

Modulations in movement by animals



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I dedicate this thesis to my family
For all that they do - my thanks could never be enough

Abstract

Movement is a fundamental aspect of life, which is intrinsically linked to almost every ecological and evolutionary process. Thus, a large fraction of an individual's energy budget is invested in movement. Managing energy expenditure in relation to energy acquisition is critical for survival and is a primary focus for natural selection. Therefore, investigating how, when and why animals modulate their movement is crucial to understand behavioural ecology and, ultimately, the driving forces shaping evolution. The aim of my DPhil is to investigate how animals modulate their movement in response to their navigational capacity, the external presence of conspecifics and their internal reproductive state using two model species: the homing pigeon (*Columba livia*) and the African savannah elephant (*Loxodonta africana*). In Chapter 2, I report that homing pigeons modulate their wingbeat characteristics as a function of navigational knowledge, which suggests, for the first time, that navigation may have physical (biomechanical) manifestations. In Chapter 3, I show that pigeons increase their wingbeat frequency by *c.*18% when flying in pairs relative to flying solo. My results demonstrate that there is a substantial cost to flying together, and that the ultimate drivers of flocking, including predator protection and navigational knowledge, must outweigh these proximate costs. By contrast, in Chapter 4 I reveal that gestation, parturition and the presence of a neonatal calf has little impact on the movements of multiparous elephants, which could suggest that elephants' unusually long gestation period evolved to facilitate an advanced stage of physical development. In my final data chapter, I show that reproductively active male elephants significantly increase their speed with age, suggesting that elephants increase energetic investments into reproduction as their probability of reproductive success increases. Overall, the results of my thesis provide key new insights into proximate and ultimate causes of movement and its modulation in animals.

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Author Contributions

Regarding the thesis of Lucy Alethea Taylor, submitted for the degree of Doctor of Philosophy, Hilary Term 2018, entitled “Modulations in movement by animals”. The author contributions towards the data chapters are as follows:

Chapter 2. Homing pigeons (*Columba livia*) modulate wing-beat characteristics as a function of route familiarity

This chapter is presented as a published manuscript. The experiment was designed between myself, Dora Biro and Steve Portugal. I collected, formatted and analysed the data and wrote the published manuscript, which was edited and modified by my supervisors Steve Portugal and Dora Biro.

Chapter 3. Birds invest wingbeats to reap the ultimate benefits of flocking

This chapter is presented as a manuscript in submission. The experiment was designed between myself, Dora Biro and Steve Portugal. I collected and formatted all of the data. I conducted the analysis in collaboration with Ben Lambert who wrote the Bayesian code to specification. I wrote the manuscript, which was edited and modified in collaboration with co-authors Dora Biro, Ben Lambert, Graham Taylor and Steve Portugal.

Chapter 4. Movement behaviour atfer birth demonstrates precocial abilities of African elephant (*Loxodonta africana*) calves

This chapter is presented in the format of a traditional thesis chapter and therefore contains more information than a chapter formatted for publication and has received minimal editing. The data was collected by Save the Elephants. I conceived the project and formatted the data. I conducted the analysis in collaboration with Ben Lambert who wrote the Bayesian three-state hidden Markov model code to specification. I wrote the chapter. I was advised by George Wittemyer, Ben Lambert, Iain Douglas-Hamilton and Fritz Vollrath.

Chapter 5. Movement-related reproductive tactics alter with age in male African savannah elephants (*Loxodonta africana*)

This chapter is presented in the format of a traditional thesis chapter and therefore contains more information than a chapter formatted for publication and has received minimal editing. The data was collected by Save the Elephants. I conceived the project, formatted the data, analysed the data and wrote the chapter. I was advised by Fritz Vollrath, Ben Lambert, Daniel Lunn, Iain Douglas-Hamilton and George Wittemyer.

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Introduction

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1.1 Movement in animals

Movement is a fundamental aspect of life, which is intrinsically linked to almost every ecological and evolutionary process, from the acquisition of food to reproduction and the avoidance of predators. Moving animals disperse seeds, spread disease, alter the structure and dynamics of populations, communities and ecosystems, and determine many other vital ecological processes (Baker, 1978; Nathan *et al.*, 2008; Côrtes & Uriarte, 2013; Dingle, 2014; Kays *et al.*, 2015). Movement occurs across every spatial and temporal scale from the smallest known Myxozoa to the blue whale (*Balaenoptera musculus*) (Biewener & Patek, 2018). Most animals

actively move from one spatial location to another, and even the comparatively few animal species that are sessile, such as corals and some molluscs, still move parts of their body and utilise external movement for fundamental processes, such as feeding and reproduction (Sebens & Johnson, 1991; Nathan *et al.*, 2008). Studying animal movement can thus provide insights into everything from individual life history to evolution and biodiversity.

The fascination with, and study of, animal movement can be traced back over 3,000 years. Ancient writers including Homer, Hesiod, Jeremiah, Herodotus, Aristotle, Pliny the Elder and others have all referred to the seasonal disappearance and reappearance of birds (Lincoln, 1950; Nussbaum, 1985; Nathan, 2008). Furthermore, Aristotle (384-322 BC) wrote in *De Motu Animalium* (Movement of Animals):

“... now we must consider in general the common reason for moving with any movement whatever (for some animals move by flying, some by swimming, some by stepping, some in other comparable ways)” (Aristotle, *De Motu Animalium*; translated by Nussbaum, 1985).

Despite the long history and importance of movement in determining ecological and evolutionary processes, the study of animal movement has generally fallen towards the margins of ecological research due to the difficulty of gathering detailed information on the movements of both individuals and groups (Nathan, 2008; Nathan *et al.*, 2008; Kays *et al.*, 2015; Westley *et al.*, 2018). Recent advances in tracking technology have removed many of these constraints by enabling the remote quantitative study of movement, which has led to an exponential growth of movement ecology research (Nathan, 2008; Nathan & Giuggioli, 2013; Kays *et al.*, 2015; Westley *et al.*, 2018). In order to facilitate the advancement of such research, Nathan *et al.* (2008) proposed a conceptual framework for movement ecology, which depicts the four basic mechanistic components of organismal movement: the individuals' internal state, capacity for motion, capacity for navigation, and external factors. Understanding how these four factors interact to produce the movement path of an individual can help identify both the ecological and evolutionary causes and consequences of movement (Nathan *et al.*, 2008; Westley *et al.*, 2018). My thesis

aims to contribute to the growing field of movement ecology by investigating how, when and why animals modulate their movements in response to their navigational capacity, external conspecifics and internal reproductive state using two very different model species: the homing pigeon (*Columba livia*) and the African savannah elephant (*Loxodonta Africana*).

1.2 Mechanistic components of animal movement

The internal state of an individual includes both physiological and, where appropriate, psychological drivers, such as energy acquisition, reproduction and safety (Nathan *et al.*, 2008). Thus, the internal state of an individual is multidimensional, as many goals can be pursued simultaneously, each of which may be operating on different temporal scales and each of which may vary in importance with time (Getz & Saltz, 2008; Nathan *et al.*, 2008). In some instances, internal states may conflict: for example, energy acquisition versus safety from predators. Dugongs (*Dugong dugong*), for example, compromise on foraging performance by foraging at a lower depth when tiger sharks (*Galeocerdo cuvier*) are common, thereby prioritising the ultimate goal of safety over the proximate cost of foraging in a sub-optimal habitat (Wirsing *et al.*, 2007). Quantifying the internal state of an animal is problematic and is either inaccessible or can only be indirectly inferred (Getz & Saltz, 2008), such as analysing the predator and forage abundance, and analysing the behaviour of the target species, as in the dugong example.

The motion capacity of an individual accounts for the ability of an organism to move from one spatial location to another by either active means or passive means (Nathan *et al.*, 2008). Active locomotion includes all self-propelled movements, such as walking, swimming and active flight. Passive mobility is externally vectored transport, such as ballooning in spiders and floating and sailing in the Portuguese man o' war (*Physalia physalis*) (Lauder, 2010; Biewener & Patek, 2018). Some forms of locomotion, such as gliding in birds, are initially self-propelled but then largely depend on passive mobility (Biewener & Patek, 2018). The motion capacity of an individual is largely determined by morphophysiology and comprises the

biomechanical component of motion (Nathan *et al.*, 2008). Most species engaging in active locomotion are capable of altering their speed to some degree, and some species are capable of engaging in multiple modes of locomotion, such as diving birds which can walk, fly and swim (Nathan *et al.*, 2008; Biewener & Patek, 2018).

The navigational capacity of an individual includes the ability to obtain, process and use spatial and/or temporal information in order to orientate and select where and/or when to move (Nathan *et al.*, 2008). Navigation tends to be utilised towards goal-oriented targets, such as navigating to a specific food resource. The information used in navigation covers both direct and indirect cues, memory and genetics (Nathan *et al.*, 2008). For example, homing pigeons navigate over unfamiliar terrain by using a combination of olfactory cues for position fixing (Gagliardo, 2013), and a solar and magnetic compass for directional guidance (Kramer, 1957; Schmidt-Koenig, 1990; Wiltschko & Wiltschko, 2005). In addition, over familiar terrain, pigeons are also able to utilise their memory of visual landmarks (Meade *et al.*, 2005).

Finally, external factors include all of the external biotic and abiotic factors which may alter the movement of the individual, such as the environment, conspecifics and predators (Nathan *et al.*, 2008). For example, the timing of migration in many migratory bird species is related to atmospheric conditions, such as the ambient temperature, which has a function in minimising thermoregulation costs (Wikelski *et al.*, 2003), and wind direction, which reduces the cost of migration itself (Alerstam, 1979; Åkesson & Hedenström, 2000; Liechti, 2006).

The combination of internal and external factors and the navigation and motion capacity determines the movement path of an individual. For example, the movement of the dugong in Wirsing *et al.* (2007) is not only affected by the internal drives to acquire food and avoid predators, but also by the external presence of predators and abundance of food, the navigational knowledge of the relative abundance of food and predators in each of the locations, and the motion capacity to be able to forage at greater depths to avoid predators. The degree to which one or more of these factors influences an individual's movement trajectory is key to understanding many life processes from proximate to ultimate causes of movement.

The challenge facing researchers is disentangling how each of these factors contribute towards the movement path of an individual. One of the key limiting factors on movement is energy.

1.3 Energy and movement

Locomotion is energetically expensive and can represent a large fraction of the total energy expended by an individual (Schmidt-Nielsen, 1972). Managing the rate at which an organism expends energy in relation to acquisition via feeding is critical for survival and is, therefore, a primary focus for natural selection (Brown *et al.*, 2004). To maximise fitness, an individual should make a movement decision which maximises on the currency (energy). Analysing the movement of an individual from the perspective of energetics can, therefore, provide insights into the factors determining movement. For instance, an animal moving between food resource A and food resource B should move in a straight line from A to B to minimise the cost of transport. Identifying the optimal decision rule is one of the primary goals of optimal foraging theory (Pyke, 1984). Quantifying how an individual actually allocates energy to movement, relative to what theory or measurement suggests is optimal, such as whether the individual moves in a straight line from A to B or whether they take an alternate route, can thus provide key insights into the underlying proximate and ultimate (evolutionary) causes of animal movement.

1.4 Navigational capacity

The navigational capacity of an individual is often considered as the information required to get from A to B. For example, an internal drive for food at point A will result in navigation to an external food resource at point B. Knowledge itself may be key in instigating a particular movement path. In African savannah elephants, older female matriarchs are able to utilise knowledge of distant water holes to lead herds to water during droughts (Foley *et al.*, 2008). Scrub jays (*Aphelocoma coerulescens*) have episodic-like memory for specific caching events and their locations, allowing

them to recover perishable wax-moth larvae or non-perishable peanuts depending on the time lapse between caching and retrieval (Clayton & Dickinson, 1998). In both of these cases, the individuals' knowledge determines which external resource to utilise and the path to satisfy the internal drive. Moreover, the navigational knowledge of the route may influence the way in which the individual moves, such as avoiding obstacles or increasing speed in areas perceived to be dangerous. What is not clear is whether the navigational process itself affects the movement path of an individual, such as the attention to navigational cues.

In terms of my own navigation, I will move more slowly when I am navigating in an unfamiliar area as I will spend longer looking at cues, such as visual landmarks, to ensure I am still moving in the correct direction. In bumblebees (*Bombus terrestris*), some bees consistently make rapid choices with low precision, whereas other bees are slower but highly accurate (Chittka *et al.*, 2003). The trade-off between speed and accuracy is well known in animal decision-making (Franks *et al.*, 2003; Burns & Dyer, 2008; Chittka *et al.*, 2009). Thus, it is conceivable that animals modulate their movements depending on their navigational familiarity of their route or environment, such as moving at a slower rate in order to increase accuracy.

1.5 Cooperation with conspecifics

In social living species, energy expenditure, and hence individual fitness, can be dependent on the presence and the behaviour of (external) conspecifics. If the benefits of cooperating with conspecifics, such as information sharing and predator protection, outweigh the costs, such as increased competition for food resources, then an individual will have higher fitness than an individual where the costs outweigh the benefits (Sumpter, 2010). For example, schooling fish benefit from increased decision-making efficiency which reduces predation risk (Ward *et al.*, 2011), ant colonies utilise pheromone trails to allocate their workforce according to the resources available which increases foraging efficiency (Sumpter & Beekman, 2003), and ducklings are able to conserve energy by swimming in a line (Fish,

1995). Despite these benefits, little is known about the energetic consequences of collective behaviour to the individual.

One of the most commonly cited reasons for travelling as a group is to reduce energy expenditure and, in the case of swimming or flying, enhance hydro- or aero-dynamic efficiency (Bill & Herrnkind, 1976; Weimerskirch *et al.*, 2001; Liao *et al.*, 2003; Portugal *et al.*, 2014; Voelkl *et al.*, 2015). Indeed, birds flying in ‘V’ formations are able to save significant amounts of energy by positioning themselves in aerodynamically optimal positions (Weimerskirch *et al.*, 2001; Portugal *et al.*, 2014). By contrast, Usherwood *et al.* (2011) found that pigeons flying in close cluster flocks increased their wingbeat frequency, and hence energetic cost, when flying in a dense cluster formation relative to a less dense formation. However, while it is apparent that flock density affects the cost incurred by individuals during cluster flocking, whether flying in a cluster flock comes at a cost relative to the alternative of flying solo is not known. Furthermore, within a group, individuals may differ in many ways, including gender, size, age and reproductive and physiological state, which means optimal movement patterns may differ between individuals.

In birds, aerodynamic theory (flight power curves) predicts that larger birds will have a higher optimal flight speed than smaller birds (Pennycuik, 1975; Ellington, 1991). This is evident both between species, and within species where individuals have a wide range of body masses (Andersson & Norberg, 1981). As a result, birds flying in flocks containing a range of body masses may not be flying at their preferred optimal speed, which may become evident when flying solo and not part of the flock. Pettit *et al.* (2013) tested the speed of individual homing pigeons during solo flights, and found that, when these birds were flown together as a group, the fastest bird was typically the bird at the front of the flock in group flight, dominating the choice of direction. If the fastest bird is leading and dominating the choice of direction, either one or more birds may have to alter their wingbeat patterns in order to stay together. A compromise of optimal movement patterns would represent an additional ‘hidden’ cost of group travel.

1.6 Conflict with conspecifics

In contrast to intraspecific cooperation, conspecifics may also alter the movement via intraspecific competition. Male guppies (*Poecilia reticulata*) adjust their aggressive and courtship behaviours to the perceived male-male competition (Price & Rodd, 2006). Home range size in female striped mice (*Rhabdomys pumilio*) is determined by intraspecific competition and food availability (Schradin *et al.*, 2010). Male mate-searching behaviour in stoats (*Mustela erminea*) is related to social status, with dominant males increasing their movement patterns (proximate cost) and thus increasing the probability of finding receptive females (ultimate gain; Sandell, 1986). In the latter example, the strategy adopted by stoats altered with social status, with the proximate costs of movement outweighed by reproductive success in dominant males, whereas the subordinate males minimised their movement costs presumably due to a lower chance of reproductive success (Sandell, 1986). Measuring how an individual modulates their movement in relation to intraspecific cooperation and/or competition, and the conditions under which they may alter their movement, can thus reveal key insights into both the internal and external factors driving movement, and their proximate and ultimate causes (Westley *et al.*, 2018).

1.7 Measuring movement

Historically, animal movement in situ has been studied by visual observations. A fundamental limitation of this technique is that the animal must be within sight, sound or leave clues, such as spoor, in order to establish when, where and how an individual is moving (Cagnacci *et al.*, 2010; Kays *et al.*, 2015). Thus, there are many species, such as migrating birds, for which observations alone may not be sufficient to identify the movements of an individual. Incomplete information may limit our understanding of the behavioural ecology of a species and can, in some cases, lead to incorrect hypotheses. For example, Charles Morton (1627-1698) hypothesised in his text *Copendium Physicae* that birds departing England with the seasons migrated to the moon (Harrison, 1954). His arguments were based both on contemporary

science and upon Scripture as, at the time, no one knew the whereabouts of migrant birds during the winter months; therefore, he concluded that they reside off the earth (Harrison, 1954). Whilst this may be an extreme example, particularly as visual observations continue to play a pivotal role in both the conceptualisation and study of animal movement, technological advancements, including radio tracking (Cochran & Lord, 1963), radar (Emlen & Demong, 1978), light-sensing geolocators (DeLong *et al.*, 1992; Wilson *et al.*, 1992) and, more recently, satellite tracking via the Argos system or Global Positioning System (GPS) (Cagnacci *et al.*, 2010; Kays *et al.*, 2015), which can be used to locate or record the physical location of an individual, have revolutionised the field of movement ecology (Kays *et al.*, 2015).

GPS is a satellite-based system owned by the United States government, which provides location and time information globally to any GPS receiver where there is an unobstructed line of sight to three satellites for a two-dimensional fix and $\geq$ four for a three-dimensional fix. In 2000, the U.S. Department of Defence stopped degrading the accuracy of civilian receivers, which has resulted in an explosion of animal movement research using GPS trackers (Kays *et al.*, 2015). GPS enables scientists to record the movements of individuals through a set of discrete spatial coordinates ordered in time. How well the discrete GPS points, or movement track, reflect the actual movements of the individual depends on the sampling frequency and accuracy of the device (Getz & Saltz, 2008). Initially, only large species, such as elephants were tracked, due to the size of devices, but technological advancements have led to the increasing miniaturisation of devices (Steiner *et al.*, 2000; Kays *et al.*, 2015). Furthermore, the temporal resolution of GPS tracking devices has increased meaning that it is now possible to track small, fast-moving species, such as homing pigeons, in high resolution (Kays *et al.*, 2015).

The precise tracking frequency used should take the species' biology and scientific question into account and must be offset by factors such as device size and battery life. For example, a small device tracking at a relatively high tracking frequency, such as 5 Hz (five positions per second), is required to study the intricate leader-follower relationships among fast moving homing pigeons (Nagy *et al.*, 2010), but, currently,

such a device would not be able to transmit the data, meaning the individual would have to be recaptured, and the device would have a battery life of less than a day. Such a device would therefore be unsuitable for long-term deployment on wild animals, for which data transmission and a lower sampling frequency to preserve battery life may be more appropriate. Nevertheless, continuing technological advancements are leading to the development of new and more sophisticated devices, which means that the compromise between size, battery life and sampling resolution is continuing to decrease.

In addition to the advances made identifying the location of an individual, technological advances have led to the introduction of devices capable of identifying other components of movement, such as the movement of body parts which can be used to identify the behaviour of the individual (Wilson *et al.*, 2006). Tri-axial accelerometers measure the acceleration, which is the rate of change of velocity, in three orthogonal directions (Brown *et al.*, 2013). Accelerometers measure the acceleration experienced by an individual at the point of attachment, which can be used to identify the movements and behaviour of an individual, and to estimate energy expenditure (Wilson *et al.*, 2006; Shepard *et al.*, 2010; Gleiss *et al.*, 2011; Halsey *et al.*, 2011; Brown *et al.*, 2013). When placed on a flat surface, the accelerometer will measure the acceleration due to the Earth's gravity straight upwards, which is equal to 1 *g*-force (gravitational force, or 9.80665 m s^{-1}). Accelerometers were pioneered by Cavagna *et al.* (1963) for studies on energy expenditure in humans, but it was not until Wilson *et al.* (2006) that accelerometers were first utilised in this context for animal studies (Halsey *et al.*, 2011). Accelerometers have been used in a variety of different species including great cormorants (*Phalacrocorax atriceps*; Wilson *et al.*, 2006), Steller sea lions (*Eumetopias jubatus*; Fahlman *et al.*, 2008), hammerhead sharks (*Sphyrna lewini*; Gleiss *et al.*, 2010), Magellanic penguins (*Spheniscus magellanicus*; Wilson *et al.*, 2010), green turtles (*Chelonia mydas*; Enstipp *et al.*, 2011), homing pigeons (Usherwood *et al.*, 2011), African savannah elephants (Soltis *et al.*, 2012),

American lobsters (*Homarus americanus*; Lyons *et al.*, 2013) and Verreaux's Sifaka (*Propithecus verreauxi*; Wunderlich *et al.*, 2014).

The limitation of attaching biologgers, such as GPS and accelerometers, to an individual to measure movement is that it will also increase the energetic cost to the animal, both through carrying additional mass and from the aerodynamic drag of a device, which may alter movement patterns (Barron *et al.*, 2010; Venabelee *et al.*, 2015). A typical rule of thumb that has developed in the literature is that biologgers must weigh less than 5% of an animal's body mass (Brander & Cochran, 1969; Aldridge & Brigham, 1988; Barron *et al.*, 2010). However, there appears to be no clear rationale or empirical evidence for the original selection of the 5% limit (Gessaman & Nagy, 1988; Barron *et al.*, 2010). Bodey *et al.* (2018) completed a meta-analysis of the effects of biologgers on birds and found that biologgers had a small but significantly negative impact on survival, reproduction and parental care. Furthermore, Chivers *et al.* (2016) found that Black-legged kittiwakes (*Rissa tridactyla*) reduced their total foraging time by 30% over three days when carrying both a GPS and accelerometer (5.2% body mass) relative to carrying just an accelerometer (1% body mass), which suggests that biologgers may alter behaviour and, more than likely, the energetic costs of movement.

Despite the disadvantage of carrying loggers, the information acquired from biologgers, such as GPS and accelerometers, can result in extremely detailed information on the movement of animals, which, in many cases, would not be possible without such a device (Barron *et al.*, 2010; Bodey *et al.*, 2018). Thus, the information ascertained from attaching a biollogger may outweigh the costs. The information that can be gained from the biollogger should be weighed against the negative effects to the individual and the potential impact on the reliability of the results (Barron *et al.*, 2010; Bodey *et al.*, 2018). Given the negative effects of biologgers, the deployment of biologgers should be carefully planned, which should include taking the species' biology, individual animal health and welfare, size of the biollogger, duration of deployment and type of attachment into account (Barron *et al.*, 2010; Bodey *et al.*, 2018).

1.8 Model species

I studied two very different model species: the homing pigeon (*Columba livia*) and the African savannah elephant (*Loxodonta africana*). Despite vast differences in size, morphology and even modes of locomotion, homing pigeons and African elephants are two ideal model species for studies on modulations in movement.

Homing pigeons are an ideal model species for studies of navigation and collective behaviour because of their innate homing motivation and tendency to form idiosyncratic homing routes, which means factors such as navigational experience, can be identified and manipulated as the birds orientate to a known location (home) (Biro *et al.*, 2006a; Flack *et al.*, 2012). As the navigational knowledge of an individual can be manipulated, homing pigeons can be used to study how they alter their movements specifically in relation to familiarity with a route. Studying navigational familiarity in wild species is difficult, as the navigational knowledge of an individual may not be known, particularly in social living species where individuals may have different levels of knowledge. Furthermore, pigeons are highly gregarious, which means flock composition can be experimentally manipulated in order to study the effects of flying solo relative to flying in groups. Forward flapping flight is one of the most energetically demanding forms of sustained locomotion vertebrates perform (Schmidt-Nielsen, 1972). Thus, pigeons are an ideal species to study modulations in movement within an energetic framework.

African savannah elephant societies represent an interesting example of a ‘fission-fusion’ system whereby groups merge (fusion) or split (fission) depending on available resources and, in the case of males, reproductive state, enabling individuals to adjust dynamically to varying costs and benefits of group living (Wittemyer *et al.*, 2005; Archie *et al.*, 2006; Couzin, 2006; Goldenberg *et al.*, 2014). Although elephant societies are known to split in times of need, it is unknown whether herds will adapt their movements in order to maintain group structure with specific individuals, such as the young or injured. Such behaviour forces all members of the group to pay the costs of benefitting the needy. Furthermore, elephants represent a complex energetic enigma. As the largest species of land animal, African savannah elephants,

theoretically, experience the lowest energetic cost to move one kg body mass one metre of any land species (Taylor *et al.*, 1982; Langman *et al.*, 1995). However, the cost of moving a 4,000 kg elephant upwards one metre is $\sim 2,500\%$ the cost of level walking. Combined with this, elephants are herbivores which combine a relatively high intake of food with a short digestive retention time, which means that they require $\sim 6\%$ body mass in wet food intake per day, which for a 6,000 kg bull elephant equates to 600 kg of forage (Owen-Smith, 1988; Clauss *et al.*, 2007). Thus, the energetic cost of locomotion is an important factor for both species. Analysing how individuals alter their movement in relation to navigational knowledge, external conspecifics and internal reproductive state could provide key insights into the proximate and ultimate causes of animal movement.

1.9 Thesis structure

The thesis is structured in four self-contained chapters followed by a general discussion. The supplementary material for each chapter can be found in the appendices.

In Chapter 2, I investigated whether flight characteristics change with a birds' familiarity with a navigational task by examining changes in wingbeat characteristics and airspeed of homing pigeons as they learned a homing task. Twenty-one pigeons were released 20 times individually equipped with 5 Hz GPS trackers and 200 Hz tri-axial accelerometers.

Chapter 3 compared the flight characteristics, in particular wingbeat frequency, of flying solo compared to flying in pairs. Twenty pigeons were released on a familiar route six times (i) individually (solo), (ii) with a bird of a similar size (pair), (iii) with a bird of a different size (pair) and finally (iv) individually six times (solo). Aerodynamic theory (flight power curves) predict that bigger birds will have an optimal flight speed that is higher than small birds, which means that, for birds of different sizes, either one or both birds may have to alter their wingbeat frequency to stay together.

Chapter 4 investigated whether gestation, parturition and lactation and the presence of a neonatal calf in African savannah elephants resulted in a change in

movement patterns. African savannah elephants have the longest gestation period of any mammal. Twenty-two months of gestation is followed by a minimum of 24 months of complete dependency on the mother, and around a further eight years where the mother plays a central role. Despite the high levels of investment in calves, little is known about how gestation, parturition and the presence of a neonatal calf affects movements in African elephants. I examined the relationship between reproductive state and movement characterized using GPS tracking data collected during 18 births from multiparous females and three births from primiparous females.

Chapter 5 investigated whether male African elephants change their movement patterns according to their reproductive state and age. I analysed the GPS tracking data of 24 male elephants on days when the musth state of the individual was known to determine how the movements of elephants change with state and age. In particular, I aimed to (1) quantify the extent to which bull elephants alter their movement patterns between musth and non-musth periods, (2) investigate whether movement patterns alter in relation to age, and (3) determine if musth periods can be detected directly from GPS tracking data.

In Chapter 6, the general discussion, I synthesise the findings of my thesis, discuss the limitations and implications of the research and provide recommendations for future research. Overall, my thesis provides novel insights into the modulations in movements animals make, allowing me to identify some of the proximate and ultimate causes of movement.

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characteristics as a function of route familiarity.
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Published version can be found in Appendix A.
Supplementary material can be found in Appendix
B.

2

Homing pigeons (*Columba livia*) modulate wingbeat characteristics as a function of route familiarity

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2.1 Abstract

Mechanisms of avian navigation have received considerable attention, but whether different navigational strategies are accompanied by different flight characteristics is unknown. Managing energy expenditure is critical for survival, therefore understanding how flight characteristics, and hence energy allocation, potentially change

with birds' familiarity with a navigational task could provide key insights into the costs of orientation. We addressed this question by examining changes in the wingbeat characteristics and airspeed of homing pigeons (*Columba livia*) as they learned a homing task. Twenty-one pigeons were released 20 times individually either 3.85 km or 7.06 km from home. Birds were equipped with 5 Hz GPS trackers and 200 Hz tri-axial accelerometers. We found that, as the birds' route efficiency increased during the first six releases, their median peak-to-peak dorsal body (DB) acceleration and median DB amplitude also increased. This, in turn, led to higher airspeeds, suggesting that birds fly slower when traversing unfamiliar terrain. By contrast, after route efficiency stabilised, birds exhibited increasing wingbeat frequencies, which did not result in further increases in speed. Overall, higher wind support was also associated with lower wingbeat frequencies and increased DB amplitude. Our study suggests that the cost of early flights from an unfamiliar location may be higher than subsequent flights because of both inefficient routes (increased distance) and lower airspeeds (increased time). Furthermore, the results indicate, for the first time, that birds modulate their wingbeat characteristics as a function of navigational knowledge, and suggest that flight characteristics may be used as "signatures" of birds' route familiarity.

2.2 Introduction

Forward flapping flight is the most energetically demanding form of vertebrate locomotion (Schmidt-Nielsen, 1972; Norberg, 1990). To reduce the energetic cost of flight, birds utilise behavioural mechanisms, such as intermittent flight patterns (Rayner, 1985; Tobalske & Dial, 1996), formation flight (Weimerskirch *et al.*, 2001), and modulation of their wingbeat frequency and amplitude (Greenewalt, 1962; Lilienthal, 2001). Whilst energy saving mechanisms have been identified, little is known about the extent to which birds employ these mechanisms in relation to navigation, for example, as a function of familiarity with a given landscape. Until now, avian navigation research has primarily focused on the sensory and cognitive underpinnings of orientation (Wiltschko & Wiltschko, 2009) and the total cost of a

flight (Flack *et al.*, 2016). However, a bird navigating from a familiar location, such as a roost or foraging site, may utilise different flight patterns compared with when flying over less familiar terrain where the distance to be covered and the route to be taken are less well known. Energy is frequently considered the currency of life (Butler *et al.*, 2004), which means that managing energy expenditure is a key aspect of survival. Thus, energy allocation is likely to play a pivotal role in dictating the flight patterns utilised whilst navigating. Investigating whether birds modulate, for example, their wingbeat patterns in relation to their familiarity with a navigational task, could provide key insights into the cost of orientation.

