in global population during the mid- to late-twentieth century (Sibley 2014, Olsen and Larsson 2004, Burger et al. 2020). The other Atlantic subspecies *intermedius* was not involved in this range expansion, and the other three recognized subspecies, *fuscus*, *heuglini*, and *taimyrensis* (Liebers and Helbig 2002, Collinson et al. 2008), are restricted to breeding and wintering sites outside the Atlantic area (Cramp and Simmons 1983, Olsen and Larsson 2004), and are very unlikely to have contributed to these movements (Sibley 2014).

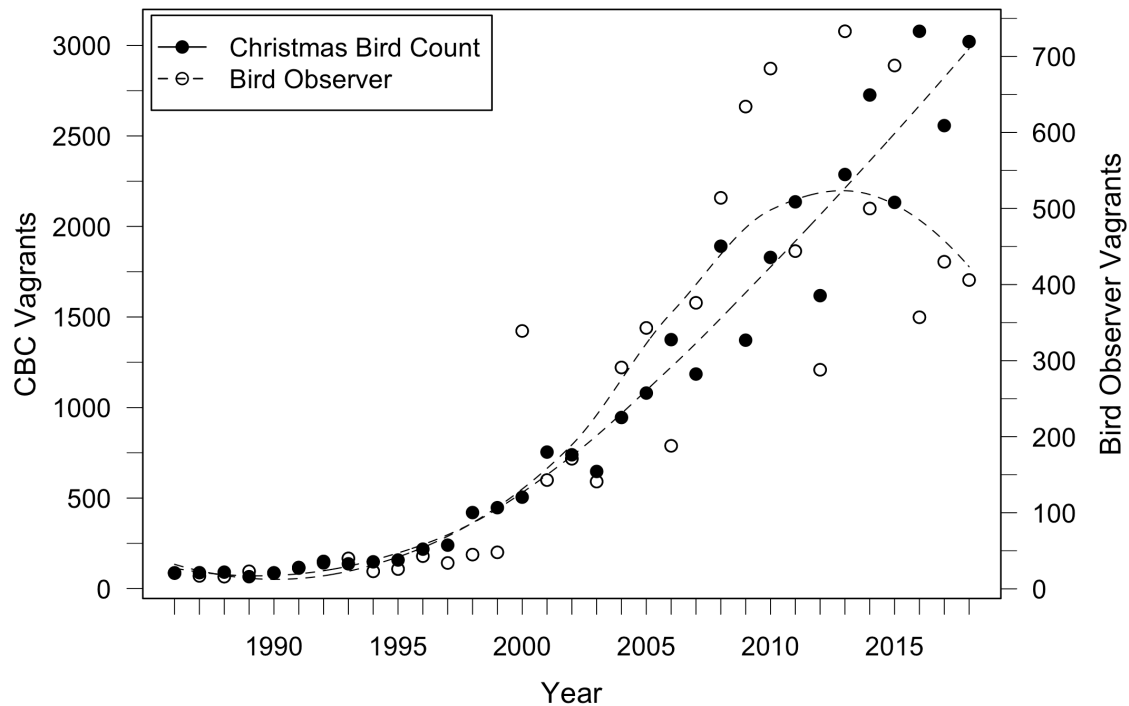


**Figure 5.2.** Monthly totals of LBBG recorded in Massachusetts from the journal *Bird Observer* between the years 1971 – 2018. LBBG are more commonly seen from September to March.

### 5.3.2 Vagrant data

We collected records of vagrant LBBGs in North America from two sources. Numbers of wintering gulls (14 December to 5 January) were taken from Christmas Bird Count (CBC) data (Figure 5.3; National Audubon Society 2020) from 1986 to 2018. All count circles with available data within the North American continent were included, covering the contiguous United States, all Canadian provinces, Central America (Mexico and Panama) and the Caribbean (Bahamas, Bermuda, the Dominican Republic, Haiti, and Puerto Rico). To correct for variation in observer effort across years, data were extracted as CBC trend estimates of median abundance (T. Meehan, pers. comm. 2020, Meehan et al. 2020), which were calculated using Bayesian hierarchical models (Soykan et al. 2016).

Additional year-round sighting records of gulls were extracted from *Bird Observer*, a Massachusetts-based journal, and used to analyse ages of vagrant LBBG. Data were available from 1973 to 2018. We chose this publication due to its intensive and consistent record-keeping of birds sighted in the state throughout the year (Veit 1997), often with individuals identified to age. Additionally, Massachusetts has a high concentration of



**Figure 5.3.** Records of individual LBBG seen in North America during yearly Christmas Bird Counts (CBC) and from *Bird Observer* records from 1986 – 2018. Data from CBC are for all of North America, while data from *Bird Observer* are just for Massachusetts. LBBG sightings increased rapidly after the early 1990s, and in the last decade, over 1000 individuals have been present each year. CBC and *Bird Observer* records are positively correlated with each other ( $r = 0.82$ ,  $p < 0.001$ ).

LBBGs each year (Veit and Petersen 1993; Nisbet et al. 2013), and is likely reflective of the pattern of sightings throughout North America (Figure 5.3; correlation between CBC and *Bird Observer* data:  $r = 0.82$ ,  $p < 0.001$ ).

While eBird has a large collection of sighting records of vagrant LBBG, we chose to use CBC and *Bird Observer* data since data from these sources are available for the entire time series of our study, and records are ensured to be single individuals (Zawadzki et al. 2019). eBird was not founded until 2002, therefore any sightings prior to this year may not be available on the platform. Additionally, eBird often reports multiple sightings for the same individual, and there are no consistent methods to distinguish single birds from multiple records. Further, standardisation of protocols used during Christmas Bird Counts ensures that vagrant data are consistent across years.

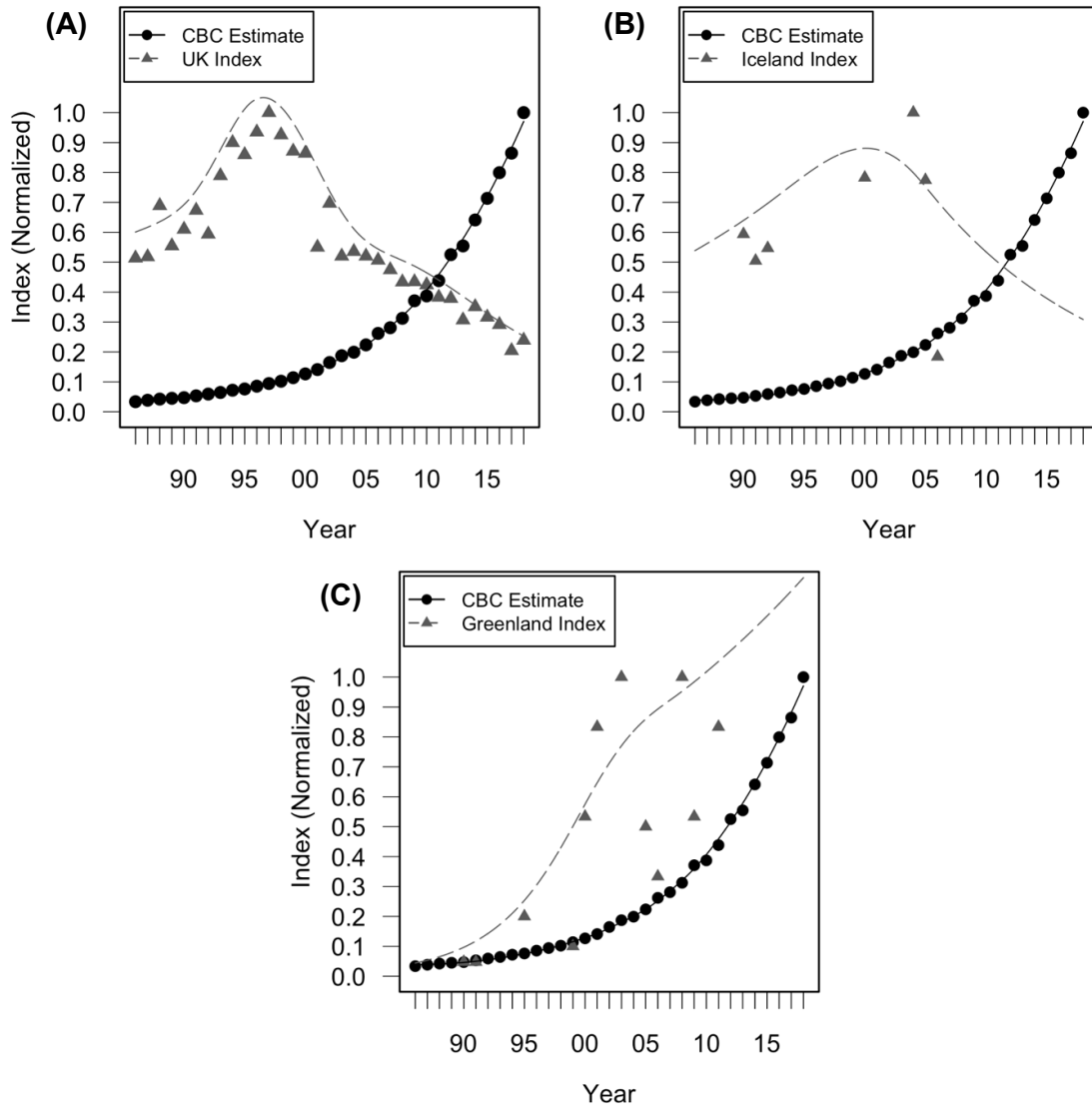
We refrain from drawing an arbitrary line over whether each particular LBBG in North

America is a vagrant, but rather define vagrancy as the process of birds moving outside of the core of their species' range, driven by growing populations (DeBenedictis 1971; DeSante 1983; Patten and Marantz 1996; Veit 1997, 2000; Zawadzki et al. 2019) and exploratory movements (Grinnell 1922, Baker 1978, Baker 1980). This definition incorporates vagrants that become recurrent seasonal visitors, and those vagrant individuals that travel to an area and stay for their lifetime. Accordingly, all sightings of LBBG in North America have been included in our analyses, including individuals that may return annually each winter.

### 5.3.3 Breeding population data

Breeding population data were extracted from countries where *graellsii* breed, i.e. the United Kingdom (hereafter, UK), Iceland, and Greenland (Figure 5.4). UK data were taken from the Seabird Monitoring Programme (SMP) (JNCC 2020), which annually monitors breeding seabird colonies in Britain and Ireland. Data are recorded as numbers of apparently occupied nests (AON), and an estimate of AON for each year is derived from these counts (I. Win, pers. comm. 2020, JNCC 2020). Data were available from 1986 to 2018.

Iceland and Greenland do not have routine monitoring programs, therefore information on breeding colonies came from other sources. Population estimates from Iceland were obtained by estimating the number of active nests at the breeding colony of Midnesheidi, Reykjanes Peninsula in southwest Iceland, the largest breeding colony in Iceland. We chose to only use data from Midnesheidi because it is the only LBBG colony that has been consistently surveyed in Iceland, and population trends at this colony are likely representative of the overall breeding population in the country (Hallgrimsson et al. 2006). The addition of limited surveys of other colonies around Iceland would only increase the estimates by a few hundred nests per year (Hallgrimsson et al. 2006), which is within the 95% confidence interval of the nest estimates at Midnesheidi. Estimates were taken between the years 1990 and 2006. Nests were counted within a sample of 4000



**Figure 5.4.** Indices of annual breeding population size from 1986 to 2018 for (A) the UK, (B) Iceland (colony of Midnesheidi), and (C) Greenland (colony of Eqaluit), and Christmas Bird Count (CBC) trend estimates of vagrants. Trend estimates are calculated from CBC surveys as estimates of median abundance, using Bayesian hierarchical methods (Soykan et al. 2016, Meehan et al. 2020). Normalized values were obtained by dividing each value in a given dataset by the maximum value of that dataset.

m<sup>2</sup> plots within the colony, and the number of plots surveyed each year ranged from 28 to 34. Outlines of the whole colony were observed and marked on a map, and the colony edge was observed from high points using a telescope and by walking with a GPS unit. The edge was determined through observations of nest defence by adults, a standard means of determining breeding status of birds (e.g. Mitchell et al. 2004). The colony area was then calculated using global information system (GIS; Esri Inc. 2008, ArcMap™9.3). To calculate the mean density, and 95% confidence limits of active nests, we used the program NEGBINOM (Krebs 1999). The size of the breeding population was found by multiplying the density by the area.

Greenland data were collected from the Greenland Seabird Colony Register. These data consisted of a series of sightings and surveys conducted across Greenland between 1986 and 2018. Data prior to 1990 were excluded from our analysis since the first confirmed case of breeding was not until 1990. Due to inconsistent survey efforts across Greenland, we used data from the most consistently surveyed colony of Eqaqut in southwest Greenland to represent breeding populations across Greenland. The first evidence of breeding LBBG was at Eqaqut in 1990, and Eqaqut has been surveyed 12 times between 1990 and 2018. Counts of LBBG were recorded as either individuals, pairs, or nests. A total pair count was calculated for each year, using the formula: pairs in year  $t$  + nests in year  $t$  + (individuals in year  $t$ )\*0.7, where 0.7 is the  $k$  value used to convert individuals to pairs (Harris et al. 2015).

Breeding data from all populations were converted to indices for model analysis. Indices were calculated as percentages relative to the base-year (first year of monitoring), which was set to 100% (Thomas 1993). Percentages were divided by 100 to derive an index value. Growth rates ( $r$ ) for each population were calculated as  $r = \ln(\lambda)$ .

### **5.3.4 Model analysis**

#### *Generalised linear models*

We constructed generalised linear models (GLMs) for each breeding population to estimate the relationship between numbers of vagrants in North America (as trend estimates from CBC data), and indices of annual breeding population size and annual growth rate ( $r$ ). We constrained our models to 1986 to 2018, when range expansion to Greenland and North America occurred. We formulated four competitive GLMs, including a null (no predictors). Models were ranked using Akaike Information Criterion (AIC) comparison, with AIC values corrected for small sample sizes (AICc) using function *aictab* from the package ‘AICcmodavg’ (Mazerolle 2020). The model with the lowest AICc value was chosen as the best model if it was at least two AICc values lower than the next most competitive model (Burnham and Anderson 2003). All analyses were conducted using R (R Core Team 2019).

#### *Generalised additive models*

Due to the nonlinear trajectory of population count data, we also constructed generalised additive models (GAMs) for each breeding population to estimate the relationship between numbers of vagrants in North America (as trend estimates from CBC data), and indices of annual breeding population size and annual growth rate ( $r$ ). GAMs are much better at dealing with variability in count data due to the nonlinear estimates calculated (Wood 2017, Knape 2016), and are often used to estimate changes in population over time (Knape 2016). Our GAMs were constrained to the same timeframe as our GLMs. A total of four models were constructed, including a null (no explanatory variables), using the package ‘mgcv’ in R (Wood 2020). We used a negative binomial distribution of errors to correct for overdispersion in our data (Lindén and Mäntyniemi 2011). Models were ranked using AIC comparison using the function *model.sel* from package ‘MuMIn’ (Bartoń 2020) to determine which model best fit our data. AIC values corrected for small sample sizes (AICc) were used. All analyses were conducted using R (R Core Team 2019).

**Table 5.1.** Parameter estimates for univariate generalised linear models (GLMs) of the relationship between trend estimates of vagrant LBBG occurrence in North America from CBC data and indices of annual breeding population size and growth rate ( $r$ ) of the breeding population in the UK, Iceland, and Greenland. Models were constrained to the years 1986 to 2018. The best model was selected based on the lowest AICc value. Effect sizes are listed for each predictor. Significant  $p$ -values ( $p < 0.05$ ) are in **bold**.

Population	Population Size	$p$ -value	Growth Rate ( $r$ )	$p$ -value	$n$	$\Delta$ AICc	AICc weight	Adj. R <sup>2</sup>
Greenland	0.13	0.08	0.36	0.53	12	0.00	0.65	0.20*
Iceland	2.11	0.03	-0.74	0.06	7	1.25	0.35	0.88
UK	-5.68	<b>&lt;0.001</b>	-4.88	<b>0.02</b>	33	89.82	0.00	0.63
Null	-	-	-	-	33	131.56	0.00	n/a

\*The best model based on the lowest AICc value

## 5.4 Results

### 5.4.1 Generalised linear models

Our most competitive model was the model for Greenland's breeding population (Table 5.1). Occurrence of vagrancy was positively correlated with both Greenland's index of population size and growth rate, albeit not significantly (Table 5.1). The model for Iceland competed with the model for Greenland as the most competitive model, differing in AICc value by only 1.25. Iceland's index of population size and growth rate were positively correlated with vagrancy, of which the index of population size was significantly correlated with vagrancy. UK breeding populations were significantly inversely related with vagrant occurrence (Table 5.1), and were the least competitive models alongside the null models.

### 5.4.2 Generalised additive models

Our most competitive GAM was the model for Iceland's breeding population (Table 5.2). Plots of this relationship indicate that Icelandic breeding populations seem to influence vagrant occurrence at two extremes (Figure 5.5b). When Icelandic populations are low or high, vagrants are abundant in North America. However, when Icelandic populations are steady, numbers of vagrants in North America are low. On the other hand, our GAM for

**Table 5.2.** Model selection for generalised additive models (GAMs) of the relationship between trend estimates of vagrant LBBG occurrence in North America from CBC data and indices of annual breeding population size and growth rate ( $r$ ) of the breeding population in the UK, Iceland, and Greenland. Models were constrained to the years 1986 to 2018. GAMs were run with negative binomial errors. The best model was selected based on the lowest AICc value. Effect sizes are listed for each predictor. Significant  $p$ -values ( $p < 0.05$ ) are in **bold**.

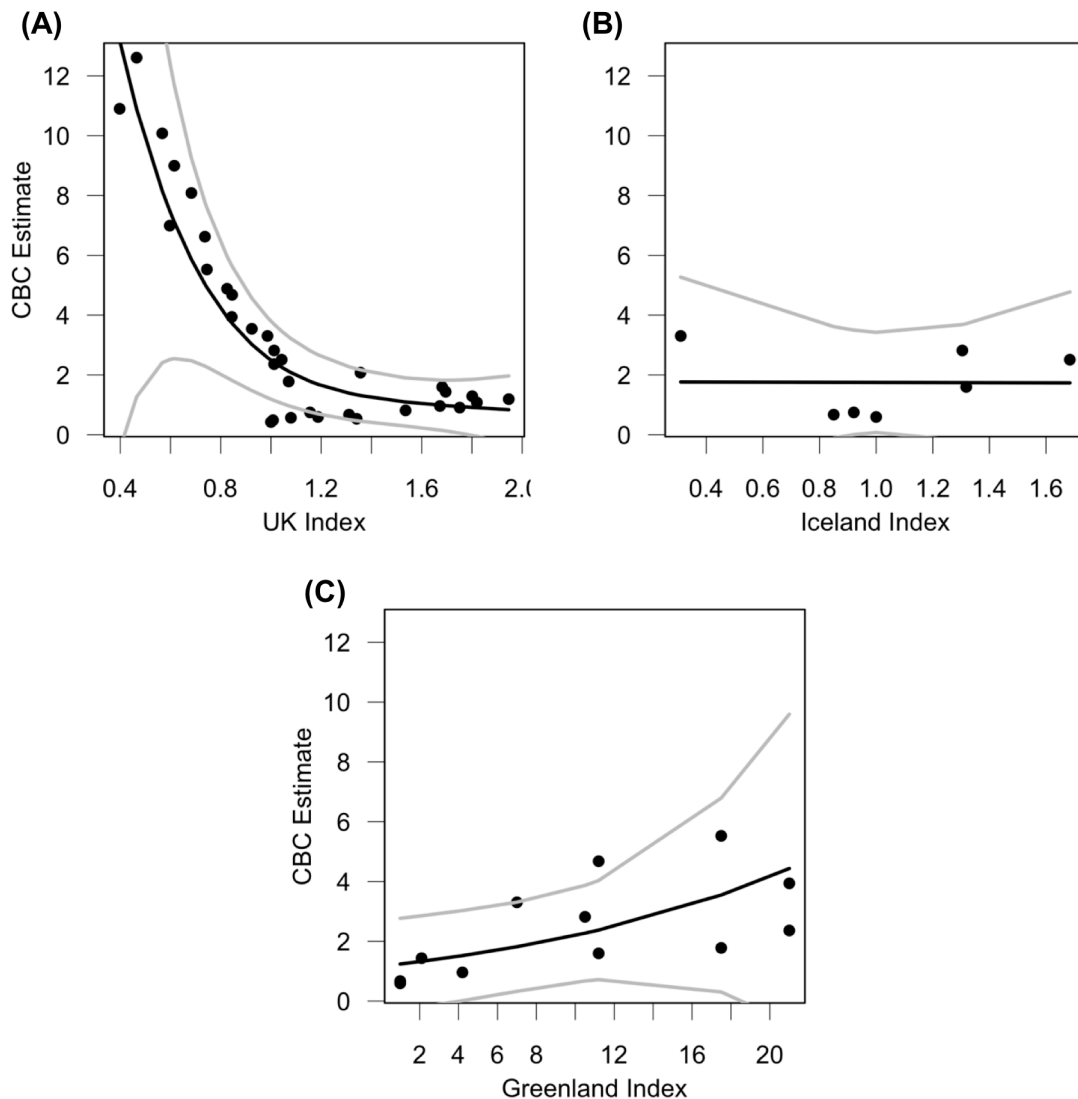
Population	Population Size	$p$	Growth Rate ( $r$ )	$p$	Deviance (%)	$k$	$n$	$\Delta\text{AICc}$	Adj. $R^2$
Iceland	0.64	0.42	0.22	0.64	41.3	4	6	0.00	0.87*
Greenland	1.22	0.27	0.20	0.66	28.9	6	11	15.02	0.05
UK	11.15	<b>&lt;0.01</b>	1.41	0.23	64.5	33	32	102.68	0.88
Null	-	-	-	-	0.0	-	33	122.27	n/a

\*The best model based on the lowest AICc value

Greenland's breeding population showed a direct positive relationship between breeding population size and occurrence of vagrants in North America (Figure 5.5c), indicating occurrence of vagrants increases with increasing breeding population size in Greenland. UK breeding populations were inversely correlated with vagrancy (Figure 5.5a), and were the least competitive models alongside the null models. The UK model was still the least competitive model despite having a higher  $R^2$  value because we selected the most competitive model based on AICc, which assesses a model's predictive power and how close it is to the underlying model, rather than its fit with existing data.

## 5.5 Discussion

We conclude that it is possible to predict potential source populations of vagrants using breeding population data. Our GLMs and GAMs for each breeding population modelled occurrence of vagrants better than the null model (Table 5.1 and 5.2). However, there are limitations present in this type of analysis if survey efforts are inconsistent or incomplete during the breeding season. For LBBG, the source population was likely derived from breeding populations in both Greenland and Iceland, though Greenland is most likely the source of the recent (since 2000) surge of vagrants to North America. The model that related Greenlandic populations to occurrence of vagrants was our most competitive model for our GLMs, while the model that related Icelandic populations to occurrence of



**Figure 5.5.** Trends between annual breeding population size and numbers of vagrants using GAM. The black line indicates the trend of the model, and the gray lines represent the lower and upper 95% confidence intervals. The graphs are allocated as follows: (A) CBC vagrants  $\sim$  UK pairs, (B) CBC vagrants  $\sim$  Iceland pairs, (C) CBC vagrants  $\sim$  Greenland pairs. CBC vagrants are calculated as trend estimates from CBC surveys, which are an estimate of median abundance, using Bayesian hierarchical methods (Soykan et al. 2016, Meehan et al. 2020). Breeding pair indices were calculated as the percent change in total breeding pairs in that year relative to the base-year (first year of monitoring), which was set to 100%. Percentages were divided by 100 to create an index.

vagrants was our most competitive model for our GAMs. While we acknowledge that other unknown or untested factors could also explain vagrancy, these are secondary to our study since we are focused on testing whether breeding population data can be used to predict a plausible source population of vagrants under the premise that population growth drives vagrancy (Patten and Marantz 1996, Ralph and Wolfe 2018, Zawadzki et al. 2019).