Homing pigeons (*Columba livia* Gmelin 1979) are an ideal model species for studies investigating flight characteristics in relation to navigational knowledge because of their innate homing ability, amenability to experimental manipulation, and body size permitting the attachment of state-of-the-art tracking devices. For research subjects, this means we can ensure that the full navigational experience of a given individual is known and can be characterised over successive flights. Although the finer details are still debated, it is generally accepted that over unfamiliar terrain, pigeons navigate by utilising a combination of olfactory cues for position fixing (Gagliardo, 2013), and a solar and magnetic compass for directional guidance (Kramer, 1957; Schmidt-Koenig, 1990; Wiltschko & Wiltschko, 2005). In addition, over familiar terrain, pigeons are also able to utilise visual landmarks (Meade *et al.*, 2005). Meade *et al.* (2005) found that homing pigeons released repeatedly from the same site gradually developed stereotypical routes, with each individual having their own, slightly indirect, route. The results of this study and others indicate that pigeons reliably adopt such individually idiosyncratic routes as familiarity with the local landscape increases, and rely more on visual landscape features as they become more experienced (Biro *et al.*, 2004; Meade *et al.*, 2005; Guilford & Biro, 2014). Correspondingly, birds' route efficiency (the straight line distance between the start and end of the route divided by the distance travelled by the bird) increases steadily during the early stages of training and then plateaus once the birds have developed stable idiosyncratic routes (Meade *et al.*, 2005; Guilford & Biro,

2014). Recapitulating a familiar but less direct route, rather than increasing route efficiency further, suggests that there could be a higher energetic and/or cognitive cost associated with navigating in an unfamiliar landscape for homing pigeons, relative to following a familiar route. However, whether different navigational strategies during route learning are accompanied by the same or different flight characteristics (e.g. wingbeat frequencies and amplitudes) is still unknown.

Our study addresses this question by quantifying changes in the flight characteristics of homing pigeons as they learn a homing task. Recent technological advances have led to the introduction of miniature GPS devices, which provide highly accurate geographical position fixes over the full duration of a flight (Steiner *et al.*, 2000), and high-frequency tri-axial accelerometers, which can measure the acceleration of an animal in three different planes, or dimensions, of movement (Wilson *et al.*, 2006; Halsey *et al.*, 2009). In turn, the combination of GPS and accelerometers allows us to simultaneously reconstruct birds' routes, speeds, wingbeat frequencies and amplitudes of dorsal body (DB) displacement. Although the precise relationship between the DB amplitude and the amplitude of wing motions is unclear, the former can nevertheless be used as an indirect measure of the latter (Hedrick *et al.*, 2004; Usherwood *et al.*, 2011). Together, wingbeat frequency and amplitude are related to the variation in power and speed of flapping flight, and thus can be used as a proxy for energy expenditure and/or work rate. By varying wingbeat frequency and amplitude, a bird is able to adjust the costs of flight. Reducing wingbeat frequency reduces the inertial power cost of the flight (i.e. power required to move the wings), as the power requirement of horizontal steady flight is proportional to the square of wingbeat amplitude but the cube of wingbeat frequency (Greenewalt, 1962; Lilienthal, 2001). By contrast, increasing wingbeat frequency and decreasing amplitude reduces the drag of the wings and body and increases lift, thereby optimising aerodynamic efficiency (i.e., optimising the forces acting on the bird relative to the air for efficient flight parameters) (Usherwood, 2009; Usherwood *et al.*, 2011). Thus, analysing variation in wingbeat characteristics and speed in

relation to navigational knowledge could shed new light on the costs of navigation and the energetic strategies employed by birds as they learn a route to a target.

2.3 Materials and methods

2.3.1 Subjects

Twenty-one homing pigeons aged either 1 or 3 years were used. All birds had prior homing experience, but had not been released at or near the sites used in the present study. The subjects were housed with ~120 other pigeons in two neighbouring lofts at the Oxford University Field Station, Wytham, UK (51°46'58.2"N, 1°19'2.7"W). Access to water, grit and a standard pigeon feed mix were available *ad libitum* at all times in the loft. All subjects were able to perform free flights around the loft on a daily basis throughout the year. In addition, in the month immediately preceding the start of the experiment, all subjects participated in a minimum of 24 solo or flock releases from four different release sites 1-3 km from home, as basic homing training, to familiarise the birds with the catch-and-release procedures and with being flown from an unfamiliar location. The protocols outlined in this paper were approved by the Local Ethical Review Committee of the University of Oxford's Department of Zoology.

2.3.2 Experimental protocols

Two release sites, both on a bearing of 282 deg from the lofts, were selected. The "far" site (Barnard Gate; 51°47'48.1" N, 1°25'3.3"W) was 7.06 km from the lofts and the "near" site (Mill Lane, Eynsham; 51°47'24.2"N, 1°22'19.5"W) was located 3.85 km from the lofts. Subjects were randomly assigned to two groups in an even age distribution. Individuals in group 1 (10 pigeons; 5 one-year-old and 5 three-year-old birds; body mass = 471 ± 39 g mean $\pm$ s.d.) were released 20 times individually from the 'far' site, and individuals in group 2 (11 pigeons; 6 one-year-old and 5 three-year-old birds; 471 ± 20 g) were released 20 times individually from the 'near' site. Releases were conducted between May and July 2015, on days when the sun was visible and the wind speed was $< 7 \text{ m s}^{-1}$ when measured

5.5 m above the ground. Subjects participated in a maximum of two releases per day, with a minimum of three hours between each release. All birds were released individually. Initially, releases occurred at 10-minute intervals; this was later reduced to a minimum of 4 minutes if it could be visually confirmed that the previously released bird had left the vicinity of the release site. If, at any point, a bird accidentally paired up with another subject, the release was excluded for both birds (18 flights). Four additional tracks were removed from the analysis. One bird failed to return home before the GPS battery ran out on its first release from the far site, a GPS fault occurred during the fifth release and the 14th release, and the devices could not be accurately synchronised for a bird on its 10th release. In addition, four birds landed during their first release. For these landings, the entire descent, stationary and ascent sections were removed from the track data from the point of first descent to the peak of ascent.

2.3.3 Data logging

The birds were tracked using 5 Hz GPS loggers (BT-Q1300ST, Qstarz International Co., Ltd., Taipei, Taiwan; 15 g) and 200 Hz tri-axial accelerometers (AX3, Axivity, Newcastle upon Tyne, UK; ± 16 g-force; 11 g). The loggers were attached to the pigeons using Velcro strips which were glued to trimmed feathers on the back (Fig. 2.1; Biro *et al.*, 2002). In total, the loggers and fastenings weighed 27 g (less than 7 % of the subjects' mean body mass). Two weeks prior to the start of the experiment, clay weights (27 g) were attached to the birds' back via Velcro to accustom them to flying with the additional mass. These were exchanged for GPS devices and accelerometers immediately prior to each release. GPS and accelerometer data were downloaded using QTravel (Qstarz International Co., Ltd., Taipei, Taiwan; version 1.48(T)) and Open Movement (Om) GUI Application (Newcastle University; version 1.0.0.28), respectively.

The weather, including mean wind speed per minute and a running mean of the wind bearing over the previous ten minutes, was recorded using a WS2083 Professional Wireless Weather Station with USB upload (Aercus Instruments,



Figure 2.1: A homing pigeon with an Axivity AX3 accelerometer (front) and QStarz BT-Q1300ST GPS logger (case removed; back) attached to the back via Velcro strip, which was glued to trimmed feathers.

Doncaster, UK) situated 5.5 m above the pigeon lofts. Weather data was logged using Cumulus Weather Station Software (Sandaysoft, Sanday, Orkney, UK; version 1.9.4).

2.3.4 Data processing

GPS and accelerometer data were synchronised to an accuracy of ± 0.2 s (GPS frequency) using the point of take-off in both the GPS and accelerometer loggers, which were identified using the marked increases in GPS speed and dorsal acceleration peaks produced during take-off. The weather data were combined with the GPS and accelerometer data using the timestamps from the weather station and the GPS loggers. For each GPS point, the orthodromic (great-circular) distance travelled and birds' final bearing from the previous point were calculated using the haversine formula and forward azimuth, respectively. For each flight, route efficiency was calculated as the ratio between the total straight-line (great-circular) distance between release and home, divided by the sum of the direct

(great-circular) distances between each successive GPS point (straightness index; Batschelet, 1981). Wind support and crosswind were calculated using the methods described in Safi *et al.* (2013): wind support represents the length of the wind vector in the direction of the bird's flight and crosswind represents the absolute speed of the wind vector perpendicular to the bird's direction of travel (Appendix B: Fig. B.1). Airspeed, the speed of the bird relative to the wind, was then calculated using the speed derived from the GPS devices while taking into account wind support and crosswind (Safi *et al.*, 2013).

The dorsal (Z-axis) accelerometer measurements were filtered by taking a running mean over five data points (0.025 s). Static acceleration (or gravity) was removed by subtracting a running mean over 15 wingbeat cycles (> 2 s). The running mean was calculated over wingbeat cycles rather than over specific time periods, because variation in wingbeat frequencies would have meant including varying quantities of partial wingbeat cycles in a time-based running mean. The dorsal acceleration signal was then used to detect each wingbeat using the upper reversal point in acceleration (Fig. B.2; Norberg, 1990; Portugal *et al.*, 2014). The peak-to-peak DB acceleration (g) and wingbeat frequency (number of wingbeats per second; Hz) were calculated for each individual wingbeat. The amplitude of the DB displacement (mm), which is the amount the body is displaced per wingbeat, was then calculated by the double integration of dorsal accelerometer measurements (Usherwood *et al.*, 2011). After the first integration, a running mean over 15 wingbeat cycles was removed from velocity to remove drift. The data were then filtered using a fourth order high-pass Butterworth filter with a cut-off frequency of 1 Hz. The procedure was repeated after the integration for displacement but with a cut-off frequency of 2.5 Hz in the Butterworth filter. The cut-off frequencies were determined by visualising the data using fast Fourier transforms. A more conservative estimate of the amplitude of the DB displacement was also calculated by passing the raw accelerometer measurements through fourth-order Butterworth filters prior to integration instead of running means, but this led to no significant difference in the results (Fig. B.3).

In order to only compare sections of steady flight, the data were trimmed in a 1000 m radius around the release site (start point) and the pigeon lofts (end point). The shortest straight-line distance of the entire steady flight therefore measured 5.08 km for the far site and 1.85 km for the near site. In addition to comparing the entire steady flight, the data were also trimmed to remove sections with lower wingbeat frequencies (≤ 3.0 Hz) and sections of tortuous flight to remove any effect of gliding, idling or circling from the dataset. Tortuosity was calculated by taking a running mean of the change in the birds' bearing over every one second of data (5 GPS points), with changes in direction of ≥ 3.0 deg removed in order to discard circling and keep only active straight-line powered flight.

2.3.5 Data analyses

Piecewise linear mixed effects (LME) models were used to investigate the effect of repeated releases on route efficiency, median peak-to-peak DB acceleration per wingbeat (g), median DB amplitude per wingbeat (mm), median wingbeat frequency (Hz) and median airspeed (m s^{-1}). Piecewise, or segmented, regression identifies an abrupt change of the dependent variable (or breakpoint) with respect to the independent variable, which allows one to fit pre- and post-event slopes (Naumova *et al.*, 2001). We used this approach to determine whether changes in wingbeat characteristics corresponded to changes in route efficiency and to identify the trends in the data either side of this change. Breakpoints were objectively estimated using one-dimensional optimisation. Piecewise LME models were fitted using the fixed-effects of release number less than the breakpoint (breakpoint – release number), release number greater than the breakpoint (release number – breakpoint), median wind support, median crosswind and group. Individual was also added as a random slope on both release number effects.

To establish the effect of wingbeat characteristics on airspeed, two LME models were used. Firstly, with median peak-to-peak DB acceleration and median wingbeat frequency as fixed-effects, and secondly with median DB amplitude per wingbeat, which is dependent on peak-to-peak DB acceleration (force exerted on the dorsal

body) and wingbeat frequency (duration of the wingbeat), as a fixed-effect. Group was added as a fixed-effect to both models but was insignificant. Individual was added as a random-effect on the intercept. In addition, LME models were used to directly relate route efficiency with wingbeat characteristics and airspeed between releases 1 and 6 using the fixed-effects of route efficiency, median wind support, median crosswind and group, and the random-effect of individual.

Route efficiency was negatively skewed, and was therefore transformed before analysis by directly inverting values and taking the logarithm using the formula $\log_{10}(1 - x)$. From the full models, simpler models were obtained by stepwise deletion of non-significant terms. Likelihood ratio tests were used to test the statistical significance of each fixed effect in the best-fitting model. LME models were calculated using maximum likelihood and the models were checked for assumptions of linearity, normality, homoskedasticity and autocorrelation by visual inspection of plotted residuals. Model fit was assessed by calculating conditional R-squared values ($R^2_{\text{LME}(c)}$) using the methods described in Nakagawa and Schielzeth (2013).

Data processing and analysis were conducted using MATLAB (MathWorks, Natick, MA, USA; version R2015a) and the open-source software R (R Core Team, 2016; version 3.2.3) using the packages lme4 (Bates *et al.*, 2015; version 1.1-8) and MuMIn (Bartoń, 2015; version 1.15.1).

2.4 Results

Route efficiency improved as the birds became more experienced (Fig. 2.2). Over the first five releases, route efficiency increased significantly from 0.46 ± 0.27 (mean $\pm$ s.d.) for release 1 to 0.82 ± 0.18 for release 5 (piecewise linear mixed model parameter estimate = 0.287; likelihood ratio test for the model without release number: $\chi^2_1 = 32.9$, $p < 0.001$). A breakpoint, which denotes a change of the dependent variable (route efficiency) in respect to the independent variable (release number), was then automatically detected between releases 5 and 6 (5.5, 95% confidence interval (CI) [4.3, 6.2]; Fig. 2.3). No significant difference in route efficiency was detected among releases ranging from release 6 (0.88 ± 0.10) to

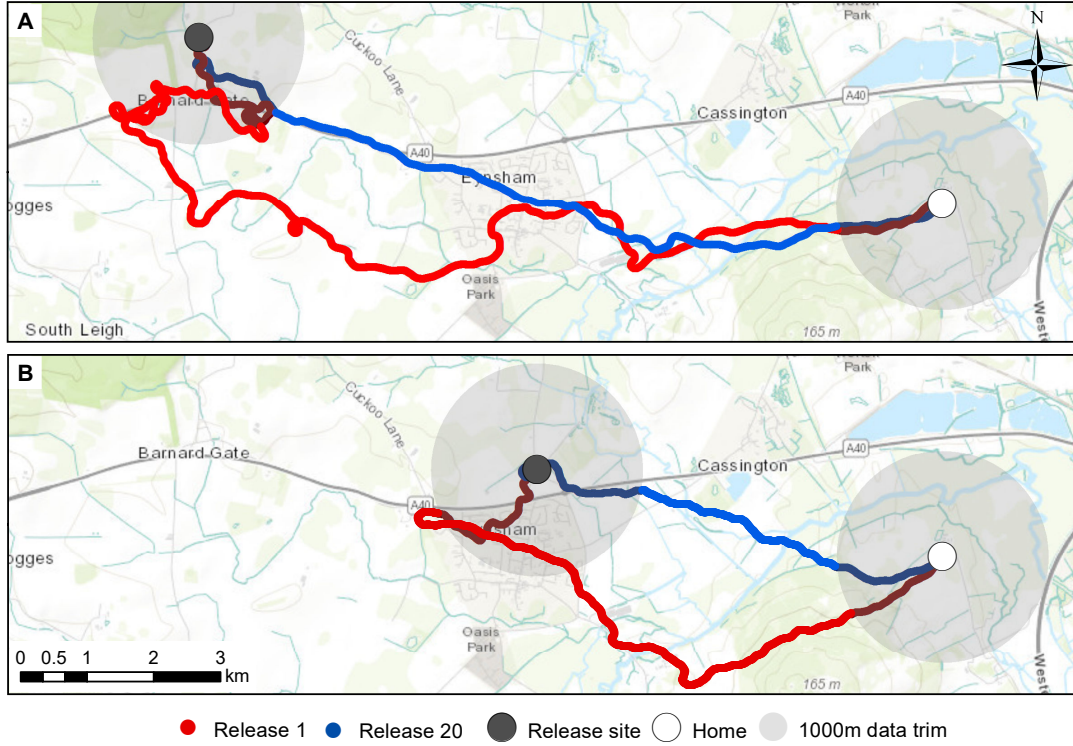


Figure 2.2: Examples of routes flown during the first (red; release 1) and last release (blue; release 20) from (A) the far site and (B) the near site. Note the increase in route efficiency at both sites. Map designed using ArcGIS 10.4.1 (Esri Inc., Redlands, USA) using the World Topographic Map (Esri *et al.*, 2013).

release 20 (0.87 ± 0.10 ; $\chi^2_1 = 0.7$, $p = 0.390$). Group (i.e. release distance) also had a significant effect on route efficiency, with birds released at the nearer site (Group 2) flying significantly more efficient routes than those released at the far site (Group 1; estimate = 0.318, $\chi^2_1 = 4.8$, $p = 0.029$). However, group had no significant effect on wingbeat characteristics or speed, thus the results from the two groups were pooled for the remainder of the analyses (Table 1). Route efficiency was also significantly affected by both median wind support (estimate = -0.05, $\chi^2_1 = 14.8$, $p < 0.001$) and median crosswind (estimate = 0.10, $\chi^2_1 = 7.9$, $p = 0.005$), with greater wind support and lower crosswinds associated with higher route efficiency.

A breakpoint was detected in the median peak-to-peak DB acceleration (5.6, 95% CI [4.1, 6.8]) and in the median DB amplitude (5.99, 95% CI [4.6, 6.9]) between the same release numbers (5 and 6) as route efficiency (5.5, 95% CI [4.3, 6.2]). Both the DB acceleration and amplitude significantly increased prior to the breakpoint

Table 2.1: Comparison of the piecewise linear mixed effects models for efficiency, wingbeat characteristics and airspeed for releases 1-20. The fixed-effects with P -values and parameter estimates (Est.) denoted in **bold** are included in the final model. Conditional R-squared values ($R^2_{\text{LME}(C)}$) are calculated using the methods described in Nakagawa and Schielzeth (2013).

Variable	Breakpoint (95% CI)	Release number < breakpoint		Release number > breakpoint		Wind support		Crosswind		Group		$R^2_{\text{LME}(C)}$
		p -value	Est.	p -value	Est.	p -value	Est.	p -value	Est.	p -value	Est.	
Efficiency (transformed)	5.5 (4.3, 6.2)	< 0.001	0.287	0.390	-	< 0.001	-0.049	< 0.001	0.099	0.029	0.316	0.69
Median peak-to-peak DB acceleration (g)	5.6 (4.1, 6.8)	0.007	0.038	0.007	-0.006	0.487	-	0.679	-	0.286	-	0.65
Median DB amplitude per wingbeat (mm)	5.99 (4.6, 6.9)	0.004	0.294	< 0.001	-0.123	< 0.001	0.195	0.430	-	0.288	-	0.70
Median wingbeat frequency (Hz)*	9.6 (4.5, 12.6)	0.159	-	< 0.001	0.016	< 0.001	-0.025	0.302	-	0.735	-	0.68
Median airspeed (m s ⁻¹)	5.2 (3.9, 7.8)	< 0.001	0.527	0.001	-0.065	N/A	-	N/A	-	0.281	-	0.22

* Note: manually moving the breakpoint for wingbeat frequency revealed a significant decrease during the early releases (breakpoint 5.6: estimate = -0.03, $\chi^2_1 = 2.83$, $p = 0.007$; breakpoint 6.0: estimate = -0.002, $\chi^2_1 = 6.88$, $P = 0.009$)

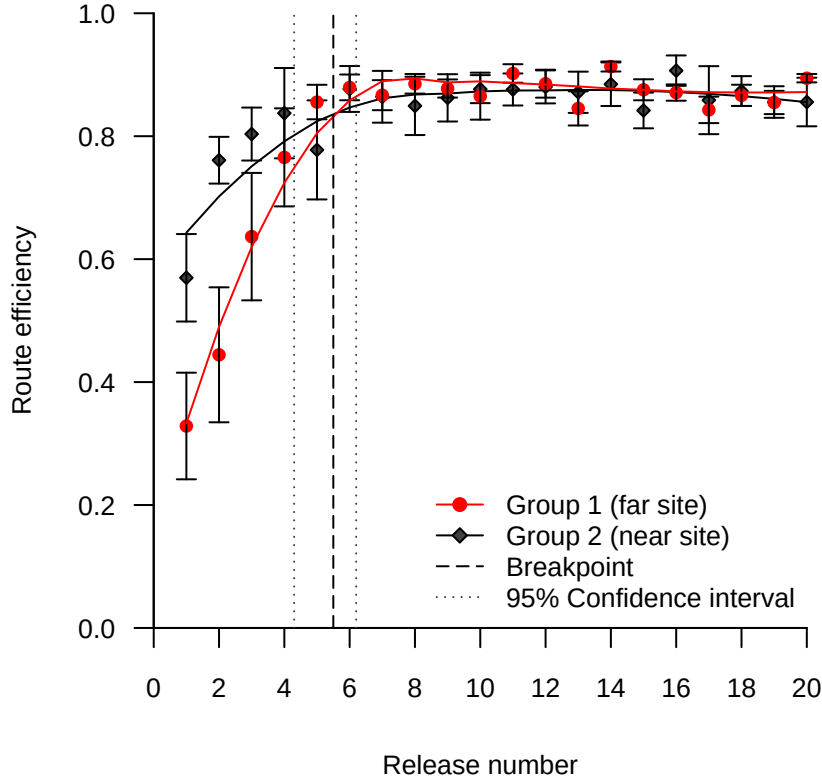


Figure 2.3: Route efficiency (mean $\pm$ s.e.m.) as a function of release number for Group 1 (far site, $n = 10$) and Group 2 (near site, $n = 11$). The dashed line indicates a computationally optimised piecewise linear mixed model breakpoint ($\pm$ 95% C.I. indicated by dotted lines) denoting a change in response function in respect to release number. Solid lines correspond to local polynomial regression fitting.

(acceleration: estimate = 0.038, $\chi^2_1 = 7.4$, $p = 0.007$; amplitude: estimate = 0.295, $\chi^2_1 = 8.5$, $p = 0.004$) before decreasing (acceleration: estimate = -0.006, $\chi^2_1 = 7.2$, $p = 0.007$; amplitude: estimate = -0.123, $\chi^2_1 = 16.4$, $p < 0.001$; Fig. 2.4). By contrast, the breakpoint for median wingbeat frequency appeared later, between releases 9 and 10 (9.6, 95% CI [4.5, 12.6]), with no significant change prior to the breakpoint ($\chi^2_1 = 2.0$, $p = 0.159$). Upon visual inspection one might argue that there is a breakpoint in the median wingbeat frequency around release 6. Indeed, manually moving the breakpoint to the breakpoints of DB acceleration (5.6) and amplitude (5.99) revealed that wingbeat frequency significantly decreased during the early releases (breakpoint 5.6: estimate = -0.03, $\chi^2_1 = 2.83$, $p = 0.007$; breakpoint 5.99: estimate = -0.02, $\chi^2_1 = 6.89$, $p = 0.009$). However, the resultant models were weaker

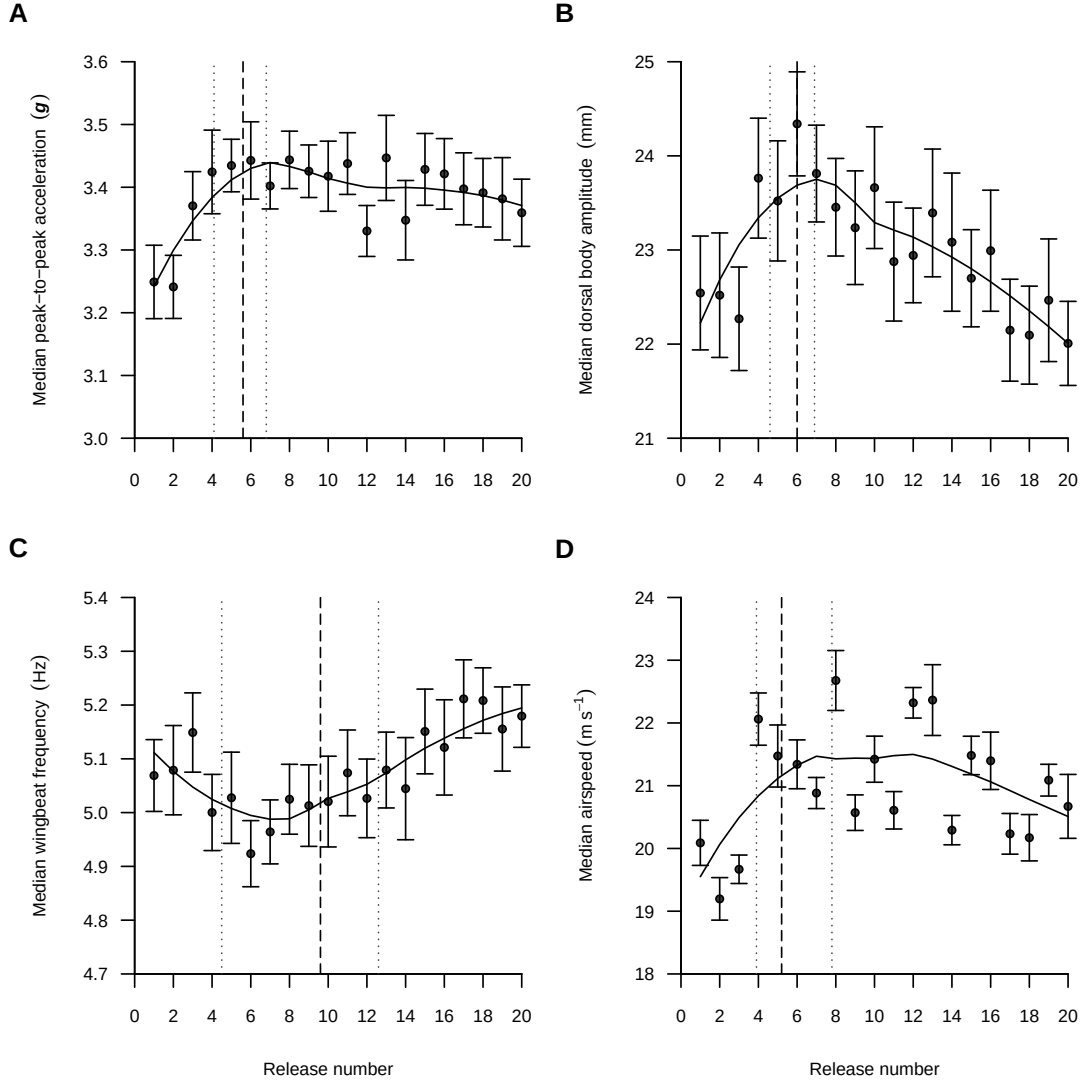


Figure 2.4: Wingbeat characteristics and airspeed (mean $\pm$ s.e.m., $n = 21$) as a function of release number. (A) Median peak-to-peak acceleration, (B) median dorsal body amplitude, (C) median wingbeat frequency and (D) median airspeed. Dashed lines indicate computationally optimised piecewise linear mixed model breakpoints ($\pm$ 95% C.I. indicated by dotted lines) denoting a change in response function in respect to release number. Solid lines correspond to local polynomial regression fitting.

and accounted for less of the variability, which is why the objective breakpoint is situated slightly later between releases 9 and 10. The visual ambiguity in the breakpoint is reflected in the confidence interval, which is large for median wingbeat frequency (95% CI [4.5, 12.6]). After the objective breakpoint, wingbeat frequency increased significantly (estimate = 0.02, $\chi^2_1 = 18.6$, $p < 0.001$).

Median wind support also had a significant effect on both median wingbeat

frequency and median DB amplitude, with higher wind support associated with lower wingbeat frequencies (estimate = -0.02, $\chi_1^2 = 26.5$, $p < 0.001$) and increased DB amplitude (estimate = 0.20, $\chi_1^2 = 25.3$, $p < 0.001$). By contrast, median wind support had no effect on peak-to-peak DB acceleration, and median crosswind had no effect on any of the wingbeat characteristics.

Median airspeed (m s^{-1}) increased during the first five releases (breakpoint 5.2, 95% CI [3.9, 7.8]; estimate = 0.53, $\chi_1^2 = 32.5$, $p < 0.001$) and thereafter decreased slightly (estimate = -0.07, $\chi_1^2 = 10.6$, $p < 0.001$; Fig. 2.4D). The mean of the median flight airspeeds for the first three releases were particularly low (release 1: $20.1 \pm 1.6 \text{ m s}^{-1}$; release 2: $19.2 \pm 1.4 \text{ m s}^{-1}$; release 3: $19.7 \pm 1.0 \text{ m s}^{-1}$). However, the coefficient of determination for the relationship between median airspeed and release number was low, even when accounting for individual variation ($R^2_{\text{LME}(C)} = 0.22$). By analysing all 20 releases in a LME model with median peak-to-peak acceleration and median wingbeat frequency as fixed-effects, we found that higher airspeeds were associated with higher peak-to-peak DB accelerations (estimate = 1.57, $\chi_1^2 = 10.3$, $p = 0.001$) and lower wingbeat frequencies (estimate = -0.78, $\chi_1^2 = 3.9$, $p = 0.048$). Furthermore, in a model with DB amplitude (displacement) as a fixed-effect, which is dependent on peak-to-peak DB acceleration (force exerted on the DB) and wingbeat frequency (duration of the wingbeat), DB amplitude was positively associated with airspeed (estimate = -0.24, $\chi_1^2 = 23.3$, $p < 0.001$).

The results thus far indicate that changes in wingbeat characteristics and airspeed correspond to changes in our route familiarity variable (i.e., route efficiency). To directly relate these findings, LME models were used with route efficiency as a fixed-effect between releases 1 and 6. The results of these analyses corroborate these findings with median peak-to-peak DB acceleration (estimate = -0.11, $\chi_1^2 = 32.5$, $p < 0.001$), median DB amplitude per wingbeat (estimate = -0.86, $\chi_1^2 = 20.9$, $p < 0.001$) and median airspeed (estimate = -0.84, $\chi_1^2 = 20.2$, $p < 0.001$) all positively related to route efficiency (negatively related to the transformed route efficiency; Table B.1 and Fig. B.4). As with release number, median peak-to-peak acceleration was only influenced by route efficiency, with no significant effect of

median wind support, median crosswind or group ($p > 0.1$). By contrast to DB acceleration, DB amplitude and airspeed, higher median wingbeat frequencies were associated with lower route efficiencies in releases 1-6 (estimate = 0.06, $\chi^2_1 = 8.1$, $p = 0.004$). Although there was a significant difference between groups in route efficiency in the piecewise LME model (estimate = 0.318, $\chi^2_1 = 4.8$, $p = 0.029$), there was no significant difference between groups when relating wingbeat characteristics and airspeed to route efficiency ($p > 0.1$).

We hypothesised that one potential explanation for differences in wingbeat characteristics could be changes in wingbeat modes with navigational experience, such as additional circling behaviour and gliding in the early releases. Analysing only data with flap frequencies > 3 Hz and tortuosity < 3 deg (i.e. without gliding and circling segments, respectively) resulted in a shift in the breakpoint in wingbeat frequency from release 9.6 (95% CI [4.5, 12.6]) to release 6.2 (95% CI [4.6, 12.5]). In addition, the wingbeat frequencies significantly decreased prior to the breakpoint (estimate = 0.02, $\chi^2_1 = 4.6$, $p = 0.03$). However, aside from the slight changes to median wingbeat frequency, removing circling and gliding had no other significant effect on the results other than decreasing median wingbeat frequency and median peak-to-peak DB acceleration, and increasing median DB amplitude and median airspeed (Fig. B.5). Furthermore, it is important to note that the confidence interval in the breakpoint for wingbeat frequency remains approximately the same and that on visual inspection one could place a breakpoint in the whole flight data at around release 6, as discussed above.