The ability to predict source populations of vagrants through breeding data alone is invaluable to studies on vagrancy, and will be widely applicable to a variety of vagrant species. Vagrants are difficult to study directly due to their inherent rarity, and have been seldom studied as a result. Having methodology available to study vagrants indirectly will increase the possibility for research in this area. This is particularly true of short-lived passerines, which are often too small for direct studies on their movement, such as through GPS-tracking. Further, this relationship between population and occurrence of vagrants has important implications for the role that vagrancy plays in both range expansion and colonisation of species. Range expansion and/or colonisation are a likely result of vagrancy, and studies on population dynamics of species can provide inference into species that are more likely to expand their range in the future (e.g. Jiguet and Barbet-Massin 2013). Since population dynamics are also tied to a species' habitat, it is imperative that we explore how habitat change influences vagrancy through its continued effect on population (DeBenedictis 1971, DeSante 1983, Patten and Marantz 1996).

Iceland's breeding population was likely to have been important during early years of colonisation in North America (either directly or indirectly; Figure 5.5b), prior to its stark decline in 2005 (82% decline between 2004 and 2006). Early colonisation of North America coincided with an increase in both the Icelandic and Greenlandic breeding populations (Figure 5.4b, c). It has been proposed that Greenland's breeding population was founded by Icelandic gulls between 1986 and 1990 (Boertmann 2008). It is therefore possible that some vagrant LBBG in North America originated from Iceland prior to their decline in 2005, either directly from Iceland, or through colonisation of Greenland and subsequent migration to North America, though any records of LBBG in North America prior to 1990 must have derived from other populations since a breeding population was not yet established in Greenland. Nevertheless, it is unambiguous that the major increase of vagrant LBBG to North America occurred during a period of growth of the Greenland population (Figure 5.4c). Greenland's population has been significantly influential across the entire time series (Figure 5.5c).

Recent tracking efforts by Pennsylvania's (PA) Game Commission provide strong support for this link (Barber et al. *in press*). Barber et al. (*in press*) affixed 9 wintering vagrant LBBG in Pennsylvania with GPS devices, and discovered that 5 of these individuals travelled to Greenland in the summer for two consecutive migrations. Additionally, a noticeable "jump" in the arrival of 1st calendar year to 3rd calendar year birds occurred in Massachusetts and Rhode Island in 2005 – 2010 (*Bird Observer*, eBird 2017), and again in 2018 – 2021, including 500 immatures (< 2 years old) at Fire Island, New York. Due to absence of breeding in North America, these birds must derive from a rapidly growing colony elsewhere. Therefore, our premise that increasing source populations are producing large numbers of vagrants is supported. Peaks of immature gulls in North America also coincide with peaks in breeding population size of Greenland LBBG (Figure S5.1).

The large number of unbanded gulls in North America also indicates that they are arriving from locations where *graellsii* remain unbanded, such as colonies in western Iceland and Greenland. In spite of considerable colour-banding effort in Iceland, the Netherlands, and the British Isles, only two banded gulls have been re-sighted in North America: (1) a juvenile gull banded in the Netherlands that was spotted as an adult in Long Island, New York on 7 October 1997, and (2) a first-winter gull from southwestern Iceland, that was seen during its first winter in Puerto Rico on 16 and 20 November 2002 (Hallgrímsson et al. 2011). No other re-sightings have been reported even though thousands of LBBG are seen in North America each year.

Our models also suggest that vagrant LBBG do not originate from the UK, and vagrancy is inversely correlated with UK LBBG populations (Table 5.1; Figure 5.5a). UK breeding populations have declined rapidly since 2000 (Figure 5.4a), as a result of increased culling practices, and changes to landfill and fishing practices (Ross-Smith et al. 2014a, b; Nager and O'Hanlon 2016). This rapid decline in UK breeders at a time when vagrants were increasing makes it unlikely that vagrant gulls originate from UK colonies. Additionally, decadal censuses of wintering gulls have found that UK-breeding LBBG are wintering more frequently in the UK (Banks et al. 2009, Burton et al. 2003, 2013, Ross-Smith et al.

2015), rather than migrating to southwest Europe and northwest Africa (Hallgrímsson et al. 2012). Since UK LBBG show high wintering site fidelity (Thaxter et al. 2012), increased residency of UK LBBG further decreases the likelihood that North American vagrants originate from UK colonies.

It has often been speculated that the recent influx of LBBG to North America is a result of breeding on the continent, rather than repeated instances of vagrancy. These breeding claims lack support. Only two instances of breeding have ever been confirmed in North America, and both cases were hybridizations between a LBBG and a Herring Gull (*Larus argentatus*) – one nesting pair in Juneau, Alaska in 1993 (vanVliet et al. 1993), and another pair on Appledore Island, Maine from 2007 to present, which has since fledged 5 hybrid chicks (Ellis et al. 2007, Ellis et al. 2014). Additionally, despite the presence of some breeding plumaged adults during summer for nearly two decades, they have not been seen visiting breeding habitats, even though LBBG are known to breed in mixed gull colonies (Camphuysen 2011). The majority of vagrant LBBG seen in North America are juveniles (*Bird Observer*; Figure S5.2a), particularly 1st calendar year birds (Figure S5.2b), and adults are mainly seen outside of the breeding season (Figure S5.3), making breeding unlikely.

Baker (1980) proposed that LBBG follow an exploratory migration model, whereby young birds explore during the first 18 months after fledging, and areas that are found to be more suitable for overwintering will facilitate a change in their migratory behaviour as adults. Tracking studies of immature LBBG also show that pre-breeding LBBG are more prone to these pre-migratory and post-migratory dispersal movements (Pütz et al. 2007, 2008; Camphuysen 2011). This coincides with the age profile we see in North America, where younger birds are seen throughout the year, while adult birds are mainly present during the winter season.

Our analysis did pose limitations due to inconsistent survey efforts during breeding. For LBBG, while surveys in the UK are annually consistent (JNCC 2020), survey efforts in Iceland and Greenland vary widely from year to year, and many years are missing

from the dataset. Furthermore, in Greenland, the same colonies are not surveyed each year, creating between-year variation that is not necessarily representative of the actual size of the breeding population (Boertmann and Frederiksen 2016, Boertmann et al. 2020), and could only be resolved by limiting analyses to one colony (which itself was under-surveyed;  $n = 12$ ; Table S5.1, S5.2). These irregularities constrained our models since we only had small sample sizes to work with. Despite these limitations, we feel that the data available faithfully identify the periods of maximum growth for each of these populations, though there is room for improvement in collecting future datasets.

Long-term, consistent, and systematic breeding bird surveys are necessary to more accurately assess patterns of vagrant occurrence and establishment of vagrant colonies. Such surveys do exist in a number of countries for other species (e.g. North American Breeding Bird Survey (Pardieck et al. 2020), Seabird Monitoring Programme (JNCC 2020), Netherlands Ecological Monitoring Network (Sovon 2019), and many others), but this is not the case globally, particularly in areas of the globe that are less accessible. Furthermore, species that are secretive or classified as pests (many gulls) may be overlooked, even in countries where robust breeding survey efforts are in place. Annual study plots with standardized protocol for each species (where possible) should be the aim, and would benefit not only future studies on LBBG vagrancy, but on vagrancy and population dynamics as a whole. For species in which frequent surveys are not possible, modelling could be supplemented by other field methods, such as tracking of vagrant individuals to their breeding/summering grounds with GPS devices, or stable isotope analysis to determine the natal origin of vagrant individuals (see Chapter 3; Fox et al. 2007, De Jong et al. 2019), but both of these methods pose additional problems themselves since vagrants are hard to catch, and isoscapes (for stable isotope analysis) are not as well-defined across Europe (Hobson et al. 2004). Improving survey efforts of native breeders would be the best way to improve studies of vagrancy since these studies often require indirect means of analysis. Furthermore, from an analytical perspective, statistical approaches must be carefully considered to improve our understanding of population dynamics of vagrants. For example, GAMs may provide a more robust alternative to GLMs when accounting for temporal variation in count data, and are

increasingly becoming the norm when modelling changes in populations over time (Knappe 2016).

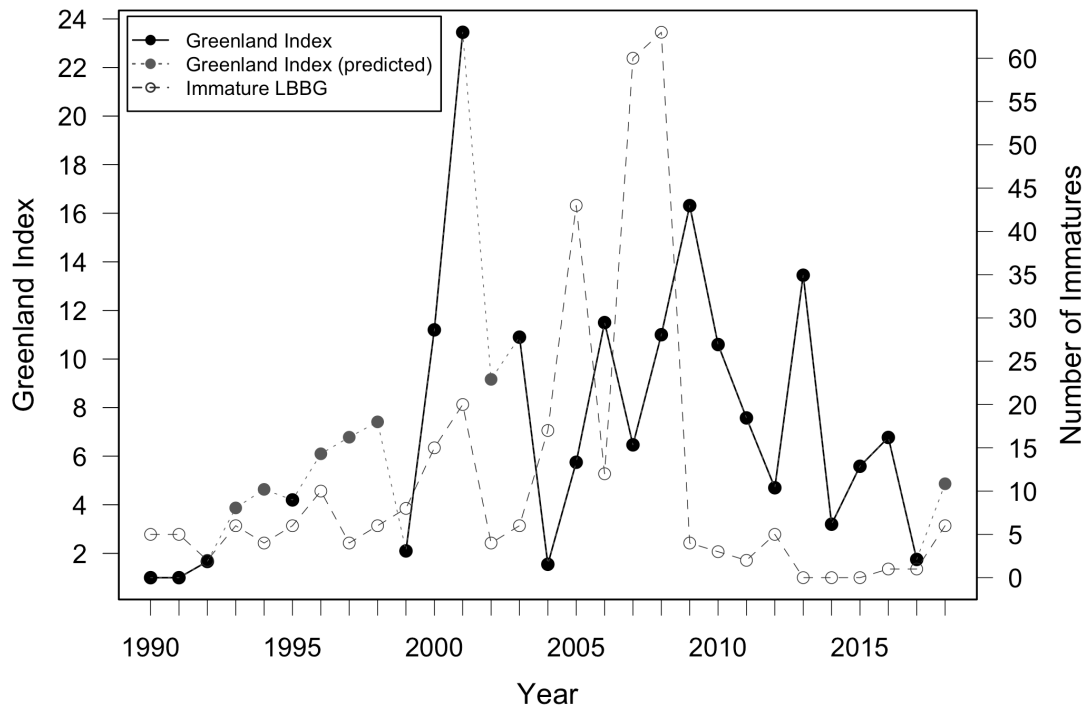
Our study shows that data on breeding populations can be used to determine plausible source populations of vagrants, but the fit of these models will be greatly improved with standardized survey efforts at breeding sites, and implementation of GAMs over GLMs for count data. For LBBG, Greenland and Iceland have influenced the increase in vagrant LBBG to North America. While Iceland may have indirectly contributed to vagrancy in early years of colonisation, Greenland populations have consistently increased alongside numbers of vagrants, suggesting Greenland is the source population of vagrant LBBG. We predict that within the next few decades LBBG will occur regularly enough in North America to be considered an established wintering population, and, following Boertmann's (2008) predictions, may even establish a small breeding population. Future studies of vagrant LBBG should incorporate GPS-tracking of wintering gulls in North America to their breeding/summering grounds to verify the results of our model analysis, and uncover the migratory routes of North American LBBG. Stable isotope analyses and mitochondrial DNA studies (Liebers and Helbig 2002) may also help to directly elucidate the origin of vagrant LBBG.

## **5.6 Acknowledgements**

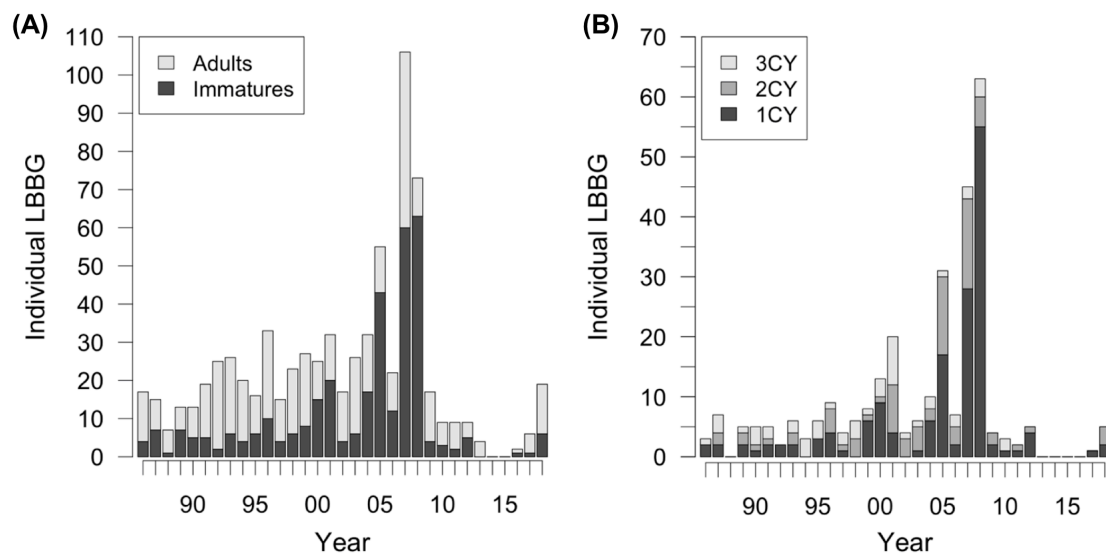
We would like to thank all that have helped with the completion of this project. Flemming Merkel answered many of our questions about Greenland data during the early stages of analyses; Ilka Win at the JNCC provided data for UK LBBG and helped us understand the dataset; and Tim Meehan and Geoff LeBaron at Audubon assisted with interpretation of CBC data. We thank Agnar Ingolfsson and Pall Hersteinsson who started the count of Icelandic gulls at Midnesheidi, and introduced the survey to G.T. Hallgrimsson. Monitoring at Midnesheidi was financially supported by ISAVIA Keflavik Airport authorities. We would also like to thank Karin Harding and four anonymous reviewers whose constructive comments and input helped greatly improve our

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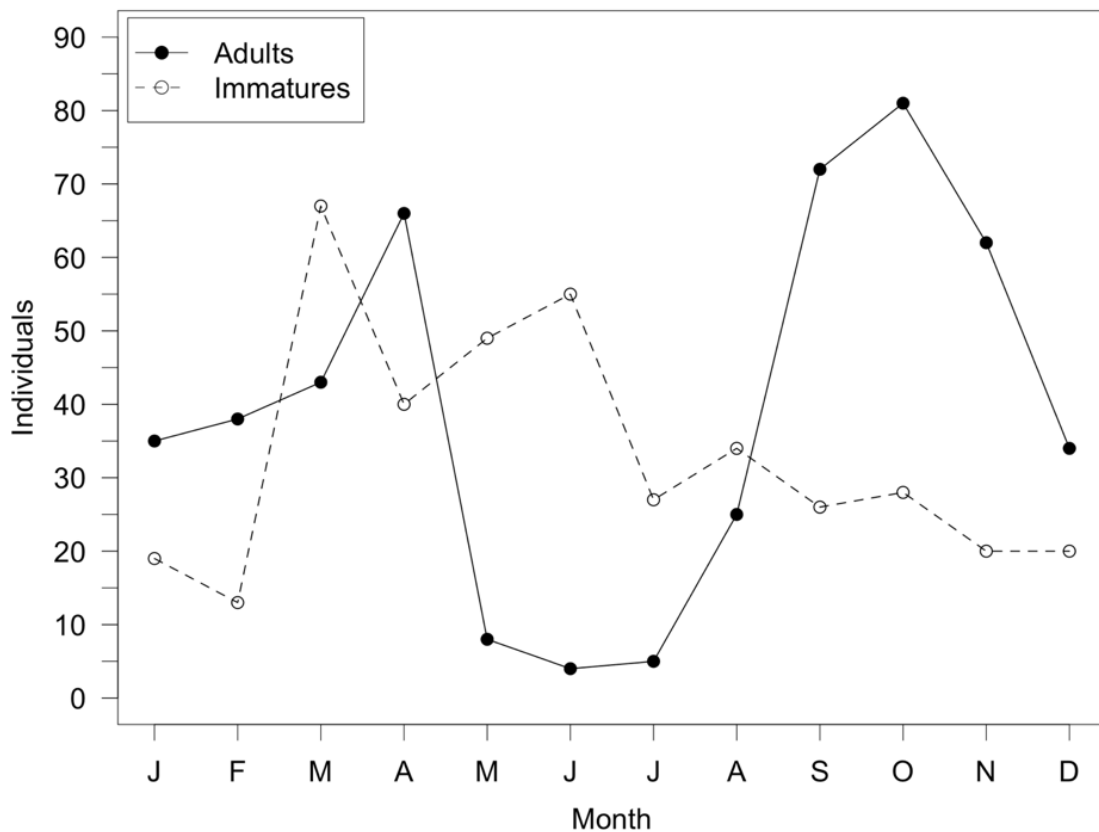
## 5.7 Supplementary Material



**Figure S5.1.** Peaks of immature LBBG (1<sup>st</sup> through 3<sup>rd</sup> calendar year birds) coincide with peaks of Greenland breeders. Data on LBBG were taken from Bird Observer, which lists records of birds found each year in Massachusetts. The index used for Greenland in this figure is an index of abundance for all Greenland colonies that has been corrected for survey effort by multiplying the average count data in one year by the total number of colonies surveyed in Greenland.



**Figure S5.2.** (A) Number of adult (4<sup>th</sup> winter and older) and immature (1<sup>st</sup> winter to 3<sup>rd</sup> summer) and (B) 1<sup>st</sup> through 3<sup>rd</sup> calendar year LBBG reported in Massachusetts annually between the years 1986 – 2018. Data were taken from the journal Bird Observer. Gulls classified to age represent 9% of the total Bird Observer dataset from 1986 – 2018.



**Figure S5.3.** Number of adult (4<sup>th</sup> winter and older) and immature (1<sup>st</sup> winter to 3<sup>rd</sup> summer) LBBG reported in Massachusetts each month between the years 1971 – 2018. Data were taken from Bird Observer. Adults are more commonly seen outside of the breeding season, from September to April, and immatures are more commonly seen from March to June. Gulls classified to age represent 11% of the total *Bird Observer* dataset from 1971-2018.

**Table S5.1.** Values of annual vagrant occurrence of LBBG from Christmas Bird Counts (CBC) and Bird Observer, and annual breeding population size of LBBG for the UK, Iceland, and Greenland. Years without survey data are years in which surveys were not conducted.

Year	Bird Observer	CBC	UK Pairs	Iceland Pairs	Greenland Pairs
1986	21	85	100687		
1987	17	88	101506		
1988	16	91	135019		
1989	23	66	108679		
1990	21	85	119540	23872	1
1991	28	113	131973	20293	1
1992	36	142	116352	21987	
1993	40	137	154642		
1994	23	148	176335		
1995	26	158	168403		4.2
1996	43	218	183223		
1997	34	240	195988		
1998	45	420	181343		
1999	48	447	170706		2.1
2000	339	505	169317	31467	11.2
2001	143	754	107788		17.5
2002	171	739	136569		
2003	141	647	101944		21
2004	291	945	104972	40204	
2005	343	1080	101963	31138	10.5
2006	188	1375	99292	7395	7
2007	376	1185	93025		
2008	514	1891	84991		21
2009	634	1372	85132		11.2
2010	684	1829	83097		
2011	444	2136	75020		17.5
2012	288	1618	74211		
2013	733	2287	60124		
2014	500	2726	68789		
2015	688	2133	61941		
2016	357	3078	57109		
2017	430	2557	40041		
2018	406	3021	46856		

**Table S5.2.** Values of Christmas Bird Count (CBC) vagrant trend estimates for LBBG and indices of annual breeding population size and growth rates for LBBG breeding populations in the UK, Iceland, and Greenland. CBC trend estimates are calculated from CBC surveys as estimates of median abundance, using Bayesian hierarchical methods (Soykan et al. 2016, Meehan et al. 2020). Breeding pairs indices were calculated as the percent change in total breeding pairs in that year relative to the base-year (first year of monitoring), which was set to 100%. Percentages were divided by 100 to create an index. Years without survey data are years in which surveys were not conducted. These data were used for model analysis of both GLMs and GAMs.

Year	CBC estimate	UK index	UK growth rate	Iceland index	Iceland growth rate	Greenland index	Greenland growth rate
1986	0.42	1.00	0.01				
1987	0.49	1.01	0.29				
1988	0.53	1.34	-0.22				
1989	0.57	1.08	0.10				
1990	0.59	1.19	0.10	1.00	-0.16	1.00	0.00
1991	0.67	1.31	-0.13	0.85	0.08	1.00	1.44
1992	0.75	1.16	0.28	0.92	0.36		
1993	0.81	1.54	0.13				
1994	0.91	1.75	-0.05				
1995	0.96	1.67	0.08			4.20	-0.69
1996	1.08	1.82	0.07				
1997	1.19	1.95	-0.08				
1998	1.29	1.80	-0.06				
1999	1.44	1.70	-0.01			2.10	1.67
2000	1.60	1.68	-0.45	1.32	0.25	11.20	0.45
2001	1.78	1.07	0.24			17.50	0.18
2002	2.08	1.36	-0.29				
2003	2.36	1.01	0.03			21.00	-0.69
2004	2.51	1.04	-0.03	1.68	-0.26		
2005	2.82	1.01	-0.03	1.30	-1.44	10.50	-0.41
2006	3.30	0.99	-0.07	0.31		7.00	1.10
2007	3.54	0.92	-0.09				
2008	3.94	0.84	0.00			21.00	-0.63
2009	4.68	0.85	-0.02			11.20	0.45
2010	4.88	0.83	-0.10				
2011	5.53	0.75	-0.01			17.50	
2012	6.62	0.74	-0.21				
2013	6.99	0.60	0.14				
2014	8.08	0.68	-0.11				
2015	9.00	0.62	-0.08				
2016	10.08	0.57	-0.36				
2017	10.90	0.40	0.16				
2018	12.61	0.47					

## References

- Baker, R. R. (1978). *The evolutionary ecology of animal migration*. Holmes; Meier Publishers.
- Baker, R. R. (1980). The significance of the Lesser Black-backed Gull to models of bird migration. *Bird Study*, 27(1), 41–50.
- Banks, A. N., Burton, N. H. K., Calladine, J. R., & Austin, G. E. (2009). Indexing winter gull numbers in Great Britain using data from the 1953 to 2004 Winter Gull Roost Surveys. *Bird Study*, 56(1), 103–109.
- Barber et al. (in press). Summer locations of LBBG (*L. fuscus*) wintering in PA.
- Bartoń, K. (2020). *Mumin: Multi-Model Inference* [R package version 1.43.17]. <https://CRAN.R-project.org/package=MuMIn>
- Bird Observer. Arlington, Massachusetts. <https://www.birdobserver.org/Issues/Complete-Archive>
- Boertmann, D. (2008). The Lesser Black-backed Gull, *Larus fuscus*, in greenland. *Arctic*, 61(2), 129–133.
- Boertmann, D., & Frederiksen, M. (2016). Status of Greenland populations of Great Black-backed Gull (*Larus marinus*). *Waterbirds*, 1, 29–35.
- Boertmann, D., Merkel, F., & Gilg, O. (2020). Seabird breeding colonies in East and North Greenland: A baseline. *Arctic*, 73(1), 20–39.
- Burger, J., Gochfeld, M., Kirwan, G. M., Christie, D. A., & Juana, E. (2020). Lesser Black-backed Gull (*Larus fuscus*), version 1.0. In J. Hoyo, A. Elliot, J. Sargatal, D. A. Christie, & E. Juana (Eds.), *Birds of the World*. Cornell Lab of Ornithology.
- Burnham, K. P., & Anderson, D. R. (2003). *Model selection and multimodel inference: A practical information-theoretic approach* (Second). Springer-Verlag.
- Burton, N. H. K., Banks, A. N., Calladine, J., & Austin, G. E. (2013). The importance of the United Kingdom for wintering gulls: Population estimates and conservation requirements. *Bird Study*, 60(1), 87–101.
- Burton, N. H. K., Musgrove, A., Rehfisch, M. M., Sutcliffe, A., & Waters, R. (2003). Numbers of wintering gulls in the United kingdom, Channel Islands, and Isle of Man: A review of the 1993 and previous Winter Gull Roost Surveys. *British Birds*, 96, 376–401.

- Camphuysen, C. J. (2011). *Lesser Black-backed Gulls nesting at Texel: Foraging distribution, diet, survival, recruitment and breeding biology of birds carrying advanced GPS loggers*. Royal Netherlands Institute for Sea Research.
- Collinson, J. M., Parkin, D. T., Knox, A. G., Sangster, G., & Svensson, L. (2008). Species boundaries in the Herring and Lesser Black-backed Gull complex. *British Birds*, *101*, 340–363.
- Cottridge, D., & Vinicombe, K. (1996). *Rare birds in Britain and Ireland - a photographic record*. Harper Collins.
- Cramp, S., & Simmons, K. E. L. (Eds.). (1983). *The birds of the Western Palearctic* (Vol. III). OUP.
- De Jong, A., Tornaiainen, J., Bourski, O. V., Heim, W., & Edenius, L. (2019). Tracing the origin of vagrant Siberian songbirds with stable isotopes: the case of Yellow-browed Warbler (*Abrornis inornatus*) in Fennoscandia. *Ornis Fennica*, *96*, 90–99.
- De Juana, E., & Garcia, E. F. J. (2010). Vagrancy or migration: Why do American Teals cross the Atlantic? *Ardeola*, *57*(2), 417–430.
- DeBenedictis, P. (1971). Wood warblers and vireos in California: The nature of the accidental. *California Birds*, *2*(4), 111–128.
- DeSante, D. F. (1973). *An analysis of the fall occurrences and nocturnal orientations of vagrant wood warblers (Parulidae) in California* (Doctoral dissertation). Stanford University. Stanford, California.
- DeSante, D. F. (1983). Annual variability in the abundance of migrant landbirds on Southeast Farallon Island, California. *The Auk*, *100*(4), 826–852.
- eBird. (2017). eBird: An online database of bird distribution and abundance [web application]. eBird, cornell lab of ornithology [Place: Ithaca, New York]. <http://www.ebird.org>
- Elkins, N. (1979). Nearctic landbirds in Britain and Ireland: A meteorological analysis. *British Birds*, *72*(9), 417–433.
- Elkins, N. (1999). Recent records of Nearctic landbirds in Britain and Ireland. *British Birds*, *92*, 83–95.
- Ellis, J. C., Bogdanowicz, S. M., Stoddard, M. C., & Clark, L. W. (2014). Hybridization of a Lesser Black-backed Gull and Herring Gulls in eastern North America. *The Wilson Journal of Ornithology*, *126*(2), 338–345.
- Ellis, J. C., Stoddard, M. C., & Clark, L. W. (2007). Breeding by a Lesser Black-backed Gull (*Larus fuscus*) on the Atlantic coast of North America. *North American Birds*, *61*(4), 546–548.
- Esri Inc. (2008). *ArcMap (version 9.3)*. Esri Inc. <https://desktop.arcgis.com/en/arcmap/>

- Farnsworth, A., La Sorte, F., & Iliff, M. J. (2015). Warmer summers and drier winters correlate with more winter vagrant Purple Gallinules (*Porphyrio martinicus*) in the North Atlantic Region. *The Wilson Journal of Ornithology*, 127(4), 582–592.
- Fox, T. A. D., Christensen, T. K., Bearhop, S., & Newton, J. (2007). Using stable isotope analysis of multiple feather tracts to identify moulting provenance of vagrant birds: A case study of the Baikal Teal *Anas formosa* in Denmark. *Ibis*, 149, 622–625.
- Grinnell, J. (1922). The role of the “accidental”. *The Auk*, 39(3), 373–380.
- Hallgrímsson, G. T., Gunnarsson, H., & Hersteinsson, P. (2006). Stærð sílamáfsvarps á álftanesi á mýrum [Size of the Lesser Black-backed Gull colony at Álftanes on Mýrar] (W-Iceland) in 2005. *Bliki*, 27, 55–57.
- Hallgrímsson, G. T., Gunnarsson, H. V., Torfason, O., Buijs, R. .-, & Camphuysen, K. C. J. (2012). Migration pattern of Icelandic Lesser Black-backed Gulls *Larus fuscus graellsii*: Indications of a leap-frog system. *Journal of Ornithology*, 153(3), 603–609.
- Hallgrímsson, G. T., Swelm, N. D., Gunnarsson, H. V., Johnson, T. B., & Rutt, C. L. (2011). First two records of Europe-banded Lesser Black-backed Gulls *Larus fuscus* in America. *Marine Ornithology*, 39, 137–139.
- Hampton, S. (1997). Rare migrants in California: The determinants of their frequency. *Western Birds*, 28, 30–42.
- Harris, M. P., Heubeck, M., Newell, M. A., & Wanless, S. (2015). The need for year-specific correction factors (k values) when converting counts of individual Common Guillemots *Uria aalge* to breeding pairs. *Bird Study*, 62(2), 276–279.
- Hengeveld, R. (1989). *Dynamics of biological invasions*. Kluwer Academic Publishers. Chapman; Hall.
- Hobson, K. A., Bowen, G. J., Wassenaar, L. I., Ferrand, Y., & Lormee, H. (2004). Using stable hydrogen and oxygen isotope measurements of feathers to infer geographical origins of migrating European birds. *Oecologia*, 141, 477–488.
- International, W. (2020). Waterbird Population Estimates. <http://wpe.wetlands.org/>
- Jiguet, F., & Barbet-Massin, M. (2013). Climate change and rates of vagrancy of Siberian bird species to Europe. *Ibis*, 155, 194–198.
- Jiguet, F., Doxa, A., & Robert, A. (2008). The origin of out-of-range pelicans in Europe: Wild bird dispersal or zoo escapes? *Ibis*, 150, 606–618.
- JNCC. (2020). Seabird population trends and causes of change: 1986-2018 report. *Online. Joint Nature Conservation Committee, Peterborough*. <https://jncc.gov.uk/our-work/smp-report-1986-2018>
- Knape, J. (2016). Decomposing trends in Swedish bird populations using generalized additive mixed models. *Journal of Applied Ecology*, 53(6), 1852–1861.

- Krebs, C. (1999). *Ecological Methodology*. Benjamin Cummings.
- Liebers, D., & Helbig, A. J. (2002). Phylogeography and colonization history of Lesser Black-backed Gulls (*Larus fuscus*) as revealed by mtDNA sequences. *Journal of Evolutionary Biology*, *15*(6), 1021–1033.
- Lindén, A., & Mäntyniemi, S. (2011). Using the negative binomial distribution to model overdispersion in ecological count data. *Ecology*, *92*(7), 1414–1421.
- Massa, C., Doyle, M., & Fortunato, R. C. (2014). On how Cattle Egret (*Bubulcus ibis*) spread to the Americas: Meteorological tools to assess probable colonization trajectories. *International Journal of Biometeorology*, *58*(9), 1879–1891.
- Mazerolle, M. J. (2020). AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). R package version 2.3-1. <https://cran.r-project.org/package=AICcmodavg>.
- McLaren, I. A. (1981). The incidence of vagrant landbirds on Nova Scotian islands. *The Auk*, *98*(2), 243–257.
- McLaren, I. A., Lees, A. C., Field, C., & Collins, K. J. (2006). Origins and characteristics of Nearctic landbirds in Britain and Ireland in autumn: A statistical analysis. *Ibis*, *148*(4), 1–20.
- Meehan, T. D., LeBaron, G. S., Dale, K., Krump, A., Michel, N. L., & Wilsey, C. B. (2020). *Abundance trends of birds wintering in the USA and Canada, from Audubon Christmas Bird Counts* (version 3.0). National Audubon Society.
- Mitchell, P. I., Newton, S. F., Ratcliffe, N., & Dunn, T. E. (2004). *Seabird Populations of Britain and Ireland*. T.; AD Poyser.
- Nager, R. G., & O'Hanlon, N. J. (2016). Changing numbers of the three gull species in the British Isles. *Waterbirds*, *39*, 15–28.
- Nisbet, I. C., Veit, R. R., Auer, S. A., & White, T. P. (2013). *Marine birds of the eastern United States and the Bay of Fundy: Distribution, numbers, trends, threats, and management*. Nuttall Ornithological Monographs No 29.
- North, M. R. (2020). Significant recoveries of banded birds. *North American Bird Bander*, *45*(3), 130–134.
- North American Breeding Bird Survey Dataset 1966 - 2019: U.S. (2020). *Geological Survey data release*.
- Olsen, K. M., & Larsson, H. (2004). *Gulls of North America, Europe and Asia*. Princeton University Press.
- Patten, M. A., & Marantz, C. A. (1996). Implications of vagrant southeastern vireos and warblers in California. *The Auk*, *113*(4), 911–923.
- Pfeifer, R., Stadler, J., & Brandl, R. (2007). Birds from the Far East in Central Europe: A test of the reverse migration hypothesis. *Journal of Ornithology*, *148*, 379–385.

- Phillips, B. L., Brown, G. P., & Shine, R. (2010). Evolutionarily accelerated invasions: The rate of dispersal evolves upwards during the range advance of cane toads. *Journal of Evolutionary Biology*, 23(12), 2595–2601.
- Post, P. W., & Lewis, R. H. (1995). The Lesser Black-backed Gull in the Americas: Occurrence and subspecific identity. *Part I: Taxonomy, distribution, and migration. Birding*, 27, 282–290.
- Pütz, K., Helbig, A. J., Pedersen, K. T., Rahbek, C., Saurola, P., & Juvaste, R. (2008). From fledging to breeding: Long-term satellite tracking of the migratory behaviour of a Lesser Black-backed Gull *Larus fuscus intermedius*. *Ringing and Migration*, 24(1), 7–10.
- Pütz, K., Rahbek, C., Saurola, P., Pedersen, K. T., Juvaste, R., & Helbig, A. J. (2007). Satellite tracking of the migration pathways of first-year Lesser Black-backed Gulls *Larus fuscus* departing from the breeding grounds of different subspecies. *Vogelwelt*, 128, 141–146.
- R Core Team. (2019). R: A language and environment for statistical computing. <https://www.R-project.org/>.
- Rabøl, J. (1969). Reversed migration as a cause of westward vagrancy by four Phylloscopus warblers. *British Birds*, 62(3), 89–92.
- Ralph, C. J., & Wolfe, J. D. (2018). Factors affecting the distribution and abundance of autumn vagrant New World warblers in northwestern California and southern Oregon. *PeerJ*, 6, 5881.
- Román-Palacios, C., & Wiens, J. J. (2020). Recent responses to climate change reveal the drivers of species extinction and survival. *Proceedings of the National Academy of Sciences*, 117(8), 4211–4217.
- Ross-Smith, V. H., Grantham, M. J., Robinson, R. A., & Clark, J. A. (2014a). *Analysis of Lesser Black-backed Gull data to inform meta-population studies*. BTO Research Report No. 654.
- Ross-Smith, V. H., Robinson, R. A., Banks, A. N., Frayling, T. D., Gibson, C. C., & Clark, J. A. (2014b). The Lesser Black-backed Gull *Larus fuscus* in England: How to resolve a conservation conundrum. *Seabird*, 27, 41–61.
- Ross-Smith, V. H., Robinson, R. A., & Clark, J. A. (2015). *Dispersal and movements of Lesser Black-backed Gull in Europe*. BTO Research Report No. 671.
- Sibley, D. A. (2014). *The Sibley Guide to Birds* (Second). Alfred A. Knopf.
- Southwood, T. R. E., May, R. M., Hassell, M. P., & Conway, G. R. (1974). Ecological strategies and population parameters. *The American Naturalist*, 108(964), 791–804.
- Sovon. (2019). Network Ecologische Monitoring (Network Ecological Monitoring). provinces & CBS. <https://www.sovon.nl/>

- Soykan, C. U., Sauer, J., Schuetz, J. G., LeBaron, G. S., Dale, K., & Langham, G. M. (2016). Population trends for North American winter birds based on hierarchical models. *Ecosphere*, 7(5).
- Szűcs, M., Melbourne, B. A., Tuff, T., & Hufbauer, R. A. (2014). The roles of demography and genetics in the early stages of colonization. *Proceedings of the Royal Society B*, 281, 20141073.
- Thaxter, C. B., Ross-Smith, V. H., Clark, N. A., J., C. G., Wade, H., Masden, E. A., Rehfish, M. M., Bouten, W., & Burton, N. H. K. (2012). *Measuring the interaction between marine features of Special Protection Areas with offshore wind farm development zones through telemetry: Second year report*. BTO Research Report No. 610.
- Thomas, G. E. (1993). Estimating annual total heron population counts. *Applied Statistics*, 42(3), 473–486.
- Thorup, K. (2004). Reverse migration as a cause of vagrancy. *Bird Study*, 51(3), 228–238.
- vanVliet, G., Marshall, B., Craig, D., & Egolf, J. (1993). First record of nesting activity by a Lesser Black-backed Gull (*Larus fuscus*) in North America. *Bulletin of the Pacific Seabirds Group*, 20, 21.
- Veit, R. R. (1990). Do vagrant birds in Massachusetts reflect population growth and dispersal rather than weather patterns? *Bird Observer*, 18(2), 86–91.
- Veit, R. R. (1997). Long-distance dispersal and population growth of the Yellow-headed Blackbird *Xanthocephalus xanthocephalus*. *Ardea*, 85(1), 135–143.
- Veit, R. R. (2000). Vagrants as the expanding fringe of a growing population. *The Auk*, 117(1), 242–246.
- Veit, R. R., & Lewis, M. A. (1996). Dispersal, population growth, and the Allee effect: Dynamics of the house finch invasion of eastern North America. *The American Naturalist*, 148(2), 255–274.
- Veit, R. R., & Petersen, W. R. (1993). *Birds of Massachusetts*. Massachusetts Audubon Society.
- Veit, R. R., Zawadzki, L. C., Manne, L. L., Cales, P., Fibikar, D., Curley, S., Dluhos, E., & Norton, R. L. (2016). Vagrancy and colonization of St. Thomas and St. John, U.S. Virgin Islands, by Adelaide's Warblers (*Setophaga adelaidae*). *The Journal of Caribbean Ornithology*, 29, 47–50.
- Williamson, K. (1959). The September drift-movements of 1956 and 1958. *British Birds*, 52, 334–377.
- Wood, S. (2017). *Generalized additive models: An introduction with r* (2nd edition). Chapman; Hall.
- Wood, S. (2020). Package 'mgcv'. <http://cran.r-project.org/web/packages/mgcv/mgcv.pdf>.

- Zawadzki, L. C., Veit, R. R., & Manne, L. L. (2019). The influence of population growth and wind on vagrancy in a North American passerine. *Ardea*, *107*(2), 131–147.

# 6

## Investigating irruption cycles of Northern Saw-whet Owls (*Aegolius acadicus*) in North America

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## 6.1 Abstract

Vagrancy occurs in irruptive cycles, whereby individual vagrants will respond to population and environmental changes, resulting in peak years when vagrants are seen. Though not a vagrant to North America, Northern Saw-whet Owls (*Aegolius acadicus*) also appear in irruption cycles during autumn migration, and causes and consequences of these peak years may be similar to fluctuations in vagrant abundance. We used banding data from the U.S. Geological Survey Bird Banding Laboratory (BBL) to determine the extent and periodicity of irruption cycles of the Northern Saw-whet Owl during autumn migration across the United States, from 1999 to 2018. We analysed 188,389 individuals of known age in this study. We also analysed population dynamics of Northern Saw-whet Owls to determine whether the population has changed since 1999, and if there are sex-specific migration trends in the species. Major irruption years occurred in 1999, 2001, 2003, 2007, 2010, 2012, 2014, 2016, and 2018, with an average irruption cycle of 2.8 years. Evidence from southern red-backed vole (*Clethrionomys gapperi*) data suggests that these cycles closely follow prey availability in the breeding range, and that the breeding success of saw-whet owls is linked to vole abundance on the breeding grounds. Additionally, populations of Northern Saw-whet Owls have remained stable from 1999 to 2018, but the ratio of hatching-year (HY) birds fluctuates with a significant periodicity of 1 to 4 years. Sex-specific trends were present, and females were more likely to be captured on migration than males. Vagrancy and irruptions may be intrinsically linked, and it is likely that vagrants also respond to food availability.

## 6.2 Introduction

Northern Saw-whet owls (*Aegolius acadicus*; hereafter "saw-whet owls"), one of the most common owls that inhabits coniferous boreal forests in southern Canada and the northern United States (Rasmussen et al. 2020), are thought to engage in irruptive or invasive movements southward (Bent 1938, Swengel and Swengel 1995, Whalen and Watts 2002). Numbers of saw-whet owls captured at banding stations fluctuate annually, with a disproportionate number of hatch year (i.e. recently fledged young; hereafter, "HY") birds present in peak years (Brinker et al. 1997, Whalen and Watts 2002, Brittain et al. 2009, Beckett and Proudfoot 2011), referred to as "irruption years" (Whalen and Watts 2002). Irruption years in saw-whet owls have been described to occur every 4 years on average (Swengel and Swengel 1995, Confer et al. 2014), the most well-known of which occurred in 1995, 1999 and 2007 (Brinker et al. 1997, Whalen and Watts 2002, Brittain et al. 2009, Beckett and Proudfoot 2011).

It was previously thought that these irruptions were similar to irruptive movements made by other boreal owl species (irruptive movements within a resident life strategy; Bent 1938, Newton 2006). However, rigorous banding efforts in North America (saw-whet owls are banded the most out of any owl species in North America (USGS Bird Banding Laboratory) have shown that saw-whet owls are actually regular migrants, rather than irruptive migrants. Many individuals embark southward on their autumn migration from September to November (Holroyd and Woods 1975, Weir et al. 1980, Duffy and Kerlinger 1992, Whalen and Watts 2002, Frye et al. 2003), with peak numbers occurring in October. It is unclear why these irruptions occur given their current migratory strategy. Unfortunately, due to their secretive nature, many aspects of their life cycle, movements, and population dynamics are still poorly understood (Rasmussen et al. 2020). Even though banding efforts indicate that they are common and widespread, saw-whet owls are seldom seen or heard, and breeding habitats where saw-whet owls can be heard calling are sparsely populated by possible observers (Swengel and Swengel 1995), making it difficult to study their life history.

For many birds that breed in the Boreal and Arctic zones of North America, species' movements and demographics closely follow resource availability (Lees and Gilroy 2009). A number of owl species that reside in these zones, including the Boreal (Tengmalm's) Owl (*Aegolius funereus*) and Great Horned Owl (*Bubo virginianus*), have been found to respond to annual variability in prey in the breeding region (Rohner 1996, Cheveau et al. 2004, Cote et al. 2007, Bowman et al. 2010). Even though saw-whet owls are migratory, it is possible that their irruptions also coincide with prey availability. Prey for boreal owl species typically consists of small rodents, such as the southern red-backed vole (*Clethrionomys gapperi*) (e.g. Cheveau et al. 2004, Cote et al. 2007, Bowman et al. 2010, Confer et al. 2014). In North America, it has recently been discovered that these rodent populations fluctuate cyclically with a periodicity of 3 to 5 years (Elias et al. 2006, Gruyer et al. 2008, Fauteux et al. 2015), which matches well-studied owl-rodent irruption cycles in Fennoscandia (see review by Stenseth 1999). Predators will respond to these changes through irruptive movements, usually when prey resources are depleted, in temporal cycles that coincide with prey abundance (Rohner 1996, Cheveau et al. 2004, Cote et al. 2007, Lees and Gilroy 2009).

Recent studies suggest that saw-whet owl populations are positively correlated with annual abundance of small rodents in the breeding range (Cote et al. 2007, Bowman et al. 2010, Confer et al. 2014). This suggests that saw-whet owls experience high breeding success in years of high prey abundance, resulting in an influx of immatures southward during their autumn migration. However, the true extent and periodicity of this relationship across North America remains understudied. Though irruptions have an estimated periodicity of 4 years, irruptions occur at irregular intervals (Confer et al. 2014). Additionally, the extent of these irruption years in North America are unknown, since the majority of studies have been confined to areas in eastern North America, within the Great Lakes Basin and the Atlantic seaboard, while studies in western North America are lacking (Frye and Gerhardt 2003).

Sex-specific migration trends have also been revealed through banding data. Female saw-whet owls are often disproportionately captured at banding stations during autumn

migration (Brinker et al. 1997, Beckett and Proudfoot 2011). Additionally, the proportion of males captured increases at more northerly latitudes (Beckett and Proudfoot 2012). This suggests that males do not migrate as far as females, potentially staying closer to the breeding area due to reluctance to leave valuable nest sites (Newton 2006, Brittain et al. 2009). This differential movement by sex has been recorded in other owl species, such as the Boreal (Tengmalm's) Owl (Korpimäki et al. 1987). Sex biases in saw-whet owls were thought to result from use of audiolures at banding stations that played a male solicitation call (Duffy and Matheny 1997). However, recent analyses have shown that while females are more likely to be captured at these stations, this sex bias is still present during passive netting (no audiolure), which is indicative of a true differential migration between the two sexes (Duffy and Matheny 1997, Neri et al. 2018). Whether this is characteristic across North America remains to be studied.