2.5 Discussion

We investigated the effect of navigational experience in relation to wingbeat characteristics and airspeed in homing pigeons. The results indicate, for the first time, that gradual increases in the birds' route efficiency, observed as birds become more experienced with a given terrain, are also accompanied by changes in wingbeat characteristics and airspeed. As the birds' route efficiency improved during the first six releases, the median peak-to-peak (DB) acceleration, median

DB amplitude and, consequently, median airspeed also increased. By contrast, after route efficiency stabilised, the birds' median DB acceleration and amplitude decreased, whereas median wingbeat frequency increased. However, decreasing DB amplitude, and hence wingbeat amplitude, in favour of increasing wingbeat frequency did not result in a higher airspeed. Taken together, our results suggest that birds may be modulating their flight characteristics as a function of navigational familiarity with the area through which they are travelling.

As with previous studies (reviewed in Guilford & Biro, 2014), route efficiency improved over consecutive releases. It increased significantly over the first five releases, with a breakpoint detected between releases 5 and 6. The breakpoint denotes a change in route efficiency (dependent variable) with respect to release number (independent variable), with the position of the breakpoint determined by where the slopes of the two segments join. We chose the piecewise linear mixed model approach to objectively identify a change of state because, as these results demonstrate, wingbeat characteristics and airspeed continue to change long after route efficiency stabilises. Whilst we could manually divide the data into segments, an automated approach enables us to objectively identify changes in wingbeat characteristics and airspeed as a function of release number and to identify whether these changes correspond to changes in route efficiency. In this study, we identified that route efficiency increases up to a breakpoint of 5.5 and thereafter stabilises. As expected, the near-site group (straight-line distance: 3.85 km) flew significantly more efficient routes home in the early stages of route learning than the far-site group (7.06 km), owing to the proximity of the near release site to the familiar area surrounding the pigeons' home lofts. However, despite these differences, no significant difference was found between groups in wingbeat characteristics and speed, and route efficiency still significantly increased over the first five releases for both groups. These results reinforce the idea that birds modulate their wingbeat characteristics in response to navigating an unfamiliar route, and that this effect is detectable even at short distances from home.

The aforementioned changes in route efficiency did correspond to changes in wingbeat characteristics, both in terms of the positioning of the breakpoint and when directly relating these factors during the first six releases. As route efficiency increased, the peak-to-peak DB acceleration and DB amplitude also increased, which indicates that the acceleration, or force, the dorsal body experienced increased over the first few releases. The median peak-to-peak DB acceleration per wingbeat was especially low during the first few releases. Although DB acceleration did decrease again after route efficiency stabilised, the DB accelerations the birds experienced during the first few releases were still much lower than in the last few releases, which could suggest that the overall flapping force was lower during the first few releases. Correspondingly, the airspeeds of the first three flights were also particularly low. By analysing the influence of peak-to-peak DB acceleration and wingbeat frequency on airspeed, we established that higher airspeeds were associated with higher peak-to-peak accelerations and lower wingbeat frequencies, with peak-to-peak acceleration having a slightly larger effect than wingbeat frequency. However, the amplitude of the DB displacement, which is dependent on the peak-to-peak acceleration (force exerted on the DB) and the wingbeat frequency (duration of the wingbeat), had the greatest overall effect on airspeed. For example, a wingbeat which is both high in force (peak-to-peak acceleration) and long in time (low wingbeat frequency) will result in a greater displacement, and hence higher airspeed, than one that is low in force or short in time. It should be noted, however, that this negative relationship between wingbeat frequency and airspeed is within the subtleties of active flight parameters, and may not represent the relationship over the entire range of the pigeons' wingbeat characteristics. Although DB amplitude is an indirect measure of wing amplitude, the two measures are likely to be related (Hedrick *et al.*, 2004). An alternative explanation for the changes in wingbeat characteristics and airspeed could be changes in flight behaviour, such as increased circling and/or gliding. However, removing both wingbeat frequencies below 3 Hz and tortuous flight made no substantial difference to the results other than shifting the breakpoint of median wingbeat frequency, suggesting that the changes

in wingbeat characteristics are occurring during straight-line powered flight. Flying at a slower speed from an unfamiliar location may be an advantage as it may enable the bird to gather more local ambient information.

Breakpoints in the median peak-to-peak acceleration (release: 5.7) and the median DB amplitude (5.99), which occur between the same release number as route efficiency (5.5), along with the fact that higher peak-to-peak acceleration and DB amplitude were associated with higher route efficiency in releases 1-6, indicate that DB movements change as a function of navigational knowledge. By contrast, during the first six releases, higher wingbeat frequencies were associated with lower route efficiencies. The large confidence interval and slightly later breakpoint in wingbeat frequency (9.6) suggest that it is likely that birds continue to learn routes home even after route efficiency initially plateaus. Indeed, removing circling and gliding behaviour resulted in a breakpoint in wingbeat frequencies being detected at release 6.2. Thus, changes in wingbeat characteristics shortly after the route efficiency breakpoint could still be related to the acquisition of navigational knowledge. An alternative explanation could be increases in the birds' physical fitness, or acclimatisation to the sensor mass or to the capture and release procedure. However, given the substantial number of releases immediately prior to the start of the experiment (≥ 24), the daily free flights around the loft and the fact that the birds were fitted with clay weights equal to the size and mass of the devices two weeks prior to the start of the experiment, this is unlikely to have been a factor. Furthermore, migratory species, such as barnacle geese (*Branta leucopsis*) undertaking 2,500 km journeys, do not increase flight behaviour prior to migratory departure (Portugal *et al.*, 2012), suggesting exercise is not a prerequisite for extended flight.

Shortly after route efficiency stabilised, changes in the birds' flight characteristics consisted largely of increases in wingbeat frequency as the birds' DB acceleration and amplitude decreased. The inertial power requirement, or cost, of horizontal steady flight is proportional to the square of wingbeat amplitude but the cube of wingbeat frequency (Greenewalt, 1962; Lilienthal, 2001), which means increasing wingbeat frequency would result in a higher inertial power cost. If this higher

wingbeat frequency translated into higher airspeeds then this strategy could be beneficial as the bird would then reach its destination in less time (Hedenström & Ålerstam, 1995). However, as already highlighted, higher wingbeat frequencies were associated with lower airspeeds. Indeed, airspeed did decrease significantly from release 6, although variability in this was high and the effect size small. Albeit increasing wingbeat frequency would increase the inertial power costs, a higher wingbeat frequency would also result in a higher aerodynamic efficiency by reducing the drag from the wings and body and increasing lift (Greenewalt, 1962; Lilienthal, 2001), which may be advantageous once the total length of the journey is known. The median wingbeat frequency increased in this study from 4.9 (release 6) to 5.2 (release 18), i.e. by 5.8%. However, these wingbeat frequencies are still considerably lower than those reported for homing pigeons participating in flight that may require a higher degree of aerodynamic efficiency or stability, such as flock flight (~6.6-7.0 Hz; Usherwood *et al.*, 2011) and during ascending and descending flight (6.1-9.6 Hz; Berg & Biewener, 2008). Thus, the increases in wingbeat frequency exhibited in the present study are more likely to be related to birds optimising their flight patterns between inertial power requirements and aerodynamic efficiency.

Increasing aerodynamic efficiency, by increasing wingbeat frequency, could help conserve energy particularly as the results of this study also indicate a strong effect of the wind on route efficiency and flight characteristics. The effect of wind on flight is well documented, particularly in relation to the timing and distance travelled during migration (Ålerstam, 1979; Liechti & Bruderer, 1998). Liechti (2006) highlighted that wind speed can easily double or halve the bird's speed and thereby affect the overall cost of the flight. Weather data used in this study (mean wind speed and bearing) were recorded 5.5 m above the pigeon lofts, 7.06 km from the "far" release site. Therefore, the accuracy of the readings decreased the further away the bird was from the lofts, which could explain some of the variation, particularly in airspeed, found in this study. Nevertheless, the results indicate that wind support, in particular, was a consistent and significant factor contributing to the work rate, with a higher wind support (tail wind) associated

with a lower wingbeat frequency, which would decrease the inertial power costs. By contrast, the birds' peak-to-peak DB acceleration was not affected by the wind, which suggests that, in winds under 7 ms^{-1} , birds compensate for the wind by modulating wingbeat frequency rather than the amplitude. Indeed, the change in breakpoint in the wingbeat frequency from the whole flight data to the active straight-line data from release 9.6 to release 6.2 could also be a reflection of the birds utilising circling and gliding behaviour to compensate for the effects of the wind. Furthermore, higher route efficiency was associated with higher wind support and lower crosswinds, which suggests that the birds may modify their route (and hence their route efficiency) depending on the wind conditions.

Regardless of the underlying cause for the changes in wingbeat characteristics, the results of this study indicate, for the first time, that pigeons modulate their wingbeat characteristics as a function of navigational knowledge, which suggests that navigation and the learning process in birds may have physical manifestations. In particular, the birds' peak-to-peak DB acceleration was especially low during the first few releases, which was unaffected by wind characteristics, and related to a lower airspeed. Thus, measuring flight characteristics could provide new insights into the cognitive state of the bird. For example, wingbeat characteristics may be used as "signatures" of birds' route familiarity, which could be utilised in navigation research to identify how familiar a bird is with a given navigational task. Furthermore, the results of this study lead us to speculate that birds may be able to orient and learn more effectively at lower speeds, in which case the flight would then become a trade-off, or compromise, between optimal navigation and learning (accuracy), and vulnerability to predators and the total flight time (speed). Moreover, these results suggest that the cost of the first flight, such as the first migration or first route out in search of a novel foraging site, may be higher than that of subsequent flights, because of both inefficiencies in the route, which increase the total distance flown, and the increased flight time, owing to lower airspeeds. This, in turn, could impact on the total time available for foraging and reproduction, and other decisions, such as whether to fly with other individuals. For example, despite the additional

energetic cost of flying in a close cluster flock (Usherwood *et al.*, 2011), a naïve individual may be able to conserve energy by flying with experienced individuals to reduce the total flight time, as well as gain protection from predators. Thus, studying intra-individual modulations of wingbeat characteristics and airspeed could provide new insights into the decision-making and navigational strategies of birds.

Taylor, L. A., Biro, D., Lambert, B. Taylor, G. K. & Portugal, S. J. (in submission) Birds invest wingbeats to reap the ultimate benefits of flocking

Supplementary material can be found in Appendix C.

3

Birds invest wingbeats to reap the ultimate benefits of flocking

Contents

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3.1 Abstract

Forward-flapping flight is the most energetically demanding form of sustained locomotion that vertebrates perform. Flock dynamics therefore have significant implications for individual energy expenditure and lifetime fitness. Despite this, no studies have yet compared the biomechanical consequences of flying in a cluster flock relative to flying solo. Here, we compared the flight characteristics of homing pigeons (*Columba livia*) completing 7km flights solo and in pairs. We found that

birds increased their wingbeat frequency by *c.*18% (1.0 Hz) when flying in pairs, by decreasing the duration of their upstroke. Thus, despite simultaneously improving route accuracy and hence reducing the distance flown by *c.*7%, flying in pairs resulted in a net energetic loss. Our results demonstrate that there is a substantial cost to flying together, and that the ultimate drivers of flocking, including predator protection and pooling of navigational knowledge, must outweigh these proximate costs even during short-range travel over familiar terrain.

3.2 Introduction

Across the animal kingdom many species travel in groups, from pairs to flocks, shoals, herds and swarms, some containing millions of individuals (Krause & Ruxton, 2002; Herbert-Read, 2016). Commonly cited benefits of group travel include the increased ability to detect and avoid predators (Krause & Ruxton, 2002; Ward *et al.*, 2011), enhanced orientational efficiency through the pooling of navigational knowledge (Simons, 2004; Biro *et al.*, 2006a; Dell’Ariccia *et al.*, 2008; Berdahl *et al.*, 2013), and energy conservation derived from the benefits of hydro- and aero-dynamic efficiency (Bill & Herrnkind, 1976; Weimerskirch *et al.*, 2001; Liao *et al.*, 2003; Portugal *et al.*, 2014; Voelkl *et al.*, 2015). Flocking in birds has received considerable attention due to the complex aerodynamic interactions that take place between group members (Weimerskirch *et al.*, 2001; Usherwood *et al.*, 2011; Portugal *et al.*, 2014; Voelkl *et al.*, 2015). Avian flock formations can be grouped into two main categories; line formations and cluster formations (Heppner, 1974; Bajec & Heppner, 2009). Line formations, which include the distinctive ‘V’ formation, are utilised by medium to large-sized birds, such as Northern bald ibis (*Geronticus eremita*) and Canada geese (*Branta canadensis*), whereas cluster formations are typically observed in smaller birds, such as pigeons (*Columba livia*) and starlings (*Sturnus vulgaris*), which fly in irregular three-dimensional shapes (Heppner, 1974; Bajec & Heppner, 2009). While birds flying in V-formations can save energy by flying in aerodynamically optimal positioning within the V (Weimerskirch *et al.*, 2001; Portugal *et al.*, 2014; Voelkl *et al.*, 2015), those species flying in cluster flocks have

been shown to incur an additional energetic cost in denser formations (Usherwood *et al.*, 2011). In homing pigeons, for example, wingbeat frequency increases by up to 0.1 Hz as flock density increases (Usherwood *et al.*, 2011). Forward-flapping flight is the most energetically demanding form of sustained locomotion that vertebrates perform (Schmidt-Nielsen, 1972; Tobalske *et al.*, 2003), and such flock dynamics will therefore have significant implications for individual energy expenditure and lifetime fitness. However, no studies have yet compared the biomechanical consequences of flying in a cluster flock relative to flying solo; therefore, the energetic impact of this form of flocking at the individual level is unknown.

To fill this fundamental gap, we recorded the position and dynamics of every wingbeat of 20 free-flying homing pigeons flying on their own (solo) and in a pair as they homed from a site 7 km east of their loft (Fig. 3.1a). The birds were equipped with 5 Hz GPS trackers and 200 Hz tri-axial accelerometer biologgers which allowed us to precisely reconstruct their trajectories and wingbeat patterns during each homeward flight (see Methods; Fig. 3.1b-f; Nagy *et al.*, 2010; Taylor *et al.*, 2017). The experiment consisted of four phases. In Phase 1, subjects first completed 21 successive solo flights (Fig. 3.1f), the final six of which provided the solo baseline (solo 1). During these six solo flights, the median wingbeat frequency and amplitude (dorsal body displacement) for all birds were 5.48 ± 0.19 Hz (mean $\pm$ s.d.) and 20.68 ± 1.17 mm, respectively (after accounting for the effects of airspeed, date of release and weather variables including wind support, crosswind, temperature, humidity and air density; Fig. 3.2a). These wingbeat frequencies match those measured previously for solo pigeon flights (Tobalske & Dial, 1996; Taylor *et al.*, 2017). In Phase 2, following the solo releases, birds were released six times from the same – now familiar – site, but in similar-sized pairs. Pairs were assigned based on similarity in body mass (g) and structural size (tarsus length, mm; Sutherland *et al.*, 2004). Body size and mass are strong predictors of preferred flight speeds in birds, both at the intra- and inter-specific levels, with optimal flight speeds usually assumed to be those for which the cost of transport (i.e. energy expenditure per unit distance) is predicted to be at its minimum (Tobalske *et al.*, 2003). Therefore,

we hypothesized that for birds of different sizes either one or both birds may have to adjust their wingbeat frequency and/or amplitude to stay together as a pair, which would represent an additional ‘hidden’ compromise cost of flying in a flock. In Phase 3, immediately following completion of the six similar-sized pair releases, each bird was then flown in size-mismatched pairs for a further six flights (different-sized pairs), again from the same site. Finally, in Phase 4, upon completion of the six size-mismatched flights, the birds flew six times solo again (Fig. 3.2d).

3.3 Results

We analysed the data from all flights using Bayesian hierarchical models (see methods). Our results show that when the birds flew in pairs, their median wingbeat frequency increased by 18.2% (1.00 Hz) relative to flying solo (95% credible interval (CrI) [0.61, 1.38]; Fig. 3.2b-c). These findings were consistent across pairs, irrespective of whether the birds were flying in similar-sized or different-sized pairs (0.01 Hz increase per mm difference in tarsus length between the pair; 95% CrI [-0.13, 0.16]; Fig. C.1), or whether the bird was in front or behind during the flight (0.01 Hz increase for travelling behind, 95% CrI [-0.10, 0.12]). These results were computed after accounting for the birds’ median airspeed, date of release and weather variables, all of which had an estimated effect on wingbeat frequency that was indistinguishable from zero (Fig. C.2, Table C.1). Furthermore, the standard deviation of wingbeat frequency remained relatively stable between solo and paired flight (2% lower standard deviation for size-matched pairs), implying that the observed increase was not associated with more variable wingbeat patterns. In addition to these results, one similar-sized pair and one different-sized pair separated during three releases each, which means we can fortuitously compare sections of paired and solo flight within the same release. The results for these six releases confirm that wingbeat frequency increases as a direct result of flying in a pair, as the birds’ median wingbeat frequency decreased by 1.01 ± 0.30 Hz (mean $\pm$ s.d.) after the birds separated and flew solo (raw values with no covariates; Fig. 3.2e-h).

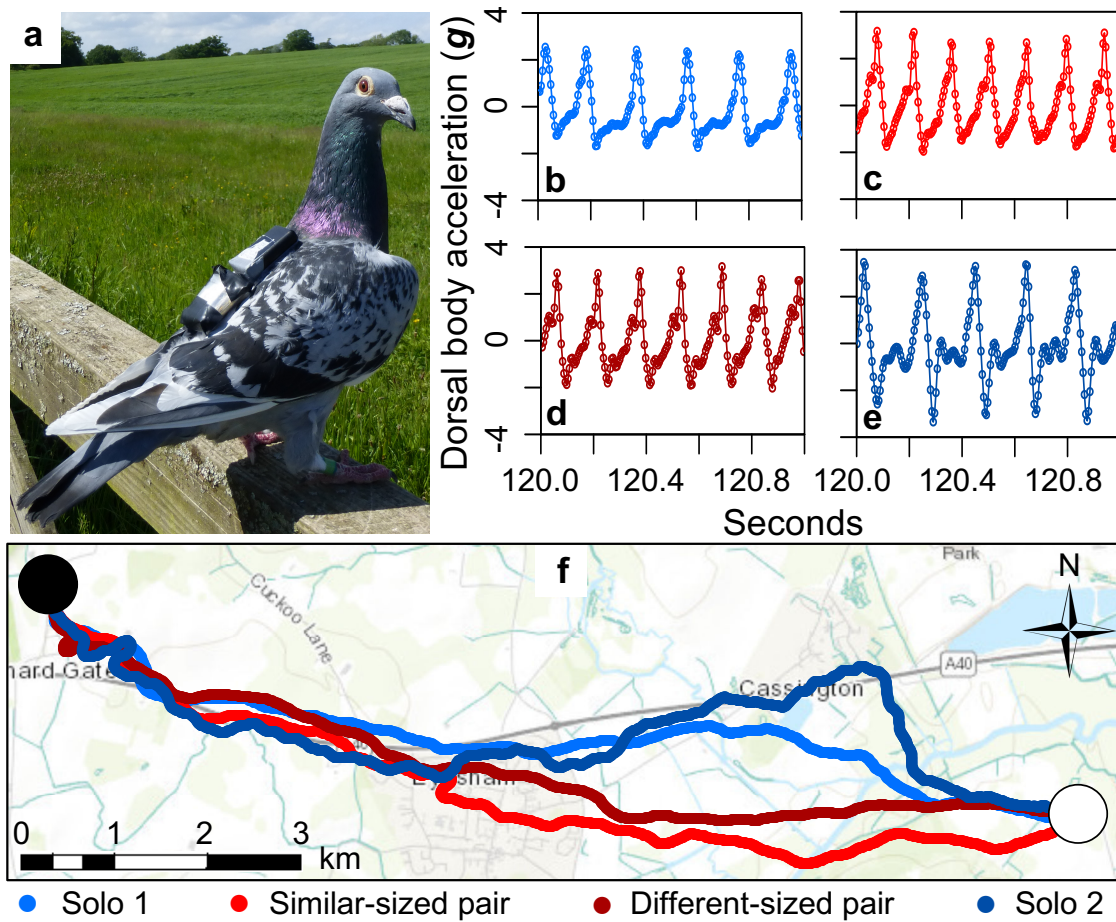


Figure 3.1: Examples of accelerometer and GPS data recorded during solo and paired flights. a, Bird S30 carrying an accelerometer (top) and GPS sensor (bottom) attached via Velcro strips. b-e, Dorsal body acceleration recorded by the accelerometer during S30's final release in each of the four conditions: b, solo flight (blue); c, paired flight with a similar-sized bird (red); d, paired flight with a different-sized bird (dark red) and e, solo flight (dark blue). Accelerometer data has been filtered and gravity removed (see Methods). Note the higher wingbeat frequency when the bird is flying in a pair. f, Routes flown by S30 during the final release of each of the four conditions (same flights as those shown in b-e). Note the straighter trajectory, and hence greater route accuracy, of the paired flights. Black circle corresponds to the release site and white circle corresponds to the home loft. Map designed using ArcGIS 10.4.1 (Esri Inc., Redlands, USA) using the World Topographic Map (Esri *et al.*, 2013). Scale bar shows 3 km.

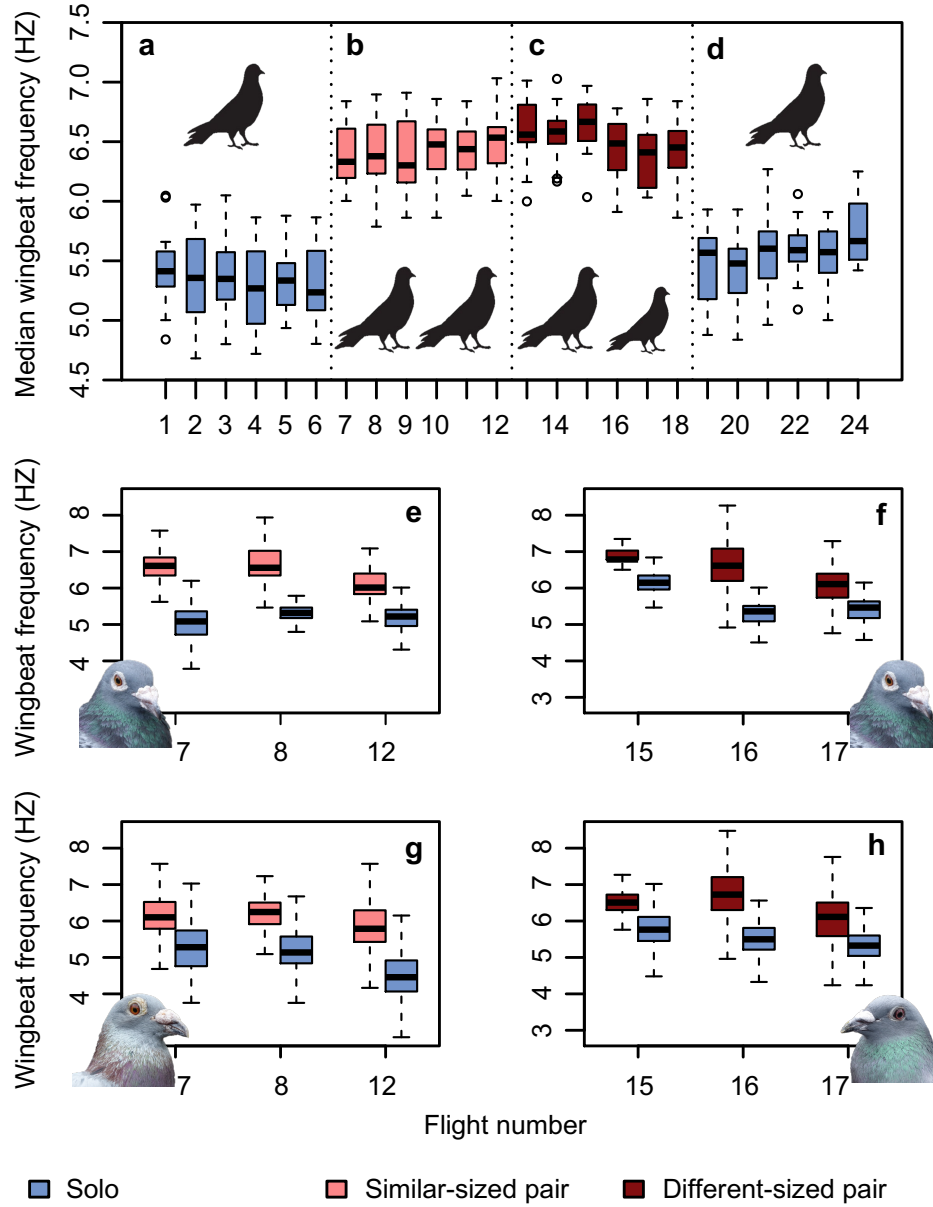


Figure 3.2: Wingbeat frequency as a function of flight number. a-d, Median wingbeat frequency (raw data with no covariates) for all 20 birds during each of the four experimental phases: a, six individual releases (solo); b, six releases with a similar-sized bird (similar-sized pair); c, six releases with a different-sized bird (different-sized pair); and d, six individual releases (solo). e-h, Raw wingbeat frequency data for birds which flew in a pair (< 50 m distance) and solo (> 300 m) during the same flight. e and g are from the similar sized pair of birds B01 and B82, respectively (pictured). f and h are from the different-sized pair B01 and B07 (pictured).

To explore the mechanism underlying this change in wingbeat frequency, we divided each wingbeat into an upstroke and downstroke phase from the peak downstroke force (maximum g -force) to the lower reversal point (minimum g -force) (see Methods). We found that birds reduced the duration of the upstroke phase by 20.6% (-27.99 ms, 95% CrI [-35.61, -19.92]) when flying in pairs, whereas the downstroke phase duration did not vary significantly (-3.53 ms, 95% CrI [-8.35, 1.38]; Fig. C.1). It is clear by inspection of the wingbeat acceleration traces (Fig. 3.1b-e) that this principally reflects the dropping of a short pause in the wing's motion during the upstroke phase so that this change in wingbeat frequency effectively represents a switching of gait. In contrast to wingbeat frequency, the median peak-to-peak dorsal body (DB) acceleration did not vary substantially between solo and paired flights (0.16 g , 95% CrI [-0.16, 0.47]). Thus, through reducing the duration of the upstroke phase by removing the short intermittent pause characteristically observed in pigeon flight (Williams & Biewener, 2015; see Fig. 3.1b-e), the birds were able to accommodate one additional wingbeat per second when flying in pairs, whilst maintaining the same range in peak-to-peak acceleration as when flying solo. It seems inevitable, therefore, that the higher-frequency gait adopted in paired flight will be associated with a higher mechanical power input than the lower-frequency gait adopted in solo flight. On the other hand, this increase in wingbeat frequency causes a 22.5% reduction in the median amplitude of dorsal body displacement (-4.65 mm, 95% CrI [-6.31, -3.06]) through the wingbeat.

In principle, a higher mechanical power input in paired flight could be associated with a lower cost of transport if the increased power were more than compensated by an increased speed. However, whilst birds migrating in V-formations increase their airspeed as flock size increases (Hedenström & Åkesson, 2017), the birds in our study did not alter their airspeed substantially when flying in pairs (3.3 %; 0.64 m s⁻¹ increase, 95% CrI [0.08, 1.2]), which indicates that the increased wingbeat frequency was not translated into increased forwards motion. Furthermore, again unlike birds in V-formations (Portugal *et al.*, 2014), there was no relationship between the front and back bird's wingbeat frequency, indicating that the birds

were not flying in phase ($\beta = -0.23$, where 1.0 corresponds to a direct correlation, 95% CrI [-1.23, 0.75]; Fig. C.3). The probability of whether the bird flew in front in a given pair was unaffected by the birds' tarsus length (0.01 per mm difference in tarsus length, 95% CrI [-2.68, 2.44]), solo airspeed (-0.22 per m s⁻¹ difference in median solo airspeed, 95% CrI [-3.08, 2.65]) and body mass (0.02 per g difference in body mass, 95% CrI [-0.10, 0.15]; Fig. C.4).

Aside from energy conservation, another key benefit often ascribed to flying in flocks is the ability to pool navigational knowledge, which should improve route accuracy (Simons, 2004; Berdahl *et al.*, 2013) and, therefore, could offset the short-term cost of additional wingbeats by a decrease in the total route distance. We calculated the birds' route accuracy flying solo and in pairs using a weighted mean cosine of the angle between the birds' heading and destination. Flying in a pair resulted in an increase in route accuracy relative to both the Phase 1 and Phase 4 solo releases (0.06, 95% CrI [0.01, 0.10] or 6.9%; Fig. 3.1), consistent with previous studies (Biro *et al.*, 2006a; Dell'Arciccia *et al.*, 2008) and with theory (Simons, 2004; Berdahl *et al.*, 2013). Thus, overall, flying in pairs resulted in an increase in wingbeat frequency of 18.2%, an increase in airspeed of 3.2% and an increase in route accuracy of 6.9%, which, extrapolated out over the straight-line route distance of 6.66 km, meant that flying in pairs resulted in a $\sim 7.1\%$ increase in the total number of wingbeats per homing flight (165 extra wingbeats; Table C.2). In essence, flying in pairs reduced the total flight time, primarily through increases in route accuracy, but the reduction in the total flight time was not sufficient to offset the increase in wingbeat frequency. Therefore, flying in pairs resulted in a net increase in the total number of wingbeats taken to reach home. As we now discuss, this surprising result indicates, first, that there must be other benefits of paired flight that outweigh the apparent energetic cost of flying in pairs, and second, that realizing those benefits must depend upon features of the higher frequency gait used when flying in pairs.

3.4 Discussion

One of the most commonly cited reasons for travelling as a group is to reduce energy expenditure and enhance locomotor performance (Weimerskirch *et al.*, 2001; Portugal *et al.*, 2014). However, increasing wingbeat frequency requires more inertial power (power required to lift the wings) than increasing wingbeat amplitude (Greenewalt, 1962; Lilienthal, 2001). Whilst aerodynamic efficiency may improve with higher wingbeat frequency, these increases in aerodynamic efficiency are unlikely to outweigh inertial power requirements, which scale approximately with the cube of wingbeat frequency (Usherwood *et al.*, 2011). Moreover, the removal of the intermittent pause on the upstroke phase will reduce the recovery time of the primary flight muscles between downstrokes. Thus, our results suggest that there is likely to be an energetic cost to flying together for pigeons, due to the increased power requirements of a higher wingbeat frequency.

The increase in wingbeat frequency – over ten times the difference reported when comparing birds in different flock densities and positions (~ 0.08 - 0.1 Hz; Usherwood *et al.*, 2011) – suggests that the majority of the additional cost comes merely from the act of flying with another individual, rather than from the relative spatial position of the bird or the size of its partner. Two key hypotheses have been proposed for the increase in wingbeat frequency seen in denser cluster flocks: (i) negative aerodynamic interactions between flock members and, (ii) increased need for control and collision avoidance (Usherwood *et al.*, 2011). The observation that both birds within our pairs increased their wingbeat frequency suggests that these effects are unlikely to have been related to negative aerodynamic flow interactions, since the bird in front does not fly in any wake created by the bird behind. As higher wingbeat frequencies can be used to increase manoeuvrability and passive stability (Hedrick *et al.*, 2009; Usherwood *et al.*, 2011; Williams & Biewener, 2015), we suggest that the increase in wingbeat frequency was related to paired flight necessitating a greater degree of control in two different ways. Firstly, flying in a flock may require enhanced manoeuvrability and control because birds will need to adjust their orientation continuously and rapidly, both to stay together and to

avoid collisions (Usherwood *et al.*, 2011). Birds make control inputs on a wingbeat-to-wingbeat basis, so increasing wingbeat frequency will increase the frequency with which control inputs can be made. Secondly, birds may require enhanced visual stability when flocking, in order to observe and coordinate with individuals whose proximity makes the effects of motion parallax significant. Other things being equal, wingbeat frequency is expected to amplify flight stability (Taylor & Thomas, 2002) but our results also show that dorsal body displacement in reaction to the wingbeat is attenuated by 22.5% in the higher-frequency gait adopted in paired flight, which should naturally translate into a reduced amplitude of head motion. Together, our results suggest that a higher wingbeat frequency may be a prerequisite for flocking flight, because of the increased demands for stability and control.