In this study, we used banding records of saw-whet owls across the United States during autumn migration to determine the extent and periodicity of irruption years, the relationship of irruption years to cycles of prey abundance in the breeding range, and sex biases in capture rates. This will be the first study to define irruption years for migrating saw-whet owls across the United States, which were previously only defined for the Great Lakes region (Confer et al. 2014). We studied the following questions: (1) How have trends in migrating saw-whet owls changed since 1999? (2) Do irruption years across the United States follow the proposed 4-year irruption cycle? (3) Do irruption cycles coincide with prey abundance in the breeding range? (4) Do saw-whet owls travel further south during irruption years? (5) Do females appear disproportionately across the United States, and does this trend coincide with latitude? We hypothesise that populations of saw-whet owls have been relatively constant since 1999, with irruptions occurring with a periodicity of 2 to 4 years in accordance with bander observations and periodicity of prey. These irruptions are hypothesised to coincide with years of high prey abundance. Furthermore, we hypothesise that saw-whet owls will move further south during irruption years, and females will migrate to more southerly latitudes than males in all years. Females are hypothesised to be captured in disproportionately high numbers to males. Increasing our understanding of how irruptions occur in migratory species may be

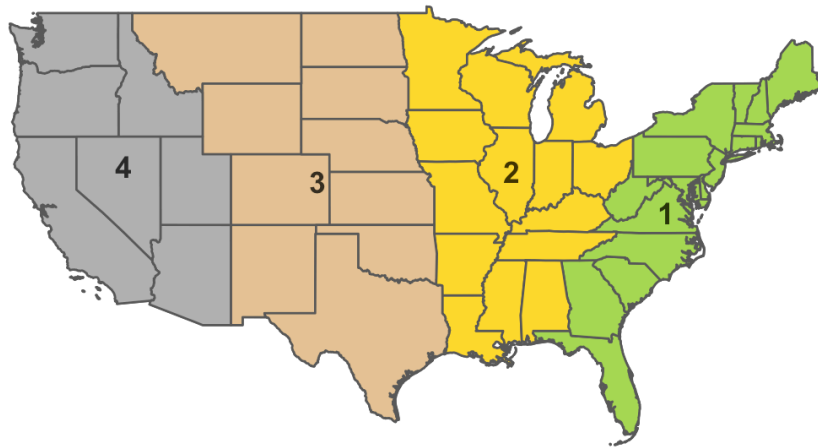
crucial in disentangling the effects that population dynamics have on vagrancy since vagrancy occurs in irruptive cycles.

## 6.3 Methods

### 6.3.1 Owl data

Data on saw-whet owls were extracted from banding records provided by the U.S. Geological Survey Bird Banding Laboratory (BBL). Extensive banding efforts for saw-whet owls are operational across North America, and a total of 325,625 individuals have been banded in the United States since 1960, 297,321 (91%) of which have been banded during autumn migration (Table S6.1, S6.2). Migratory pathways along the Atlantic coastal lowlands from Maine to North Carolina (Holroyd and Woods 1975, Duffy and Kerlinger 1992), within the Great Lakes region (the Middle Atlantic) from Michigan to Pennsylvania (Holroyd and Woods 1975, Brinker et al. 1997), and a possible pathway along the Pacific coast of North America in central Oregon (Frye and Gerhardt 2003) have been revealed from banding data. For this study, records of newly banded birds captured during autumn migration (1 September to 31 December) from 1999 to 2018 were collected, across all four flyways within the United States (Figure 1), which encompass known migratory pathways of saw-whet owls.

Birds banded prior to 1999 were excluded from our analysis since methods of capture for saw-whet owls were not standardised across stations until the late 1990s. Audiolures were introduced in 1986 at Little Suamico Ornithological Station (Erdman and Brinker 1997) to increase capture rates of saw-whet owls in mist-nets. By 1999, most saw-whet owl banding stations were using audiolures. Though Duffy and Matheny (1997) found no significant difference in age composition of owls captured with passive mist-netting versus active mist-netting with audiolures ( $F = 0.08$ ), data prior to 1999 was still excluded to ensure that records across banding stations were comparable (Confer et al. 2014). Additionally, criteria used to accurately sex saw-whet owls were not published until 1997



**Figure 6.1.** The four different migratory flyways in the United States as defined by the Bird Banding Laboratory (BBL).

(Brinker et al. 1997), therefore any owls classified to sex prior to this year are not reliable. A total of 188,389 saw-whet owls were captured during the study period (Table 6.1). Owls of unknown age (owls not aged by the bander; age = “0”) were excluded from all analyses involving age, and owls of unknown sex (owls not sexed by the bander; sex = “0”) were excluded from all analyses involving sex.

### 6.3.2 Temporal trends

Linear regressions were used to assess population trends of saw-whet owls over the course of the study period. Regressions were analysed for the total number of HY saw-whet owls and after hatch-year (i.e. adult birds; hereafter, "AHY") saw-whet owls captured, as well as the total number of owls captured regardless of age during the study period. Owls of unknown age (owls not aged by the bander; age = "0") were excluded from analyses.

### 6.3.3 Irruption years

Temporal autocorrelations were conducted to detect potential periodicity in presence of HY saw-whet owls across the United States, using the *pacf* function in the ‘forecast’

**Table 6.1.** Annual ratios of Northern Saw-whet Owls (*Aegolius acadicus*) banded in North America by age and sex from 1999 to 2018. The overall ratios over the 20 year time-series, and the 20 year mean ratios, are included. Owls of unknown age (age = "0") and sex (sex = "0") were excluded from calculations.

Year	Age Class		Sex Class	
	Hatch Year	After Hatch Year	Females	Males
1999	0.66	0.34	0.83	0.17
2000	0.40	0.60	0.91	0.09
2001	0.58	0.42	0.87	0.13
2002	0.48	0.52	0.89	0.11
2003	0.56	0.44	0.88	0.12
2004	0.40	0.60	0.90	0.10
2005	0.49	0.51	0.88	0.12
2006	0.62	0.38	0.92	0.08
2007	0.62	0.38	0.85	0.15
2008	0.22	0.78	0.93	0.07
2009	0.54	0.46	0.93	0.07
2010	0.62	0.38	0.88	0.12
2011	0.47	0.53	0.91	0.09
2012	0.68	0.32	0.86	0.14
2013	0.26	0.74	0.92	0.08
2014	0.63	0.37	0.90	0.10
2015	0.55	0.45	0.89	0.11
2016	0.62	0.38	0.88	0.12
2017	0.43	0.57	0.87	0.13
2018	0.65	0.35	0.89	0.11
<b>Overall<sup>1</sup></b>	<b>0.55</b>	<b>0.45</b>	<b>0.88</b>	<b>0.12</b>
<b>20-yr mean<sup>2</sup></b>	<b>0.52</b>	<b>0.48</b>	<b>0.89</b>	<b>0.11</b>

<sup>1</sup> Overall ratios for each age group and sex class were calculated as the ratio of the total number of each age group or sex class to the total owls captured between 1999 to 2018

<sup>2</sup> The 20-yr mean for each age group and sex class was calculated as the average of all of the ratios from 1999 to 2018

package in R (Hyndman et al. 2020). A partial-autocorrelation was used instead of an autocorrelation to remove indirect relationships between intervening time steps. Autocorrelations were assessed for both the total number of HY saw-whet owls captured per year, and the annual ratio of HY saw-whet owls.

Irruption years were determined for each state across the United States. Irruptions were classified as years in which the ratio of HY saw-whet owls captured was at least 20% greater than the weighted mean ratio of HY owls from 1999 to 2018 in that region.

The weighted mean ratio was calculated as an average of the HY ratios calculated for each year between 1999 to 2018, and each value was weighted by the number of HY owls captured in that year. Irruption years were also classified as those that were not already preceded by an irruption year.

The criterion of 20% or greater was derived from studies on breeding success of nesting saw-whet owls (Marks and Doremus 2000, Buidin et al. 2006, Nightingale et al. 2013, Drilling 2013, Marks et al. 2015, Domahidi et al. 2020, Rasmussen et al. 2020), based on the premise that irruptions are linked to high productivity in those years. The mean clutch size and the mean number of owls fledged from successful nests were extracted from each study (Table S6.3). A weighted mean was calculated for both the clutch size, and number of owls fledged, where weights were the sample size ( $n$ ) that was used to derive the mean value for the clutch size or number fledged in each study. We then used the weighted means to calculate the percent increase from the weighted mean number of owls fledged to the weighted mean clutch size. That is, in an irruption year, all eggs may hatch to fledging, therefore the number fledged will increase from 4.34 (the mean fledged) to 5.27 (the mean clutch size). We found that if saw-whet owls from these studies fledged all of their young, this would result in a 21.5% increase in population of HY owls. We lowered our estimate to 20%, as a broad estimate, and to account for the fact that even in good years, not all adults will fledge all of their young. Additionally, we chose not to classify years with preceding irruption years as irruption years themselves, because irruptions are linked to prey abundance, and the first year of the irruption is the initial year of high food availability. If, in the subsequent year, numbers of saw-whet owls are still high, this is likely linked to the boom in the previous year, and not a separate irruption itself.

We classified irruptions in terms of ratios of HY birds, rather than raw totals, due to varied catch effort across banding stations (Beckett and Proudfoot 2011, Confer et al. 2014). Saw-whet owls were captured in 44 U.S. states between 1999 and 2018. For each state, years in which the number of owls captured was less than 20 were excluded from analysis ( $n = 466$ ). After site years were filtered, states with less than 10 years of banding data were excluded from analysis ( $n = 25$ ) – Alabama, Arkansas, California,

Connecticut, Delaware, Georgia, Iowa, Kansas, Kentucky, Missouri, Nebraska, Nevada, New Hampshire, New Mexico, North Carolina, North Dakota, Oklahoma, Oregon, South Carolina, South Dakota, Tennessee, Texas, Utah, Washington and Wyoming. We chose 10 years as our cut-off point because we need more than 8 years of data if we want to detect a possible periodicity of 4 years. Nineteen states were kept for analysis ( $n = 487$  site years).

Irruption years were also calculated for flyways (Figure 6.1). All 44 states were included in this analysis, since data were grouped by flyway, and years would not be missing in the dataset like they are when grouped by state. Since irruptive migrants may only be irruptive in some parts of their range (Newton 2006), an Analysis of Variance (ANOVA) was used to test for the effect of flyway on the average irruption cycle for that region. ANOVAs used data on the average irruption cycle per region for the 19 states studied instead of all 44 states, because the average irruption cycle per state will be more informative for the states that were filtered based on annual data availability.

### 6.3.4 Prey abundance

Since irruptions in other boreal owl species are known to coincide with prey availability, we tested whether the annual ratio of HY saw-whet owls during autumn migration was linked to prey availability during breeding. Red-backed voles were chosen for this analysis since they are a known prey item for breeding saw-whet owls (Underwood and Sealy 2002, Rasmussen et al. 2020), and are a key part of their diet during early spring (Catling 1972, Cannings 1987, Marks and Doremus 1988, Rains 1997). Data on red-backed voles were extracted from Bowman et al. (2010), which were presented as the number of captures per trap night during the summer (late May to late August) in Algonquin Provincial Park, Oregon (45.3°N, 78.4°W). Surveys for voles were conducted within saw-whet owl breeding territory. Data were available from 1995 to 2006.

Bowman et al. (2010) analysed the relationship between the percent of HY saw-whet owls during autumn migration at Long Point Bird Observatory, Ontario, and the summer abundance of red-backed voles in central Ontario. They found a “weak” relationship

between the two variables ( $F_{1,9} = 2.51$ ,  $p = 0.148$ ,  $R^2 = 0.22$ ). We used a linear regression to measure the relationship between the percent of HY owls captured during autumn migration across the United States from BBL data, and the number of voles present during the summer in the breeding range of saw-whet owls. Percent HY was used to mirror analyses conducted by Bowman et al. (2010). We also reanalysed available data on percent of HY saw-whet owls from Bowman et al. (2010) against numbers of voles during the summer. Our regressions were constrained to years in which vole data were collected by Bowman et al. (2010), from 1995 to 2006. We conducted a cross correlation analysis between the percent of HY saw-whet owls and vole abundance (Cheveau et al. 2004) to determine the time lag at which the correlation between vole abundance and percent of HY owls was the strongest.

### 6.3.5 Southerly movements

To determine whether HY birds migrate further south in irruption years, we used a two-tailed  $t$ -test to compare the median latitude of HY saw-whet owls captured during irruption years, and the median latitude of HY saw-whet owls captured during non-irruption years from 1999 to 2018. Irruption years were those calculated as years in which the ratio of HY owls for the 19 states analysed was 20% greater than the average ratio of HY owls for that region.

### 6.3.6 Sex trends

Female saw-whet owls are captured much more frequently than male saw-whet owls at banding stations (Brinker et al. 1997, Beckett and Proudfoot 2011). We used a two-tailed  $t$ -test to determine if there was any significant difference between the ratio of female owls captured, and the ratio of male owls captured from 1999 to 2018. We also assessed sex-based capture biases along lines of latitude (Brittain et al. 2009, Beckett and Proudfoot 2012), with a linear regression analysis. Owls of unknown sex (owls not sexed by the bander; sex = "0") were excluded from analyses.

All analyses were conducted using R (R Core Team 2020).

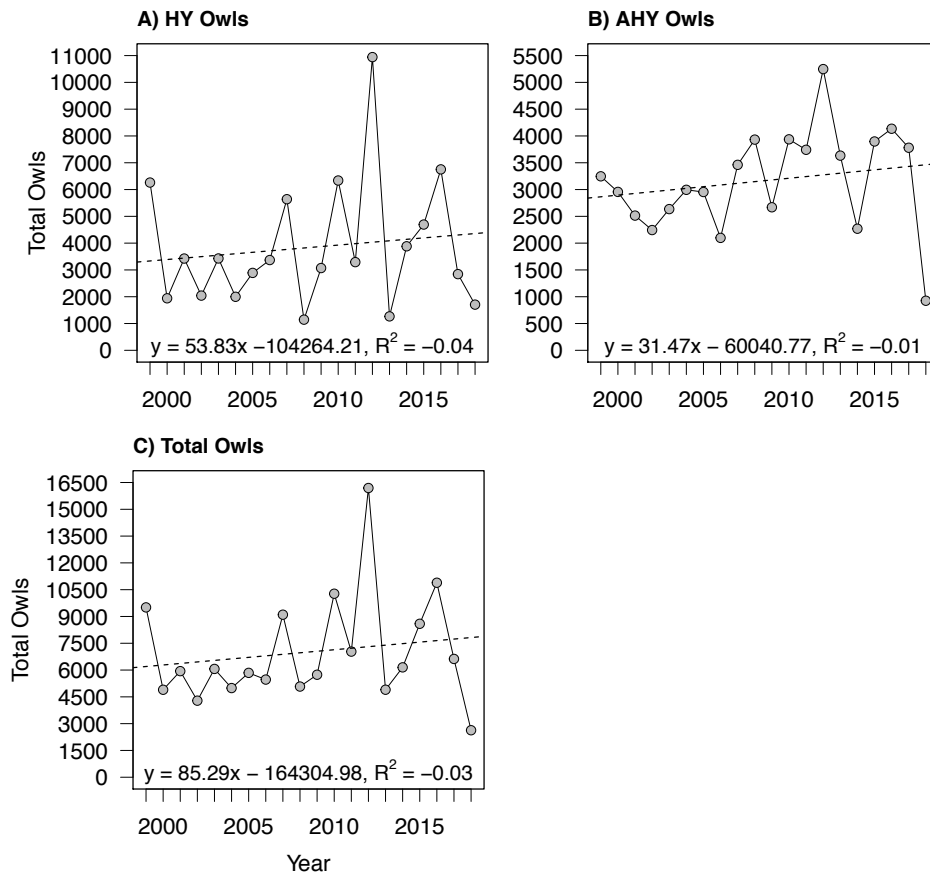
## 6.4 Results

### 6.4.1 Temporal trends

Populations of migrating saw-whet owls have remained stable between 1999 to 2018, as evidenced by banding data. We found that the relationships between the year of capture, and the total number of HY saw-whet owls captured ( $y = 53.83x - 104,264.21$ ,  $F_{1,18} = 0.33$ ,  $p = 0.57$ ,  $R^2 = -0.04$ ; see Figure 6.2a), the total number of AHY saw-whet owls captured ( $y = 31.47x - 60,040.77$ ,  $F_{1,18} = 0.73$ ,  $p = 0.40$ ,  $R^2 = -0.01$ ; see Figure 6.2b), and the total number of saw-whet owls captured regardless of age ( $y = 85.29x - 164,304.98$ ,  $F_{1,18} = 0.51$ ,  $p = 0.48$ ,  $R^2 = -0.03$ ; see Figure 6.2c) were not significant. Though population trends have remained relatively stable over the past 20 years, fluctuations in age groups across years were observed from plotted trends (Figure 6.2, Figure S6.1).

### 6.4.2 Irruption years

Partial autocorrelation analysis of the total number of HY saw-whet owls revealed no significant lags from 1999 to 2018 (Figure 6.3a), while partial autocorrelation analysis of the annual ratio of HY saw-whet owls revealed a significant periodicity of -1 years from 1999 to 2018 (Figure 6.3b). Since time series are heavily dependent on the length of the datasets used, we also conducted a temporal partial autocorrelation for the years 1960 to 2018, which offers a much longer timeseries than our study period ( $n = 58$  versus  $n = 20$ ). A significant lag was found at 1, 2, and 4 years for the total number of HY saw-whet owls (Figure 6.3c). A significant lag was also found at 4 years for the annual ratio of HY saw-whet owls (Figure 6.3d). Calculated irruption cycles varied among states (Table 6.2), with an average irruption cycle of 2.8 years for the 19 states studied (Table 6.3). Overall irruption years were determined to occur in 1999, 2001, 2003, 2006, 2009, 2012, 2014, 2016 and 2018 (Figure 6.4, Table 6.2). Years 2007 and

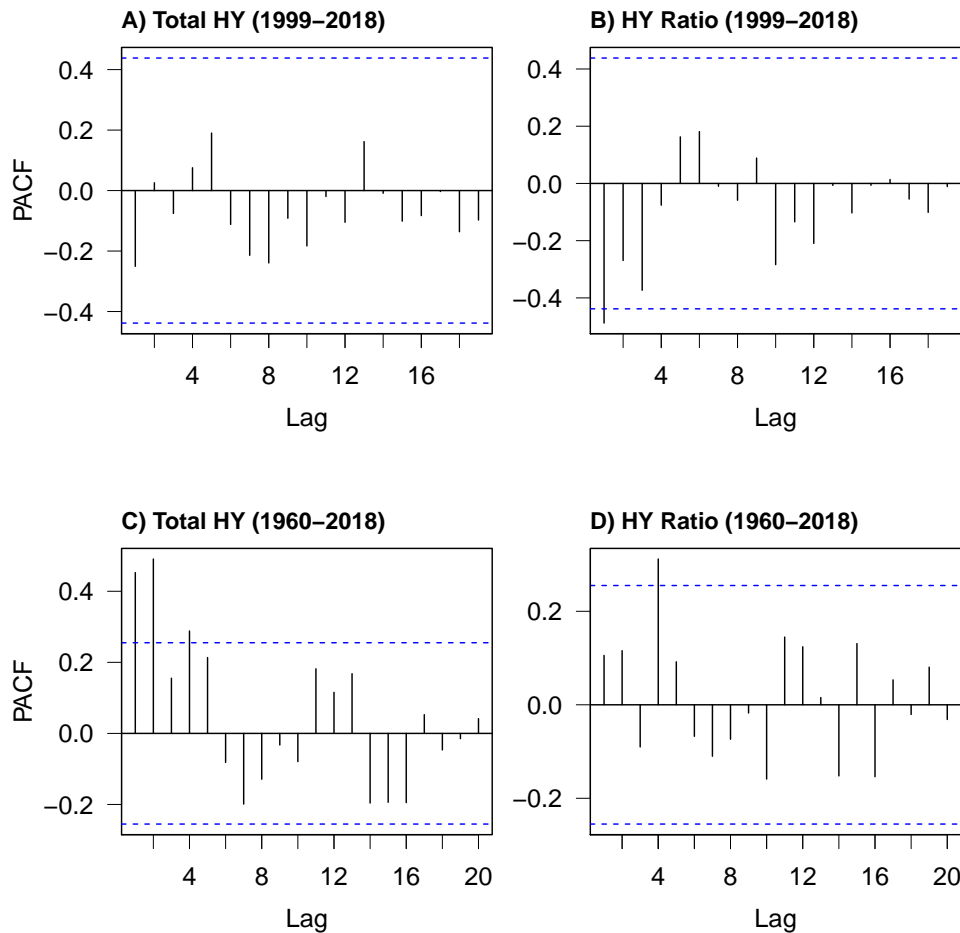


**Figure 6.2.** Total number of (A) HY (B) AHY, and (C) the total saw-whet owls captured per year in North America from 1999 to 2018 based on 140,190 banding events. The dotted line represents the linear regression between the number of owls and year. The relationship was not significant for all age groups: (A) HY owls ( $F_{1,18} = 0.33$ ,  $p = 0.57$ , adj.  $R^2 = -0.04$ ), (B) AHY owls ( $F_{1,18} = 0.73$ ,  $p = 0.40$ , adj.  $R^2 = -0.01$ ), (C) Total ( $F_{1,18} = 0.51$ ,  $p = 0.48$ , adj.  $R^2 = -0.03$ ). Linear regression results are located in the lower right corner of each graph. Individuals not identified to age (age = 0; “unknown”) were excluded from ratio calculations.

2010 also matched irruption year criteria (i.e. the ratio of HY saw-whet owls captured in that year was at least 20% greater than the mean for the United States). However, because they had a preceding irruption year, they were excluded from classification. The average periodicity of 2.8 years coincides with the 2 to 4 year-range determined by partial autocorrelation for the years 1960 to 2018.

The average irruption cycle for flyways was 2.6 years (Tables 6.4, 6.5). Overall irruption years occurred in 1999, 2001, 2003, 2006, 2009, 2012, 2014, 2016 and 2018. Years 2007, 2010, and 2015 also matched irruption year criteria, however, because they had a preceding irruption year, they were excluded from classification. Average irruption

cycles across the four different flyways were not statistically differ from one another ( $F_{1,17} = 1.65$ ,  $p = 0.22$ ; Figure 6.5).



**Figure 6.3.** Partial temporal autocorrelation analyses for the total number of HY saw-whet owls (A) 1999 to 2018, and (C) 1960 to 2018, and the ratio of HY saw-whet owls from (B) 1999 to 2018, and (D) 1960 to 2018. Though our study focuses on the years 1999 to 2018, we included a time series for 1960 to 2018 since analysis of a longer time series ( $n = 58$ ) may pick up cycles that are missed in a shorter time series ( $n = 20$ ). No lags were significant for (A). Lags were significant at (B) -1 years, (C) 1, 2, and 4 years, and (D) 4 years. Blue lines represent the 95% level of statistical significance.

**Table 6.2.** Ratio of hatching-year (HY) saw-whet owls for each state from 1999 to 2018, for the 19 states that had sufficient data to calculate irruption years (years with less than 20 owls captured, and states with less than 10 years of data, were omitted). Irruption years were classified as years where the ratio of HY saw-whet owls was at least 20% greater than the weighted mean ratio of HY owls from 1999 to 2018 for that region, and when the preceding year was not an irruption. Irruption years were classified to occur in 1999, 2001, 2003, 2006, 2009, 2012, 2014, 2016, and 2018 for all of North America. The overall and weighted mean ratios for all of North America in each year are included.