Managing energy expenditure is critical for survival and is a primary focus for natural selection, but, rather than conserving energy as birds do flying in V-formations, pigeons flying in pairs opt for a more energetically expensive flight strategy. While our results demonstrate that birds can derive navigational benefits from flying in pairs even during short-range flights along familiar routes, the 7% increase in route accuracy did not counterbalance the cost of the 18% increase in wingbeat frequency energetically, as the total number of wingbeats increased by $\sim 7\%$ overall. Despite this, only six releases had to be repeated due to birds separating at the start, and twelve out of 116 pair releases (10%) resulted in separation part-way through the release. The observed preference for paired flight suggests that additional benefits outweighed the increase in energy expenditure required to fly in pairs. We suggest that perceived safety-in-numbers is the most likely candidate: during a predation event, flying with just one additional bird dilutes the chance of fatality by 50% (Kenward, 1978). Therefore, for pigeons, the ultimate benefits of flocking, such as protection from predators and the pooling of navigational knowledge, together outweigh the energetic cost of flying with conspecifics. These results suggest that anti-predator protection and navigational knowledge may act as selective drivers, in terms both of individual behavioural responses and the evolution of flocking. Whilst the birds in our study apparently

experienced a net energetic loss as a result of flying in pairs, in circumstances where an individual has substantially less navigational knowledge than the flock, the increases in route accuracy gained from flying with the flock could result in energetic savings due to the overall shorter flight time. In this scenario, birds would experience short-term energetic costs which would be compensated by overall net energetic savings and reduced risk of predation. Nevertheless, the birds in our study still opted to fly in pairs despite collective travel resulting in an energetic loss at the individual level. Our results thus provide key new insights into the energetic investments pigeons make to gain access to collective navigational knowledge and predator protection. Taken together, our results demonstrate that flocking is, for pigeons, both fundamentally important and fundamentally expensive.

3.5 Methods

3.5.1 Subjects

Twenty homing pigeons aged 1 or 3 years were used. Body size was quantified by measuring tarsus length (mm) and body mass (g). Tarsus length was measured with callipers sensitive to 0.1 mm using the methods described in Sutherland *et al.* (2004). Body mass was measured using digital scales (Salter ARC Electronic Kitchen Scales, Salter, UK; ± 1 g). All subjects completed a minimum of 15 solo flights from the release site used in this study immediately preceding the start of the experiment. The subjects were housed with ~ 120 other pigeons in two neighbouring lofts at the Oxford University Field Station, Wytham, UK ($51^{\circ}46'58.2''\text{N}$, $1^{\circ}19'2.7''\text{W}$). Access to water, grit and a standard pigeon feed mix were available *ad libitum* at all times in the loft. The protocols outlined in this paper were approved by the Local Ethical Review Committee of the University of Oxford's Department of Zoology.

3.5.2 Data logging

The birds were tracked using 5 Hz GPS loggers (QStarz BT-Q1300ST, 15 g) and 200 Hz tri-axial accelerometers (± 16 g; Axivity AX3, 11 g), which were attached via Velcro strips glued to trimmed feathers on the birds' back. In total, the

loggers and fastenings weighed 27 g. To enable subjects to adapt to carrying the additional mass, clay weights were attached to them throughout the pre-training and experimental periods, which meant the weights were attached for a minimum of 43 days prior to the start of the experiment. The weights were exchanged for the loggers immediately prior to each release. GPS and accelerometer data were downloaded using QTravel (Qstarz International Co., Ltd., Taipei, Taiwan; version 1.48(T)) and Open Movement (Om) GUI Application (Newcastle University, UK; version 1.0.0.28), respectively.

The weather, including mean wind speed per minute (m s^{-1}), a running mean of the wind bearing over the previous ten minutes, temperature ($^{\circ}\text{C}$), humidity (%) and barometric pressure (hPa), were recorded using WS2083 Professional Wireless Weather Station with USB upload (Aercus Instruments, UK) situated 5.5 m above the pigeon lofts and Cumulus Weather Station Software (Sandaysoft; version 1.9.4).

3.5.3 Experimental procedures

The release site was located 7.06 km from the loft on a bearing of 282° (Barnard Gate; $51^{\circ}47'48.1''\text{N}$, $1^{\circ}25'3.3''\text{W}$). The experiment consisted of four phases: Phase 1 - six individual releases (solo 1); Phase 2 - six releases with a bird of a similar size (similar-sized pair); Phase 3 - six releases with a bird of a different size (different-sized pair); and Phase 4 - six individual releases (solo 2). Bird pairings can be found in Table C.3. Releases were conducted between June and September 2015, on days when the sun was visible and the wind speed was $< 7 \text{ ms}^{-1}$. Subjects participated in a maximum of two releases per day, with a minimum of three hours between each release. The birds had to complete a minimum of one third of the flight together for the flight to be included in the analysis. If the birds spent less than one third of the flight together, the flight was repeated. In total, six releases out of 116 pair releases had to be repeated. One different-sized pair did not complete the final pair release after repeatedly separating. The Velcro failed on bird S27 after the third release with a different-sized bird therefore the pairing S27 and S84 only completed three different size pair releases and S27 did not complete the final

solos. In addition, S13 only completed one final solo before the Velcro failed, S87 completed four final solos, and S05 and S25 completed five final solos each. The remaining 15 birds all completed the final solo releases.

3.5.4 Data processing

Data were processed using the procedures outlined in Taylor *et al.* (2017). For each GPS point, the orthodromic (great-circular) distance travelled and birds' final bearing from the previous point were calculated using the haversine formula and forward azimuth, respectively. The dorsal accelerometer measurements were filtered by taking a running mean over three data points (0.015 s). Static acceleration (or gravity) was removed by subtracting a running mean over 15 wingbeat cycles (> 2 s; Fig C.5). The wingbeat frequency (number of wingbeats per second; Hz) and peak-to-peak dorsal body (DB) acceleration (g) using the dorsal acceleration signal (Z-axis) were calculated for each individual wingbeat. The amplitude of the DB displacement (mm) was then calculated by the double integration of dorsal accelerometer measurements (Usherwood *et al.*, 2011; Taylor *et al.*, 2017). In addition, we calculated the duration of the “downstroke” from the peak downstroke force (maximum g -force) to the lower reversal point (minimum g -force). The “upstroke phase” duration, which included the start of the downstroke, was measured from minimum g -force to the maximum. We used the maximum and minimum g -force peaks to divide the wingbeat for consistency as the start of the downstroke was not distinguishable in the data from paired flights.

Wind support, crosswind and airspeed were calculated using the methods described in Safi *et al.* (2013) using the measurements from the weather station and speed derived from the GPS devices. Humid air density (kg m^{-3} ; ρ_{air}) was calculated from measures of barometric pressure (hPa; P), temperature ($^{\circ}\text{C}$; T_c) and relative humidity (%; Φ) recorded by the weather station, using the following calculation derived from the ideal gas law:

$$\rho_{\text{air}} = \left(\frac{P_d}{R_d T} \right) + \left(\frac{P_v}{R_v T} \right) \quad (3.1)$$

where P_d is pressure of dry air (Pa), P_d is gas constant for dry air [287.05 J/(kg * K)], P_v is pressure of water vapour (Pa), R_v is gas constant for water vapour [461.495J/(kg * K)] and T is ambient temperature (K). P_v can be calculated from the saturation of vapour pressure (P_{sat}) and relative humidity (Φ):

$$P_v = \Phi P_{sat} \quad (3.2)$$

We used the Arden-Buck (Buck, 1981, 1996) equation to calculate P_{sat} , where P_{sat} (hPa) is calculated as:

$$P_{sat} = 0.61121 \exp \left(\left(18.678 - \frac{T_C}{234.5} \right) \left(\frac{T_C}{257.14 + T_C} \right) \right) \quad (3.3)$$

P_d can then be calculated from the barometric pressure (P) and the vapour pressure of water (P_v):

$$P_d = P - P_v \quad (3.4)$$

The birds' route accuracy was calculated using a weighted mean cosine of the angle (θ) between the birds bearing and the bearing to the loft for each timestep, where θ is equal to the smallest angle difference so that θ ranged from 0 (heading directly to the loft) and 180 (heading directly away from the loft), and the orthodromic distance between each GPS point (d) using the following calculation:

$$\frac{1}{D} \sum_{i=1}^n d_i \cos \theta_i \quad (3.5)$$

where D is the total distance flown. Route accuracy is, therefore, on a scale of -1 (heading in a straight-line away from the destination) to 1 (straight-line to the destination). For orientated movement, route accuracy is >0 , which means route accuracy is akin to the straight-line index (Batschelet, 1981), but enables us to calculate the accuracy for sections of a flight, rather than a whole flight, which is necessary if the birds separate during the flight and fly solo.

The data were trimmed within a 200m radius around the release site and the loft to remove take-off and landing. When analysing the pair tracks, sections of

flight where the birds were ≥ 50 m apart was excluded. In addition, if the birds swapped front-vs-back positions, the bird who spent the majority of the flight in front based on GPS positioning was identified and the rest of the data from when the other bird was in front was excluded.

3.5.5 Data analysis

We analysed the data using a range of Bayesian hierarchical models, which are similar to mixed models in frequentist methods. The median wingbeat frequency ($\bar{W}_{i,j}$) for the pair (i, j) is assumed to be normally distributed,

$$\bar{W}_{i,j} \sim N(\delta_0 + \delta_1 \|T_i - T_j\| + \omega_i \mu_i + (1 - \omega_i) \mu_j + \gamma X, \sigma) \quad (3.6)$$

where δ_0 is the difference in wingbeat frequency between the solo and paired flight. δ_1 is the difference in wingbeat frequency for every mm absolute difference in tarsus length (T) between the pair (i, j) . For solo flights, the term involving δ_1 equals zero. The expression $\omega_i \mu_i + (1 - \omega_i) \mu_j$ represents a weighted average of the solo wingbeat frequency (μ) of birds i and j with a mixing weighting (ω_i), which determines the weight placed on the bird's own solo wingbeat frequency (μ_i) relative to that of its partner (μ_j). This weighting is bounded to lie between 0 and 1 and was determined by a logistic sigmoid function of the absolute difference in tarsus length,

$$\omega_i = \text{logit}^{-1}(\eta_1 + \eta \|T_i - T_j\|) \quad (3.7)$$

However, across all cases, there was no consistent effect of tarsus difference on the mixing weighting.

Finally, γX represents the effect of the covariates, which are median wind support (m s^{-1}), median crosswind (m s^{-1}), median temperature ($^{\circ}\text{C}$), median humidity (%), humid air density (kg m^{-3}) and the date of release treated as a categorical variable. The birds' median airspeed (m s^{-1}) was also added as a covariate on all models except for models of airspeed. We used airspeed rather than ground speed as a covariate because ground speed and wind support were correlated (Fig. C.5). In terms of the response variable, there was almost no difference between the models of airspeed

and ground speed as the model takes into account the effect of wind (0.64, 95% CrI [0.08, 1.20] compared to 0.69, 95% CrI [0.10, 1.28]). For consistency with the covariates, we present the results of the model for airspeed. A covariate indicating whether the bird was a leader or follower was also added to the model in a secondary analysis to determine the effect of the birds' position on wingbeat frequency.

To investigate whether the birds were flying in phase, we used the following model to identify whether the median wingbeat frequency of the follower ($\bar{W}_F$) is related to the leader ($\bar{W}_L$) in pair (P):

$$\bar{W}_F \sim N(\alpha_P + \beta_P \bar{W} + \gamma X, \sigma') \quad (3.8)$$

We also investigated whether the difference between the leader and follower's tarsus length, body mass or solo airspeed (S) predicted why the bird was a leader (L) in the pair using a Bernoulli regression:

$$L_i \sim \text{Bernoulli}(\alpha_P + \beta_P S_i) \quad (3.9)$$

The model priors were centred on the null hypothesis using the mean, standard deviation and square root standard deviation of the solo data (Table C.4). Eight Markov chain Monte Carlo (MCMC) chains were run simultaneously, each with 12,500 warm-up and 12,500 model iterations, which resulted in 100,000 samples for each posterior distribution. Across all estimated models and parameters, we detected convergence in the sampling distribution as determined by using a criterion $\hat{R} \leq 1.1$ (Gelman & Rubin, 1992). The number of divergent iterations was 0.0-1.3% of the total sample size. The code for the wingbeat frequency model and the model output can be found in the Supplementary Materials in Appendix C.

In addition to these results, one similar-sized pair (birds B01 and B82 with a tarsus length of 32.4 mm and 33.3 mm, respectively) and one different-sized pair (birds B01 and B07 with a tarsus length of 32.4 mm and 35.2 mm, respectively) split and flew solo for more than 30% of the flight for three of their six releases. As the sample size is low, only descriptive statistics can be performed comparing the paired (< 50 m distance between birds) and solo flight (> 300 m distance).

We approximated the number of wingbeats difference between the solo and paired flight using the total flight distance (excluding the 200m take-off and landing) and the model results from route accuracy, airspeed and wingbeat frequency (Table C.2). We calculated the number of wingbeats difference as not all of birds completed 100% of the paired flights together or with one leader.

Data processing and analysis were conducted using MATLAB (MathWorks, Natick, USA; version R2015a) and the open-source software R (version 3.4.2; R Core Team, 2017). Bayesian models were written in Stan (Carpenter *et al.*, 2017) using the R interface RStan (version 2.16.2; Stan Development Team, 2017).

Traditional thesis chapter

Supplementary material can be found in Appendix D.

4

Movement behaviour after birth demonstrates precocial abilities of African savannah elephant (*Loxodonta africana*) calves

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4.1 Abstract

African savannah elephants (*Loxodonta africana*) have the longest gestation period of any mammal. Twenty-two months of gestation is followed by a minimum of

24 months of complete dependency on the mother, and around a further eight years where the mother plays a central role. Despite the high levels of investment in calves, little is known about how gestation, parturition and the presence of a neonatal calf affects movements in African savannah elephants. We examined the relationship between reproductive state and movement characterized using GPS tracking data collected during 18 births from multiparous females ($\geq$ second calving) and three births from primiparous females (first calf). We analysed the data using three-state hidden Markov models to determine whether parturition results in a distinctive change in movement behaviour, characterized as hourly and daily speed, 95% minimum convex polygon (MCP) and sinuosity index. Overall, parturition had little impact on movement in multiparous females. In some cases, parturition was indistinguishable from normal movement patterns. Using linear mixed-effects models, we determined that speed increased and sinuosity index decreased during the ~ 18 days after parturition, but, overall, movements before and after birth were not significantly different. By contrast, two primiparous females remained almost stationary for ~ 22 and ~ 27 hours on the estimated parturition day itself, which may be attributed to the smaller stature of primiparous females. The ability of calves to move soon after parturition could be advantageous given the mothers nutritional and water requirements, and their matriarchal fission-fusion social structure. We speculate that, alongside cognitive development, elephants may have evolved an unusually long gestation period to facilitate an advanced stage of physical development.

4.2 Introduction

In social living species, energy expenditure, and hence individual fitness, can be dependent on the presence and, crucially, on the behaviour of conspecifics. If the benefits of cooperating with conspecifics, such as information sharing and predator protection, outweigh the costs, such as increased competition for food resources, then an individual will on balance benefit from cooperating (Sumpter, 2006, 2010). However, little is known about the energetic consequences of collective behaviour

to the individual. Locomotion in particular is energetically expensive and can make up a substantial proportion of the daily energy budget for an individual (Schmidt-Nielsen, 1972). Within a group itself, individuals may differ in many ways, including gender, size, age and reproductive and physiological state. As a result, optimal movement patterns may differ between individuals. Although there could be some benefit from assisting related individuals as it may increase the fitness of the actors, a compromise of optimal movement patterns could also result in a reduction in energy acquisition and reproductive performance (Sumpter, 2006, 2010). When extrapolated over a group, the costs could be greater than the benefits of increasing the reproductive output of the helped relative. Understanding how and to what extent groups will compromise on optimal movement patterns in order to maintain group structure with specific individuals, such as the young or injured, could provide key insights into collective behaviour.

African savannah elephants (*Loxodonta africana*) have the longest gestation period of any land animal (Moss, 1988). One calf is born after a 22-month gestation period. Twins are rare (Moss, 1988). After birth, the calf is completely dependent on the mother for a minimum of 24 months, although more often weaning occurs after the birth of another calf after 3-5 years (Lee & Moss, 1986). The mother continues to play a crucial role for the calf for the first five to ten years of life. Despite the comparatively high levels of investment involved in reproduction, little research has been conducted into how parturition impacts the herd, particularly the movement patterns. African savannah elephant societies represent an interesting example of a ‘fission-fusion’ system whereby groups merge (fusion) or split (fission) depending on available resources, enabling individuals to adjust dynamically to varying costs and benefits of group living (Wittemyer *et al.*, 2005; Archie *et al.*, 2006; Couzin, 2006). Although elephant societies are known to split in times of need, it is unknown whether herds will adapt their movements in order to maintain group structure with specific individuals. Thus, reproductive behaviour in female elephants may provide an ecologically relevant example of how a group may need to dynamically adjust to requirements of group members.

One of the reasons that little research has been conducted into the movements of elephants around parturition is that observations of births are relatively rare. Despite the long gestation period, neonatal calves only weigh 110-120 kg, which is comparatively small relative to a $\sim 2,500$ -3,000 kg mature female (Hanks, 1972; Lee & Moss, 2011). This means that, for females over the age of 20, there is little outward sign of pregnancy in late gestation, except for breast enlargement (Moss, 1988). In late gestation, cows can appear lethargic and visually may appear to slow their movements (Nicholson, 1954; Sikes, 1971; Moss, 1988). Some females separate from herd with one or two other females (Nicholson, 1954), whilst others remain with the herd and continue engaging in activities, such as foraging, even whilst in labour (Douglas-Hamilton, 1972; Leuthold & Leuthold, 1975). Parturition itself is usually rapid due to the size of the calf and the vertical position of the birth canal, and often occurs at night (Moss, 1988; Allen *et al.*, 2003). Calves are born fully developed and are capable of standing and then walking a few steps within an hour of birth. Initially, calves tend to be very unsteady on their feet but continue to become more stable with the passing of hours and days and are assisted with standing and walking by their mother and other females, often teenage allomothers (non-maternal infant carers; Moss, 1988; Lee & Moss, 2011). Elephants present at parturition have been observed becoming excited and exhibiting rumbling, trumpeting and guarding behaviour (Poppleton, 1957; Leuthold & Leuthold, 1975; Jones, 1985; Mutinda, 1996). However, after the initial postpartum period, herds often resume their normal activities and move away from the birth site, at which point either the mother and calf move off with the herd at a slow pace (Douglas-Hamilton, 1972; Jones, 1985; McKnight, 1991; Church, 1992) or they are left behind either with (Leuthold & Leuthold, 1975; Moss, 1988) or without other individuals (Poppleton, 1957). Some mother-calf units left behind will re-join the herd later in the day (Leuthold & Leuthold, 1975) and others several days later (Nicholson, 1954).

The separation of elephant herds both peri- and post-partum could suggest that, in some cases, the costs to the group of staying with a female in late gestation or a neonatal calf outweigh the benefits that could be attained from foraging

elsewhere. This study aims to quantify the extent to which gestation, parturition and a neonatal calf affects the movement patterns of elephants, and hence the degree to which elephants must adapt their movement patterns in order to stay together. We analysed the global positioning system (GPS) tracking data of 18 births from multiparous females ($\geq$ second calving) and three births from primiparous females (first time mothers) throughout the peri- and post-partum periods. We used a fixed three-state hidden Markov model to determine whether the mother made distinctive changes in her daily mean speed, daily home range size and track tortuosity during the peri- and post-partum period. We analysed whether these changes in state corresponded with the estimated parturition date. As we selected collared elephants that gave birth to understand movement patterns, the analysis was limited to calves born in or near Samburu and Buffalo Springs National Reserves, thus, we did not analyse environmental characteristics of the birth site. The results of our study reveal the precocial movement abilities of neonatal elephant calves.

4.3 Methods

4.3.1 Study population

Since 1997, demographic data has been collected as part of an ongoing long-term monitoring project on the elephants inhabiting the unfenced Samburu and Buffalo Springs National Reserves in northern Kenya (0.3-0.8°N, 37-38°E; Wittemyer, 2001). The study area consists of semiarid savanna bushland along the semi-permanent Ewaso N'giro River, which is the largest river in the region and a focal point for wildlife. Rainfall averages approximately 350mm per year and occurs biannually during April-May and November-December. The study population, which uses both the reserves and the surrounding area ($> 3,500 \text{ km}^2$), consists of approximately 900 individuals, which can be individually identified using ear and tusk idiosyncrasies (Wittemyer, 2001). The elephants have become habituated to vehicles as a result of tourism which has enabled detailed behavioural and demographic monitoring of the population. Between 1997 and 2017, over 1,000 births have been recorded. Each calf was aged at first sighting using established aging techniques (Moss, 1996,

2001), which means that, for calves under one month old, the age can be accurately estimated to within one week (Wittemyer *et al.*, 2007a).

4.3.2 Study subjects

As elephant herds sometimes separate during the initial post-partum period, we limited our analyses to births from individuals fitted with a GPS tracking collar to ensure the data represented the movement of the mother and calf. In total, 22 calves were born to elephants being actively tracked. Two births were excluded due to GPS data gaps within 10 days of the estimated birth date. One additional birth was added to the sample size from a non-collared elephant as the herd, which included a collared elephant, were being filmed by a television crew from the BBC Natural History Unit who were able to confirm that the collared elephant remained with the mother and calf throughout the peri- and post-partum periods. The 21 births were from 18 females that ranged in age from 12 to 48 at time of birth and included five matriarchs, three primiparous females (first time mothers) and two elephants from orphan herds (Table 4.1). As the results of this study were highly individualistic, we refer to these individuals by their given name, or name followed by year in the case of multiple births, rather than their identification number for ease of reading. We divided the dataset into multiparous females ($\geq$ second calving) and primiparous females (first calf). Of the 18 births from multiparous females, six calves were observed within five days of birth and no other births or deaths occurred within the herd ± 30 days. The remaining 12 calves were observed between 0 and ~ 33 days after birth. We analysed the data both with the dataset of six individuals with accurate birth estimates and the expanded dataset including the 12 other births from multiparous females.

The three primiparous females had different levels of experience with young calves. Habiba, a 12-year-old female, was a matriarch of an orphan herd, the Swahilis, which consisted of two young females (aged six and ten) and one male (aged nine). Habiba's herd often associated with a herd with an experienced matriarch. Luna (2014; aged 14) belonged to the remnants of the Planets, which

consisted of two females, aged 22 and 19, and their calves aged 11, 8, and 18 months. Luna also spent time associating with another unrelated herd. Luna lost her first calf (2014) for unknown reasons aged ~ 3.5 months and had a second calf two years later, which is included in the sample of multiparous females (Luna, 2016 calf). The remainder of the Swahilis and the Planets were poached or went missing during poaching and drought periods between 2009-2012. Finally, Soutine (aged 14) was a primiparous female from a relatively large herd consisting of eight parous females and their calves. Soutine's mother was poached when she was aged eight. Four calves were born within this herd during the two years prior to the birth of Soutine's calf, including Flaubert's calf, which means Soutine had experience as an allomother (non-maternal infant care).

4.3.3 Movement data

The GPS collars were fitted by Save the Elephants under the supervision from a veterinarian from the Kenya Wildlife Service. The GPS collars used were African Wildlife Tracking models A and MT2000 (African Wildlife Tracking cc, Pretoria, South Africa), LOTEK model 2000 (LOTEK Engineering Ltd., Newmarket, ON, Canada), Savannah Tracking models GL100 and GL200 (Savannah Tracking Ltd., Nairobi Kenya) and TVP models SIMPLEX and T5HS (Televilt Positioning AB, Lindesberg, Sweden). The collars recorded positions at 15-minute, 30-minute or one-hour intervals. To maintain consistency, the four births recorded at 30-minute intervals and one birth at 15-minute intervals were systematically down-sampled to one-hour sampling frequencies on the hour. We fitted a continuous-time correlated random walk model to predict temporally-regular locations for missing data points ≤ 4 hours (Johnson *et al.*, 2008). Data gaps > 4 hours were excluded from the analysis. For each GPS point, the orthodromic (great-circular) distance from the previous point was calculated using the haversine formula. Speed (km hour^{-1}) was then calculated using distance over the total time between each GPS fix in hours. Daily tortuosity was estimated using the sinuosity index (*SI*) proposed

Table 4.1: Study subject information, including the name and age of the mother and details of birth. Individuals with two births are referred to by their name followed by the year of birth studied.

Parity	Group	Mother	Herd	Age	GPS collar	n calves in study	Estimated date of parturition	Estimated calf age (days) at first sighting	Calf sex	Notes	Days until other calves born	
Multiparous	Accurate	Amina	Swahilis	48	Yes	1	27/04/2004	2	M			
		Delaware	Native Americans	22	Yes	1	03/11/2015	1	M			
		Flaubert	Artists	28	Yes	1	04/02/2016	0	M			
		Maya Churchill	First Ladies	27	Yes	1	17/01/2003	4	M		22*	
		Ngalatoni	Samburu Ladies	34	Yes	1	15/02/2003	2	F	Matriarch		
	Expanded	Rosemary (2005)	Spice Girls	39	Yes	2	21/10/2005	0	M	Matriarch		
		Annabelle	Royals	27	Yes	1	21/10/2013	1	F			-26; 1
		Aztec	American Indians	28	Yes	1	22/10/2003	1	F			-8
		Chyulu	Ol Donyos	21	Yes	1	01/12/2016	13	M			
		Jerusalem (2003)	Biblical Towns	35	Yes	2	17/11/2003	16	M			
		Jerusalem (2008)	Biblical Towns	40	Yes	2	13/12/2008	33	M			
		Karoo	Acacias	23	Yes	1	29/10/2017	6	F			0; 3; 15
		Luna (2016)	Planets	16	Yes	2	08/03/2016	30	F	Orphan herd		
		Nutmeg	Spice Girls	21	Yes	1	15/11/2016	15	M			
		Rosemary (2003)	Spice Girls	37	Yes	2	28/02/2003	0	M	Matriarch		-17
		Salma Kikwete	First Ladies	18	Yes	1	03/11/2017	13	M			0; 5; 7
		Wendy	Poetics 1	35	Yes	1	29/01/2018	15	F	Matriarch		-28
		Cyclone	Storms 1	44	No	1	28/10/2017	0	F	Matriarch		-17
		Primiparous	Habiba	Swahilis	12	Yes	1	30/11/2013	3	M	Matriarch; Orphan herd	
Luna (2014)	Planets		14	Yes	2	28/01/2014	1	F	Orphan herd			
Soutine	Artists		14	Yes	1	16/02/2018	2	M				

*Not observed with this individual during birth period.

by Benhamou *et al.* (2004):

$$SI = 2 \left[p \left(\frac{1 + c^2 - s^2}{(1 - c)^2 + s^2} + b^2 \right) \right]^{-0.5} \quad (4.1)$$

where p and b are the mean and the coefficient of the variation of step length (distance), and c and s are the mean cosine and sine of the turning angle between each step (Benhamou, 2004). Daily home range size was estimated using a 95% Minimum Convex Polygon (MCP) (Mohr, 1947).

4.3.4 Covariates

For each GPS point, the slope (0-90°) was calculated using the Shuttle Radar Topography Mission (SRTM) 90m version 4 elevation dataset (Jarvis *et al.*, 2008). To measure time-specific vegetation productivity, we used NASA's Terra Moderate Resolution Imaging Spectroradiometer (MODIS) 16-day 250m composites of normalised difference vegetation index (NDVI; DOI: 10.5067/MODIS/MOD13Q1.006 Didan., 2015). A binary covariate was added to distinguish whether an elephant was in or out of a protected area. For the hourly level models, the day and night movements were differentiated between 06:30 and 18:30. As Samburu and Buffalo Springs National Reserves are situated near the equator (0.3-0.8°N) the timing of sunrise and sunset is relatively consistent throughout the year. The elevation and NDVI datasets were downloaded from Google Earth Engine (Gorelick *et al.*, 2017). Maps of protected areas were developed by Save the Elephants.

4.3.5 Data analyses

To determine whether elephants changed their movement patterns around parturition, we analysed the data using three-state Bayesian hidden Markov models (HMM), which identify distinctive changes in movement. We analysed the data using HMMs at two different resolutions. Firstly, we analysed the daily mean speed, sinuosity index and 95% MCP within ± 90 days and ± 30 days of the estimated date of parturition to determine whether there were distinct changes in state affecting daily movement patterns above normal movement patterns. We analysed daily

mean speed an analogue of distance, which enabled us to include days with a small amount of missing GPS fixes (≥ 20 samples). MCP was positively skewed and was therefore log-transformed before analysis. As mean speed, sinuosity index and log-transformed 95% MCP are related to each other (Figure S1), we also ran a principle component analysis (PCA) but analysing the principle components led to no improvement in detection, therefore we just present the results of these variables separately. Secondly, we analysed the data at a finer resolution looking at the hourly level speed after accounting for the effects of the day or night, NDVI, slope and protected area, which have all been shown to affect movement patterns in elephants (Wall *et al.*, 2006; Wittemyer *et al.*, 2008; Boettiger *et al.*, 2011; Bohrer *et al.*, 2014; Ihwagi *et al.*, 2018). We analysed the hourly level data with both ± 30 days and ± 10 days either side of the estimated date of parturition.

HMMs have two parts: the states, which are unobserved, and the observations, which are modelled as originating from an emission probability distribution, which is conditional on the latent states. In a HMM, we suppose that the different states have probability distributions of the same form, but differing parameter values (speeds). We centred the HMM priors on the hypothesis that elephants decrease their speed around parturition. The three states comprised the speed at the start of the selected time period (State 1), followed by a slower speed in State 2 and then a higher speed in State 3 (Fig. 4.1). The three latent states were ordered so no other sequence of moves was possible but allowed for differences in peri- and post-partum movement patterns. HMMs were run separately on each individual and determined from the speed data alone when the elephant changed state. We analysed whether these changes in state corresponded with the estimated parturition date.