State	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009
Colorado								*0.73	0.62	0.25	*0.82
Idaho	0.56	0.63	*0.72	0.81	*0.81	0.66	*0.81	0.83	*0.79	0.59	*0.89
Illinois	*0.66	0.51	0.46	0.54	*0.61	0.51	0.15	*0.78	0.36		*0.59
Indiana				*0.67	0.62	0.32	0.46	*0.66	0.67	0.14	0.58
Maine	*0.71	0.20	*0.66	0.48	*0.68	0.37	0.62	0.44	*0.71	0.24	0.58
Maryland	*0.77	0.39	*0.66	0.44	0.54	0.42	0.50	0.60	*0.73	0.16	0.61
Massachusetts	*0.88	0.30	*0.77	0.54	*0.60	0.28	*0.66	0.42	*0.68	0.22	0.49
Michigan	*0.67	0.28	0.48	*0.63	0.56	0.39	0.46	*0.60	0.59	0.34	0.54
Minnesota	*0.56	0.47	0.47	0.51	*0.63	0.43	0.46	*0.70	0.43	0.29	0.52
Montana			0.71	*0.84	0.92	*0.78	0.64	*0.77			0.70
New Jersey	0.77		*0.84	0.61	0.61	0.60	0.74	0.72	*0.84		0.70
New York			*0.69	0.41	*0.57	0.42	0.52	*0.59	0.57	0.14	0.56
Ohio						0.35	0.48	0.39	*0.71	0.25	0.56
Pennsylvania	*0.65	0.34	*0.64	0.47	0.51	0.42	0.41	0.61	*0.67	0.16	0.56
Rhode Island	*0.88	0.81	0.80	0.65	0.86		*0.98				0.85
Vermont	*0.81	0.18	*0.71	0.39	0.49	0.35	0.57	0.51	*0.65	0.27	*0.65
Virginia	*0.75	0.24	*0.71	0.38	0.50	0.37	0.41	0.36	*0.72	0.08	0.39
West Virginia	*0.54	0.40	0.35	0.39	0.36	0.36	0.57	0.62	*0.76	0.11	0.59
Wisconsin					*0.48	0.35	0.38	*0.51	0.37	0.23	0.41
<b>Overall<sup>1</sup></b>	<b>*0.66</b>	<b>0.39</b>	<b>*0.58</b>	<b>0.48</b>	<b>*0.56</b>	<b>0.40</b>	<b>0.49</b>	<b>*0.62</b>	<b>0.62</b>	<b>0.22</b>	<b>*0.54</b>
<b>Weighted Mean<sup>2</sup></b>	<b>*0.73</b>	<b>0.49</b>	<b>*0.66</b>	<b>0.59</b>	<b>*0.64</b>	<b>0.47</b>	<b>*0.61</b>	<b>*0.64</b>	<b>0.70</b>	<b>0.29</b>	<b>*0.63</b>

<sup>1</sup> Overall ratios for each year were calculated as the ratio of the total number of HY owls to total owls captured in all 19 states in that year

<sup>2</sup> Weighted mean of the HY ratios for each year, where the weight is the number of HY owls captured per state in that year

\* Irruption year (HY ratio is at least > 20% the weighted mean HY ratio from 1999 to 2018 for that region)

**Table 6.2 (cont.).** Ratio of hatching-year (HY) saw-whet owls for each state from 1999 to 2018, for the 19 states that had sufficient data to calculate irruption years (years with less than 20 owls captured, and states with less than 10 years of data, were omitted). Irruption years were classified as years where the ratio of HY saw-whet owls was at least 20% greater than the weighted mean ratio of HY owls from 1999 to 2018 for that region, and when the preceding year was not an irruption. Irruption years were classified to occur in 1999, 2001, 2003, 2006, 2009, 2012, 2014, 2016, and 2018 for all of North America. The overall and weighted mean ratios for all of North America in each year are included.

State	2010	2011	2012	2013	2014	2015	2016	2017	2018	Total HY	Weighted Mean HY Ratio <sup>3</sup>
Colorado	0.58	0.43	*0.73	0.58	0.67	*0.87	0.53	0.52	0.42	349	0.69
Idaho	0.95	0.67	0.66	0.58	*0.74	0.82	0.65	*0.77	0.74	3973	0.72
Illinois	0.62	0.50	*0.61		*0.58	0.66	*0.67		0.27	555	0.58
Indiana	*0.68	0.41	*0.77	0.15	0.57	0.61	*0.80	0.34	0.51	1522	0.66
Maine	*0.74	0.49	*0.79	0.34	*0.75	0.77	*0.77	0.59	*0.82	3202	0.65
Maryland	*0.67	0.44	*0.77	0.25	*0.74	0.57	*0.69	0.36	*0.91	4955	0.67
Massachusetts	0.56	0.33	*0.62	0.14	*0.74	0.37	0.57	0.24	*0.62	4699	0.60
Michigan	0.55	0.50	*0.73	0.25	*0.59	0.32	*0.68	0.49		3279	0.57
Minnesota	*0.63	0.43	*0.59	0.25	*0.58	0.54	*0.56	0.38	*0.62	16360	0.54
Montana		0.67	*0.76	0.56	*0.74	0.76	0.62	*0.88		1586	0.74
New Jersey	*0.85	*0.82	*0.90	0.15	*0.85	0.56	0.75	0.37	*0.92	1717	0.79
New York	*0.57	0.48	*0.68	0.17	*0.60	0.50	*0.60	0.37	*0.69	4301	0.57
Ohio	*0.75	0.45	*0.81	0.31	*0.82	0.70	*0.75	0.50	0.65	1019	0.68
Pennsylvania	*0.65	0.52	*0.71	0.31	*0.69	0.51	*0.62	0.35	*0.68	11096	0.62
Rhode Island		0.55	0.86		*1.00		*1.00			549	0.88
Vermont	0.73	0.49	*0.61	0.25	*0.76	0.49	0.50	0.33		854	0.59
Virginia	0.53	0.30	*0.71	0.11	0.39	0.29	0.55	0.23	*0.69	3641	0.63
West Virginia	0.60	0.33	0.62	0.17	*0.68	0.60	0.63	0.07	*0.80	790	0.64
Wisconsin	*0.54	0.32	*0.48	0.25	*0.53	0.38	*0.53	0.28	0.31	8712	0.44
<b>Overall<sup>1</sup></b>	<b>0.62</b>	<b>0.46</b>	<b>*0.68</b>	<b>0.26</b>	<b>*0.63</b>	<b>*0.53</b>	<b>*0.62</b>	<b>0.41</b>	<b>*0.67</b>	<b>73159</b>	<b>0.52</b>
<b>Weighted Mean<sup>2</sup></b>	<b>0.67</b>	<b>0.52</b>	<b>*0.70</b>	<b>0.32</b>	<b>*0.69</b>	<b>*0.61</b>	<b>*0.68</b>	<b>0.55</b>	<b>*0.67</b>	<b>3382</b>	<b>0.59</b>

<sup>1</sup> Overall ratios for each year were calculated as the ratio of the total number of HY owls to total owls captured in all 19 states in that year

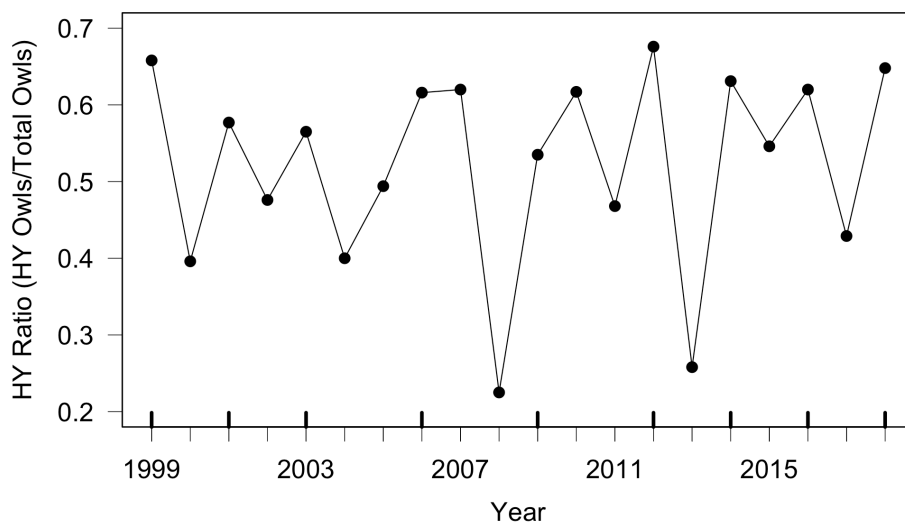
<sup>2</sup> Weighted mean of the HY ratios for each year, where each value is weighted by the number of HY owls captured per state in that year

<sup>3</sup> Weighted mean of the HY ratios for each state, where each value is weighted by the number of HY owls captured per year

\* Irruption year (HY ratio is at least > 20% the weighted mean HY ratio from 1999 to 2018 for that region)

**Table 6.3.** The average irruption cycle per state based on irruption years calculated in Table 6.2.

State	Years of Data	# of Irruptions	Average Cycle
Colorado	12	4	3.0
Idaho	20	8	2.5
Illinois	17	8	2.1
Indiana	17	6	2.8
Maine	19	8	2.4
Maryland	20	7	2.9
Massachusetts	20	8	2.5
Michigan	19	6	3.2
Minnesota	20	8	2.5
Montana	14	7	2.0
New Jersey	17	6	2.8
New York	18	8	2.2
Ohio	15	5	3.0
Pennsylvania	20	8	2.5
Rhode Island	11	4	2.8
Vermont	17	5	3.4
Virginia	20	5	4.0
West Virginia	19	4	4.8
Wisconsin	20	7	2.9
<b>Overall</b>	<b>20</b>	<b>9</b>	<b>2.2</b>
<b>Average</b>	<b>18</b>	<b>6</b>	<b>2.8</b>



**Figure 6.4.** Ratio of HY saw-whet owls banded per year in North America from 1999 to 2018, based on 76,919 banding events. The black lines on the x-axis represent irruption years (see Table 6.2).

**Table 6.4.** Ratio of hatching-year (HY) saw-whet owls for each flyway from 1999 to 2018. All 44 states were included in this analysis (i.e. all available data). Irruption years were classified as years where the ratio of HY saw-whet owls was at least 20% greater than the weighted mean ratio of HY owls from 1999 to 2018 for that region, and when the preceding year was not an irruption. Irruption years were classified to occur in 1999, 2001, 2003, 2006, 2009, 2012, 2014, 2016 and 2018 for all of North America. The overall and weighted mean ratios for all of North America in each year are included.

Flyway	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009
1	*0.75	0.30	*0.68	0.46	*0.56	0.39	*0.54	0.52	*0.69	0.16	*0.54
2	*0.56	0.43	0.40	0.45	*0.54	0.40	0.44	*0.63	0.50	0.25	*0.50
3		*0.70	0.60	*0.82	0.90	0.60	0.60	*0.75	0.59	0.24	*0.74
4	0.57	0.62	*0.69	0.75	*0.78	0.59	0.63	*0.78	0.62	0.57	*0.82
<b>Overall<sup>1</sup></b>	<b>*0.66</b>	<b>0.40</b>	<b>*0.58</b>	<b>0.48</b>	<b>*0.56</b>	<b>0.40</b>	<b>0.49</b>	<b>0.62</b>	<b>*0.62</b>	<b>0.22</b>	<b>*0.54</b>
<b>Weighted Mean<sup>2</sup></b>	<b>*0.64</b>	<b>0.56</b>	<b>*0.62</b>	<b>0.66</b>	<b>*0.73</b>	<b>0.52</b>	<b>*0.56</b>	<b>0.69</b>	<b>*0.61</b>	<b>0.39</b>	<b>*0.68</b>

Flyway	2010	2011	2012	2013	2014	2015	2016	2017	2018	Total HY	Weighted Mean HY Ratio <sup>3</sup>
1	*0.62	0.45	*0.71	0.22	*0.69	0.51	*0.65	0.37	*0.74	36355	0.53
2	0.60	0.41	0.61	0.24	0.57	0.48	0.59	0.36	0.52	32312	0.47
3	0.65	*0.64	0.70	0.35	0.62	*0.76	0.67	0.62	0.47	3266	0.63
4	0.80	0.64	0.64	0.58	*0.74	0.79	0.61	*0.77	0.68	4986	0.68
<b>Overall<sup>1</sup></b>	<b>0.62</b>	<b>0.47</b>	<b>*0.68</b>	<b>0.26</b>	<b>*0.63</b>	<b>0.55</b>	<b>*0.62</b>	<b>0.43</b>	<b>*0.65</b>	<b>76919</b>	<b>0.52</b>
<b>Weighted Mean<sup>2</sup></b>	<b>0.68</b>	<b>*0.56</b>	<b>*0.67</b>	<b>0.41</b>	<b>*0.66</b>	<b>0.67</b>	<b>*0.63</b>	<b>0.59</b>	<b>*0.62</b>	<b>19230</b>	<b>0.52</b>

<sup>1</sup> Overall ratios for each year were calculated as the ratio of the total number of HY owls to total owls captured in all 4 flyways in that year

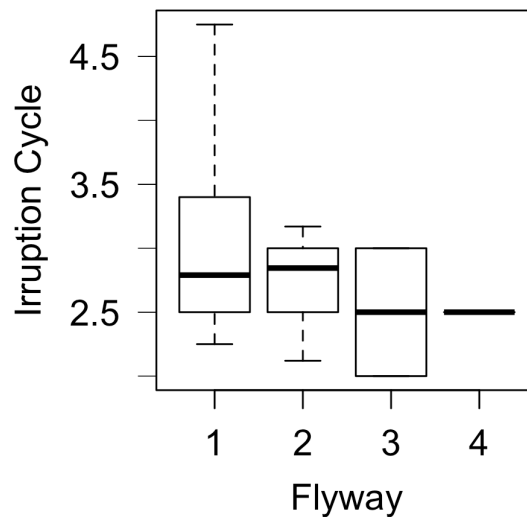
<sup>2</sup> Weighted mean of the HY ratios for each year, where each value is weighted by the number of HY owls captured per flyway in that year

<sup>3</sup> Weighted mean of the HY ratios for each state, where each value is weighted by the number of HY owls captured per year

\* Irruption year (HY ratio is at least > 20% the weighted mean HY ratio from 1999 to 2018 for that region)

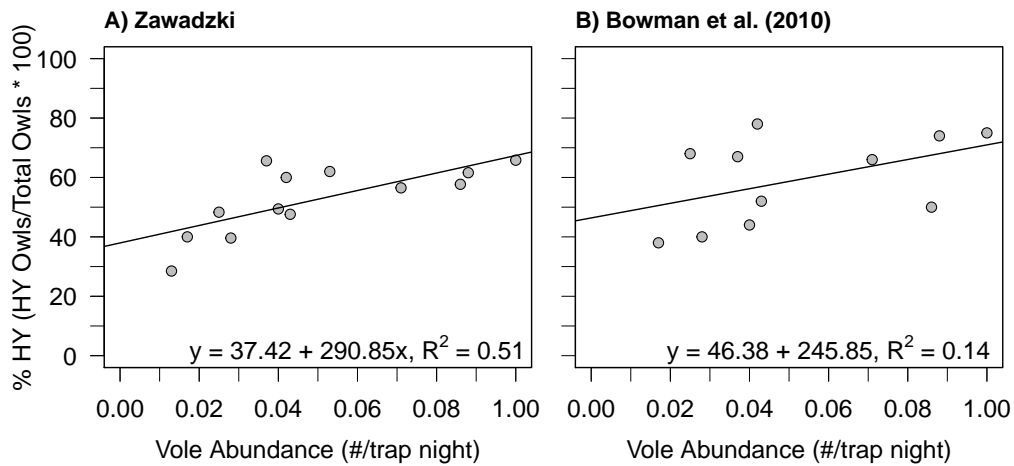
**Table 6.5.** The average irruption cycle per migratory flyway based on irruption years calculated in Table 6.4.

Flyway	Years of Data	# of Irruptions	Average Cycle
1	20	10	2.0
2	20	8	2.5
3	19	7	2.7
4	20	6	3.3
<b>Overall</b>	<b>20</b>	<b>9</b>	<b>2.2</b>
<b>Average</b>	<b>20</b>	<b>8</b>	<b>2.6</b>

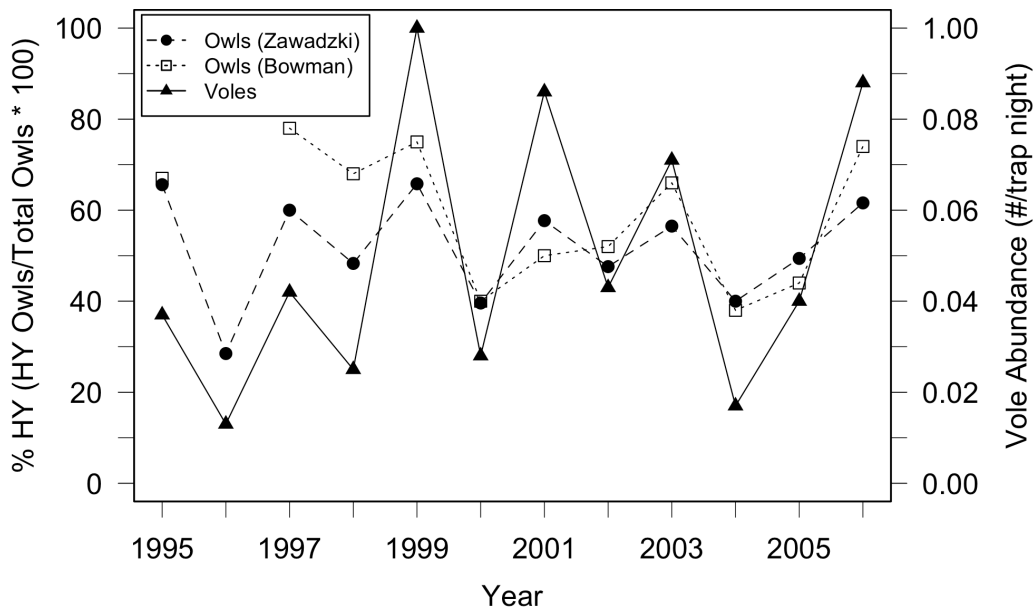
**Figure 6.5.** The irruption cycle does not differ significantly per flyway ( $F_{1,17} = 1.65$ ,  $p = 0.22$ ).

### 6.4.3 Prey abundance

The percent of HY saw-whet owls in the United States was strongly correlated with summer abundance of red-backed voles ( $y = 37.42 + 290.85x$ ,  $F_{1,10} = 12.35$ ,  $p < 0.01$ ,  $R^2 = 0.51$ ; see Figure 6.6a). This suggests that abundance of saw-whet owls in the United States during autumn migration is linked to prey availability on the breeding grounds. In contrast, HY owls from Bowman et al. (2010) were not correlated with summer abundance of red-backed voles ( $y = 46.38 + 245.85x$ ,  $F_{1,9} = 12.35$ ,  $p = 0.14$ ,  $R^2 = 0.14$ ; see Figure 6.6b). The non-significant relationship using Bowman et al. (2010) data might be due to the small area in which saw-whet owl numbers were extracted.

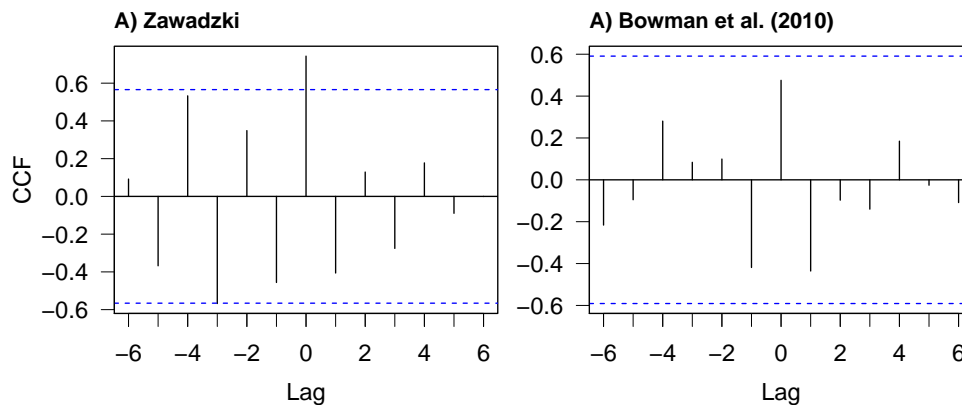


**Figure 6.6.** Percent of HY saw-whet owls banded during (A) autumn migration in the United States, and (B) autumn migration at Long Point Bird Observatory, Ontario from Bowman et al. (2010), compared to the summer abundance of red-backed voles (*Myodes gapperi*) in central Ontario from 1995 to 2006. Vole abundance was expressed as the number captured per trap-night. The relationship was significant for (A) HY saw-whet owls in North America ( $F_{1,10} = 12.35$ ,  $p < 0.01$ , adj.  $R^2 = 0.51$ ), but not for (B) HY saw-whet owls from Bowman et al. (2010) ( $F_{1,9} = 12.35$ ,  $p = 0.14$ , adj.  $R^2 = 0.14$ ). Black lines represent the linear regression between the ratio of saw-whet owls and voles. Linear regression results are located in the lower right corner of each graph.



**Figure 6.7.** Percent of two groups of banded HY saw-whet owls in North America compared to summer abundance of red-backed voles (*Myodes gapperi*) in central Ontario from 1995 to 2006. The abundance of saw-whet owls and voles are variable and cyclical from year to year, and fluctuations of saw-whet owls closely track fluctuations in vole populations.

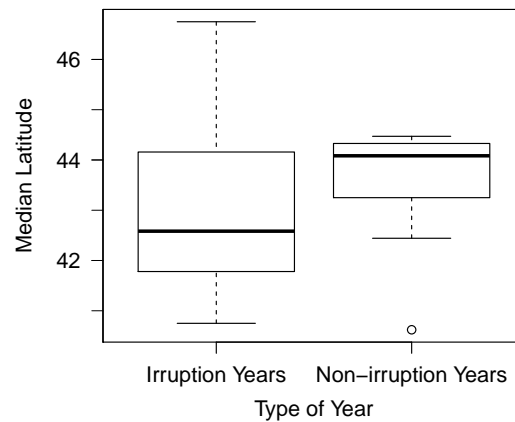
Visual analysis of these trends over time shows that the percent of HY saw-whet owls closely tracks the periodicity in vole abundance from 1995 to 2006 (Figure 6.7). Our cross-correlation analysis supports this. The relationship between HY saw-whet owls from BBL data and vole abundance was strongest at a lag of 0 (Figure 6.8a), meaning that HY saw-whet owls fluctuate alongside vole populations with a time lag of less than one year. No significant periodicity was found between HY saw-whet owl data from Bowman et al. (2010) and vole abundance (Figure 6.8b).



**Figure 6.8.** Cross correlation for the percent of HY saw-whet owls banded during A) autumn migration in the United States, and B) autumn migration in Ontario from Bowman et al. (2010), compared to the summer abundance of red-backed voles (*Myodes gapperi*) from 1995 to 2006. A) Migrant owls and vole populations fluctuate simultaneously at a lag of 0, while B) owls from Ontario show no relationship with vole populations. The blue lines represent the 95% level of statistical significance.

#### 6.4.4 Southerly movements

There was no significant difference between the median latitude during irruption years and the median latitude during non-irruption years ( $t_{13.8} = -0.73$ ,  $p = 0.48$ ; see Figure 6.9). The mean latitude for irruption years was 43.07, and the mean latitude for non-irruption years was 43.57.



**Figure 6.9.** The median latitude during irruption years does not significantly differ from the median latitude in non-irruption years ( $n = 20$ ,  $t_{18} = -0.73$ ,  $p = 0.48$ ). The mean latitude for irruption years is 43.07, and the mean latitude for non-irruption years is 43.57.