We modelled the daily speed of the elephants using a normal sampling HMM whose parameters depended on the estimated state of the elephant, thus the emission of mean speed ($\bar{S}$) at time (t) followed:

$$\bar{S}_t \mid k \sim \text{normal}(\alpha_{t,k}, \sigma_k) \quad (4.2)$$

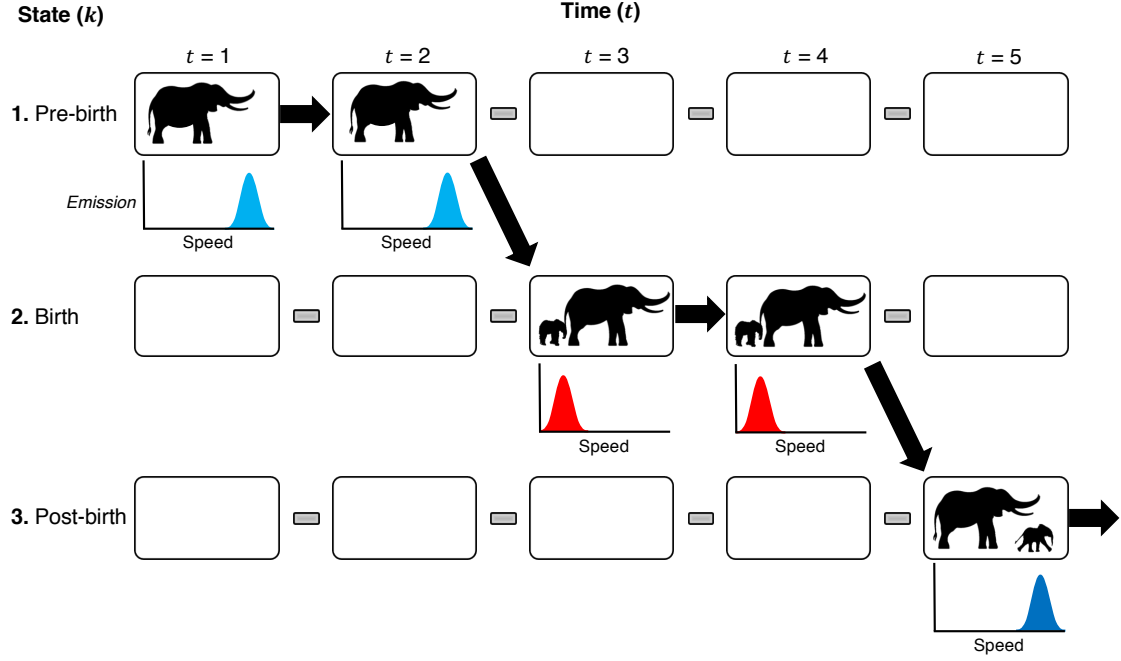


Figure 4.1: Three-state hidden Markov model for daily mean speed. The model assesses the probability of the elephant being in state k at time t based on the emission distribution of speed. For our model, we tested the hypothesis that elephants slow down during the birth period.

where k is the latent state, α is the parameter value in that state and σ_k is the standard deviation. In the daily model, there were no covariates and so $\alpha_{t,k}$ is time independent:

$$\alpha_{t,k} = \beta_k \quad (4.3)$$

where β_k is the unconstrained parameter. The model priors can be found in Table D.1. By using priors in the Bayesian HMM, we give a degree of meaning to each state, for example the second state as a lower speed state. We modelled the hourly speed (S) of the elephants using an exponential distribution so the emission distribution at time (t) followed:

$$S_t \mid k \sim \text{exponential}(\alpha_{t,k}) \quad (4.4)$$

The parameter (α) value was equal to:

$$\alpha_{t,k} = \log(\beta_k + \gamma X_t) \quad (4.5)$$

where β_k is the unconstrained parameter and X_t represents the covariates of day-night, NDVI, slope and in-out of a protected area. We used a log link function to ensure that $\alpha_{t,k}$ was always positive, to match the support of the exponential distribution. In both HMM models, we treated missing points by assuming that the latent state of the elephant in these periods was the same as it was in the most recent non-missing period. Eight Markov chain Monte Carlo (MCMC) chains were run simultaneously, each with 5,000 warm-up and 5,000 model iterations, which resulted in 40,000 samples for each posterior distribution. We detected convergence in the sampling distribution as determined by using a criterion $\hat{R} \leq 1.1$ (Gelman & Rubin, 1992). The HMM code and an example model output can be found in the supplementary materials in Appendix D.

To compare the movements on the date of birth itself, we first extracted the lowest daily mean speed and log-transformed 95% MCP and highest sinuosity index within an error margin of the estimated parturition date to account for any slight inaccuracies in the estimated parturition date. As the error margin of the calf age is expected to increase with the age of the calf, we gave age estimates of 0-1 day old a margin of ± 2 day to account for the effects of labour, 2-7 days ± 2 days and then added ± 1 day for every week thereafter. For example, a calf aged 28 days at first sighting was given an error margin of ± 5 days. We then analysed the number of standard deviations the minimum value (or maximum in the case of sinuosity index) was away from the mean of the yearly data. The year data made up the remainder of the year of tracking data outside the error margin, ideally taken evenly before and after parturition. If this was not possible, we took as much sequential data either side of the error margin as possible for a total of 365 days minus the size of the error margin. Days with < 20 GPS fixes were excluded from the analysis and not replaced.

For the multiparous females, linear mixed effects (LME) models were used to analyse changes in daily mean speed, sinuosity index and log-transformed 95% MCP before and after birth. The LME models were run on both dataset of the six births with accurate birth estimates and the expanded dataset of all 18 births from 90 and 30 days to the day before birth, and from one day to 30 and 90 days after

birth. We also ran the linear mixed-effects models using the day with the lowest detected daily means speed within the error margin of the birth estimate as the estimated parturition date, but this led to no significant alteration of the results so we just present the results from the estimated date of parturition. We added the fixed effects of the number of days since the estimated parturition date, the number of days squared, daily mean NDVI, NDVI², daily mean slope, slope² and protected area. In order to avoid possible computer rounding errors, all continuous covariates were standardised by subtracting the mean and dividing by the standard deviation $\left(\frac{x-\bar{x}}{\sigma}\right)$ once at the start of the analysis and thus were on the same scale for all analyses. Protected area was rounded to a binary covariate. The identity of the mother, rather than birth, was added as a random effect on the intercept to account for the multiple births from two multiparous females. To account for the temporal relatedness of observations, we added a continuous time autoregressive lag-1 correlation (corCAR1) to the models (Pinheiro & Bates, 2000).

We used the function ‘dredge’ in the R package MuMIn (Bartoń, 2017) to compare all possible combinations of the model and then selected the model with the lowest second-order Akaike information criterion with the models fitted with maximum likelihood (Burnham & Anderson, 2002). Likelihood ratio tests (LRT) were used to test the statistical significance of each fixed effect in the best-fitting model. The models were then refitted using restricted maximum likelihood to obtain parameter estimates and confidence intervals. Models were checked for assumptions of linearity, normality, homoscedasticity and autocorrelation by visual inspection of plotted residuals and autocorrelations. Model fit was assessed by calculating marginal ($R^2_{\text{LME}(m)}$) and conditional R-squared values ($R^2_{\text{LME}(c)}$) using the methods described in Nakagawa and Schielzeth (2013).

Data processing and analysis was conducted in the open-source software R (version 3.4.3; R Core Team, 2017), using the packages adehabitatHR (version 0.4.15; Calenge, 2006), MomentuHMM (version 1.4.0; McClintock & Michelot, 2018), MuMIn (version 1.40.0; Bartoń, 2017), nlme (version 3.1-131.1; Pinheiro *et al.*, 2018), raster (version 2.6-7; Hijmans, 2017), rgdal (version 1.2-16; Bivand *et al.*,

2017), rgeos (version 0.3-26; Bivand & Rundel, 2017), sp (version 1.2-7; Pebesma & Bivand, 2005; Bivand *et al.*, 2008) and spatialEco (version 1.0-1; Evans, 2017). HMMs were written in Stan (Carpenter *et al.*, 2017) using the R interface RStan (version 2.17.3; Stan Development Team, 2017).

4.4 Results

4.4.1 Multiparous females

Overall, the results of the individual three-state HMMs were highly variable both in terms of the timing of the detected state changes and, in some cases, between models of the same birth. Only two individuals (Flaubert aged 28 and Luna (2016) aged 16) decreased their movement patterns around the estimated parturition date itself. Flaubert dropped her speed from 0.97 km h⁻¹ (30-day hourly model, 95% Bayesian credible interval (CrI) [0.91, 1.00]) to 0.43 km h⁻¹ (95% CrI [0.36, 0.51]) from 5.12 days prior to the estimated parturition date (both hourly level models 95% CrI [-5.12, -5.12]) to between 4 and 8 days after birth (hourly ± 30 days: 6.9, 95% CrI [4.62, 8.21]; ± 10 days: 7.61, 95% CrI [4.62, 8.21]; Fig. 4.2e-f). Luna (2016) decreased her movements from -0.53 days before the estimated parturition date (± 30 days hourly HMM, where 0.0 represents 12:00 on the estimated date of parturition, 95% CrI [-0.54, -0.54]) to 0.17 days after parturition (95% CrI [0.12, 0.25]), which is a total of ~ 17 hours. During this time, Luna (2016) remained almost stationary (0.05 km h⁻¹, 95% CrI [0.02, 0.09]), but then increased her speed to approximately the same speed as before (before 0.50 km h⁻¹, 95% CrI [0.38, 0.64] and after 0.48 km h⁻¹, 95% CrI [0.37, 0.62]; Fig. 4.2e-f). However, the daily level HMMs were unable to detect parturition due to other dips in speed. Luna (2016) was the only multiparous female where the specific day of parturition was detected.

In eight out of 18 births, the HMM detected a state change at the start of the allotted time period, followed by a second state change later in the period, which indicates that the elephants were travelling at a slower speed followed by a faster speed (Fig. 4.3). Indeed, Aztec exhibited just two movement states, with a slower movement pattern from the start of the 30 days until 2-3 days after

parturition (daily mean speed ± 30 days: 1.58 days, 95% Bayesian credible interval (CrI) [1,2]; ± 10 days: 2.93, 95% CrI [2.92, 4.25]; Fig. 4.2c-d). At which point, Aztec increased her speed by 101% from 0.27 km h⁻¹ (95% CrI [0.27, 0.31]) to 0.58 km h⁻¹ (95% CrI [0.52, 0.64]). Aztec's log-transformed 95% MCP also increased by 113% and her sinuosity index decreased by 35% (straighter trajectory). Karroo also demonstrated consistent changes across all but the 90 day model with an increase in her speed slightly prior to parturition at -2.94 days (daily ± 30 days: 95% CrI [-3,-3]). The remainder of the individuals which exhibited two states either had state changes apparently unrelated to day of parturition (Annabelle and Delaware), had relatively wide credible intervals (Chyulu and Rosemary 2005) or the timing of the changes varied between models indicating a potential effect of environmental covariates (Nutmeg and Salma Kikwete).

The remaining eight individuals had wide credible intervals on all or most of the HMMs, suggesting a large degree of uncertainty in the state changes and, in some cases, exhibited state changes apparently unrelated to parturition (Fig. 4.2, Fig. D2-D7). In addition, Ngalatoni, a matriarch, migrated from the Ewaso N'giro river in Buffalo Springs National Reserve to the Ndare forest in the south, starting at 16:00 on the 9th day after birth and reaching the border to Ndare at 22:00 on the 15th day, which was a journey of 64.83km (linear interpolation between data points). In the process, Ngalatoni and her herd climbed from an elevation of 859 m above sea level to a maximum of 2,143 m, with the cumulative change in elevation over the course of five days totalling 2,026 m, which is a substantial undertaking relatively soon after parturition.

Visually, some individuals had dips in their daily mean speed either on the estimated date of birth or on the day before, but these dips in speed were not present in all individuals (Fig. D.2-7; Table D.2). Although dips in speed may be indicative of parturition, the dips were not distinctive when placed in the context of speed over a two-month period as there were multiple dips in speed over this time period. Indeed, when examining the lowest daily mean speed within the potential error of the estimated parturition date (see methods), no multiparous

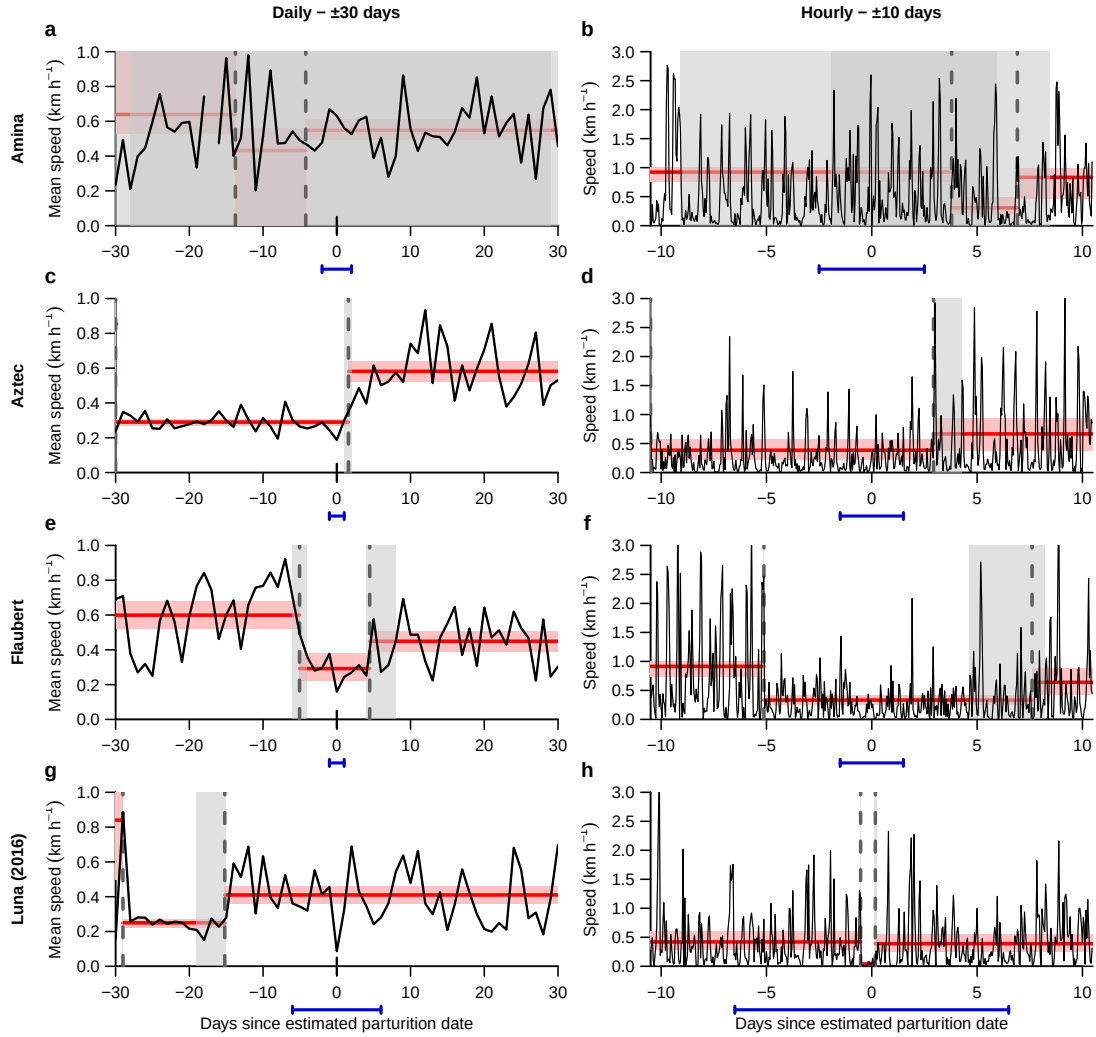


Figure 4.2: Three-state hidden Markov model results for (a, c, e, g) daily mean speed ± 30 days either side of midday of the estimated date of parturition, and (b, d, f, h) hourly speed for (a-b) Amina, (c-d) Aztec, (e-f) Flaubert and (g-h) Luna (2016). Grey dashed lines denote the timing of the mean state change and grey shaded area indicates the corresponding credible interval ($\pm 95\%$). Red lines are the estimated mean speed during each state with the red shaded area corresponding to the 95% credible interval. Horizontal blue lines indicate the potential error margin on the estimated parturition date (day 0).

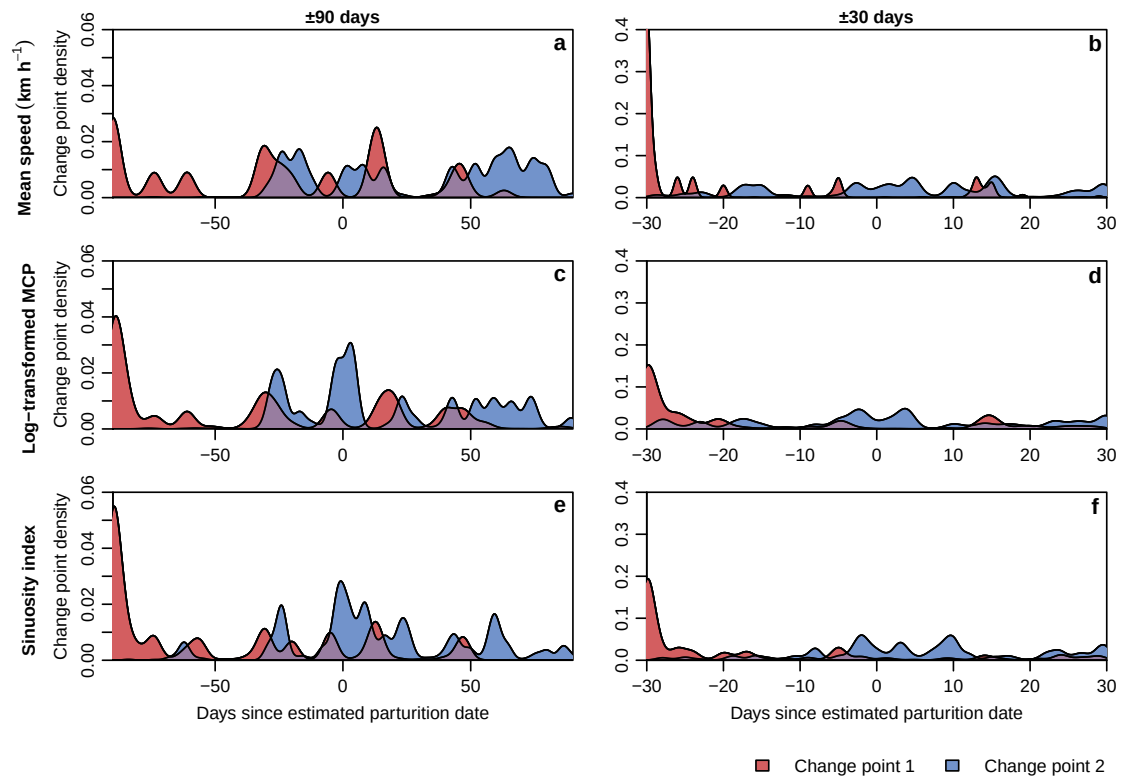


Figure 4.3: The estimated posterior probability distribution of change point timing for all iterations of the three-state hidden Markov model of daily mean speed (km h^{-1}), log-transformed 95% MCP and sinuosity index for ± 30 days and ± 90 days for all multiparous females. Each model on each individual resulted in 40,000 samples for each posterior distribution. High probability of change point one occurring at the onset of the dataset indicates a general trend in the data to change point 2.

females had daily mean speeds outside of two standard deviations from the mean of the yearly data, and only five out of 18 individuals (Aztec, Delaware, Flaubert, Luna (2016) and Maya Churchill) were outside one standard deviation from the mean (e.g. outside 68% of the data; Table 4.2). By contrast, six individuals had log-transformed 95% MCP's and/or sinuosity indices outside of two standard deviations from the mean (e.g. outside of 95% of the data), which suggests that home range size and the straightness of the trajectory were significantly lower and higher than the normal for these individuals, respectively. As with the other results, this result was not consistent across all individuals. In total, six out of 18 individuals had values inside one standard deviation from the yearly mean of daily mean speed, log-transformed 95% MCP and sinuosity index, which indicates

that, for these individuals, the movements on the estimated parturition date were well inside the range of normal movements.

In all cases, during the first complete day of the calf's life the daily mean speed, log-transformed 95% MCP and sinuosity index were all inside two standard deviations of the yearly mean when the first day was taken as either the day after the estimated parturition date or as the mode of the days detected for low speed, low 95% MCP and sinuosity index within the error margin of the birth date. The total distance travelled by the calf using linear interpolation between data points was between a mean of 8.16 ± 3.42 km (mode day plus one) and 9.88 ± 2.83 km (Day 1; after accounting for the effects of multiple calves from two females). The mean daily distance travelled in the remainder of the year was 8.80 ± 2.49 km.

Overall, the results of the HMMs suggest that there were no consistent state changes in relation to parturition behaviour. However, the HMMs detect distinct state changes and not gradual changes in movement. The results of the linear mixed-effects models revealed that the multiparous females significantly increased their daily mean speed and sinuosity index between 1 and 30 days after parturition (speed estimate (scaled) for all multiparous females 0.50, 95% confidence interval (CI) [0.13, 0.88], likelihood ratio test (LRT): = 6.83, $p = 0.009$; day2: -0.70, 95% CI [-1.28, -0.12], LRT: = 5.52, $p = 0.019$). Daily mean speed peaked 18 days after parturition, at which point the estimated speed was $\sim 24\%$ higher than on day 1, but the speed decreased again so that at the end of the 30-day period the speed was only 12% higher than day 1 (Fig. 4.4). Days since parturition was not a significant factor on the model of 95% MCP or on any of the variables between 1-90 days after parturition.

The results prior to parturition were a little more variable. The analysis of the six births with accurate parturition dates indicated that the speed and 95% MCP decreased, and sinuosity increased, prior to parturition. By contrast, day was not a significant factor on any of the movement variables between -90 or -30 days and 1 day prior to parturition (Tables D.3-D.4). There was no significant difference between the daily mean speed, log-transformed 95% MCP or sinuosity index before and after birth (± 30 days, excluding the estimated date of parturition).

Table 4.2: Comparison of the lowest daily mean speed, log-transformed 95% MCP and sinusity index within the potential error of the estimated parturition date to the yearly values of each variable. Birth value's more than two standard deviations from the yearly mean (e.g. outside of 95% of the data) are highlighted in **bold**.

Group	Name	Female age	Estimated parturition		Year sample		Daily mean speed (km h ⁻¹)					Log-transformed 95% MCP					Sinuosity index			
			Days since	Search range	Start day	End day	n days	Day	Yearly mean $\pm$ SD	Birth value	SD from mean	Day	Yearly mean $\pm$ SD	Birth value	SD from mean	Day	Yearly mean $\pm$ SD	Birth value	SD from mean	
Multiparous	Accurate	Amina	48	2 $\pm$ 2	-182	182	357		-2	0.45 $\pm$ 0.19	0.48	0.1	-2	1.47 $\pm$ 1.01	1.44	0.0	-2	3.23 $\pm$ 1.16	2.68	-0.5
		Delaware	22	1 $\pm$ 1	-182	182	349		0	0.38 $\pm$ 0.17	0.12	-1.5	0	1.04 $\pm$ 1.00	-0.69	-1.7	0	3.79 $\pm$ 1.27	5.42	1.3
		Flaubert	28	0 $\pm$ 1	-268	96	362		0	0.46 $\pm$ 0.15	0.16	-1.9	0	1.52 $\pm$ 0.90	-0.38	-2.1	0	3.09 $\pm$ 0.97	4.58	1.5
		Maya Churchill	27	4 $\pm$ 2	-77	287	345		-1	0.44 $\pm$ 0.18	0.17	-1.5	-1	1.52 $\pm$ 0.86	-0.30	-2.1	-1	3.22 $\pm$ 1.11	6.30	2.8
		Ngalatoni	34	2 $\pm$ 2	-103	261	257		2	0.43 $\pm$ 0.23	0.25	-0.8	-1	1.29 $\pm$ 1.24	0.23	-0.9	2	3.90 $\pm$ 2.36	4.48	0.2
		Rosemary (2005)	39	0 $\pm$ 1	-182	182	335		0	0.38 $\pm$ 0.15	0.19	-1.2	0	1.09 $\pm$ 0.89	0.55	-0.6	0	3.96 $\pm$ 1.27	7.09	2.5
	Expanded	Annabelle	27	1 $\pm$ 1	-182	182	362		0	0.36 $\pm$ 0.17	0.19	-1.0	-1	1.10 $\pm$ 0.96	0.30	-0.8	-1	3.74 $\pm$ 1.21	3.99	0.2
		Aztec	28	1 $\pm$ 1	-194	164	356		0	0.37 $\pm$ 0.13	0.19	-1.4	-1	1.26 $\pm$ 0.76	-0.43	-2.2	0	3.62 $\pm$ 0.94	6.19	2.7
		Chyulu	21	13 $\pm$ 3	-182	182	356		2	0.39 $\pm$ 0.24	0.32	-0.3	-2	1.05 $\pm$ 1.07	0.31	-0.7	2	3.61 $\pm$ 1.42	4.15	0.4
		Jerusalem (2003)	35	16 $\pm$ 4	-182	182	356		4	0.40 $\pm$ 0.14	0.31	-0.7	-4	1.32 $\pm$ 0.87	0.69	-0.7	-4	3.40 $\pm$ 0.94	4.50	1.2
		Jerusalem (2008)	40	33 $\pm$ 6	-182	182	352		-4	0.33 $\pm$ 0.16	0.17	-1.0	-4	0.73 $\pm$ 1.04	-0.18	-0.9	-4	4.05 $\pm$ 1.26	5.84	1.4
		Karoo	23	6 $\pm$ 2	-233	131	360		-1	0.27 $\pm$ 0.14	0.27	0.0	-1	0.23 $\pm$ 1.22	0.50	0.2	-1	4.73 $\pm$ 1.59	4.49	-0.2
		Luna (2016)	16	30 $\pm$ 6	-92	272	352		0	0.37 $\pm$ 0.15	0.09	-1.9	0	1.15 $\pm$ 0.93	-1.12	-2.4	0	3.62 $\pm$ 1.11	6.87	2.9
		Nutmeg	21	15 $\pm$ 4	-182	182	350		-2	0.24 $\pm$ 0.13	0.20	-0.4	2	0.32 $\pm$ 0.93	-0.08	-0.4	-2	4.68 $\pm$ 1.21	5.19	0.4
Primiparous	Rosemary (2003)	37	0 $\pm$ 1	-102	262	277		-1	0.40 $\pm$ 0.19	0.22	-1.0	-1	1.18 $\pm$ 1.00	-1.26	-2.4	-1	3.59 $\pm$ 1.28	9.12	4.3	
	Salma Kikwete	18	13 $\pm$ 3	-166	100	182		-3	0.32 $\pm$ 0.16	0.20	-0.8	-2	0.69 $\pm$ 1.02	-0.24	-0.9	-3	4.12 $\pm$ 1.36	6.07	1.4	
	Wendy	35	15 $\pm$ 4	-325	39	353		-1	0.30 $\pm$ 0.13	0.20	-0.8	-2	0.54 $\pm$ 1.14	-0.22	-0.7	-1	4.26 $\pm$ 1.30	5.90	1.3	
	Cyclone	44	0 $\pm$ 1	-232	132	362		-1	0.33 $\pm$ 0.13	0.20	-1.0	-1	0.83 $\pm$ 1.02	-0.49	-1.3	0	4.03 $\pm$ 1.16	5.12	0.9	
	Habiba	12	3 $\pm$ 2	-159	197	310		1	0.48 $\pm$ 0.37	0.34	-0.4	-1	1.47 $\pm$ 1.05	1.18	-0.3	-2	3.27 $\pm$ 1.39	3.88	0.4	
	Luna (2014)	14	1 $\pm$ 1	-182	182	359		0	0.44 $\pm$ 0.17	0.04	-2.3	0	1.50 $\pm$ 0.97	-3.57	-5.2	0	3.24 $\pm$ 1.20	9.41	5.2	
	Soutine	14	2 $\pm$ 2	-343	21	360		-2	0.46 $\pm$ 0.16	0.07	-2.5	-2	1.42 $\pm$ 1.11	-2.08	-3.2	-1	3.17 $\pm$ 1.31	6.93	2.9	

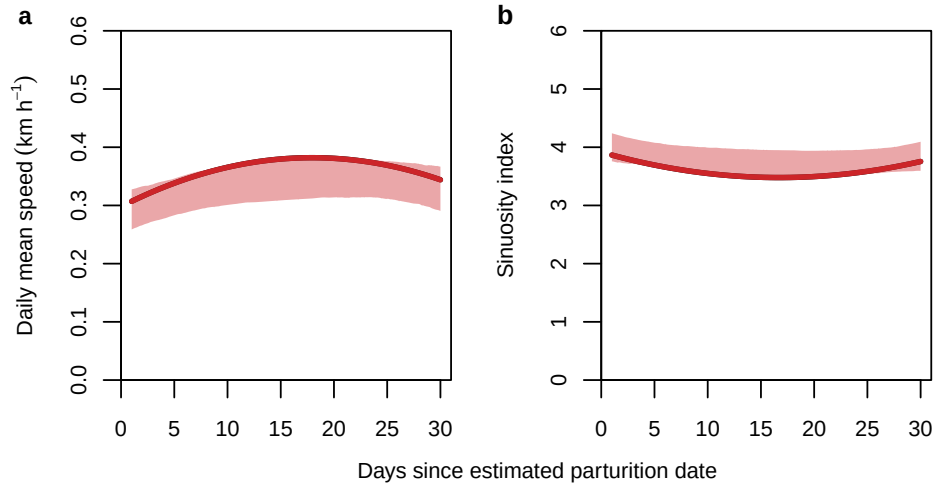


Figure 4.4: Linear mixed-effects models of (a) daily mean speed (km h^{-1}) and (b) sinuosity index for all multiparous females between 1 and 30 days after the estimated date of parturition. Shaded area corresponds to the 95% confidence interval from a non-parametric bootstrap of 1,000 resampled data points.

4.4.2 Primiparous females

In contrast to the multiparous females, both Luna (2014) and Soutine displayed significant drops in movement on the days around the estimated parturition date. Luna (2014) dropped her hourly speed from a mean of 0.56 km h^{-1} (± 30 -day model; 95% CrI [0.45, 0.69]) to just 0.03 km h^{-1} (95% CrI [0.02, 0.05]) at $\sim 01:00$ on the estimated date of parturition (-0.46 days, 95% CrI [$-0.50, -0.46$]; Fig 5b), which is -2.3 standard deviations away from the yearly mean. Furthermore, Luna's log-transformed MCP and sinuosity index were significantly lower than normal (5.2 standard deviations away from the yearly mean). The hourly level HMM detected that Luna commenced moving at $\sim 04:00$ the day after birth (0.70 days, 95% CrI [0.67, 0.71]), which means Luna remained almost stationary for ~ 27 hours. The broader daily level model found that Luna's daily mean speed remained lower than normal until 18.05 days after birth (95% CrI [17, 22]; 0.26 km h^{-1} , 95% CrI [0.21, 0.32]). At which point, Luna's mean speed returned to approximately the same speed as before birth (before 0.49 km h^{-1} , 95% CrI [0.42, 0.56]; after 0.46 km h^{-1} , 95% CrI [0.38, 0.53]). Despite the dip in speed, Luna's mean speed on the day after parturition was $0.30 \pm 0.53 \text{ km h}^{-1}$, which is a total distance travelled of 7.31 km .

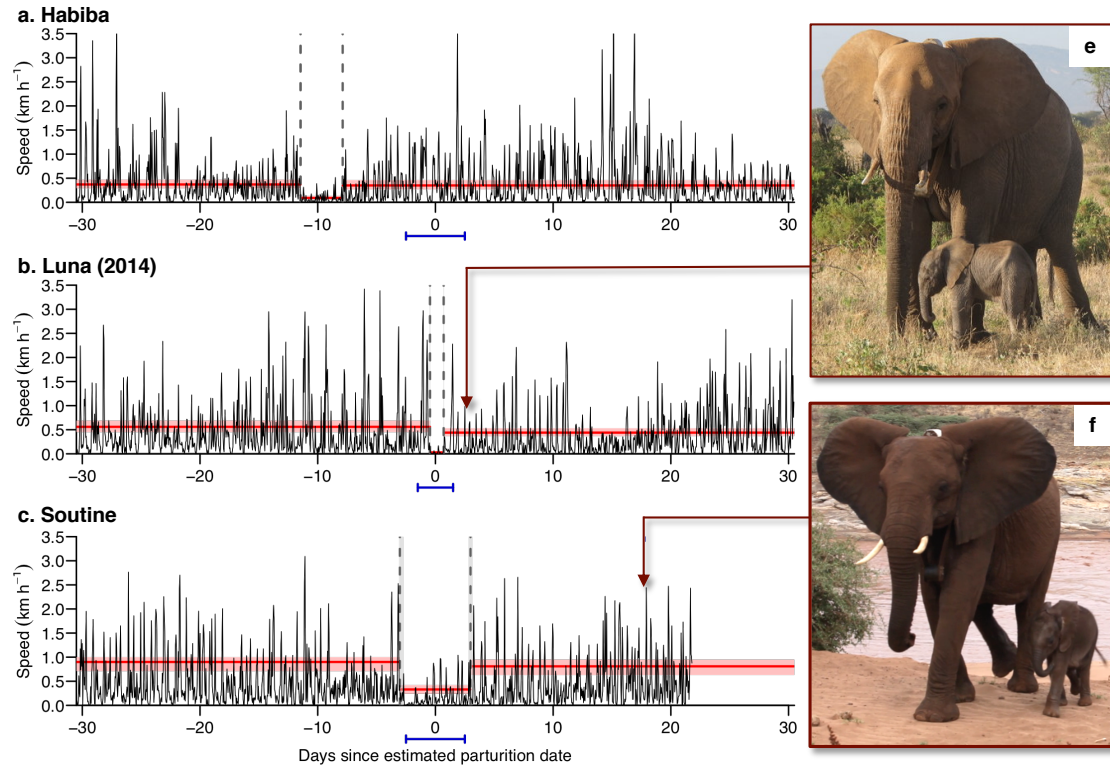


Figure 4.5: Three-state hidden Markov models for (a) Habiba, (b) Luna (2014) and (c) Soutine for hourly speed with the covariates of day-night, NDVI, slope and protected area for ± 30 days either side of the estimated date of parturition. Day 0.0 represents 12:00 on the estimated date of parturition. Grey dashed lines correspond to the mean detected state changes with the grey shaded area denoting the 95% credible interval. Red lines are the estimated mean speed during each state with the red shaded area corresponding to the 95% credible interval. Horizontal blue lines indicate the potential error margin on the estimated parturition date (day 0). (e) Luna and (f) Soutine carrying GPS tracking collars with their newborn calves (Photos: David Daballen and Matt Brierley, respectively).

Soutine displayed a similar pattern of behaviour and slowed her movements from -3.02 days (hourly ± 30 -day model 95% CrI [-3.08, -2.71]) to 2.98 days after birth (95% CrI [2.79, 317]; Fig. 4.2c). Within this seven-day period, Soutine remained almost stationary from 21:00 on day -3 until 19:00 on day -2, which is a total of ~ 22 hours. Indeed, the lowest daily mean speed and log-transformed 95% MCP and highest sinuosity index occurred two days before the estimated parturition date, at which point the values were -2.5, -3.2 and 2.9 standard deviations away from the yearly mean. On day -1, Soutine's speed was still low 0.09 ± 0.12 km h⁻¹ or a total distance of 2.23 km. In both Luna (2014) and Soutine, the daily level models were, mostly, unable to detect the state changes around parturition (Fig. D.9-10).

For the final primiparous female, Habiba, the HMM models did not detect any state changes around the estimated parturition date. Furthermore, the daily mean speed, log-transformed 95% MCP and sinuosity index were all within one standard deviation of the yearly mean (-0.4, -0.3 and 0.4, respectively). However, the HMM models detected an unusually low level of movement between -11.46 days (hourly ± 30 days: 95% CrI, [-11.46, -11.46]) and -7.88 days [-7.88, -7.88]; Fig. 5a). During this period, Habiba's hourly speed dropped to 0.09 km h⁻¹. In comparison to the rest of the year (using -11 to -8 days), the lowest daily mean speed (0.08 km h⁻¹) occurred on day -10, which was -1.1 standard deviations away from the yearly mean, and the lowest log-transformed 95% MCP and highest sinuosity index occurred on day -11 which were -4.2 and 3.2 standard deviations away from the yearly mean, respectively. These results show that the period of movement 11-8 days prior to parturition was unusual, but unfortunately there are no observations of Habiba from this time period as she was outside of the protected reserves.

4.5 Discussion

The results of this study suggest that gestation, parturition and the presence of a neonatal calf have very little impact on the movement of multiparous African savannah elephant females. Only two out of 18 multiparous births resulted in a dip in movements around parturition and only one of these, a young 16-year-old female, slowed on the day of parturition itself. In some cases, parturition was completely indistinguishable from normal movement patterns. Only six out of 18 births resulted in log-transformed 95% MCP's and sinuosity indices outside two standard deviations of the yearly mean within the error margin of the estimated parturition date. Furthermore, on the first complete day of the calf's life, taken as the day after the lowest movement patterns within the error margin of the estimated parturition date, the neonatal calves in this study travelled a mean of 8.16 ± 3.42 km, which is well within normal movement parameters, especially given the yearly mean of 8.80 ± 2.49 km. The results of linear mixed-effects models revealed a slight increase in the daily mean speed and a decrease in sinuosity index, during the

first 1 to ~ 18 days after the estimated parturition date. A corresponding decrease before parturition was not consistently found and, overall, there was no significant difference between all of the movement variables before and after parturition. Our results suggest that neonatal calves from multiparous females are capable of keeping up with elephant herds within hours of birth.

The finding that parturition has little impact on movement in multiparous females is concurrent with the ensemble of individual visual observations of births from the literature. Both Leuthold and Leuthold (1975) and Douglas-Hamilton (1972) noted that the birth of young caused minimal disruption of the normal activities and spacing of the mother and her group. Furthermore, McKnight (1991) observed a calf that walked fairly steadily within 30 minutes of birth and had no difficulty keeping up with the mother by the third day after birth. Indeed, by the day after parturition, the neonatal calves in our study were moving within normal movement parameters, which means overall the calf had very little impact on the broad scale movement patterns. Moss (1988) noted that neonatal calves are considered “precocious” as they are able to walk and keep up, but are otherwise completely dependent on the mother and other family members. Furthermore, in our study Ngalatoni, a matriarch, embarked on a 65 km trek climbing over 2,000m in six days starting when the calf was only nine days old, which is a substantial undertaking. Whilst the calf is still young, the energetic cost of moving ~ 120 kg 2,000m upwards will be considerably less than the cost of both moving ~ 2,500 kg upwards and lactating for Ngalatoni (Wall *et al.*, 2006). Thus, the mother, rather than the calf, could become the limiting factor on movement in some situations, which, in this case, would be a limitation caused by the matriarch herself.

The ability of a calf to move soon after parturition has several advantages. Firstly, and most importantly, the nutritional and water requirements of the mother herself, which is essential in order to provide care for the neonatal calf. Lactation can increase the energy requirement of an individual by 150% in ungulates (Clutton-Brock *et al.*, 1989; Blanchard, 2005). Alternate strategies, such as hiding the calf, may not be effective for elephants due to the distance travelled between resources.

Secondly, the ability to remain with the herd would enable both the mother and calf to benefit from the collective abilities of the herd. In cases where the mother is the matriarch, or an experienced female, the herd will also benefit from group fusion. This includes the benefits of shared knowledge, predator protection and neonatal care from other members of the herd, such as allomothering from teenagers (Douglas-Hamilton, 1972; Dublin, 1983). The inclusion of a neonatal calf within the herd also has the added advantage of enabling teenagers to gain experience with calves prior to the birth of their own calves (Dublin, 1983). Finally, the ability to move, including movement away from the birth site, may aid in predator protection. Although elephant herds will fiercely defend young calves, neonatal calves are vulnerable to predators, such as lions (Sikes, 1971; Loveridge *et al.*, 2006), which could be attracted to the birth site by the smell of the placenta. Indeed, many elephants have been observed covering the placenta with soil (Leuthold & Leuthold, 1975; McKnight, 1991; Church, 1992), which may act as a form of predator avoidance, although this behaviour is not consistently performed. Overall, the ability of a calf to keep up with a herd could enhance both the individual fitness of the calf and the inclusive fitness of the herd. Thus, alongside the development of advanced cognitive abilities, the long gestation period of elephants may facilitate an advanced state of physical development.

In terms of peripartum behaviour, our results did not support the observation that elephants tend to move more slowly in late gestation (Nicholson, 1954; Sikes, 1971; Moss, 1988), although there was a slight decrease in speed in the dataset of six individuals with accurate birth estimates. This does not negate the fact that individuals in late gestation may appear lethargic, but their broad scale movements do not appear to be significantly affected. One factor that could contribute to this is the timing of elephant calving, which often occurs at the start of the wet season in order to benefit from the highest vegetation productivity during early lactation (Wittemyer *et al.*, 2007b). This means that elephants are often in the late stages of gestation during the dry season when herds tend to move at a slower rate (Wittemyer *et al.*, 2008; Bohrer *et al.*, 2014). The timing of parturition

could thus factor into both the lack of a visible decrease in movements prior to parturition, and the presence of increases in speed, which occurred both before and after parturition in the HMMs and after parturition in the LME models. Furthermore, elephant herds consist of a mixture of individuals, all at different life stages (Moss, 1988), which means the combined herd movement may already factor in a degree of inter-individual differences.

In contrast to the results of the multiparous females, two out of three primiparous females decreased their movements around parturition. Luna stayed almost stationary for ~ 27 hours on the estimated date of parturition itself, and Soutine remained almost stationary for ~ 22 hours two days prior to parturition and overall remained slow over a ~ 7 -day period. Given that Soutine remained stationary for ~ 22 hours on day -2, which is significantly less movement than normal (2.5 standard deviations away from the yearly mean), parturition probably occurred slightly earlier than the estimated parturition date. Calves from primiparous females are more difficult to age as they tend to look younger for longer (pers. comm. D. Daballen). By contrast, Habiba continued moving throughout the estimated parturition date, but displayed an unusually low level of movement 11 days earlier. One potential hypothesis is that this calf was mis-aged and the calf was in fact born at this earlier date. Out of all three of these primiparous females, Habiba was the youngest and had the least experience of young calves within her own direct family, although she may have gained some experience from the unrelated herd she associated with. The reactions of Luna (2014) and Soutine, coupled with Habiba's own level of experience, lend support to the hypothesis that the birth occurred earlier than estimated. However, due to the lack of observations of Habiba during this time, the small sample size of primiparous females and the fact that parturition could not be detected from GPS tracking data in the multiparous females, we are unable to determine when parturition occurred with complete certainty retrospectively. Despite this, both Luna (2014) and Soutine displayed unusually low movement patterns, which was a behaviour only repeated by Luna's second parturition in 2016 in the multiparous females.

Aside from difficulties during parturition or problems with the calf, three potential reasons could account for the depressed movement patterns observed in the primiparous females in this study. Firstly, physical trauma and exhaustion in the mother caused by the first parturition. Although calf size is comparatively small relative to the mother, female African elephants do not undergo epiphyseal fusion of their long bones, and hence attain their full height, until around age 25 (Laws, 1966; Lee & Moss, 2011). The spine, and hence back length, continues to grow until death (Laws, 1966), which means that the primiparous females in our study, aged 12-14, are smaller than the multiparous females. Indeed, Lee and Moss (2011) estimated the mass at conception (22 months prior to parturition) in primiparous females was $\sim 1,200$ kg, which is substantially smaller than a mature female which may weigh $\sim 2,500$ - $3,000$ kg. Moss (1988) noted that there is little outward sign of pregnancy after about age 20, but younger females look visibly fuller or more rounded. Thus, calves born to primiparous females may be larger in size relative to the mother, which could result in more difficulty and pain associated with parturition.

Parturition itself in elephants leads to considerable intrauterine haemorrhaging, which is most likely caused by the placenta being wrenched off the endometrium as the foetus is delivered rapidly through the vertical birth canal and leads to significant intrauterine scarring (Allen *et al.*, 2003). In addition, during the first calving, the calf will rupture the permanent hymeneal membrane (Balke *et al.*, 1988). These factors could contribute to the observation that the physical stress resulting from pain associated with parturition may be elevated in primiparous females (Hermes *et al.*, 2008). Furthermore, Douglas-Hamilton and Douglas-Hamilton (1975) reported two separate cases of young females that had given birth who looked exhausted and were unwilling to move after parturition, which is not a factor noted during other observations of births. Together, these results suggest that parturition may be more of a physical exertion and/or result in more pain in primiparous females than older females. Indeed, many of the older multiparous females in our study showed almost no alteration in movement and the only female that did slow was Luna for her second birth in 2016 when she was still only 16 years old.

The second potential reason of an altered movement pattern could be caused by the calf itself. Due to the smaller stature of primiparous females, the foetus may have less space to develop, which may lead to the calf being more tightly furled during development. Douglas-Hamilton and Douglas-Hamilton (1975) noted that calves from still growing adolescents tend to be smaller than average. As already noted, calves from primiparous females tend to look younger for a longer period of time. The restricted growth space could lead to two potential limiting factors. Firstly, the calf may be weaker at birth, and, secondly, it may take the calf longer to straighten out and then strengthen their leg muscles. Further research is required into the early development of calves from young females compared to older females.

Finally, the experience of the mother may factor into movement decisions. McKnight (1991) noted that an elephant mother's reactions to her neonatal calf appear to be quite varied depending on prior experience. For example, Moss (1988) reported a case of an inexperienced primiparous female almost burying a calf in dirt as she appeared not to have learnt the skills required to lift a calf. In captive elephants, maternal experience can significantly influence reproductive success, with a lack of calf experience increasing the likelihood of both calf rejection and calf mortality (Hartley & Stanley, 2016). Furthermore, Lee (1987) found that the calves of wild young females were involved in more distress events, as defined by distress vocalisations, than the calves of middle-aged mothers or matriarchs. In this study, both Luna and Habiba had disrupted social structures due to the loss of all mature females within their herds, which could have impacted on their experience levels at parturition. Soutine lost her mother to poaching aged eight but had experience of allomothering other calves within her herd. Thus, the fact Soutine remained almost stationary for a day would seem to indicate a physical trauma rather than a psychological one, although this is speculative. Regardless of whether experience contributed to the decrease on the day of birth itself, calf survival in the long-term is greater in herds with more experienced matriarchs, which suggests that experience, both of the mother and the herd, is a significant factor in calf survival (Foley *et al.*, 2008; McComb *et al.*, 2011). The combined evidence from the GPS tracks in our

study and the literature suggests that births from primiparous females and within orphan herds warrant further investigation to establish what impact inexperience and a small stature have on the long-term development of elephant calves.

Although we have shown that in most cases multiparous females do not alter their movement patterns on the broad scale except for slight increases in movement after birth, two key points must be taken into consideration. Firstly, this dataset only contains elephants born in or near the relative safety of a National Reserve and none of the elephant families recorded were travelling at speed for any length of time. Whilst neonatal calves are capable of keeping up with normal herd movements, moving at high speed has a considerable energetic cost and thus could foreseeably impact on calf survival. Secondly, adaptations in movement may still have occurred at a finer resolution. For example, selecting a flatter route to a water source. Nevertheless, the large-scale movement patterns over each hour tended to remain the same throughout the peri- and postpartum period.

A compromise in optimal movement patterns could result in a cost to foraging performance but could result in a potential gain in inclusive fitness. In our study, births from multiparous females had little impact on movement meaning that staying with a multiparous female and calf would incur minimal costs. By contrast, if parturition in primiparous females necessitates remaining stationary or a slower movement pattern, the herd must weigh up the cost to foraging performance versus the potential gain in inclusive fitness. The fact that female elephants are capable of giving birth, which leads to considerable intrauterine haemorrhaging, and continuing moving is an incredible feat of strength. The ability of both mother and calf to move soon after birth would be a significant advantage to elephants given their biology and social structure, thus elephants may have evolved strategies which enable both mother and calf to continue moving throughout. We speculate that, alongside cognitive development, elephants may have evolved an unusually long gestation period to facilitate an advanced stage of physical development. Thus, results of our study provide crucial new insights into the reproductive behaviour of African savannah elephants, including the precocial abilities of calves.

5

Movement-related reproductive tactics alter with age in male African savannah elephants (*Loxodonta africana*)

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5.1 Abstract

In polygynous mating systems, intrasexual competition, in particular, can lead to the evolution and escalation of traits which are advantageous in conflict situations. Thus, males may adopt different reproductive strategies according to their relative

condition, strength and experience, which can drive differentiation in energy allocation between current and future reproduction. In the largest land mammal, the African savannah elephant (*Loxodonta africana*), male elephants continue to grow throughout their life, which means reproductive strategies may alter with age. However, the degree to which elephants allocate energy to movement related-tactics in relation to reproductively active periods (musth), and how this changes with age, is not currently known. We analysed the GPS tracking data of 24 male elephants in musth and non-musth. The results of our study demonstrate that mature male elephants significantly increase their daily mean speed, daily home range size (95% minimum convex polygon) and proportion of exploratory behaviour when in musth. Furthermore, movement patterns significantly increased with age in musth. Thus, despite no differences in musth and non-musth movements at age 20, by age 50, males were travelling 1.98 times faster per day in a daily home range that was 3.40 times larger in musth relative to non-musth. The increase in contrast between musth and non-musth movements with age meant that a three-state hidden Markov model was able to detect musth in bulls over 35 with a sensitivity of 97% and a specificity of 88%. The movements in younger males were less distinctive, which led to a lower level of sensitivity (66%) and specificity (77%). Our results demonstrate that, as age increases, bulls invest more energy into movement and searching behaviour during musth when the probability of reproductive success is higher. Thus, African savannah elephants may invest in future reproductive potential, by minimising the proximate costs of movement at a younger age when the probability of reproductive success is lower.

5.2 Introduction

In polygynous mating systems, variation in reproductive success is greater in males than females (Emlen & Oring, 1977; Clutton-Brock *et al.*, 1989; Andersson, 1994). One male may mate with a number of females thereby increasing the reproductive fitness of that individual. The resultant selective pressure from male-male competition for access to females (intrasexual selection) and/or female mate

choice (intersexual selection) has been suggested to be the driving force behind the evolution of exaggerated traits in species with polygynous mating systems (Darwin, 1871; Emlen & Oring, 1977; Andersson, 1982, 1994; Kodric-Brown & Brown, 1984). Intrasexual competition, in particular, can lead to the evolution and escalation of traits which are advantageous in conflict situations, such as increased size and the development of physical weapons (Darwin, 1871; Andersson, 1994). In life history theory, a central concept is the trade-off between key traits, such as current reproductive effort and future fecundity and survival, which is based on the assumption of limited resources (Stearns, 1992). Investing significant resources into reproduction can lead to a shorter life-expectancy (Andersson, 1994). Thus, males may adopt different reproductive strategies according to their relative condition, strength and experience, which can drive differentiation in energy allocation between current and future reproduction. As energy is a finite resource, analysing how an individual allocates their energy, such as to movement, can help elucidate reproductive strategies.

In the largest land mammal, the African savannah elephant (*Loxodonta africana*), the combination of longevity, indeterminate growth and sexual dimorphism means that old males can reach over twice the body mass of both females and young males (Laws, 1966). Thus, the reproductive success of a male elephant increases with age, both through reductions in intrasexual competition by the escalation of size-related dominance (Poole, 1989a), and an increase in intersexual selection by females for older males (Moss, 1983; Poole, 1989b). However, despite the reproductive dominance of older males, younger males still contribute significantly to the gene pool (Hollister-Smith *et al.*, 2007; Rasmussen *et al.*, 2008). Investigating how reproductive strategies, and hence investment in life history traits, varies with age is therefore crucial to our understanding of the behavioural ecology of the African elephant and, ultimately, the driving forces shaping evolution.

Both male and female elephants are promiscuous, with males supplying no parental care (Sukumar, 2003). Male elephants are physiologically able to reproduce by 14-17 years of age, which means a potential reproductive lifespan of over 40

years (Rasmussen, 2005). Beyond age ~ 30 , males start to display regular periods of heightened sexual and aggressive activity termed musth (Poole & Moss, 1981). Musth is likened to rutting behaviour in deer, and is characterised by conspicuous signalling, such as urine dribbling and temporal gland secretion, and increased aggression, which is likely linked to highly elevated levels of androgens, such as testosterone (Rasmussen *et al.*, 1984, 1996; Poole, 1987; Ganswindt *et al.*, 2005). Musth, itself an exaggerated trait, temporarily raises the dominance status of an individual to above that of those individuals not in musth, which means a younger male in musth may displace an older non-musth male (Poole, 1987, 1989a).

The duration of musth is positively related to age, with young bulls between ~ 26 -35 coming into musth for approximately two weeks several times a year, and males over 35 coming into musth once a year with the duration increasing to around 10 weeks by age 46-50, before a slight decrease (Poole, 1987; Poole *et al.*, 2011). Females can come into oestrus at any time of the year for only 2-6 days and, assuming reproductive success, will not come into oestrus again for 3-9 years (Moss, 1983), which means musth can occur at any time of the year, but typically peaks around the wet seasons coinciding with the highest female receptivity (Barnes, 1982; Poole, 1987; Ganswindt *et al.*, 2005; Poole *et al.*, 2011). Although the timing of musth varies, individuals tend to show annual periodicity (Poole, 1987). Whilst males can, and do, mate out of musth (Hollister-Smith *et al.*, 2007; Rasmussen *et al.*, 2008), the large older males in musth tend to monopolise female herds both through size- and musth-related increases in dominance, particularly as older males tend to remain in musth longer (Hollister-Smith *et al.*, 2007; Poole *et al.*, 2011). However, the degree to which elephants invest energy in reproductive tactics, such as investing in searching behaviour, and how this changes with age is not currently known.

The aim of this study was to use GPS tracking data from male elephants in and out of musth to (1) quantify the extent to which bull elephants alter their movement patterns between musth and non-musth periods, (2) investigate whether movement patterns alter in relation to age, and (3) determine if musth periods can be detected directly from GPS tracking data. We hypothesised that bulls in musth

would increase their movement patterns relative to non-musth in order to increase the probability of finding receptive females. Given older males display distinctive musth periods whereas younger males tend to be more opportunistic in their mating strategies (Poole, 1989a; Rasmussen, 2005; Rasmussen *et al.*, 2008; Poole *et al.*, 2011), we hypothesised that the contrast between musth and non-musth movements would be higher in older males. The ability to detect musth from GPS tracking data would enable detailed analysis of the musth behaviour in bull elephants, such as interactions with females and landscape usage, which could provide crucial new insights into African savannah elephant behavioural ecology.

5.3 Methods

5.3.1 Study area and population

The study population of elephants inhabits the semi-arid region in and around the unfenced Samburu and Buffalo Springs National Reserves in northern Kenya (0.3-0.8°N, 37-38°E). The area is dominated by *Acacia-Commiphora* savanna and scrub bush along the semi-permanent Ewaso N'giro River, which is the major water source in the region. Rainfall averages approximately 350mm per year and occurs biannually during April-May and November-December (Wittemyer, 2001). The study population has been monitored since 1997 and consists of ~900 individuals, of which ~150 are bulls and ~220 are breeding females and their calves that can all be individually identified using ear and tusk idiosyncrasies (Wittemyer, 2001; Rasmussen *et al.*, 2008). All adult individuals have been aged based on physical appearance using individuals aged from molar progression as reference points (Rasmussen *et al.*, 2005). Age was rounded down to the nearest year to account for variability in the age estimate. All males were assigned the birth date of the 31st August, which is the mid-point of a four-month period during the dry season when few bulls were in musth and meant that bulls did not change age category during the peak musth periods November-February and April-June (Table E.1).

5.3.2 Movement data

GPS tracking collars were fitted to 30 bull elephants inhabiting Samburu and Buffalo Springs National Reserves, of which 24 bulls were observed either in and/or out of musth with a GPS tracking frequency of 1-hour intervals or less. The GPS collars used were African Wildlife Tracking models A, AM, MT1000 and MT2000 (African Wildlife Tracking cc, Pretoria, South Africa), LOTEK models 1000 and 2000 (LOTEK Engineering Ltd., Newmarket, ON, Canada), Savannah Tracking models NHDS and GL200 (Savannah Tracking ltd., Nairobi Kenya), TVP models SIMPLEX and T5HS (Televilt Positioning AB, Lindesberg, Sweden) and the VECTRONIC model VERTEX Survey Iridium (VECTRONIC Aerospace GmbH, Berlin, Germany). The collars were fitted by a veterinarian from the Kenya Wildlife Service (KWS). To maintain consistency, the four collars from three different bulls with 30-minute fixes were systematically down-sampled to one-hour sampling frequencies on the hour. A continuous-time correlated random walk model was fitted to predict temporally-regular locations for missing data points ≤ 4 hours (Johnson *et al.*, 2008). Data gaps > 4 hours were excluded from the analysis. For each GPS point, the orthodromic (great-circular) distance from the previous point was calculated using the haversine formula. We calculated the daily mean speed (km hour⁻¹) as an analogue for distance using the distance over the time between each GPS fix, which enabled us to include days with a small amount of missing GPS fixes (≥ 20 samples). Daily home range size was estimated using a 95% Minimum Convex Polygon (MCP) (Mohr, 1947).

For each GPS fix, we determined whether the bull was moving in slow undirected way (encamped behaviour) or in a faster, more directed movement pattern (exploratory behaviour). We used an unfixed two-state hidden Markov model in the R package *momentuHMM* (McClintock & Michelot, 2018). Hidden Markov models are able to distinguish the unobserved (hidden) states from the observable combinations of movement distance (step length) and turning angles. To do this, the model uses the Viterbi algorithm which uses the probabilities of being in a state, the probability to switch between states and the previous hidden states to determine the most

likely sequence of states. We fitted the model using a gamma distribution for step length and wrapped Cauchy distribution for the turning angle. We summed the total number of hours engaged in exploratory behaviour and encamped behaviour for analysis. We also calculated the sinuosity index proposed by Benhamou *et al.* (2004), but, as speed, 95% MCP and sinuosity index were highly correlated in this study (Fig. E.1), we present just the results for speed and 95% MCP.

5.3.3 Musth observations

All elephants encountered during regular patrols of Samburu and Buffalo Springs National Reserves have been recorded since 1998, including the identity of the individual(s) present, date and time, location and notes on reproductive behaviour. For males, the degree of temporal gland swelling, temporal gland secretion and urine dribbling were recorded following Poole (1987). We analysed the data using musth as a categorical covariate as either musth or non-musth. A total of 553 non-musth and 193 musth observations were made of bulls with GPS tracking collars on days with ≥ 20 GPS fixes. We assumed that the bull was in the same state both the day before and the day after a field observation. In total, we compared 1,403 non-musth days to 482 musth days from bulls ranging in age from 20-52 at the time of observation (Table 1)

5.3.4 Environmental covariates

Movement patterns of elephants have been shown to be affected by vegetation productivity, terrain slope and ruggedness, distance to the nearest water source and whether the elephant is in or out of a protected area (Wall *et al.*, 2006; Wittemyer *et al.*, 2008; Boettiger *et al.*, 2011; Bohrer *et al.*, 2014; Ihwagi *et al.*, 2018). Therefore, we included these environmental factors as covariates for each GPS point. We used NASA's Terra Moderate Resolution Imaging Spectroradiometer (MODIS) 16-day 250m version 6 composites of normalised difference vegetation index (NDVI) to measure time-specific vegetation productivity (Didan., 2015). Slope (0-90°) and vector ruggedness measure (VRM; Sappington *et al.*, 2007) were calculated using

Table 5.1: Sample information, including minimum and maximum age and the number of non-musth and musth days analysed for each bull. The observations include all days where the bull was observed with ≥ 20 GPS fixes. The total GPS tracking days analysed includes one day either side of the day the bull was observed. Note for some observations, GPS tracking data was missing for the date of the observation itself, but data was available from the days either side. Individuals are ordered by the maximum age attained during the study period.

Individual		Age (years)		Observations with GPS tracking data		Total GPS tracking days analysed	
ID	Name	Min	Max	Non-musth	Musth	Non-musth	Musth
B1316	Bahati/Nusura	20	20	2	1	4	3
B1039	Ansel	22	24	29	0	69	0
B1044	Columbus	26	27	36	0	88	0
B1264	Lemaiyan	27	27	1	1	3	3
B1052	Nehru	28	29	9	1	25	3
B1045	Thoreau	23	31	5	1	13	3
B1082	Edison	29	32	8	14	21	30
B1041	Picasso	31	32	9	3	25	5
B1324	Frank	33	33	1	8	2	21
B1122	Uffe	21	34	28	2	77	13
B1026	Winston	28	34	90	19	223	47
B1059	Theresai	33	34	7	3	20	7
B1252	Boru	32	35	4	0	14	0
B1011	Nelson Mandela	36	37	12	0	28	0
B1016	MLK	37	37	4	3	7	10
B1033	Apollo	36	38	60	20	142	51
B1018	Boone	39	39	4	6	11	13
B1223	Leakey	40	41	2	0	3	2
B1013	Lewis	41	41	7	0	18	0
B1027	Esidai	35	44	86	30	233	75
B1023	Kenyatta	42	44	53	21	139	44
B1009	PrettyBomBom	44	45	35	32	95	80
B1001	Mungu	46	48	59	22	138	51
B1158	Matt	40	52	2	6	5	21
Total				553	193	1,403	482

the Shuttle Radar Topography Mission (SRTM) 30m V3 elevation dataset using the eight neighbouring cells (Farr *et al.*, 2007). Distance to water (km) was estimated as the distance to nearest permanent rivers, lakes and swamps. A binary covariate was added to distinguish whether an elephant was in or out of a protected area. The NDVI and elevation datasets were downloaded from Google Earth Engine. Maps of protected areas and water sources were developed by Save the Elephants.

5.3.5 Movements in musth and non-musth

We analysed daily mean speed and 95% MCP using linear mixed-effects (LME) models. Both daily mean speed and 95% MCP were positively skewed and were therefore log-transformed prior to analysis. For a single level of grouping (in this case elephant ID) with m groups and n_i the size of the i^{th} group (in this case the number of measurements taken on the i^{th} elephant), the linear mixed-effects model can be expressed mathematically in the form

$$\mathbf{y}_i = \mathbf{X}_i\boldsymbol{\beta} + \mathbf{Z}_i\mathbf{b}_i + \boldsymbol{\epsilon}_i, \quad i = 1, \dots, m,$$

where $\mathbf{b}_i \sim N(\mathbf{0}, \boldsymbol{\Psi})$, $\boldsymbol{\epsilon}_i \sim N(\mathbf{0}, \boldsymbol{\Sigma}_i)$.