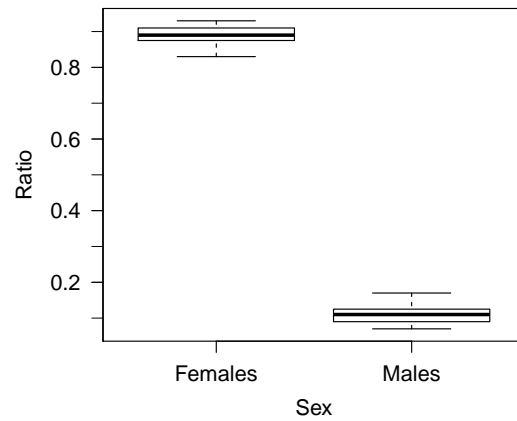
### 6.4.5 Sex trends

Females were found to be disproportionately captured during autumn migration ( $n = 40$ ,  $t_{38} = 93.13$ ,  $p < 0.001$ ; Figure 6.10). The mean ratio of females captured was 0.89, while the mean ratio of males captured was 0.11. This relationship seems to be latitude-based, as we also found a strong relationship between sex and latitude (Figure 6.11). The ratio of female to male saw-whet owls increased with decreasing latitude ( $y = 2.18 - 0.023x$ ,  $F_{1,14} = 5.70$ ,  $p < 0.05$ , adj.  $R^2 = 0.24$ ; see Figure 6.11). These results indicate that females migrate to more southerly locations than males.

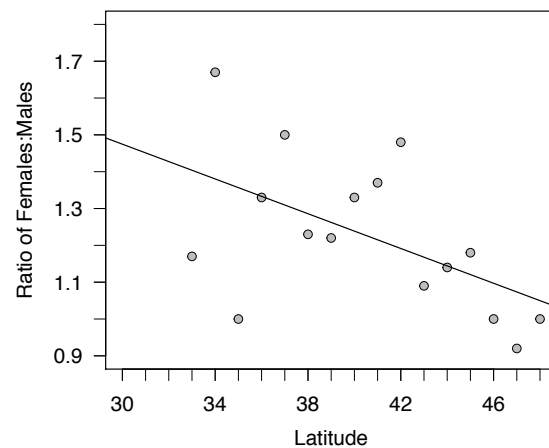
## 6.5 Discussion

### 6.5.1 Irruption cycles of saw-whet owls

Our results show that while population trends of migrating saw-whet owls have remained stable over the past 20 years, saw-whet owls exhibit irruption cycles during autumn migration, with a possible periodicity of 1 to 4 years. Irruption years were identified to occur in 1999, 2001, 2003, 2006, 2009, 2012, 2014, 2016, and 2018 (Figure 6.4, Table



**Figure 6.10.** Females are much more common than males during autumn migration at banding sites across North America from 1999 to 2018 ( $n = 40$ ,  $t_{38} = 93.13$ ,  $p < 0.001$ ). The mean ratio for females captured per year is 0.89, and the mean ratio for males captured per year is 0.11.



**Figure 6.11.** Linear regression plot of the ratio of female to male saw-whet owls by latitude. A strong relationship was found between sex and latitude. The ratio of females to males had a strong negative relationship with latitude ( $y = 2.18 - 0.023x$ ,  $F_{1,14} = 5.70$ ,  $p < 0.05$ , adj.  $R^2 = 0.24$ ), indicating that more females are present at southerly latitudes than males during autumn migration.

6.2), with an average periodicity of 2.8 years, and a range of 1.6 to 3.3 years (Table 6.3). This finding coincides with previous studies that have proposed that saw-whet owls follow a 4-year irruption cycle (Swengel and Swengel 1995, Confer et al. 2014).

Irruptive movements occur in nomadic species, which employ a facultative migration strategy to follow spatially and temporally unpredictable food availability (Newton 2006). The most well-known irruptive migrants are boreal songbirds (e.g. finches and crossbills) which feed on tree-seed crops (e.g. Red Crossbill (*Loxia curvirostra*); Benkman and Young 2020), and species of boreal owl that feed upon cyclically-fluctuating rodent populations (Rohner 1996, Cheveau et al. 2004, Newton 2006, Cote et al. 2007, Bowman et al. 2010). For boreal owls, irruptive movements have been found to be negatively correlated with prey availability, whereby individuals will move to a new area in response to low density of prey (Cheveau et al. 2004, Newton 2006, Cote et al. 2007). Breeding success in a number of boreal owl species has also been directly linked to high prey abundance during breeding (e.g. Great Horned-Owl (*Bubo virginianus*) (Rohner 1996); Boreal (Tengmalm's) Owl (*Aegolius funereus*), Ural Owl (*Strix uralensis*), and Long-eared Owl (*Asio otus*) (Sundell et al. 2004)).

For saw-whet owls, we discovered a strong positive relationship between the ratio of migrating HY owls, and summer abundance of red-backed vole populations (Figure 6.6a). The periodicity of this relationship had a significant lag at 0 years (Figure 6.8a), which suggests that fluctuations in both populations occur simultaneously. Saw-whet owls are nomadic (Bowman et al. 2010), and respond to the cyclic abundance of their prey, exhibiting cyclic populations themselves. This relationship indicates that breeding success of saw-whet owls is directly linked to prey availability on the breeding grounds (Cote et al. 2007, Bowman et al. 2010). In years of high prey abundance, AHY saw-whet owls may be able to successfully fledge an increased number of young, resulting in a large influx of HY saw-whet owls the following autumn.

Our partial autocorrelation analysis did not show significant lags for the study period at the predicted periodicity for saw-whet owls (Figures 6.3a–b). However, significant

lags of 1, 2 and 4 years were detected when we used a longer time-series, from 1960 to 2018 (Figures 6.3c–d). Based on the strong correlation between HY saw-whet owls and cyclic vole populations, we do not think the lack of significant lags from 1999 to 2018 reflects real trends. Rather, the interval at which we attempted to detect a periodicity was too small for analysis ( $n = 20$ ). Once we added the full 58-year time-series, lags at predicted intervals were shown to be significant.

### **6.5.2 Irruption year classification**

Our finding that migrant saw-whet owls cyclically track prey abundance supports our hypothesis that irruption years are years in which the ratio of HY owls is greater than the ratio of HY owls in years of low prey availability. However, our designation that an irruption year has a ratio of HY owls that is at least 20% greater than the weighted average, based on available nesting data (Marks and Doremus 2000, Buidin et al. 2006, Nightingale et al. 2013, Drilling 2013, Marks et al. 2015, Domahidi et al. 2020, Rasmussen et al. 2020), may not be the best way to define an irruption year. It may be that the actual breeding success of saw-whet owls is dramatically different from our estimate of 20%, though this will require additional studies of breeding populations of saw-whet owls.

### **6.5.3 Differential movements**

Latitudinally, saw-whet owls did not appear at more southerly latitudes during irruption years (Figure 6.9). However, differential sex trends were present. Females migrated to more southerly latitudes in all years, while males stayed at more northerly latitudes (Figure 6.11). Females were also much more common than males during autumn migration (Figure 6.10). This is thought to result from males staying closer to the breeding range to defend their nest sites (Brittain et al. 2009), since nesting sites in boreal habitat are scarce (Korpimäki et al. 1987). In Boreal Owls, females have also been found to move much further than males, travelling distances up to 500 km more than males in years of poor vole abundance (Korpimäki et al. 1987). Korpimäki et al. (1987) explained that this

was due to scarcity of nesting habitat, combined with the larger size of females. Males are hesitant to travel away from nest sites since knowledge of the territory is beneficial during breeding – males feed the female and young throughout the breeding season, and need to be familiar with hunting in the area. Their smaller size makes this possible since they are able to survive harsh winter conditions closer to the breeding grounds by switching to more agile prey, such as songbirds, in lieu of small mammals. Since saw-whet owls also show sexual dimorphism based on size (Brinker et al. 1997), it is possible that the same, or similar, mechanisms apply.

#### **6.5.4 Vagrancy and irruptions**

Many irruptive migrants have been known to occur as vagrants during years of extremely low food availability in search of new feeding grounds, as well as during years of high food availability, when incursions of young occur, typically southward of natal sites (Lees and Gilroy 2009). Vagrancy and irruptions may thus be intrinsically linked (Williamson 1969, Veit 2005), since rates of vagrancy are thought to be influenced by population dynamics (see Chapters 4 and 5). When populations experience rapid growth in the breeding range, rates of vagrancy of juveniles increase, similar to irruptions in juvenile saw-whet owls in years of high breeding success. Similarly, if populations exceed the available food supply, vagrancy may increase to seek out new food resources. Patten and Burger (1998) found that occurrence of vagrant New World wood warblers to eastern North America were correlated with spruce budworm (*Choristoneura fumiferana*) population outbreaks, identifying a connection between resources and rates of vagrancy. We may be able to learn more about how and why vagrancy occurs within migratory populations by studying patterns of irruptive migrants. Irruptive migrants, such as the saw-whet owl, need to be flexible during migration in order to employ a nomadic life strategy in the face of unpredictable resource availability. Vagrants are also flexible, travelling to habitat far outside of the known species' range, and this flexibility may be driven by similar mechanisms that drive irruptive migration. Irruptive migration is accepted as a normal part of the migratory programme. We propose that vagrancy is

also a normal part of the migratory programme based on the strong similarities evident between vagrancy and irruptive migration.

### **6.5.5 Future directions**

While this study is a step towards understanding patterns of irruptive migrations in saw-whet owls, additional studies will need to be conducted directly on the breeding grounds to confirm this link between saw-whet owl populations and vole abundance. Furthermore, banding efforts should be increased in Flyways 3 and 4 in the mid-western to western United States. Very little is known about migratory patterns of saw-whet owls in these regions of the United States (Frye and Gerhardt 2003, Brenner and Jorgensen 2020), even though saw-whet owls migrate through this region. Since 1999, only 5,063 and 7,732 individuals have been banded in Flyways 3 and 4, respectively, compared to the 72,283 and 103,306 individuals banded in Flyways 1 and 2. While current banding data are invaluable for providing key insights into irruptive movements of this species, increased efforts across the United States will help us improve our understanding of this cryptic species.

## **6.6 Acknowledgements**

We would like to thank all of the banders and volunteers who have captured and collected information on saw-whet owls in North America during autumn migration. This study relied heavily on banding data collected by these dedicated banders and volunteers across North America, and we are grateful for their continued efforts. We also thank Danny Bystrak at the North American Bird Banding Laboratory (BBL) for providing access to these banding records. Additional thanks to Tom Brown for sparking initial interest in this study from our many nights of banding saw-whet owls together in Sandy Hook, NJ.

## 6.7 Supplementary Material

**Table S6.1.** Annual ratio of Northern Saw-whet Owls captured from 1960 to 2018 classified to age. Individuals were assigned as “Unknown” (age = 0), “Hatch Year” (age = 2; HY), or “After Hatch Year” (age = 1, 5, 6, 7, 8; AHY). AHY birds are not included in this table. HY ratios shown were calculated with and without owls of unknown age in the total. Ratios without unknowns (“Without Unk” columns) were used in analyses. The ratio of HY saw-whet owls and unknown saw-whet owls do not add up to 1.00 because the ratio of after hatch-year saw-whet owls needs to be considered.

Year	Unknown Ratio	Hatch Year Ratio		Total Unknown	Total Banded	
		With Unk	Without Unk		With Unk	Without Unk
1960	0.54	0.10	0.22	32	59	27
1961	0.50	0.06	0.12	57	115	58
1962	0.63	0.07	0.19	73	116	43
1963	0.46	0.25	0.46	76	167	91
1964	0.24	0.33	0.44	30	126	96
1965	0.75	0.08	0.32	213	285	72
1966	0.27	0.07	0.10	45	169	124
1967	0.32	0.36	0.53	42	132	90
1968	0.30	0.45	0.65	117	384	267
1969	0.40	0.36	0.60	70	177	107
1970	0.55	0.24	0.54	58	106	48
1971	0.39	0.30	0.49	53	135	82
1972	0.37	0.31	0.50	116	312	196
1973	0.43	0.26	0.46	128	297	169
1974	0.27	0.37	0.51	158	592	434
1975	0.23	0.35	0.45	133	587	454
1976	0.10	0.46	0.51	65	649	584
1977	0.19	0.42	0.52	81	429	348
1978	0.08	0.47	0.51	65	765	700
1979	0.11	0.42	0.47	39	367	328
1980	0.09	0.54	0.59	63	699	636
1981	0.03	0.42	0.43	28	892	864
1982	0.02	0.43	0.44	17	772	755
1983	0.04	0.40	0.42	17	403	386
1984	0.01	0.46	0.46	9	868	859
1985	0.03	0.50	0.51	17	537	520
1986	0.02	0.48	0.49	13	735	722
1987	0.03	0.44	0.46	47	1446	1399
1988	0.02	0.49	0.50	33	2190	2157
1989	0.08	0.32	0.36	227	2729	2502
1990	0.03	0.52	0.53	68	2634	2566

**Table S6.1 (cont.).** Annual ratio of Northern Saw-whet Owls captured from 1960 to 2018 classified to age. Individuals were assigned as “Unknown” (age = 0), “Hatch Year” (age = 2; HY), or “After Hatch Year” (age = 1, 5, 6, 7, 8; AHY). AHY birds are not included in this table. HY ratios shown were calculated with and without owls of unknown age in the total. Ratios without unknowns (“Without Unk” columns) were used in analyses. The ratio of HY saw-whet owls and unknown saw-whet owls do not add up to 1.00 because the ratio of after hatch-year saw-whet owls needs to be considered.

Year	Unknown Ratio	Hatch Year Ratio		Total Unknown	Total Banded	
		With Unk	Without Unk		With Unk	Without Unk
1992	0.02	0.42	0.43	50	2039	1989
1993	0.00	0.50	0.50	14	3207	3193
1994	0.00	0.56	0.56	14	3539	3525
1995	0.02	0.65	0.66	96	6324	6228
1996	0.01	0.28	0.28	38	2623	2585
1997	0.01	0.59	0.60	35	3364	3329
1998	0.02	0.47	0.48	68	3713	3645
1999	0.00	0.66	0.66	44	9552	9508
2000	0.01	0.39	0.40	45	4942	4897
2001	0.00	0.57	0.58	23	5962	5939
2002	0.00	0.48	0.48	15	4301	4286
2003	0.01	0.56	0.56	35	6098	6063
2004	0.02	0.39	0.40	75	5067	4992
2005	0.01	0.49	0.49	49	5892	5843
2006	0.00	0.61	0.62	18	5485	5467
2007	0.00	0.62	0.62	42	9142	9100
2008	0.02	0.22	0.22	105	5181	5076
2009	0.02	0.53	0.54	93	5832	5739
2010	0.01	0.61	0.62	146	10420	10274
2011	0.01	0.46	0.47	96	7129	7033
2012	0.01	0.67	0.68	107	16298	16191
2013	0.00	0.26	0.26	3	4902	4899
2014	0.00	0.63	0.63	17	6168	6151
2015	0.01	0.54	0.55	56	8647	8591
2016	0.00	0.62	0.62	19	10907	10888
2017	0.00	0.43	0.43	27	6650	6623
2018	0.00	0.65	0.65	5	2635	2630
<b>Overall<sup>1</sup></b>	<b>0.02</b>	<b>0.53</b>	<b>0.54</b>	<b>3,559</b>	<b>188,389</b>	<b>184,830</b>
<b>55-yr mean<sup>2</sup></b>	<b>0.13</b>	<b>0.43</b>	<b>0.48</b>	<b>60</b>	<b>3,193</b>	<b>3,133</b>

<sup>1</sup> Overall for each column was calculated using all of the data from 1960 to 2018

<sup>2</sup> The 55-yr mean for each column was calculated as the average of each column from 1960 to 2018

**Table S6.2.** Annual ratio of Northern Saw-whet Owls captured from 1960 to 2018 classified to sex. Individuals were assigned as “Unknown” (sex = 0), “Female” (sex = 5), or “Male” (sex = 4). Female and male ratios shown were calculated with and without owls of unknown sex in the total. Ratios without unknowns (“Without Unk” columns) were used in analyses.

Year	Unknown Ratio	Female Ratio		Male Ratio		Total Unk	Total Banded	
		With Unk	Without Unk	With Unk	Without Unk		With Unk	Without Unk
1960	0.97	0.02	0.50	0.02	0.50	57	59	2
1961	0.91	0.04	0.50	0.04	0.50	105	115	10
1962	0.97	0.01	0.33	0.02	0.67	113	116	3
1963	0.99	0.00	0.00	0.01	1.00	166	167	1
1964	1.00	0.00		0.00		126	126	0
1965	0.89	0.08	0.73	0.03	0.27	255	285	30
1966	0.98	0.01	0.67	0.01	0.33	166	169	3
1967	0.98	0.02	1.00	0.00	0.00	130	132	2
1968	0.99	0.01	0.50	0.01	0.50	380	384	4
1969	0.95	0.04	0.88	0.01	0.12	169	177	8
1970	0.97	0.02	0.67	0.01	0.33	103	106	3
1971	0.99	0.01	1.00	0.00	0.00	134	135	1
1972	0.99	0.01	0.50	0.01	0.50	308	312	4
1973	0.80	0.08	0.39	0.12	0.61	238	297	59
1974	0.96	0.02	0.57	0.02	0.43	571	592	21
1975	0.93	0.03	0.45	0.04	0.55	545	587	42
1976	0.94	0.02	0.39	0.03	0.61	613	649	36
1977	0.87	0.04	0.31	0.09	0.69	375	429	54
1978	0.93	0.02	0.35	0.04	0.65	714	765	51
1979	0.90	0.04	0.42	0.06	0.58	331	367	36
1980	0.87	0.04	0.33	0.09	0.67	607	699	92
1981	0.84	0.06	0.38	0.10	0.62	751	892	141
1982	0.94	0.02	0.24	0.05	0.76	722	772	50
1983	0.82	0.05	0.27	0.13	0.73	332	403	71
1984	0.98	0.01	0.44	0.01	0.56	852	868	16
1985	0.93	0.03	0.46	0.04	0.54	500	537	37
1986	0.69	0.07	0.23	0.24	0.77	504	735	231
1987	0.75	0.06	0.25	0.19	0.75	1086	1446	360
1988	0.77	0.07	0.31	0.16	0.69	1693	2190	497
1989	0.76	0.08	0.33	0.16	0.67	2076	2729	653
1990	0.83	0.07	0.39	0.10	0.61	2182	2634	452
1991	0.78	0.07	0.30	0.15	0.70	1945	2496	551
1992	0.92	0.06	0.73	0.02	0.27	1871	2039	168
1993	0.94	0.05	0.74	0.02	0.26	2999	3207	208

**Table S6.2 (cont.).** Annual ratio of Northern Saw-whet Owls captured from 1960 to 2018 classified to sex. Individuals were assigned as “Unknown” (sex = 0), “Female” (sex = 5), or “Male” (sex = 4). Female and male ratios shown were calculated with and without owls of unknown sex in the total. Ratios without unknowns (“Without Unk” columns) were used in analyses.

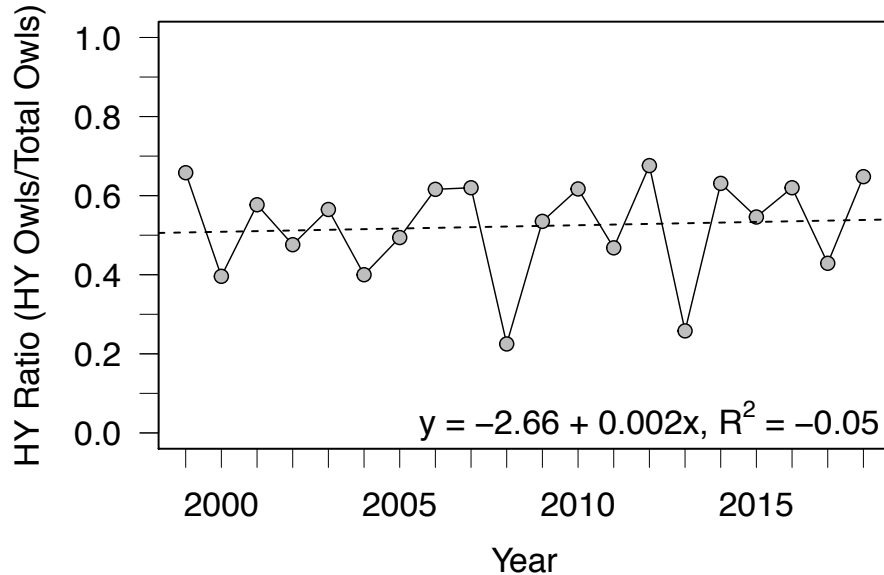
Year	Unknown Ratio	Female Ratio		Male Ratio		Total Unk	Total Banded	
		With Unk	Without Unk	With Unk	Without Unk		With Unk	Without Unk
1994	0.90	0.08	0.83	0.02	0.17	3197	3539	342
1995	0.92	0.05	0.65	0.03	0.35	5819	6324	505
1996	0.92	0.06	0.81	0.01	0.19	2426	2623	197
1997	0.90	0.06	0.67	0.03	0.33	3039	3364	325
1998	0.86	0.11	0.81	0.03	0.19	3199	3713	514
1999	0.66	0.29	0.83	0.06	0.17	6260	9552	3292
2000	0.73	0.25	0.91	0.02	0.09	3602	4942	1340
2001	0.57	0.38	0.87	0.06	0.13	3371	5962	2591
2002	0.66	0.30	0.89	0.04	0.11	2844	4301	1457
2003	0.61	0.34	0.88	0.05	0.12	3706	6098	2392
2004	0.50	0.45	0.90	0.05	0.10	2545	5067	2522
2005	0.55	0.40	0.88	0.05	0.12	3227	5892	2665
2006	0.54	0.42	0.92	0.04	0.08	2964	5485	2521
2007	0.40	0.51	0.85	0.09	0.15	3689	9142	5453
2008	0.50	0.47	0.93	0.03	0.07	2570	5181	2611
2009	0.42	0.54	0.93	0.04	0.07	2435	5832	3397
2010	0.43	0.50	0.88	0.07	0.12	4527	10420	5893
2011	0.50	0.45	0.91	0.05	0.09	3588	7129	3541
2012	0.39	0.53	0.86	0.09	0.14	6287	16298	10011
2013	0.27	0.67	0.92	0.05	0.08	1346	4902	3556
2014	0.33	0.60	0.90	0.07	0.10	2035	6168	4133
2015	0.33	0.59	0.89	0.08	0.11	2884	8647	5763
2016	0.32	0.60	0.88	0.09	0.12	3473	10907	7434
2017	0.37	0.55	0.87	0.08	0.13	2446	6650	4204
2018	0.24	0.67	0.89	0.09	0.11	630	2635	2005
<b>Overall<sup>1</sup></b>	<b>0.56</b>	<b>0.38</b>	<b>0.86</b>	<b>0.06</b>	<b>0.14</b>	<b>105,828</b>	<b>188,389</b>	<b>82,561</b>
<b>55-yr mean<sup>2</sup></b>	<b>0.76</b>	<b>0.19</b>	<b>0.64</b>	<b>0.06</b>	<b>0.36</b>	<b>1,794</b>	<b>3,193</b>	<b>1,399</b>

<sup>1</sup> Overall for each column was calculated using all of the data from 1960 to 2018

<sup>2</sup> The 55-yr mean for each column was calculated as the average of each column from 1960 to 2018

**Table S6.3.** The mean clutch size and mean number of owls fledged taken from publications on breeding success of nesting saw-whet owls. A weighted mean was calculated for both the clutch size and the number of owls fledged. Publications with missing data were excluded from calculations. The weight for each datapoint was the sample size (*n*) from which the mean clutch size and number of owls fledged were derived. The weighted mean clutch size was 5.27, and the weighted mean owls fledged was 4.34.