$\mathbf{y}_i$ is the n_i -dimensional vector of responses of the i^{th} group,

$\mathbf{X}_i$ is the $(n_i \times p)$ matrix of p fixed-effects explanatory variables,

$\boldsymbol{\beta}$ is the p -dimensional vector of fixed-effects coefficients,

$\mathbf{Z}_i$ is the $(n_i \times q)$ matrix of q random effects,

$\mathbf{b}_i$ is the q -dimensional vector of random-effects,

$\boldsymbol{\epsilon}_i$ is the n_i -dimensional vector of within-group errors (Pinheiro & Bates, 2000).

In this case, the fixed-effects explanatory variables ($\mathbf{X}_i$) consisted of musth state as a binary covariate interacting with age at observation (years), age², daily mean NDVI, mean NDVI², mean slope, mean slope², mean VRM, mean VRM², mean distance to water, mean distance to water² and protected area (Fig. E.2). In order to avoid possible computer rounding errors and confine coefficient estimates

to a reasonable scale, all continuous environmental covariates were standardised by subtracting the mean and dividing by the standard deviation $\left(\frac{x-\bar{x}}{\sigma}\right)$ prior to analysis. Age was kept in years and was centred on age 35, which is the age bulls start to exhibit clear musth periods (Poole, 1987; Poole *et al.*, 2011), to aid in interpretation. Protected area was rounded to a binary covariate as either in (1) or out (0) of a protected area. Log-likelihood tests revealed that the elephants responded differently to NDVI ($p < 0.001$), and therefore the random-effect of elephant ID (i) was added on both the intercept and NDVI ($\mathbf{Z}_i$). $\mathbf{b}_i$ is assumed to be normally distributed with a symmetric, positive-definite covariance matrix Ψ .

The entries of the vector ϵ_i are usually taken to be independent, normally distributed and homoscedastic with variance σ^2 , so that $\Sigma_i = \sigma^2 \mathbf{I}$ (Pinheiro & Bates, 2000). However, different within-group correlation structures can be incorporated, which means $\Sigma_i = \sigma^2 \mathbf{R}_i$, where $\mathbf{R}_i$ is a within-group ($n_i \times n_i$) correlation matrix. In this case, we added two different within-group structures. Firstly, whilst homoscedasticity was found within both musth state and non-musth state, their variances were not the same and therefore a weighting factor was added to the model to cater for this distinction. Secondly, to account for the temporal relatedness of observations, we added a continuous time autoregressive lag-1 correlation (corCAR1) to the models (Pinheiro & Bates, 2000). If ρ_{jk} is the correlation between times t_j and t_k and if φ is the lag-1 correlation, then $\rho_{jk} = \varphi^{t_k - t_j}$, $t_k > t_j$.

LME models were fitted with the R package ‘nlme’ (Pinheiro *et al.*, 2018). From the full models, parsimonious models were obtained by deletion of non-significant terms using likelihood-ratio tests (LRT). We selected the model with the lowest Akaike information criterion with the model fitted with maximum likelihood (Burnham & Anderson, 2002). LRTs were used to test the statistical significance of each fixed effect in the best-fitting model. The models were then refitted using restricted maximum likelihood to obtain parameter estimates and confidence intervals. Models were checked for assumptions of linearity, normality, homoscedasticity and autocorrelation by visual inspection of plotted residuals and autocorrelations (Fig. E.2-4). Marginal ($R^2_{\text{LME}(m)}$) and conditional R-squared

values ($R^2_{\text{LME}(c)}$) were calculated using the methods described in Nakagawa and Schielzeth (2013).

In addition to speed and MCP, we analysed the proportion of exploratory behaviour per day using a binomial generalised linear mixed-effects model (GLMM). Aside from having no weightings in the binomial GLMM, the global model set-up was the same for both the LME models and the binomial GLMM. The binomial GLMM was fitted using the function ‘glmmPQL’ from the R package ‘MASS’ (Venables & Ripley, 2002). Wald tests were used to determine the best fitting model.

5.3.6 Musth detection

To determine whether musth can be detected from GPS data, we analysed the data using the fixed three-state hidden Markov model described in Chapter 4, which detects distinct changes in movement. The HMM priors were centred on the results from the linear mixed-effects models, which showed that bulls increased their movement patterns in musth. Thus, the three states comprised a slower speed at the start of the selected time period (State 1), followed by an increase in speed in State 2 and a decrease in speed in State 3. The three latent states were ordered so no other sequence of moves was possible. We modelled the log-transformed daily mean speed and log-transformed 95% MCP of the elephants using a normal sampling HMM whose parameters depended on the estimated state of the elephant, thus the emission of the log-transformed mean speed ($\bar{S}$) at time (t) followed:

$$\bar{S}_t \mid k \sim \text{normal}(\beta_k, \sigma_k) \quad (5.1)$$

where k is the latent state, β_k is the unconstrained parameter in that state and σ_k is the standard deviation. The model priors can be found in Table E.2.

To test whether the HMM correctly identified the musth period, we selected data containing a known musth period which had both a minimum of six observations of the bull, at least one of which was when the bull was in musth, and minimum of 120 days of corresponding GPS tracking data with $\geq 90\%$ of the data. Where possible, we took 120 days either side of the midpoint of the musth observations. In total, 15

musth periods from 10 bull elephants ranging in age from 28-52 years were analysed. Eight Markov chain Monte Carlo (MCMC) chains were run simultaneously, each with 5,000 warm-up and 5,000 model iterations, which resulted in 40,000 samples for each posterior distribution. We detected convergence in the sampling distribution as determined by using a criterion $\hat{R} \leq 1.1$ (Gelman & Rubin, 1992). To test the sensitivity and specificity of the three-state HMM, we examined whether the states detected in the HMM correctly corresponded to the visual observations of the bulls in musth or non-musth. We calculated the standard deviation in the estimated duration of musth from the posterior samples.

Data processing and analysis was conducted in the open-source software R (version 3.4.3; R Core Team, 2017), using the packages *adehabitatHR* (version 0.4.15; Calenge, 2006), *MASS* (version 7.3-48; Venables & Ripley, 2002), *MomentuHMM* (version 1.4.0; McClintock & Michelot, 2018), *nlme* (version 3.1-131.1; Pinheiro *et al.*, 2018) *raster* (version 2.6-7; Hijmans, 2017), *rgdal* (version 1.2-16; Bivand *et al.*, 2017), *rgeos* (version 0.3-26; Bivand & Rundel, 2017), *sp* (version 1.2-7; Pebesma & Bivand, 2005; Bivand *et al.*, 2008) and *spatialEco* (version 1.0-1; Evans, 2017). Three-state HMM's were written in Stan (Carpenter *et al.*, 2017) using the R interface RStan (version 2.17.3; Stan Development Team, 2017).

5.4 Results

5.4.1 Movements in musth and non-musth

The comparison of 1,403 days of GPS tracking data of bulls in non-musth to 482 musth days from 24 bulls ranging in age from 20 to 52 years revealed that reproductive state had a significant effect on daily mean speed and home range size (daily 95% MCP). Daily mean speed increased 1.47 times (LRT: $\chi^2_1 = 67.66$, $p < 0.001$) and 95% MCP 2.21 times ($\chi^2_1 = 66.19$, $p < 0.001$) in musth relative to non-musth for a bull aged 35 years under average environmental conditions (Table 5.2). There was weak evidence to suggest that bulls decreased their speed with age, but the relationship could not be considered significant ($\chi^2_1 = 2.91$, $p = 0.088$). However, there was strong evidence to suggest that the interaction between

Table 5.2: Results of the linear mixed-effects models for log-transformed daily mean speed and log-transformed 95% MCP, and the binomial generalised linear mixed-effects model for the proportion of exploratory behaviour per day. Blank cells correspond to variables which were removed from the model and are therefore not significant. Note: Estimates for age are in years centred on a reference point of age 35, whereas the environmental covariates are standardised by removing the mean and dividing by the standard deviation. Marginal ($R^2_{\text{LME}(m)}$) and conditional R-squared values ($R^2_{\text{LME}(c)}$) were calculated using the methods described in Nakagawa and Schielzeth (2013).

Fixed-effect	Log-transformed speed	Log-transformed 95% MCP	Proportion exploratory behaviour
	(Estimate [95% CI])	(Estimate [95% CI])	(Estimate [95% CI])
(Intercept)	-1.05 [-1.17, -0.93]	1.05 [0.8, 1.3]	-0.26 [-0.68, 0.17]
Musth	0.39 [0.30, 0.47]	0.79 [0.61, 0.98]	0.94 [0.63, 1.25]
Age	-0.01 [-0.02, 0.00]	-0.01 [-0.03, 0.01]	0.00 [-0.03, 0.03]
Age ²		0.00 [0.00, 0.01]	
NDVI	0.17 [0.09, 0.25]	0.34 [0.16, 0.51]	0.39 [0.27, 0.51]
NDVI ²	-0.05 [-0.08, -0.02]	-0.08 [-0.15, -0.01]	-0.08 [-0.15, -0.02]
Slope		-0.06 [-0.14, 0.01]	
Slope ²	-0.01 [-0.02, 0.00]	-0.03 [-0.06, -0.01]	-0.03 [-0.05, 0.00]
VRM	0.04 [0.02, 0.06]	0.06 [0.01, 0.11]	0.06 [0.00, 0.12]
VRM ²	-0.03 [-0.04, -0.02]	-0.09 [-0.13, -0.06]	-0.05 [-0.08, -0.01]
Water	0.07 [0.03, 0.11]	0.24 [0.15, 0.33]	0.24 [0.11, 0.37]
Water ²	-0.01 [-0.01, 0.00]	-0.03 [-0.04, -0.02]	-0.06 [-0.10, -0.02]
Protected	0.16 [0.11, 0.21]	0.37 [0.25, 0.49]	0.48 [0.34, 0.61]
Musth * Age	0.02 [0.01, 0.03]	0.03 [0.01, 0.05]	0.03 [0.00, 0.05]
Musth * Age ²			
Musth * NDVI			
Musth * NDVI ²	-0.08 [-0.12, -0.03]	-0.14 [-0.24, -0.04]	-0.15 [-0.25, -0.04]
Musth * Slope			
Musth * Slope ²	0.03 [0.00, 0.06]	0.04 [0.00, 0.07]	
Musth * VRM			
Musth * VRM ²			
Musth * Water		-0.26 [-0.45, -0.07]	
Musth * Water ²		0.06 [0.01, 0.10]	
Musth * Protected		-0.37 [-0.67, -0.08]	
$R^2_{\text{LME}(m)}$	0.22	0.19	0.06
$R^2_{\text{LME}(c)}$	0.45	0.36	0.19

musth and age was significant ($\chi^2_1 = 11.65$, $p < 0.001$). The resultant combination meant that speed diverged, with speed in non-musth tending to decrease with age, whereas speed in musth increased with age (Fig. 5.1a). Thus, there was no significant difference between musth and non-musth daily mean speed at age 20 ($\chi^2_1 = 0.79$, $p = 0.375$), but, by age 50, males were travelling 1.98 times faster in musth than non-musth ($\chi^2_1 = 63.79$, $p < 0.001$).

Home range size (95% MCP) also significantly increased with age in musth ($\chi^2_1 = 5.91$, $p = 0.015$), but, unlike speed, non-musth 95% MCP did not alter with age ($\chi^2_1 = 1.40$, $p = 0.236$; Fig. 5.1b). As a result, the home range size (95% MCP) of a 50-year-old male in musth was 3.40 times larger than when in a non-musth state

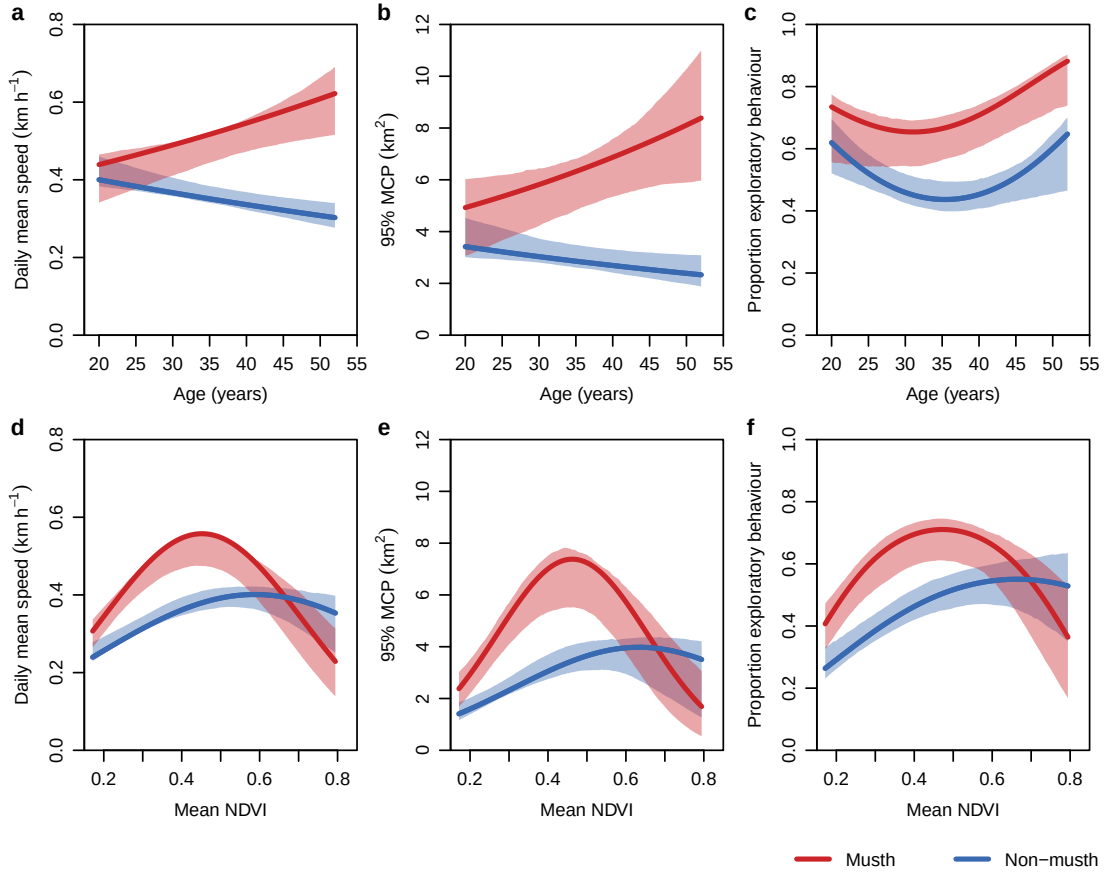


Figure 5.1: Relationship between daily mean speed (km h⁻¹), 95% MCP (km²) and the proportion of exploratory behaviour, and age (years) and mean NDVI in musth (red) and non-musth (blue). Shaded area corresponds to the 95% confidence interval from a non-parametric bootstrap of 1,000 resampled data points.

($\chi^2_1 = 49.26$, $p < 0.001$). The 95% MCP of a 20-year-old male did not significantly differ between musth and non-musth ($\chi^2_1 = 2.76$, $p = 0.097$).

The proportion of exploratory behaviour per day also significantly differed between musth and non-musth, with the odds-ratio for musth equal to 2.55 (binomial GLMM: $t\text{-value} = 5.94$, $df = 1843$, $p < 0.001$), which means other things being equal, a 35-year-old male elephant is 2.55 times as likely to explore in musth relative to non-musth. However, age, age² and the interaction between musth and age also had a significant effect on exploratory behaviour ($p < 0.05$), with age increasing, age² decreasing and the interaction between musth and age increasing exploratory behaviour (Table 2). Overall, this meant that the proportion of exploratory behaviour in both musth and non-musth behaviour initially decreased

before increasing with age (Fig. 5.1c).

As expected, the environmental covariates significantly influenced movement patterns. As already mentioned, the relationship between movement patterns and mean NDVI varied between individuals ($p < 0.001$), which led us to add NDVI to the random effects. After accounting for individual reactions to NDVI, as a fixed-effect, NDVI significantly increased daily mean speed, 95% MCP and proportion of exploratory behaviour ($p < 0.001$), whereas NDVI² significantly decreased movements ($p < 0.05$). Furthermore, the interaction between musth and NDVI² was significant, with movements decreasing with NDVI² for bulls in musth ($p < 0.01$). Overall, this meant that daily mean speed in musth increased with NDVI up to a moderately high NDVI of 0.45, before decreasing, whereas non-musth movements gradually increased up to a higher NDVI of 0.59 before a slight decrease (Fig 5.1d).

In a protected area, male elephants moved 1.18 times faster ($\chi^2_1 = 1.40$, $p < 0.001$) in a 1.45 times greater home range size ($\chi^2_1 = 35.44$, $p < 0.001$) and were 1.61 times more likely to engage in exploratory behaviour (t-value = 6.92, df = 1843, $p < 0.001$). Predictably, mean slope² (degrees) significantly decreased speed and 95% MCP, which meant the negative effect of slope on movement increased as the slope increased. Slope tended to decrease exploratory behaviour and slope² decreased non-musth movements. Mean VRM and distance to water both initially increased movements before decreasing in more rugged terrain and further from water ($p < 0.05$; Fig. E5).

5.4.2 Musth detection

Overall, the fixed three-state HMM of log-transformed daily mean speed detected musth periods which resulted in 90% of all observations being correctly identified (musth or non-musth) across the 10 bulls studied. A total of 106 musth observations were correctly assigned with 8 false-positives (84% sensitivity after accounting for the effects of individual; Table 5.2) and 162 non-musth observations were correctly assigned with 39 false-negatives (84% specificity). Aside from one bull, Edison,

the models of bulls under the age of 35 tended to have a lower sensitivity (66%; true positive) and specificity (77%; true negative) compared to the bulls over 35, where the models had quite a high sensitivity (97%) and specificity (88%). Furthermore, the standard deviation in the estimated duration of musth from the 40,000 iterations of the model were lower in the bulls over 35 (5.1 days compared to 18.3 days) indicating a higher degree of certainty in the timing of the detected state changes between musth and non-musth in the older individuals (Fig. 5.2). The results for the three-state HMM for log-transformed 95% MCP were similar, as speed and MCP are correlated, but the models had slightly lower levels of sensitivity and specificity (Fig. E.2, Table E.4).

Consistent with the results of the LME models, the daily mean speed during the detected musth periods of the males over 35 was ~ 2.14 times faster than non-musth periods (Fig. 5.3). Furthermore, the standard deviation between the daily mean speeds during musth also increased ~ 2.11 times, suggesting more variable movement patterns during musth in older males. The males under 35 also displayed an increase in speed during musth but, given that these results include all of the data from the detected musth periods from the HMM models and thus contain both the false-positive and false-negative results, the interpretations that can be drawn from the speed data in the males under 35 is limited due to the lower levels of sensitivity and specificity.

5.5 Discussion

The results of this study show that mature male African savannah elephants significantly increase their daily mean speed, daily home range size and proportion of exploratory behaviour when in musth. As locomotion is energetically expensive, our results demonstrate that musth comes at a significant energetic cost to African savannah elephants. Moreover, the increase in exploratory behaviour in musth means that bulls are simultaneously reducing the total foraging and rest time available, which may impact on energy acquisition. Whilst non-musth movements remained consistent or tended to decrease with age, bulls in musth significantly

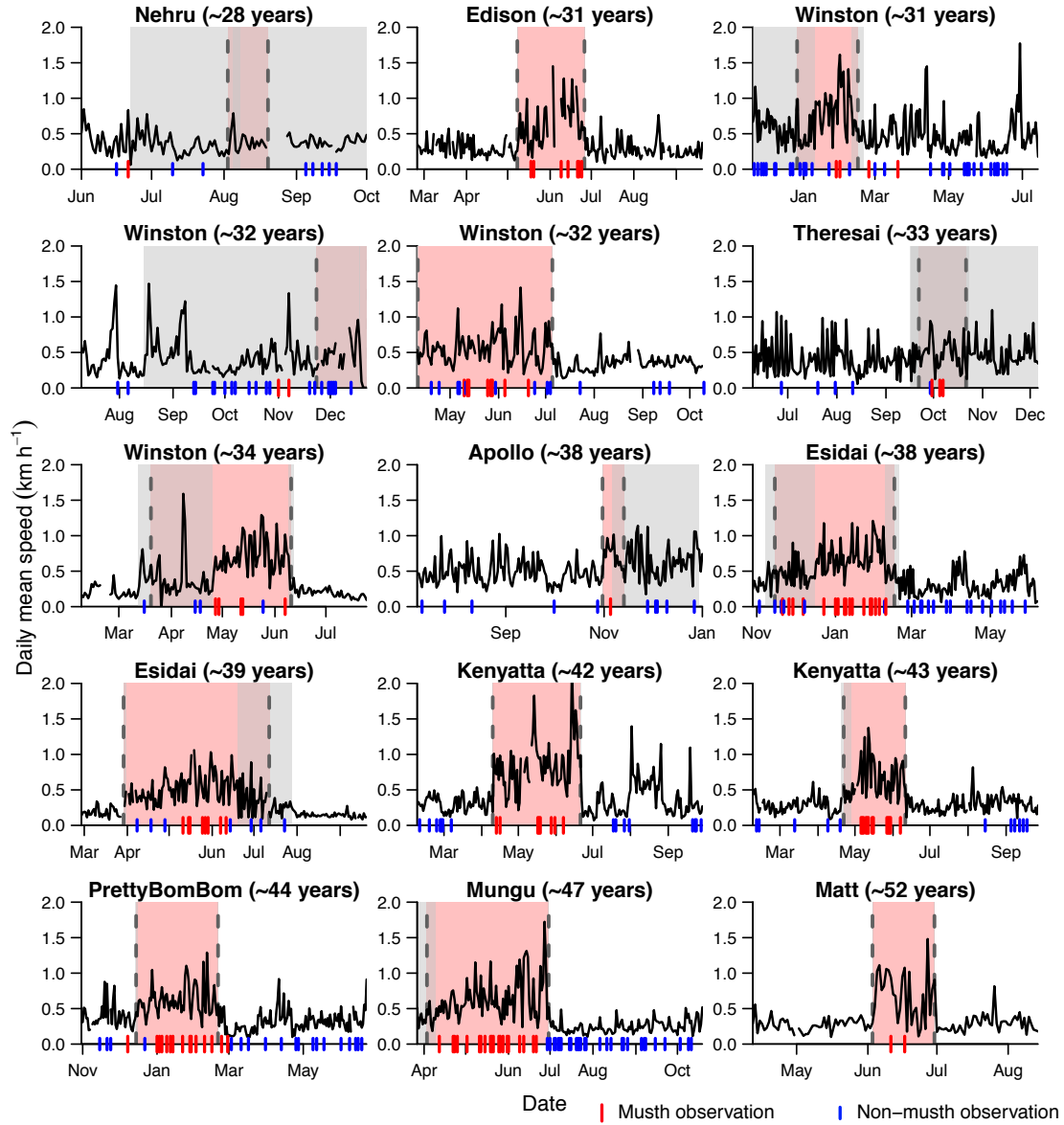


Figure 5.2: Three-state hidden Markov model results of the model for log-transformed daily mean speed aiming to detect musth periods in bull elephants. Plots show the untransformed daily mean speed with the detected musth periods shaded in red. Grey shaded area indicates the corresponding credible interval ($\pm 95\%$). Visual observations of the bull in musth or non-musth are denoted by the red and blue lines at the base of the plot. Plots are ordered by age from youngest to oldest.

Table 5.3: Results of the three-state hidden Markov model of log-transformed daily mean speed (km h^{-1}) aiming to detect musth in male elephants. The number of observations corresponds to the number of visual observations correctly or incorrectly assigned by the three-state HMM. Note that the values for daily mean speed during the detected states includes all of the data within the detected time frames and thus contains both the false-positive and false-negative results.

Name	Age (years)	Three-state HMM		Musth observations						Daily mean speed (km h^2) during detected state					
		Detected musth length (days)	SD of detected length (days)	Non-musth			Musth			Total % correct	Mean			Standard deviation	
				Correct	Incorrect	% Correct	Correct	Incorrect	% Correct		Non-musth	Musth	% Change	Non-musth	% Change
Nehru	28	17	23.6	9	0	100	0	1	0	90	0.37	0.38	3	0.14	-3
Edison	31	49	0.7	0	0	-	7	0	100	100	0.28	0.66	131	0.12	162
Theresai	33	30	28.9	4	1	80	3	0	100	88	0.42	0.50	19	0.23	-12
Winston	31	50	27.5	27	7	79	2	2	50	76	0.49	0.76	55	0.25	38
	32	30	33.1	15	7	68	0	2	0	63	0.42	0.43	3	0.26	-5
	32	86	2.4	5	9	36	8	0	100	59	0.34	0.56	66	0.11	116
	34	83	17.3	1	3	25	5	0	100	67	0.22	0.56	154	0.12	177
Apollo	38	13	10.9	10	0	100	1	0	100	100	0.53	0.73	38	0.21	-24
Esidai	38	93	13.7	18	4	82	17	0	100	90	0.32	0.61	92	0.16	48
	39	105	6.7	1	6	14	8	0	100	60	0.17	0.49	184	0.06	235
Kenyatta	42	72	0.0	15	0	100	8	0	100	100	0.34	0.85	151	0.20	77
	43	50	2.8	11	0	100	13	0	100	100	0.29	0.64	124	0.11	143
PrettyBomBom	44	67	1.7	18	1	95	12	3	80	88	0.33	0.62	87	0.15	36
Mungu	47	88	5.2	28	1	97	20	0	100	98	0.25	0.63	152	0.10	206
Matt	52	27	0.9	0	0	-	2	0	100	100	0.29	0.67	134	0.12	196
Total count/ mean value		51*	10.4*	162	39	84*	106	8	84*	90*	0.34*	0.61*	91*	0.15*	89*
Under 35		40*	18.3*	61	27	77*	25	5	66*	86*	0.36*	0.53*	56*	0.17*	57*
Over 35		59*	5.1*	101	12	88*	81	3	97*	94*	0.33*	0.66*	114*	0.14*	111*

*After accounting for the effects of repeated individuals

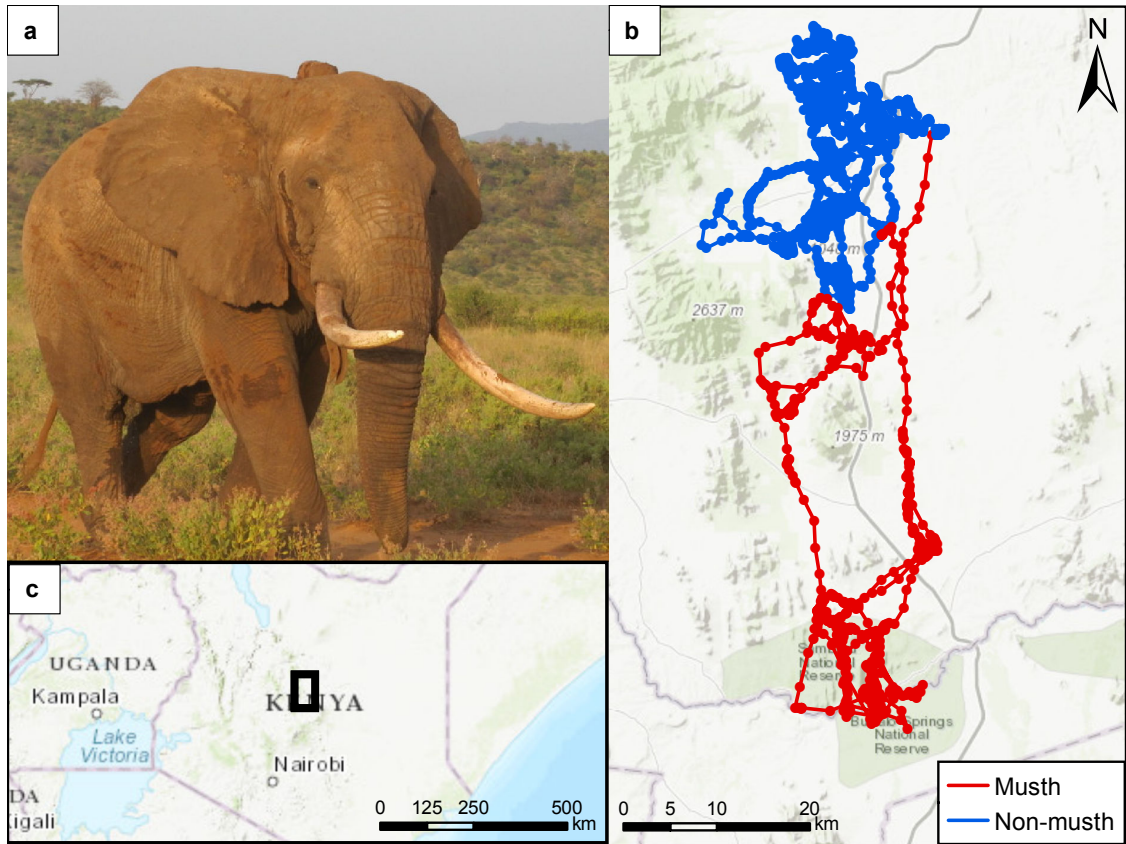


Figure 5.3: Map of the detected musth and non-musth periods for the bull ‘Matt’ (B1158) aged 52 years. (a) Photo of Matt in musth aged 49 (Photo courtesy of Save the Elephants). Note the temporal gland secretion and swelling and urine dribble, which are indicative of musth (Poole, 1987). (b) The musth periods detected for Matt aged 52 years using the three-state hidden Markov models. (c) Map inset showing the location of Matt’s tracks in relation to Kenya. Maps were designed using ArcGIS 10.4.1 (Esri Inc., Redlands, USA) using the World Topographic Map (Esri *et al.*, 2013).

increased their movements with age. Thus, despite there being no difference in musth and non-musth movements for 20-year-old males, 50-year-old males were travelling twice as fast in a home range size that was nearly three and a half times larger than normal. The higher contrast between musth and non-musth movements in older individuals led to the detection of musth periods using a fixed-order three-state hidden Markov model with a sensitivity of $\sim 97\%$ in males over 35 years, although the specificity was lower at 88% (true negative). Musth movements in younger males were less distinctive, which meant the three-state HMM had more difficulty differentiating musth movements (66% sensitivity and 77% specificity). In addition, the HMM results indicated that, during the detected

musth periods, bull elephants also increase the variability of speeds over the whole musth period, which may represent travelling and then following and/or guarding a receptive female. Overall, our results suggest that movement related strategies in African savannah elephants alter with age.

The increase in exploratory behaviour and the daily mean speed during musth is congruent with behavioural observation studies showing that bulls spend more time walking and less time foraging and resting in musth (Poole, 1989a). The higher daily home range size, as measured by 95% MCP, is also consistent with the observation that bulls cover large distances in a short amount of time when in musth (Hall-Martin, 1987). Unlike Whitehouse and Schoeman (2003), the bulls in this study significantly increased their daily mean speed in musth, which could be attributed to the fact that the bulls in this study were not in a small enclosed park. Barnes (1982) postulated that under extremely low elephant densities, a bull that remains with a herd will encounter more females than a roving male. However, both observational studies (Barnes, 1982; Poole, 1987, 1989a; Rasmussen, 2005) and the increased movement observed in this study suggests that elephants tend to adopt a roving strategy and only remain with females to guard or follow individuals in oestrus. Thus, the increased probability of finding receptive females may outweigh the energetic cost in African elephants due to the potential to increase an individuals' reproductive success.