Publication	Country	State/Province	Clutch size		Owls fledged	
			Mean	<i>n</i>	Mean	<i>n</i>
Marks and Doremus (2000)	USA	Idaho	-	-	4.8	29
Buidin et al. (2006)	Canada	Quebec	3.5	9	2.9	9
Nightingale et al. (2013)	USA	Oregon	5.8	22	4.4	20
Drilling (2013)	USA	South Dakota	5.2	127	4.4	104
Marks et al. (2015)	USA	Oregon	5.7	37	4.2	29
Domahidi et al. (2020)	Canada	Alberta	5.0	4	4.2	29
Rasmussen et al. (2020)	Canada	Alberta	-	-	5.5	4
Rasmussen et al. (2020)	USA	Oregon	5.2	12	-	-



**Figure S6.1.** Ratio of HY saw-whet owls captured per year in North America from 1999 to 2018 based on 140,190 banding events. The dotted line represents the linear regression between the ratio of saw-whet owls and year. The relationship was not significant for HY saw-whet owls ( $F_{1,18} = 0.11$ ,  $p = 0.75$ , adj.  $R^2 = -0.05$ ). Linear regression results are located in the lower right corner of the graph. Individuals not identified to age (age = 0; “unknown”) were excluded from ratio calculations. Though populations remain stable across the study period, fluctuations in ratios of HY owls are evident.

## References

- Andersson, M. (1980). Nomadism and site tenacity as alternative reproductive tactics in birds. *Journal of Animal Ecology*, 49, 175–184.
- Beckett, S. R., & Proudfoot, G. A. (2011). Large-scale movement and migration of Northern Saw-whet Owls in eastern North America. *The Wilson Journal of Ornithology*, 123(3), 521–535.
- Beckett, S. R., & Proudfoot, G. A. (2012). Sex-specific migration trends of Northern Saw-whet Owls in eastern North America. *The Journal of Raptor Research*, 46(1), 98–108.
- Benkman, C. W., & Young, M. A. (2020). Red Crossbill (*Loxia curvirostra*), version 1.0. In S. M. Billerman, B. K. Keeney, P. G. Rodewald, & T. S. Schulenberg (Eds.), *Birds of the World*. Cornell Lab of Ornithology.
- Bent, A. C. (1938). Life histories of North American birds of prey part II: Orders *Falconiformes* and *Strigiformes*. *Bulletin of the United States National Museum*.
- Bowman, J., Badzinski, D. S., & Brooks, R. J. (2010). The numerical response of breeding Northern Saw-whet Owls *Aegolius acadicus* suggests nomadism. *Journal of Ornithology*, 151, 499–506.
- Brinker, D., Duffy, K., & Whalen, D. (1997). Autumn migration of Northern Saw-whet Owls (*Aegolius acadicus*) in the middle atlantic and northeastern united states: What observations from 1995 suggest. In J. R. Duncan, D. H. Johnson, & T. H. Nicholls (Eds.), *Biology and conservation of owls of the northern hemisphere: Second international symposium* (pp. 74–89). St. Paul.
- Brittain, R. A., Meretsky, V. J., Gwinn, J. A., Hammond, J. G., & Riegel, J. K. (2009). Northern Saw-whet Owl (*Aegolius acadicus*) autumn migration magnitude and demographics in south-central Indiana. *Journal of Raptor Research*, 43(3), 199–209.
- Buidin, C., Rochepault, Y., Savard, M., & Savard, J.-P. L. (2006). Breeding range extension of the Northern Saw-whet Owl in Quebec. *The Wilson Journal of Ornithology*, 118(3), 411–413.
- Cannings, R. J. (1987). The breeding biology of Northern Saw-whet Owls in southern British Columbia. *General technical report: U.S. forest service*.
- Catling, P. M. (1972). Food and pellet analysis studies of the Saw-whet Owl (*Aegolius acadicus*). *Ontario Field Biologist*, 26, 72–85.

- Cheveau, M., Drapeau, P., Imbeau, I., & Bergeron, Y. (2004). Owl winter irruptions as an indicator of small mammal population cycles in the boreal forest of eastern North America. *Oikos*, *107*, 190–198.
- Confer, J. L., Kanda, L. L., & Li, I. (2014). Northern Saw-whet Owl: Regional patterns for fall migration and demographics revealed by banding data. *The Wilson Journal of Ornithology*, *126*(2), 305–320.
- Cote, M., Ibarzabal, J., St-Laurent, M.-H., Ferron, J., & Gagnon, R. (2007). Age-dependent response of migrant and resident *Aegolius* owl species to small rodent population fluctuations in the eastern Canadian boreal forest. *Journal of Raptor Research*, *41*(1), 16–25.
- De Juana, E., & Garcia, E. F. J. (2010). Vagrancy or migration: Why do American Teals cross the Atlantic? *Ardeola*, *57*(2), 417–430.
- DeBenedictis, P. (1971). Wood warblers and vireos in California: The nature of the accidental. *California Birds*, *2*(4), 111–128.
- DeSante, D. F. (1983). Annual variability in the abundance of migrant landbirds on Southeast Farallon Island, California. *The Auk*, *100*(4), 826–852.
- Domahidi, Z., Nielsen, S. E., Bayne, E. M., & Spence, J. R. (2020). Boreal owl (*Aegolius funereus*) and Northern Saw-whet Owl (*Aegolius acadicus*) breeding records in managed boreal forests. *The Canadian Field-Naturalist*, *134*, 125–131.
- Drilling, N. E. (2013). *Studies of nesting Northern Saw-whet Owls in northwestern South Dakota* (Tech. Rep. M-SDOWL BAND-03.). Rocky Mountain Bird Observatory. Brighton, CO.
- Duffy, K., & Kerlinger, P. (1992). Autumn owl migration at Cape May Point, New Jersey. *The Wilson Bulletin*, *104*(2), 312–320.
- Duffy, K., & Matheny, P. E. (1997). Northern Saw-whet Owls (*Aegolius acadicus*) captured at Cape May Point, NJ, 1980-1994: Comparison of two capture techniques. In J. R. Duncan, D. H. Johnson, & T. H. Nicholls (Eds.), *Biology and conservation of owls of the northern hemisphere: Second international symposium* (pp. 131–137). St. Paul.
- Elias, S. P., Witham, J. W., & Hunter, M. L., Jr. (2006). A cyclic red-backed vole (*Clethrionomys gapperi*) population and seedfall over 22 years in Maine. *Journal of Mammalogy*, *87*(3), 440–445.
- Erdman, T. C., & Brinker, D. F. (1997). Increasing mist net captures of migrant Northern Saw-whet Owls (*Aegolius acadicus*) with an audiolure. In J. R. Duncan, D. H. Johnson, & T. H. Nicholls (Eds.), *Biology and conservation of owls of the northern hemisphere: Second international symposium* (pp. 553–544). St. Paul.
- Fauteux, D., Cheveau, M., Imbeau, L., & Drapeau, P. (2015). Cyclic dynamics of a boreal southern red-backed vole population in northwestern Quebec. *Journal of Mammalogy*, *96*(3), 573–578.

- Frye, G. G., & Gerhardt, R. P. (2003). Northern Saw-whet owl (*Aegolius aegolius*) migration in the Pacific Northwest. *Western North American Naturalist*, *63*(3), 353–357.
- Gruyer, N., Gauthier, G., & Berteaux, D. (2008). Cyclic dynamics of sympatric lemming populations on Bylot Island, Nunavut, Canada. *Canadian Journal of Zoology*, *86*, 910–917.
- Hampton, S. (1997). Rare migrants in California: The determinants of their frequency. *Western Birds*, *28*, 30–42.
- Holroyd, G. L., & Woods, J. G. (1975). Migration of the Saw-whet Owl in eastern North America. *Bird-Banding*, *46*(2), 101–105.
- Hyndman, R. J., Athanasopoulos, G., Bergmeir, C., Caceres, G., Chhay, L., O'Hara-Wild, M., Petropoulos, F., Razbash, S., Wang, E., & Yasmeeen, F. (2020). forecast: Forecasting functions for time series and linear models. R package version 8.13. <https://pkg.robjhyndman.com/forecast/>
- Johnson, A., & Anderson, S. H. (2003). *Conservation assessment for the Northern Saw-whet Owl in the Black Hills National Forest, South Dakota and Wyoming*. USDA Forest Service, Rocky Mountain Region.
- Korpimäki, E., Lagerström, M., & Saurola, P. (1987). Field evidence for nomadism in Tengmalm's Owl *Aegolius funereus*. *Ornis Scandinavia*, *18*, 1–4.
- Lees, A. C., & Gilroy, J. J. (2009). Vagrancy mechanisms in passerines and near-passerines. In R. Slack (Ed.), *Where and When: An analysis of status and distribution in Britain and Ireland. Volume 1: Sandgrouse to New World orioles*. Rare Bird Books.
- Marks, J. S., & Doremus, J. H. (1988). Breeding-season diet of Northern Saw-whet Owls in southwestern Idaho. *The Wilson Bulletin*, *100*(4), 690–694.
- Marks, J. S., & Doremus, J. H. (2000). Are Northern Saw-whet Owls nomadic? *Journal of Raptor Research*, *34*(4), 299–304.
- Marks, J. S., Nightingale, A., & McCullough, J. (2015). On the breeding biology of Northern Saw-whet Owls (*Aegolius acadicus*). *Journal of Raptor Research*, *49*(4), 486–497.
- McLaren, I. A. (1981). The incidence of vagrant landbirds on Nova Scotian islands. *The Auk*, *98*(2), 243–257.
- Neri, C. M., Mackentley, N., Dykema, Z. A., Bertucci, E. M., & Lindsay, A. R. (2018). Different audio-lures lead to different sex-biases in capture of Northern Saw-whet Owls (*Aegolius acadicus*). *Journal of Raptor Research*, *52*(2), 245–249.
- Newton, I. (2006). Advances in the study of irruptive migration. *Ardea*, *94*(3), 433–460.
- Patten, M. A., & Burger, J. C. (1998). Spruce budworm outbreaks and the incidence of vagrancy in eastern North American wood-warblers. *Canadian Journal of Zoology*, *76*, 433–439.

- Patten, M. A., & Marantz, C. A. (1996). Implications of vagrant southeastern vireos and warblers in California. *The Auk*, *113*(4), 911–923.
- Pfeifer, R., Stadler, J., & Brandl, R. (2007). Birds from the Far East in Central Europe: A test of the reverse migration hypothesis. *Journal of Ornithology*, *148*, 379–385.
- R Core Team. (2020). R: A language and environment for statistical computing. <https://www.R-project.org/>.
- Rains, C. (1997). Comparison of food habits of the Northern Saw-whet Owl (*Aegolius acadicus*) and the Western Screech-owl (*Otus kennicottii*) in southwestern Idaho. In J. R. Duncan, D. H. Johnson, & T. H. Nicholls (Eds.), *Biology and conservation of owls of the northern hemisphere: Second international symposium* (pp. 339–346). St. Paul.
- Ralph, C. J., & Wolfe, J. D. (2018). Factors affecting the distribution and abundance of autumn vagrant New World warblers in northwestern California and southern Oregon. *PeerJ*, *6*, 5881.
- Rasmussen, J. L., Sealy, S. G., & Cannings, R. J. (2020). Northern Saw-whet Owl (*Aegolius acadicus*), version 1.0. In A. F. Poole (Ed.), *Birds of the World*. Cornell Lab of Ornithology.
- Rohner, C. (1996). The numerical response of Great Horned Owls to the snowshoe hare cycle: Consequences of non-territorial 'floaters' on demography. *Journal of Animal Ecology*, *65*, 359–370.
- Southwood, T. R. E., May, R. M., Hassell, M. P., & Conway, G. R. (1974). Ecological strategies and population parameters. *The American Naturalist*, *108*(964), 791–804.
- Stenseth, N. C. (1999). Population cycles in voles and lemmings: Density dependence and phase dependence in a stochastic world. *Oikos*, *87*, 427–461.
- Sundell, J., Huitu, O., Henttonen, H., Kaikusalo, A., Korpimäki, E., Pietiäinen, H., Saurola, P., & Hanski, I. (2004). Large-scale spatial dynamics of vole populations in Finland revealed by the breeding success of vole-eating avian predators. *Journal of Animal Ecology*, *73*, 167–178.
- Swengel, A. B., & Swengel, S. R. (1995). Possible four-year cycle in amount of calling by Northern Saw-whet Owls. *The Passenger Pigeon*, *57*(3), 149–155.
- Thorup, K. (2004). Reverse migration as a cause of vagrancy. *Bird Study*, *51*(3), 228–238.
- Underwood, T. J., & Sealy, S. G. (2002). Breeding status and notes on diet of the Northern Saw-whet Owl at Delta Marsh, Manitoba. *Blue Jay*, *60*(3), 130–135.
- USGS Bird Banding Laboratory. (2018). *North American bird banding and band encounter data set*. Patuxent Wildlife Research Center, Bird Banding Laboratory. <http://www.pwrc.usgs.gov/bbl>.
- Veit, R. R. (1997). Long-distance dispersal and population growth of the Yellow-headed Blackbird *Xanthocephalus xanthocephalus*. *Ardea*, *85*(1), 135–143.

- Veit, R. R. (2000). Vagrants as the expanding fringe of a growing population. *The Auk*, *117*(1), 242–246.
- Veit, R. R. (2005). Yellow-nosed Albatross at Tuckernuck Island, Massachusetts. *Bird Observer*, *33*(5), 284–288.
- Weir, R. D., Cooke, F., Edwards, M. H., & Steward, R. B. (1980). Fall migration of Saw-whet owls at Prince Edward Point, Ontario. *The Wilson Bulletin*, *92*(4), 475–488.
- Whalen, D. M., & Watts, B. D. (1999). The influence of audio-lures on capture patterns of migrant Northern Saw-whet Owls. *Journal of Field Ornithology*, *70*(2), 163–168.
- Whalen, D. M., & Watts, B. D. (2002). Annual migration density and stopover patterns of Northern Saw-whet Owls (*Aegolius acadicus*). *The Auk*, *119*(4), 1154–1161.
- Williamson, K. (1969). Weather systems and bird movements. *Quarterly Journal of the Royal Meteorological Society*, *95*(404), 414–423.
- Zawadzki, L. C., Veit, R. R., & Manne, L. L. (2019). The influence of population growth and wind on vagrancy in a North American passerine. *Ardea*, *107*(2), 131–147.

# 7

## Discussion

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### 7.1 Introduction

The aim of this thesis was to use a novel combination of experimental field studies and mathematical modelling to quantitatively investigate patterns and drivers of vagrancy in migratory birds. There currently exist very few published studies that quantitatively assess vagrancy, and even fewer that study vagrancy directly in the field. I aimed to cover topics to address the biggest misconception about vagrants, which claims them to be aberrant, and to begin to fill in gaps in the literature in an attempt to piece together the

plausible causes of vagrancy in migrants. In this final chapter, I outline the main results and findings of this thesis, and link together the narrative of each chapter to explain what my results have shown about vagrant behaviour. I also discuss the limitations posed by the methodology used in this thesis, and explain potential solutions to improve these studies in the future. Finally, I highlight the areas that will require future study, of which there are many, as well as the key questions that remain unanswered about vagrancy.

## **7.2 Main results and future directions**

### **7.2.1 Are vagrants aberrant?**

The initial motivation for this thesis was to test the assumption that vagrants are aberrant, which has been proposed multiple times by many scientists and birdwatchers alike over the last century. Vagrants are often thought to be ‘lost’ birds, and it is as rare an occurrence as vagrancy itself that I have ever heard somebody refer to a vagrant as anything but. Though the chapters in my thesis do not directly study whether vagrants are aberrant, overall, the findings from my work emphasise that they are not, and that rather, vagrancy is more likely to be a natural part of the migratory programme.

Chapter 2 is the only study where I address whether vagrants are aberrant directly, since the orientation experiments themselves were meant to test if vagrants differ behaviourally from non-vagrants. In this study, I found that vagrants were capable of demonstrating a preferred orientation during autumn migration, and the mean orientation of vagrant individuals was not statistically different from the mean orientation of non-vagrants. That is, both vagrants and non-vagrants reacted similarly during experimentation, orienting towards the N/NNW. This implies that the vagrants in this study were capable of actively orienting similarly to non-vagrants during migratory flights, and thus the behaviour of vagrants may not differ from non-vagrant migrants.

Though my main hypothesis for the other chapters of this thesis did not directly test whether vagrants were aberrant, results from each study lend their support to the

hypothesis that vagrants are not aberrant. Particularly, in Chapters 4 and 5, occurrence of vagrant New World warblers and Lesser Black-backed Gulls (*Larus fuscus*), respectively, were correlated with population size and growth in some portion of their breeding range. Additionally, the number of vagrant records each year for all the species I studied in Chapters 4 and 5 are substantial. For example, thousands of vagrant Lesser Black-backed Gulls are recorded in North America each year. Density-dependence in occurrence of vagrants, or any patterns on vagrant occurrence in general, should not be evident if vagrancy is aberrant (Phillips 2000). If vagrants are actually aberrant, this behaviour should be selected out of a population since it will likely be detrimental to an individual's survival if they cannot navigate, or navigate in the wrong direction (Ralph 1978). Likewise, we would not expect to see such large numbers of vagrants (Phillips 2000), especially in consistent patterns of occurrence, since the inheritance of these defective behaviours would not be passed on if birds do not survive their first winter.

How Chapter 3 demonstrates that vagrants are not aberrant may not be immediately clear, however, the patterns present in predicted natal origins of vagrants suggest that vagrancy does not occur at random. In Chapter 3, I found that vagrants derive mainly from the edge of the breeding range in various species, which may be linked to population growth, or other factors within the breeding range such as habitat or food availability. This pattern suggests that vagrancy may be selected for under certain conditions and is not an aberrant trait. Additionally, the majority of vagrants I captured in Chapter 2 were in good body condition, and had high fat scores upon capture. Vagrants must be normal migrants if they experience similar physiological changes during the migratory period (DeJuana 2008, Veit 2008). Body size has been found to predict vagrant abundance (Robbins 1980, McLaren et al. 2006), which implies that those with the capacity to maintain greater fat stores are more likely to become vagrants.

Grinnell (1922) was the first to propose that vagrancy may be an adaptive trait, suggesting that vagrancy was “the regular thing, to be expected” and that “the process is part of the normal evolutionary program”. Williamson (1959, 1969) also emphasised the adaptive value of this behaviour, due to its facilitation of exploration and pioneering by young birds.

While both Grinnell (1922) and Williamson (1959, 1969) explained vagrancy as if it were selected for at the species-level (which it cannot be), vagrancy may still be adaptive at the individual-level. The ability to maintain some level of behavioural flexibility, particularly upon migration, can be highly beneficial to the individual (DeBenedictis 1971; Ralph 1978; Veit 1989, 2008; Phillips 2000). By being flexible, birds can respond to changing environmental conditions, and may be able to escape deteriorating habitat by locating and occupying habitat with access to suitable resources (Ralph 1978, Veit 1989). This is particularly important for species that occupy early seral stage (DeBenedictis 1971) or ephemeral habitat (Farnsworth et al. 2015), where the access to resources is constantly shifting. The results from Chapter 6 are pertinent in this regard. In Chapter 6, I showed that irruptions of Northern Saw-whet Owls (*Aegolius acadicus*) during autumn migration are linked to prey availability in the breeding range. Though irruptive Northern Saw-whet Owls are not vagrants, the process by which irruptions occur is similar to vagrancy, and may reflect how vagrants disperse in relation to food availability.

Vagrancy does not need to end in breeding for it to be adaptive either, and importantly, most vagrant events do not end in reproduction. Vagrants are typically young migrants on their first autumn migration (Williamson 1959, 1969; DeSante 1973; Baker 1977; Ralph 1971, 1978; Elkins 1979). The ability to find suitable non-breeding habitat may increase chances of survival of the individual, which in turn, will increase the chances that they will breed the following spring. That is, vagrancy just has to be a “slightly better option than staying at home” for it to persist in a given population (Veit 2008). Little evidence exists to suggest that the mortality rate of vagrants is any higher than that of non-vagrants (Veit 2008). If all vagrants that occurred on the coasts of North America perished, 1 to 10% of the annual migratory population would be lost (Ralph 1978). Normal migratory populations in North America are estimated to lose, on average, 25 to 35% of their populations each winter (Dokter et al. 2018).

It is possible, however, that vagrancy is not adaptive, and may occur as either the unexpected outcome of an adaptive behaviour (i.e. migration), or as the result of bet-hedging, which is advantageous for the parents rather than their offspring (Reilly and

Reilly 2009). The former of the two is the basis for the suggestion that vagrants are aberrant – this behaviour should not occur, but arises as a mistake during post-juvenile dispersal or migration, which themselves are adaptive behaviours to help individuals survive the seasonal cycle. While it is possible that some instances of vagrancy are mistakes (e.g. being displaced by a storm (Kinsky 1968, Bugoni et al. 2007), or calibrating the magnetic compass during a magnetic anomaly (Winklhofer et al. 2013)), the fact that patterns are evident in vagrant occurrence, and the high occurrence of vagrants each year, suggests that this is not the cause. As for the latter, bet-hedging occurs when parents impart a trait on their young that ensures their genes will be passed on. For vagrancy, parents may impart an array of migratory orientations that create within-clutch phenotypic variation in migratory orientation. While this is not adaptive to the individual since travel in a direction that differs from the normal migratory orientation may end in mortality, it is adaptive to the parents since it increases their chances that at least one of their offspring will survive and pass on their genes. Though this is not adaptive to the individual, this does not detract from the hypothesis that vagrancy is evolutionarily advantageous. Whether it is adaptive for the parents or young, it is still adaptive to some degree, and will result in repeated instances of vagrancy across generations.

Studies on the genetic makeup of vagrants and normal migrants from the same population of individuals will help elucidate whether vagrants actually differ from migrants, and whether these traits are genetically encoded or triggered through epigenetic processes. While I have discussed the potential adaptive value of vagrancy, it is not known whether this type of behaviour is inherited, though it has been hypothesised for theories on reverse migration and mirror-image misorientation (Rabøl 1969, Desante 1973). Furthermore, possible studies on the exploratory acumen of vagrants, particularly in regard to ‘boldness’ or neophobia, may highlight differences between vagrants and migrants of the same species, since it is thought that vagrants must be highly flexible in order to end up at locations far from the normal species’ range (Ralph 1978).

### **7.2.2 Why do vagrants increase with decreasing population growth?**

This thesis focused heavily on patterns found in occurrence of vagrants for a multitude of species. Based on previous studies (DeBenedictis 1971; DeSante 1983b; Veit 1990, 1997, 2000; Thorup 2004; Pfeifer et al. 2007; Jiguet and Robert 2008; De Juana and Garcia 2010; Ralph and Wolfe 2018; Zawadzki et al. 2019) I had hypothesised that population size and growth will highly predict abundance of vagrants. While I did find a similar relationship in Chapter 4, my species-specific results were surprising, and warranted a re-examination of how population growth may influence vagrancy. I found that occurrence of vagrant New World warblers was predicted by both a larger population size, which was expected from results of the studies cited above. However, when each species was examined separately to highlight trends from specific regions within the breeding range, both population size and population growth were negatively correlated with vagrant abundance. This led me to propose an extension to the ‘population hypothesis’.

The underlying premise of the ‘population hypothesis’ is that vagrants will increase when the population increases, simply because a larger population will produce more vagrants. However, this does not consider the various interactions that individuals will have with themselves or the environment. In times of increased food supply, populations will increase due to an abundance of available resources, resulting in more vagrants – this is known as an irruption. However, during the next (or a following) breeding season, the population of potential breeders may now exceed the available food supply (Newton 2006), and population growth will slow or decrease. Normally, when resources are no longer abundant, or do not meet the needs of a current population, individuals will emigrate out of the region in search of new resources – known as an eruption (Newton 2006, Lees and Gilroy 2009). Consequently, while one would assume numbers of vagrants would decrease when population growth has slowed, they may actually increase in response to poor conditions to find suitable habitat, similar to many species of boreal owl (e.g. Cheveau et al. 2004).

The models in Chapter 4 demonstrate this – vagrants increase in years of slowed population growth, likely in search of new resources. This may also be the case if habitats are deteriorating in the region (DeBenedictis 1971, DeSante 1983b). A deteriorating habitat will no longer be able to support the entire population, population growth will decrease, and individuals will emigrate outside of their range to find suitable habitat. Results from Chapter 5 also suggest that vagrants can derive from decreasing populations. In Chapter 5, I found that occurrence of vagrant Lesser Black-backed Gulls to North America was best predicted by generalised linear models (GLMs) with Greenlandic populations, which have been increasing since the late 1990s, but for generalised additive models (GAMs), vagrant Lesser Black-backed Gulls were best predicted by Icelandic populations, which experienced a stark decline in 2005. It is possible that individuals from the Icelandic population left as a result of deteriorating food resources during that period, and added to the influx of vagrants to North America from Greenland. Future studies will need to incorporate the possibility that vagrants respond to density quadratically, whereby during slowing population growth, vagrants will increase, just as they will when populations experience heightened population growth. We may find that we can predict vagrancy much more accurately if it is studied under this premise.

### **7.2.3 Where do vagrants come from?**

Another topic I explored in this thesis was the origin of vagrants. Knowing the origin of vagrants will not only improve our understanding of vagrancy, but will also allow us to directly study how and why vagrants occur. We may be able to backtrack possible migratory directions, ask particular questions about the region and habitat in which an individual vagrant fledged, and examine the population of individuals that produced this vagrant. Theories of reverse migration, mirror-image misorientation, and displacement by wind will also be able to be examined more critically since we will know the origin of the vagrants we are studying (De Jong et al. 2019), rather than having to assume their starting point (e.g. Rabøl 1969; Baker 1977; Van Impe and Derasse 1994; Williamson 1959, 1961;

McLaren 1981). In Chapter 3, I examined the origin of vagrants through stable isotope analysis and assessed the use of this methodology for future studies on vagrants. Though this method does require capture of individuals (museum specimens can also be used; Fox et al. 2007), it is highly cost-effective, and only needs the individual to be captured once, which is imperative for individuals whose appearance is already unpredictable.

I expected that vagrants would mainly originate from the edge of their range, since dispersing individuals are often described as those that occur at the range edge (Veit and Lewis 1996; Phillips et al. 2008, 2010). I found that the majority of vagrants originated along the edge of their breeding range. This is an interesting result, since it suggests that vagrants are primarily those at the range edge, and vagrancy may reflect ecosystem interactions along range edges of populations. Liebl and Martin (2012, 2014) found that House Sparrows (*Passer domesticus*) at the edge of their range presented with increased exploratory behaviour, and were more likely to interact with novel food resources, than those within the centre of the range. This suggests that birds at the range edge have a higher likelihood of interacting with new resources and environments. These individuals, thus, may have a higher propensity to disperse and become vagrant. Results from Chapter 4 add support to these findings. In Chapter 4, I found that regions of the breeding area that best predicted occurrence of vagrant New World warblers to New England (based on annual population size and growth in those regions) were those located on the edge of the breeding range. Since vagrants are often recently fledged young, it is possible that vagrants that occurred in New England originated from those regions along the range edge.

Future studies on vagrants should incorporate the use of stable isotope analysis to determine natal origin. Two studies have already used stable isotope analysis to examine the natal origin of vagrants in Europe. Fox et al. (2007) used this technique to assess whether a vagrant Baikal Teal (*Anas formosa*) in Denmark was an escaped captive or a wild bird. They were able to determine that it was in fact a wild bird, emphasising that vagrant Baikal Teal in Europe are genuine vagrants (and likely most vagrants that are deemed to be escaped cage birds). De Jong et al. (2019) later used this technique to determine the origin of vagrant Yellow-browed Warblers (*Phylloscopus inornatus*),

however, they were unable to pinpoint a precise region of origin since Yellow-browed Warblers have a broad longitudinal range, and isoscapes in Europe are less well-defined (Hobson et al. 2004). Nonetheless, my results in Chapter 2 highlight the potential for this methodology to be used in future studies on vagrants.

Additionally, in Chapter 5, I attempted to determine the origin of vagrants indirectly, by predicting a location based on population growth in the breeding range. While results of this study were promising, the limitations imposed by availability of breeding data restricted analyses and their interpretation. This method should be explored in species of vagrants that have abundant breeding data to determine if it is a viable option to study vagrants indirectly. The ability to study vagrants indirectly is highly important since vagrant events are often rare and unpredictable.

## **7.3 Limitations**

### **7.3.1 Orientation experiments**

Experiments on orientation behaviour of migrants often test individuals on subsequent nights to obtain a mean orientation for each individual (e.g. DeSante 1973, Thorup 1998, Thorup et al. (2011, 2012)). This is likely to ensure that any confounds during testing nights are averaged out of results to reflect the ‘true’ orientation of individuals. In Chapter 2, however, I was not able to test birds on subsequent nights because the weather conditions on Nova Scotian islands are not ideal for holding birds in captivity for long periods of time. The weather on Bon Portage and Seal Island is highly variable, since both islands are heavily impacted by prevailing easterlies and passing storms throughout the autumn season, and are subject to periods of wet, cold, and foggy weather in which birds in outdoor cages may not survive. Therefore, our results reflect only orientation of individuals on their first day of capture.

Sandberg et al. (1991) and Thorup (1998) have suggested that orientation on the first night of capture may reflect a “default” orientation, rather than the actual preferred

migratory orientation of the individual. This is presumed to result from a stress response to immediate conditions. While I cannot say for certain whether vagrants in Chapter 2 demonstrated a stress response rather than true orientation, the experimental design makes it highly unlikely that birds were exhibiting a “default” orientation during experimentation. In most orientation experiments, individuals are kept in a separate holding cages prior to testing in Emlen funnels (e.g. Åkesson 1993, Mouritsen and Larsen 2001, Muheim et al. 2002). However, I housed individuals in the same cage that they were tested in, based on designs by Toews et al. (2017). This was to ensure that individuals had time to adjust to their surroundings prior to experimentation, so they would exhibit their preferred orientation during experimentation. In the future, it would be ideal to test vagrants on subsequent nights to confirm whether demonstrated orientation changes with each test.

Furthermore, orientation experiments were subject to environmental and external factors since the field is not a closed system. Though I found that the wind direction did not affect chosen orientation during experiments, it is possible that other factors such as cloud cover, moon visibility, and even activity from animals or other migrants nearby may have influenced the experimental results. A model that tested for the effect of cloud cover, moon visibility, and wind direction on orientations observed would help identify whether these factors impact observed orientations. In the future, the experimental design could be altered to minimise the impact of external factors. If vagrants can be kept in captivity for multiple days, the effects of weather and astronomical conditions on the orientation demonstrated by each individual could be analysed from multiple experiments. Additionally, individuals could be tested on nights that have similar weather and astronomical conditions to remove this possible confound.

Lastly, although we were able to conclude that vagrants and non-vagrants (Blackpoll Warblers (*Setophaga striata*)) exhibited a mean NNW and N heading, respectively, we can only hypothesise why this heading was chosen in our experiments. Though I was able to infer natal origin of vagrants from the stable isotope analysis in Chapter 3, we do not know why vagrants flew to Bon Portage or Seal Island. We can infer that they oriented directly to these islands from their natal sites, but we cannot determine from

our orientation data whether the initial overseas crossing was directed. Unfortunately for most vagrants, we will never know what occurs during the outward journey since we cannot track their movements. Though we can track movements after their arrival at vagrant sites with nanotags (such as the MOTUS network; Taylor et al. 2017), nanotags in our experiments did not stay on long enough to permit observation of a second autumn migration the following year. This may however, be possible for larger individuals with GPS devices that do not require recovery, as has been recently demonstrated through tracking of vagrant Lesser Black-backed Gulls in North America (Barber et al. in press).

### **7.3.2 Data availability and how we define vagrants**

Chapters 4, 5, and 6 relied on data collected by both citizen scientists and bird banders. This presented limitations for analysis, particularly in Chapter 5, since breeding data collected in both Iceland and Greenland on breeding Lesser Black-backed Gulls were inconsistent across years and colonies. In Iceland, only one colony was surveyed, and surveys did not continue past 2006. In Greenland, though breeding population surveys have occurred nearly annually since 1990, different colonies are surveyed each year. Lack of consistent survey data introduces complications into model analysis, and interpretation of these models. Though time-series of vagrant occurrence of Lesser Black-backed Gulls support the hypothesis that they have originated from both Iceland and Greenland, instead of the UK, improved breeding survey data will improve the quality of these inferences. Many studies on migratory ecology of populations rely on this data, and the link that I have found between breeding populations and vagrancy emphasises the need for accurate breeding data to study this topic in more detail in the future. Calculating indices from breeding data (Jiguet et al. 2008) to use in analyses may also improve the fit and interpretation of models.

Citizen science data, particularly for vagrant sightings, are not without their own limitations. Vagrancy is defined as the movement of an individual into an area where its species is not known to breed, winter, or migrate through (DeSante 1973). At what point,

however, do we stop defining a vagrant as a vagrant? This issue has impacted which species of vagrants are reported in rarities reports, and which are deemed too common to make a note of. For example, in North America, Cave Swallows (*Petrochelidon fulva*), previously a rare vagrant to New York, are now such a common autumn visitor that they are overlooked. Additionally, in Chapter 4, a few warbler species, including Hooded Warbler (*Setophaga citrina*), Worm-eating Warbler (*Helmitheros vermivorum*), and Yellow-throated Warbler (*Setophaga dominica*), have become a common vagrant to certain parts of the study area (according to editors of the journals themselves), and have subsequently ceased to be highlighted or even reported as important rarities.

This decision as to when a vagrant is defined as a common vagrant, or “pseudo-vagrant” (Gilroy and Lees 2003), is completely arbitrary, and to date, no formal classification has been developed. Having clear definitions of how many individuals it takes to still be considered a vagrant species is important if we are to fully understand how and why this behaviour unfolds in populations. Williamson (1975, p. 161) stressed the danger in declaring species as “non-rarities” once they exceed an arbitrary threshold, particularly in regards to conservation efforts, since vagrants may serve as important indicators of ecosystem health.

In Chapter 6, our study was limited by the availability of prey data in the breeding range, particularly for southern red-backed voles (*Clethrionomys gapperi*). Though a database used to exist with data on mammal populations in Quebec (Atlas des Micromammifères du Québec, Desrosiers and Jutras 2002), it is no longer a functionally accessible database. Studies on red-backed vole populations in North America are also few and far between (Bowman et al. 2010, Elias et al. 2006, Fauteux et al. 2015), and have limited datasets confined to specific study sites. Future studies on Northern Saw-whet Owls and prey availability may benefit from using a combination of all available red-backed vole data to improve analysis. It is also imperative that the relationship between cyclical timing of prey and irruptions of these species is identified, which will require intensive investigation of the current populations of prey available to these species.

## 7.4 Concluding remarks

At the beginning of my thesis, little was known about vagrancy, and I had many unanswered questions about how vagrancy occurs in migratory birds. This is still true, though now, I have even more questions. However, I hope that the findings in this thesis serve as a new starting point from which vagrancy may be viewed as not only an exciting topic of research, but a valuable one. I have found evidence that vagrants are not aberrant – they can effectively orient, and in the same direction as non-vagrants. Vagrants also originate from the edge of their ranges more often than other regions, and this behaviour is density-dependent, linked to food availability, and possibly habitat change. The methods used in this thesis to study vagrancy have exciting implications for future studies and will help accelerate our understanding of this behaviour. In light of current climatic changes, disease spread, and general uncertainty, understanding how and why this exploratory behaviour arises in individuals, will improve conservation efforts for all migratory species. Vagrancy is likely a part of the natural migratory programme, and is not an aberrant trait, but rather “the regular thing, to be expected” (Grinnell 1922).

## References

- Able, K. P. (1977). The orientation of passerine nocturnal migrants following offshore drift. *The Auk*, *94*(2), 320–330.
- Åkesson, S. (1993). Effect of geomagnetic field on orientation of the Marsh Warbler, *Acrocephalus palustris*, in Sweden and Kenya. *Animal Behaviour*, *46*, 1157–1167.
- Baker, K. (1977). Westward vagrancy of Siberian passerines in autumn 1975. *Bird Study*, *24*(4), 233–242.
- Barber et al. (in press). Summer locations of LBBG (*L. fuscus*) wintering in PA.
- Bowman, J., Badzinski, D. S., & Brooks, R. J. (2010). The numerical response of breeding Northern Saw-whet Owls *Aegolius acadicus* suggests nomadism. *Journal of Ornithology*, *151*, 499–506.
- Cheveau, M., Drapeau, P., Imbeau, I., & Bergeron, Y. (2004). Owl winter irruptions as an indicator of small mammal population cycles in the boreal forest of eastern North America. *Oikos*, *107*, 190–198.
- De Jong, A., Tornaiainen, J., Bourski, O. V., Heim, W., & Edenius, L. (2019). Tracing the origin of vagrant Siberian songbirds with stable isotopes: the case of Yellow-browed Warbler (*Abroornis inornatus*) in Fennoscandia. *Ornis Fennica*, *96*, 90–99.
- De Juana, E. (2008). Where do Pallas's and Yellow-browed Warblers (*Phylloscopus proregulus*, *Ph. inornatus*) go after visiting northwest Europe in autumn? an Iberian perspective. *Ardeola*, *55*(2), 179–192.
- De Juana, E., & Garcia, E. F. J. (2010). Vagrancy or migration: Why do American Teals cross the Atlantic? *Ardeola*, *57*(2), 417–430.
- DeBenedictis, P. (1971). Wood warblers and vireos in California: The nature of the accidental. *California Birds*, *2*(4), 111–128.
- DeSante, D. F. (1973). *An analysis of the fall occurrences and nocturnal orientations of vagrant wood warblers (Parulidae) in California* (Doctoral dissertation). Stanford University. Stanford, California.
- DeSante, D. F. (1983). Annual variability in the abundance of migrant landbirds on Southeast Farallon Island, California. *The Auk*, *100*(4), 826–852.

- Desrosiers, N. R., & Jutras, M. J. (2002). Atlas des micromammifères du Québec. *Société de la faune et des parcs du Québec. Direction du développement de la faune. Québec* (p. 92).
- Dokter, A. M., Farnsworth, A., Fink, D., Ruiz-Gutierrez, V., Hochachka, W. M., La Sorte, F. A., Robinson, O. J., Rosenberg, K. V., & Kelling, S. (2018). Seasonal abundance and survival of North America's migratory avifauna determined by weather radar. *Nature Ecology & Evolution*, 2, 1603–1609.
- Elias, S. P., Witham, J. W., & Hunter, M. L., Jr. (2006). A cyclic red-backed vole (*Clethrionomys gapperi*) population and seedfall over 22 years in Maine. *Journal of Mammalogy*, 87(3), 440–445.
- Elkins, N. (1979). Nearctic landbirds in Britain and Ireland: A meteorological analysis. *British Birds*, 72(9), 417–433.
- Farnsworth, A., La Sorte, F., & Iliff, M. J. (2015). Warmer summers and drier winters correlate with more winter vagrant Purple Gallinules (*Porphyrio martinicus*) in the North Atlantic Region. *The Wilson Journal of Ornithology*, 127(4), 582–592.
- Fauteux, D., Cheveau, M., Imbeau, L., & Drapeau, P. (2015). Cyclic dynamics of a boreal southern red-backed vole population in northwestern Quebec. *Journal of Mammalogy*, 96(3), 573–578.
- Fox, T. A. D., Christensen, T. K., Bearhop, S., & Newton, J. (2007). Using stable isotope analysis of multiple feather tracts to identify moulting provenance of vagrant birds: A case study of the Baikal Teal *Anas formosa* in Denmark. *Ibis*, 149, 622–625.
- Gilroy, J. J., & Lees, A. C. (2003). Vagrancy theories: Are autumn vagrants really reverse migrants? *British Birds*, 96, 427–438.
- Grinnell, J. (1922). The role of the "accidental". *The Auk*, 39(3), 373–380.
- Hobson, K. A., Bowen, G. J., Wassenaar, L. I., Ferrand, Y., & Lormee, H. (2004). Using stable hydrogen and oxygen isotope measurements of feathers to infer geographical origins of migrating European birds. *Oecologia*, 141, 477–488.
- Jiguet, F., Doxa, A., & Robert, A. (2008). The origin of out-of-range pelicans in Europe: Wild bird dispersal or zoo escapes? *Ibis*, 150, 606–618.
- Lees, A. C., & Gilroy, J. J. (2009). Vagrancy mechanisms in passerines and near-passerines. In R. Slack (Ed.), *Where and When: An analysis of status and distribution in Britain and Ireland. Volume 1: Sandgrouse to New World orioles*. Rare Bird Books.
- Liebl, A. L., & Martin, L. B. (2012). Exploratory behaviour and stressor hyper-responsiveness facilitate range expansion of an introduced songbird. *Proceedings of The Royal Society B*, 279(1746), 4375–4381.
- Liebl, A. L., & Martin, L. B. (2014). Living on the edge: Range edge birds consume novel foods sooner than established ones. *Behavioral Ecology*, 25(5), 1089–1096.

- McLaren, I. A. (1981). The incidence of vagrant landbirds on Nova Scotian islands. *The Auk*, 98(2), 243–257.
- McLaren, I. A., Lees, A. C., Field, C., & Collins, K. J. (2006). Origins and characteristics of Nearctic landbirds in Britain and Ireland in autumn: A statistical analysis. *Ibis*, 148(4), 1–20.
- Mouritsen, H., & Larsen, O. N. (2001). Migrating songbirds tested in computer-controlled Emlen funnels use stellar cues for a time-independent compass. *The Journal of Experimental Biology*, 204, 3855–3865.
- Muheim, R., Bäckman, J., & Åkesson, S. (2002). Magnetic compass orientation in European robins is dependent on both wavelength and intensity of light. *The Journal of Experimental Biology*, 205, 3845–3856.
- Newton, I. (2006). Advances in the study of irruptive migration. *Ardea*, 94(3), 433–460.
- Pfeifer, R., Stadler, J., & Brandl, R. (2007). Birds from the Far East in Central Europe: A test of the reverse migration hypothesis. *Journal of Ornithology*, 148, 379–385.
- Phillips, B. L., Brown, G. P., & Shine, R. (2010). Evolutionarily accelerated invasions: The rate of dispersal evolves upwards during the range advance of cane toads. *Journal of Evolutionary Biology*, 23(12), 2595–2601.
- Phillips, B. L., Brown, G. P., Travis, J. M., & Shine, R. (2008). Reid's paradox revisited: The evolution of dispersal kernels during range expansion. *The American Naturalist*, 172, 34–48.
- Rabøl, J. (1969). Reversed migration as a cause of westward vagrancy by four *Phylloscopus* warblers. *British Birds*, 62(3), 89–92.
- Ralph, C. J. (1971). An age differential of migrants in coastal California. *The Condor*, 73(2), 243–246.
- Ralph, C. J. (1978). Disorientation and possible fate of young passerine coastal migrants. *Bird-banding*, 49(3), 237–247.
- Ralph, C. J., & Wolfe, J. D. (2018). Factors affecting the distribution and abundance of autumn vagrant New World warblers in northwestern California and southern Oregon. *PeerJ*, 6, 5881.
- Robbins, C. S. (1980). Predictions of future Nearctic landbird vagrants to Europe. *British Birds*, 73, 448–457.
- Sandberg, R., Ottoson, U., & Pettersson, J. (1991). Magnetic orientation of migratory wheatears (*Oenanthe oenanthe*) in Sweden and Greenland. *Journal of Experimental Biology*, 155, 51–64.
- Thorup, K. (1998). Vagrancy of yellow-browed warbler *Phylloscopus inornatus* and pallas's warbler *Ph. proregulus* in north-west Europe: misorientation on great circles? *Ringing and Migration*, 19(1), 7–12.

- Thorup, K. (2004). Reverse migration as a cause of vagrancy. *Bird Study*, 51(3), 228–238.
- Thorup, K., Ortvad, T. E., Holland, R. A., Rabøl, J., Kristensen, M. W., & Wikelski, M. (2012). Orientation of vagrant birds on the Faroe Islands in the Atlantic Ocean. *Journal of Ornithology*, 153(4), 1261–1265.
- Thorup, K., Ortvad, T. E., Rabøl, J., Holland, R. A., Tøttrup, A. P., & Wikelski, M. (2011). Juvenile songbirds compensate for displacement to oceanic islands during autumn migration. *PLoS One*, 6(3), 17903.
- Toews, D. P. L., Delmore, K. E., Osmond, M. M., Taylor, P. D., & Irwin, D. E. (2017). Migratory orientation in a narrow avian hybrid zone. *PeerJ*, 5, 3201.
- Van Impe, J., & Derasse, S. (1994). De recente toename van Bladkoninkje *Phylloscopus inornatus* en Pallas' Boszanger *P. proregulus* in Europa: zijn dwaalgasten werkelijk dwalende vogels. *Oriolus*, 60, 3–17.
- Veit, R. R. (1989). Vagrant birds: Passive or active dispersal? *Bird Observer*, 17(1), 25–29.
- Veit, R. R. (1990). Do vagrant birds in Massachusetts reflect population growth and dispersal rather than weather patterns? *Bird Observer*, 18(2), 86–91.
- Veit, R. R. (1997). Long-distance dispersal and population growth of the Yellow-headed Blackbird *Xanthocephalus xanthocephalus*. *Ardea*, 85(1), 135–143.
- Veit, R. R. (2000). Vagrants as the expanding fringe of a growing population. *The Auk*, 117(1), 242–246.
- Veit, R. R. (2008). Why expect clusters of vagrants? *Bird Observer*, 36(4), 213–217.
- Veit, R. R., & Lewis, M. A. (1996). Dispersal, population growth, and the Allee effect: Dynamics of the house finch invasion of eastern North America. *The American Naturalist*, 148(2), 255–274.
- Williamson, K. (1959). The September drift-movements of 1956 and 1958. *British Birds*, 52, 334–377.
- Williamson, K. (1961). The concept of 'cyclonic approach'. *Bird Migration*, 1, 235–240.
- Williamson, K. (1969). Weather systems and bird movements. *Quarterly Journal of the Royal Meteorological Society*, 95(404), 414–423.
- Williamson, K. (1975). Birds and climatic change. *Bird Study*, 22(3), 143–164.
- Zawadzki, L. C., Veit, R. R., & Manne, L. L. (2019). The influence of population growth and wind on vagrancy in a North American passerine. *Ardea*, 107(2), 131–147.