The increase in musth movements with age suggests that the energetic investment in reproduction also increases with age. Although male elephants continue to grow throughout their entire life, elephants do not have a strong allometry between speed and leg length, meaning that young male elephants can move as fast as older elephants (Hutchinson *et al.*, 2006). Thus, differences in size are unlikely to account for the observed increase in musth movements with age. Moreover, alongside increases in speed, musth duration increases with age (Poole *et al.*, 2011), which means older bulls are both moving faster and for longer than younger males, which suggests older males are investing significant energetic resources into musth periods. Indeed, Poole (1989a) found that the body condition of bulls significantly

declines during musth, with the older bulls tending to lose the most condition, which suggests that bulls experience a negative energy balance with energy expenditure exceeding energy acquisition. Thus, the combined evidence of the extended duration of musth in older individuals (Poole *et al.*, 2011), the greater degree of body mass loss in older individuals (Poole, 1989a), and the increase in movement patterns in musth in relation to age found in this study, suggests that the energetic investment into locating receptive females in musth significantly increases with age.

Elephants are unusual in that reproductive success peaks so late in life (Andersson, 1994). A key life history trait that may skew the reproductive success of male African savannah elephants towards older age is the trait of indeterminate growth, which means that male-male competition will be at its lowest, and female mate-choice at its highest, over the lifetime of an individual in musth between the ages of 45-50 years old through the dominance gained by both size and musth state. Bulls older than 50 may yet be more dominant but are unable to sustain musth as long (Poole *et al.*, 2011). Furthermore, as residual life expectancy decreases, the balance in the trade-off between potential gains in reproductive success versus risk to life expectancy may alter, which means that older male elephants may take more risks. Thus, older males may increase their energetic investments into musth periods when they can achieve the highest lifetime dominance rank, at a time when residual life expectancy is low, and thus have the highest reproductive success. By contrast, in younger elephants, both the probability of reproductive success is lower and the residual life expectancy is higher, which means the proximate costs of movement may not outweigh the benefits gained through the increased potential of finding receptive females. Furthermore, younger males will have higher energetic costs in relation to growth (Laws, 1966; Poole *et al.*, 2011). Thus, younger male elephants may invest in future reproductive success rather than expending energy on locating females when their current reproductive potential is lower.

The increased contrast between musth and non-musth movements with age meant that the three-state HMM's were able to detect musth with a relatively high level of sensitivity and specificity in males over 35, although the sample size in this study

was small. We used the fixed three-state HMM specifically to test the hypothesis of whether musth behaviour could be detected. The traditional usage of HMM models is to detect short-term state changes, such as resting versus moving behaviour or movements with distinctive patterns, such as migrations (McClintock & Michelot, 2018). By contrast, musth is a prolonged period, which, as our results show, is characterised by both an increase in movement patterns and an increase in the variability of movement patterns meaning that movement patterns are constantly fluctuating. One of the reasons the fixed three-state HMM was successful was because the model searched for just two change points within the data, thereby detecting the start and end of musth. The disadvantage of this approach is that the three-state model requires a set period to run over and the model will always detect a period of increased speed within that period, whether this corresponds to musth or not. One potential confounding factor in terms of elephant movements would be the increased movement patterns associated with high vegetation productivity observed in this study and in others (Boettiger *et al.*, 2011; Bohrer *et al.*, 2014), which could lead to false-positive results. Another potential caveat is that the younger bulls do not demonstrate distinctive musth periods, which means the technique would only be viable for a subsample of the total male population. Despite these drawbacks, our results demonstrate that musth can be detected clearly in some individuals, which means that musth behaviour in bulls could potentially be studied directly from GPS tracking data in the future. One potential future avenue is machine learning, which could be used to automatically detect alterations in movement.

As expected, environmental covariates had a significant impact on movements, with male elephants moving 1.18 times faster in daily home range size that was 1.45 times larger in protected area relative to a non-protected area, regardless of reproductive state. Furthermore, our results show that movement in relation to vegetation productivity (NDVI) varied between individuals and with reproductive state. Both musth and non-musth movements were lower in areas with low vegetation productivity. Thereafter, musth movements significantly increased up to a moderate-high level of vegetation productivity before decreasing sharply. The increase in

movements in moderate-high vegetation productivity is likely to reflect the increase in vegetation productivity during the wet season (Boettiger *et al.*, 2011; Bohrer *et al.*, 2014), which may facilitate energy acquisition and enable males to maintain musth movements. One potential reason for the sharp decrease in movements thereafter in areas of high vegetation productivity is that there are more environmental obstacles which may impede movement. The results of our study therefore suggest that, alongside impacting on the timing of musth through the increase in receptive females (Barnes, 1982; Poole, 1987; Rasmussen, 2005; Poole *et al.*, 2011), movements in musth may alter in relation to NDVI. which means musth may need to be factored into movement models of elephants.

Overall, our results indicate that musth in African savannah elephants comes at a significant energetic cost due the increased cost of locomotion. Furthermore, the results indicate that movement-related reproductive tactics change with age, which may have implications on elephant population management and conservation. Older male elephants tend to be the target of both legal trophy hunting and illegal poaching. As reproductive investment increases with age, removing dominant older males from the population could impact on the reproductive dynamics in African savannah elephants, either through a lower density of roving males, which may decrease the probability of female reproductive success, or by changing the dynamics of male-male competition which may lead to males increasing their movement at a younger age, which could impact on long-term health. The ability of African savannah elephants to increase their reproductive investment with age is the ultimate test of endurance as an individual must survive to old age in order to maximise fitness. Thus, African savannah elephants may invest in future reproductive potential, by minimising the proximate costs of movement at a younger age when the probability of reproductive success is lower.

6

General Discussion

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My thesis provides new insights into how, when and why two very different species modulate their movement in response to their navigational capacity, external conspecifics and internal reproductive state.

Firstly, in Chapter 2, I demonstrated that homing pigeons modulate their wingbeat patterns as a function of navigational knowledge, which suggests that the navigation and learning process in birds may have physical manifestations. Moreover, the results demonstrate that the energetic cost of the first flight may be higher than subsequent flights both due to inefficient routes (increased distance) and lower airspeeds (increased time).

In Chapter 3, I showed that pigeons increase their wingbeat frequency by *c.*18% when flying in pairs relative to flying solo, which suggests that there is a substantial

cost to flying together, and that the ultimate drivers of flocking, including predator protection and pooling of navigational knowledge, must outweigh these proximate costs even during short-range travel over familiar terrain.

In Chapter 4, I found that gestation, parturition, lactation and the presence of a neonatal calf have very little impact on the movement of multiparous African savannah elephants. The results of this study could suggest that, alongside cognitive development, African savannah elephants have developed an unusually long gestation period in order to facilitate an advanced state of physical development.

Finally, in Chapter 5, I showed that male African savannah elephants significantly increase their movement patterns in relation to musth behaviour and age, which suggests that males increase their energetic investments into reproduction as probability of reproductive success increases. Thus, African savannah elephants may invest in future reproductive potential, by minimising the proximate costs of movement at a younger age when the probability of reproductive success is lower.

6.1 Limitations

Before discussing the results in more detail, the broad limitations of this thesis must first be stated. Firstly, all studies could have benefited from a larger sample size, particularly the sample of primiparous females in Chapter 4, which consisted of three births, and the sample of bulls used to detect musth periods in Chapter 5, which consisted of 15 musth periods from 10 bulls. In all cases, the sample size was limited by the availability of animals and/or data. Nevertheless, the results were consistent across the individuals studied with either a clear effect (Chapters 2, 3 and 5) or no effect (Chapter 4). The results from the primiparous females will require a larger sample size before population generalisations can be drawn.

The sample size also impacted on how I designed the studies. For example, in Chapter 3, the pigeons flew in pairs firstly with a similar-sized partner and then a different-sized partner. At the time, I considered using a crossover design so that some birds started with a similar-sized and some with a different-sized partner, but I could only divide the pigeons into four and six pairs in each condition at

any one time due to the way in which the birds swapped partners, so I decided to keep the pigeons in blocks. In hindsight, I should have used the crossover design regardless to account for any effects related to the order of releases. Fortuitously, the results of the model with tarsus length on a continuous scale revealed that tarsus length was not a significant factor.

The observations of bulls in musth and non-musth from Chapter 5 were also very unbalanced due some bulls being observed regularly whereas other bulls visited the Samburu and Buffalo National Springs reserves infrequently. The linear mixed-effects model with the random effect of individual should account for the correlation among observations within an individual (Pinheiro & Bates, 2000), but this study could have benefited from more consistent longitudinal observations across age classes.

As highlighted in the Introduction, one of the limitations of studying movement by attaching devices is that the devices will increase the energetic cost of movement. For the pigeons, the biologgers and fastenings weighed 27 g. The lowest body mass recorded for the smallest pigeon (B84) was 402 g, which means the devices weighed 6.7% body mass. This is slightly heavier than the rule of thumb of 5% of an animals body mass (Brander & Cochran, 1969; Aldridge & Brigham, 1988; Barron *et al.*, 2010), although there is no clear scientific rationale for this figure. Although this may have impacted on energy expenditure, the experimental questions were related to how individuals altered their movement in relation to a repeated route or a conspecific which was under the same experimental conditions. Thus, the overall findings are unlikely to have been affected by the presence of a device as we were comparing individuals against themselves in a situation where they should aim to reduce energy expenditure. For the African savannah elephants, a ~ 15 kg collar, including device, strapping and counterweight, weighed less than <1.25% body mass for the smallest elephants studied, which means the presence of a collar probably had very little impact on the results.

The resolution of the environmental covariates was another limiting factor on all studies. In the pigeon studies, the weather station recorded the weather data at the pigeon's home loft, which was 7.06 km away from the furthest release site,

and recorded wind speed every minute and the wind bearing as a running mean over the previous ten minutes. Given that the pigeons completed the release in <10 minutes when experienced, the accuracy of the weather data in this study was relatively low, which means the effects of weather may not fully be accounted for.

In the elephant studies, both the GPS tracking frequency and the resolution of the environmental covariates was low. Whilst this is sufficient for studies of broad-scale movements as in this thesis, a higher resolution is advantageous when analysing modulations in animal movements. For example, the results of Chapter 4 indicate that the broad scale movements of multiparous African savannah elephants remained the same both before and after parturition, but I could not investigate whether movements at fine scale changed, such as selecting flatter routes. The continuing advancement of both GPS tracking collars and remote sensing data means that it may soon be possible to track elephants for long periods of time with a high resolution (Kays *et al.*, 2015).

Finally, both elephant chapters were reliant on observational data, which required the observer to make an accurate identification of the individual, accurately estimate the age of neonatal calves to within days and to identify reproductive state in males. Although the whole team at Save the Elephants endeavour to keep the data as accurate as possible, the data may contain some small errors.

6.2 Navigational capacity

At the start of my thesis, I aimed to investigate whether the process of navigation itself altered the movement path of an individual. The results of Chapter 2 revealed that homing pigeons do indeed modulate their wingbeat patterns as a function of navigational knowledge. At the start of the releases, we found that the birds' median peak-to-peak dorsal body (DB) acceleration was lower, which in turn resulted in lower airspeeds. The navigational capacity of an individual is often considered as the information required to get from A to B in order to pursue a specific goal, such as foraging. Our results demonstrate that the navigational capacity of an individual may not only alter when and where individuals move, but the process of navigation

itself may alter the movement path. In this case, our results demonstrate that the cost of early flights from an unfamiliar location may be higher than subsequent flights both due to inefficient routes (increased distance) and lower airspeeds (increased time). The finding that navigation itself may impact on movement is important both in terms of understanding individual decision making and our understanding of movement ecology. For the individual, if navigation itself is costly, this could factor into other decisions, such as whether to move with other individuals or even to move at all. In terms of movement ecology, recognising that the navigation itself can affect movement opens up new avenues of research, such as using an individual's movement patterns to help elucidate the cognitive underpinnings of navigation.

6.3 Cooperation with conspecifics

The second objective of this thesis was to investigate how individuals modulate their locomotion in relation to conspecifics. I used two different study systems to investigate this question. In the homing pigeons, I found that birds significantly increase their wingbeat frequency when flying in pairs relative to flying solo (Chapter 3). By contrast, I found that gestation, parturition, lactation and the presence of a neonatal calf had very little impact on the movements of multiparous African savannah elephants (Chapter 4). Although, at first glance, these results may seem very different, there are some key commonalities within these results. Crucially, Chapter 3 also investigated whether bird size, as measured by tarsus length, altered the wingbeat patterns of pigeons flying in pairs. Aerodynamic theory (flight power curves) predicts that larger birds will have a higher optimal flight speed than smaller birds (Pennycuick, 1975; Ellington, 1991) and indeed the fastest homing pigeon is often at the front in flocks (Pettit *et al.*, 2015). Despite this, we found no difference in wingbeat patterns as the inter-individual difference in tarsus length increased. Furthermore, the presence of a neonatal calf had very little impact on the movement of African savannah elephants. Thus, despite differences in size, and hence motion capacity, both pigeons and elephants did not alter their movements specifically in relation to physical size differences.

Cooperating with conspecifics has many benefits including predator protection (Krause & Ruxton, 2002), navigational knowledge (Simons, 2004; Biro *et al.*, 2006a; Dell’Ariccia *et al.*, 2008) and, in some cases, energy conservation (Fish, 1995; Weimerskirch *et al.*, 2001; Portugal *et al.*, 2014). The ability of an animal to continue moving with a group, despite physiological differences, could be a significant advantage for social living species. Indeed, the results from the multiparous African savannah elephants in Chapter 4 show that both the mother and the neonatal calf were capable of moving soon after parturition, which would enable them to remain with the herd and benefit from the collective knowledge and safety of the group. The results from the primiparous females suggest that parturition may have more impact on a physiologically smaller individual, although the sample size was low. This could impact on the ability of primiparous females to remain with their herd as the herd would have to compromise on optimal foraging in order to remain with the mother and calf. Thus, the ability of both the mother and calf to move soon after birth could enhance both the individual fitness of the calf and the inclusive fitness of the herd. The fact that a significant life event, such as parturition, had such little impact on movement in multiparous females suggests that social living species may evolve strategies in order to remain together. Nevertheless, the pigeons in my thesis did incur a significant energetic cost when flying in pairs.

As tarsus length had little effect on wingbeat characteristics, the observed increase in wingbeat frequency is likely to be a functional product of this type of coordinated movement. Indeed, birds that fly in aerodynamically optimal V-formations tend to be larger, which means that the wingbeat frequency will be lower (Weimerskirch *et al.*, 2001; Portugal *et al.*, 2014). By contrast, coordinating fast three-dimensional movement in smaller species that are more agile and have a higher wingbeat frequency may require a greater degree of stability and control of movement. What is interesting about this finding is that these pigeons had already flown the route a minimum of 21 times solo before embarking on the paired releases, which meant the birds knew the route home and could have flown home alone, yet they still opted to fly with another individual and incur an energetic cost.

Thus, our results demonstrate the importance of flying in a flock to pigeons and suggests that the ultimate drivers of flocking, such as predator protection, outweigh the proximate costs. Overall, the results of both of these two studies provide new insights into collective animal movement and their underlying mechanisms.

6.4 Conflict with conspecifics and internal reproductive state

Finally, I aimed to identify how male African savannah elephants altered their movement in relation to their reproductive state and age. My results revealed that male elephants significantly increase their investments into musth periods as their probability of reproductive success increases. African savannah elephants are an intriguing study species for this question due to the life history traits of indeterminate growth, sexual dimorphism and longevity. Thus, male-male competition is at its lowest and female mate choice is at its highest late in life. The results of my study suggest that rather than investing in movement at a young age when the probability of reproductive success is lower, African savannah elephants may invest in future reproductive potential. Thus, my results suggest that male-male competition and female mate choice may influence the movement-related reproductive strategies employed in African elephants. A key question moving forward is whether males will dynamically adapt their strategy depending on the level of male-male competition.

6.5 Modulating movement in pigeons and elephants

In addition to the key results from my thesis, the contrast within the two pigeon and two elephant chapters provides some interesting insights into intra-species modulations in movement. For example, in the two pigeon studies, the birds altered their movement patterns by two different mechanisms. When navigating an unfamiliar terrain, the pigeons decreased their peak-to-peak DB acceleration, or the force of the wingbeat, whereas, when flying in pairs, the birds increased their wingbeat frequency and the DB acceleration remained stable. Whilst the birds

navigating unfamiliar routes did alter their wingbeat frequency, the primary mode of modulating the wingbeat was the force. Indeed, the ~ 0.3 Hz increase in median wingbeat frequency between releases 6 and 18, respectively, was slight in comparison to the 1.0 Hz increase exhibited when flying in pairs, which suggests that the increase was well within the normal wingbeat parameters of this species and such slight adjustments may be the individual optimising on wingbeat characteristics for that particular route.

The most parsimonious explanation for the different mechanisms is that, over the range of speeds the pigeons were travelling at, the pigeons used their peak-to-peak DB acceleration to modulate their speed, as demonstrated in Chapter 2, and altered their wingbeat frequency to increase stability and control. Indeed, Tobalske and Dial (1996) found that pigeons flying in wind-tunnels did not alter their wingbeat frequency appreciably with speed. By contrast, increasing wingbeat frequency can increase manoeuvrability and passive stability (Hedrick *et al.*, 2009; Usherwood *et al.*, 2011; Williams & Biewener, 2015). My results therefore provide ecologically relevant examples of the mechanism pigeons use to modulate their movements.

In the elephants, the differences in movement between the female herds and males were evident within the distribution of the data. Whereas daily mean speed (km h^{-1}) in the female elephants was normally distributed, with a very slight positive skew, the male elephant data was positively skewed, which required transformation prior to analysis. Non-musth males moved in a similar way to female herds, although the data had a slightly larger positive skew (Fig. 6.1). By contrast, males in musth moved substantially faster and in a larger home range size per day than both females and non-musth males. Thus, the results of my thesis show that musth state in males is an important factor to consider when modelling the movements of African savannah elephants.

6.6 Future directions

The results of my thesis open up many avenues for future research both in terms of broad research areas and species-specific projects.

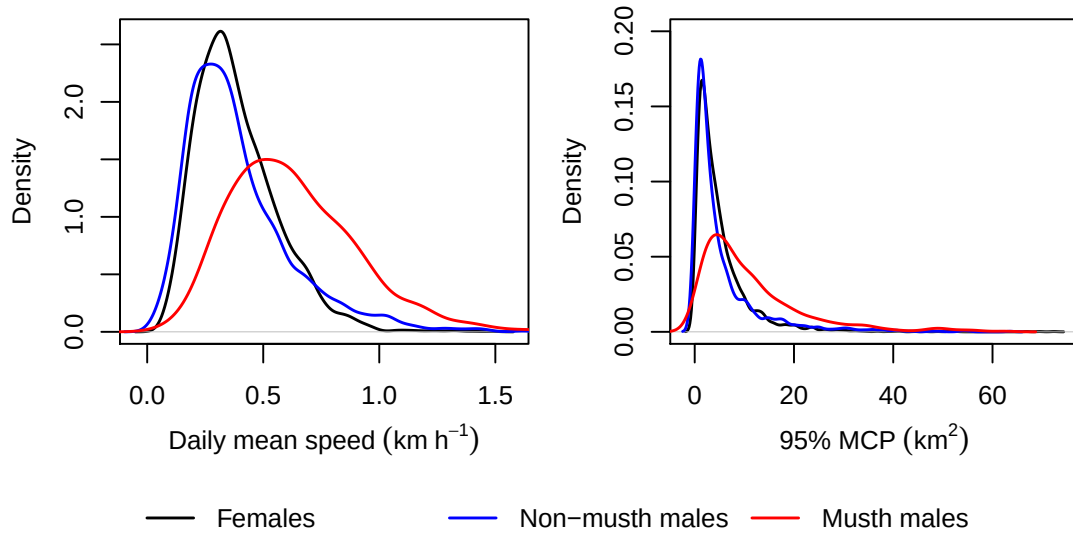


Figure 6.1: Distribution of the daily mean speeds (km h⁻¹) and 95% MCP (km²) of female and both musth and non-musth male African savannah elephants used in this thesis.

The discovery in Chapter 2, that pigeons modulate their wingbeat characteristics as a function of navigational knowledge, could be utilised in navigational research to identify how familiar a bird is with a given navigational task. For example, pigeons use the sun compass in navigation and can be “clock-shifted” by artificially altering the timing of the sunrise and sunset, which results in the pigeon deviating from their desired destination (home) through mis-information (Biro *et al.*, 2007; Guilford & Taylor, 2014). Biro *et al* (2007) released clock-shifted pigeons over a familiar terrain, which puts the landmark and sun-compass information directly in conflict, and found that pigeons were able to follow their known routes but the route was consistently offset in the expected compass direction. An extension of this study would be to analyse the wingbeat patterns of clock-shifted pigeons flying both highly familiar and less familiar routes to determine if, and when, the conflict in navigational cues results in the pigeon altering their wingbeat patterns, which may provide new insights into the cognitive underpinnings of navigational decisions.

Homing pigeons are an ideal model species for studies of navigation because of their innate homing ability and tendency to form idiosyncratic homing routes, which means factors, such as navigational experience, can be identified and manipulated

(Biro *et al.*, 2006b). Investigating how other species modulate their movements in response to information will be more complex because the navigational knowledge of an individual or the desired destination may not be known. Nevertheless, one potential application of this technique would be to investigate how animals move in relation to changes in the environment, such as a physical fence or a new wildlife corridor. The information gained from analysing how movement changes as the study subjects negotiate and then learn to alter their behaviour in relation to the new environment could provide key new insights into both species-specific biology and land management plans.

In Chapter 3, my results show that pigeons significantly increase their wingbeat frequency when flying in pairs. The first, and most crucial, extension of this research is to replicate this study in flocks of pigeons ranging in size from small to large to confirm that the increase in wingbeat frequency also occurs in flocks, and to determine if there is any interaction effect with flock size. Data from head mounted accelerometers in pigeons does suggest that the observed increase in wingbeat frequency does occur in flocks (James Walker and Graham Taylor, pers. comm.), but this needs to be systematically tested. Secondly, the energetic cost of flying in flocks relative to flying solo should be measured. Quantifying the cost would provide vital insight into the magnitude of the cost pigeons are prepared to pay to fly together. After establishing points 1 and 2, the next key extension would be to establish if this increase in wingbeat frequency is specific to pigeons or if it is a function of the cluster flock formation itself and thus applies to other species. Close cluster flock formations are typically made up of large numbers of smaller birds, such as pigeons and starlings (*Sturnus vulgaris*), which fly in irregular three-dimensional shapes (Heppner, 1974; Bajec & Heppner, 2009). One phenomenon that has long fascinated scientists is starling murmurations. If the increase in wingbeat frequency is a function of close cluster flocking, starling murmurations could come at a significant energetic cost. Investigating whether the increase in wingbeat frequency is a function of cluster flock formations could therefore provide crucial new insights into the behavioural ecology of species flying in cluster formations.

In chapters 2 and 3, I demonstrated that pigeons modulate their movements in relation to both navigational knowledge and the presence of conspecifics. Crucially, when considering a naïve bird, both of these modulations may result in a net energetic loss - either from the additional cost derived from navigating through unfamiliar terrain or the cost of increasing wingbeat frequency to fly in a flock. The key question that arises from this is whether the net energetic loss from flying an unfamiliar route can be offset by flying in an energetically expensive mode with conspecifics. The ‘many wrongs’ principle suggests that the navigational accuracy of a group increases as group size increases because individual orientation error is suppressed by group cohesion (Bergman & Donner, 1964; Hamilton, 1967; Wallraff, 1978; Simons, 2004). Biro *et al.* (2006a) found that pairs of pigeons flew more efficient (shorter) routes than the individuals that comprised the pairs. Furthermore, Dell’Ariccia *et al.* (2008) found that groups of homing pigeons homed more efficiently than individuals, with groups selecting more direct routes, whereas individuals tended to navigate using familiar landmarks. Indeed, within Chapter 3, I found that pigeons flying in pairs flew more direct routes, but, in this case, the birds were already flying a familiar route, which meant that the gains in route accuracy were not sufficient to offset the additional cost of flying in a flock. Thus, a key experiment moving forward would be to compare the routes and wingbeat patterns of naïve birds released from an unfamiliar location individually and in groups with varying degrees of experience to establish whether a naïve bird can incur a short-term energetic cost (flying in a flock) to make a net energetic saving.

In terms of the elephants, the combined evidence from the GPS tracks in my thesis and the literature suggests that births from primiparous females and within orphan herds warrant further investigation to establish what impact inexperience and a small stature have on the long-term development of elephant calves. Early life experiences can have long term impacts on the development of elephant calves (Lee *et al.*, 2013). In my thesis, two primiparous females slowed their movements around parturition in contrast to the multiparous females, which could result in

separation from the herd. However, the sample size was very low in my thesis so further research is required to confirm this result.

The results of Chapter 5 suggest that musth behaviour in bulls has physical movement manifestations, particularly in older bulls. The fixed three-state hidden Markov model used in this study had a relatively high success rate, but it cannot be easily applied to data, particularly as the fixed three-state model will always detect an increase in movement whether the bull is in musth or not. However, the results demonstrate, for the first time, that it may be possible to detect musth from GPS tracking data. One potential future avenue is machine learning algorithms, which could run on live GPS tracking data and relate information directly to fieldworkers. The ability to detect musth from GPS tracking data would open up a range of research possibilities including more detailed analyses of musth and non-musth movements, factors affecting movement, musth and non-musth associations with other individuals and reproductive dynamics in a population.

Finally, the fixed three-state hidden Markov models (HMMs) that were written for this thesis by Ben Lambert could be utilised to investigate distinctive changes in movement in other species or scenarios. For example, African savannah elephants make a distinctive dietary switch from browse to grass at the onset of the wet season (Wittemyer *et al.*, 2009). The three-state HMM could be used to identify whether there is also a distinctive change in movement corresponding with the dietary switch.

6.7 Concluding remarks

Overall, my thesis has provided many new insights into the modulations in movements by animals and their underlying proximate and ultimate causes. The results of my research have opened up many new avenues for future research which I hope will be explored in more depth. Ultimately, I hope that I have demonstrated that studying animal movements within an energetic framework can help elucidate how, when and why animals move. Modulations in movement are a fundamental aspect of life which have implications ranging from individual health to population dynamics and evolution - no matter whether you are a pigeon or an elephant.

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Appendices



Published version of Chapter 2

Taylor, L.A., Portugal, S.J., Biro, D. (2017) Homing pigeons (*Columba livia*) modulate wingbeat characteristics as a function of route familiarity. *Journal of Experimental Biology* 220: 2908-2915

RESEARCH ARTICLE

Homing pigeons (*Columba livia*) modulate wingbeat characteristics as a function of route familiarity

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ABSTRACT

Mechanisms of avian navigation have received considerable attention, but whether different navigational strategies are accompanied by different flight characteristics is unknown. Managing energy expenditure is critical for survival; therefore, understanding how flight characteristics, and hence energy allocation, potentially change with birds' familiarity with a navigational task could provide key insights into the costs of orientation. We addressed this question by examining changes in the wingbeat characteristics and airspeed of homing pigeons (*Columba livia*) as they learned a homing task. Twenty-one pigeons were released 20 times individually either 3.85 or 7.06 km from home. Birds were equipped with 5 Hz GPS trackers and 200 Hz tri-axial accelerometers. We found that, as the birds' route efficiency increased during the first six releases, their median peak-to-peak dorsal body (DB) acceleration and median DB amplitude also increased. This, in turn, led to higher airspeeds, suggesting that birds fly slower when traversing unfamiliar terrain. By contrast, after route efficiency stabilised, birds exhibited increasing wingbeat frequencies, which did not result in further increases in speed. Overall, higher wind support was also associated with lower wingbeat frequencies and increased DB amplitude. Our study suggests that the cost of early flights from an unfamiliar location may be higher than subsequent flights because of both inefficient routes (increased distance) and lower airspeeds (increased time). Furthermore, the results indicate, for the first time, that birds modulate their wingbeat characteristics as a function of navigational knowledge, and suggest that flight characteristics may be used as 'signatures' of birds' route familiarity.

KEY WORDS: Airspeed, Flight, Navigation, Route learning, Wingbeat amplitude, Wingbeat frequency

INTRODUCTION

Forward flapping flight is the most energetically demanding form of vertebrate locomotion (Norberg, 1990; Schmidt-Nielsen, 1972). To reduce the energetic cost of flight, birds utilise behavioural mechanisms, such as intermittent flight patterns (Rayner, 1985; Tobalske and Dial, 1996), formation flight (Weimerskirch et al., 2001) and modulation of their wingbeat frequency and amplitude (Greenewalt, 1962; Lilienthal, 2001). Whilst energy-saving mechanisms have been identified, little is known about the extent

to which birds employ these mechanisms in relation to navigation, for example, as a function of familiarity with a given landscape. Until now, avian navigation research has primarily focused on the sensory and cognitive underpinnings of orientation (Wiltschko and Wiltschko, 2009) and the total cost of a flight (Flack et al., 2016). However, a bird navigating from a familiar location, such as a roost or foraging site, may utilise different flight patterns compared with when flying over less familiar terrain where the distance to be covered and the route to be taken are less well known. Energy is frequently considered the currency of life (Butler et al., 2004), which means that managing energy expenditure is a key aspect of survival. Thus, energy allocation is likely to play a pivotal role in dictating the flight patterns utilised whilst navigating. Investigating whether birds modulate, for example, their wingbeat patterns in relation to their familiarity with a navigational task could provide key insights into the cost of orientation.

Homing pigeons (*Columba livia* Gmelin 1789) are an ideal model species for studies investigating flight characteristics in relation to navigational knowledge because of their innate homing ability, amenability to experimental manipulation, and body size permitting the attachment of state-of-the-art tracking devices. For research subjects, this means we can ensure that the full navigational experience of a given individual is known and can be characterised over successive flights. Although the finer details are still debated, it is generally accepted that over unfamiliar terrain, pigeons navigate by utilising a combination of olfactory cues for position fixing (Gagliardo, 2013), and a solar and magnetic compass for directional guidance (Kramer, 1957; Schmidt-Koenig, 1990; Wiltschko and Wiltschko, 2005). In addition, over familiar terrain, pigeons are also able to utilise visual landmarks (Meade et al., 2005). Meade et al. (2005) found that homing pigeons released repeatedly from the same site gradually developed stereotypical routes, with each individual having their own, slightly indirect, route. The results of this study and others indicate that pigeons reliably adopt such individually idiosyncratic routes as familiarity with the local landscape increases, and rely more on visual landscape features as they become more experienced (Biro et al., 2004; Guilford and Biro, 2014; Meade et al., 2005). Correspondingly, birds' route efficiency (the straight line distance between the start and end of the route divided by the distance travelled by the bird) increases steadily during the early stages of training and then plateaus once the birds have developed stable idiosyncratic routes (Guilford and Biro, 2014; Meade et al., 2005). Recapitulating a familiar but less direct route, rather than increasing route efficiency further, suggests that there could be a higher energetic and/or cognitive cost associated with navigating in an unfamiliar landscape for homing pigeons, relative to following a familiar route. However, whether different navigational strategies during route learning are accompanied by the same or different flight characteristics (e.g. wingbeat frequencies and amplitudes) is still unknown.

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Our study addresses this question by quantifying changes in the flight characteristics of homing pigeons as they learn a homing task. Recent technological advances have led to the introduction of miniature GPS devices, which provide highly accurate geographical position fixes over the full duration of a flight (Steiner et al., 2000), and high-frequency tri-axial accelerometers, which can measure the acceleration of an animal in three different planes, or dimensions, of movement (Halsey et al., 2009; Wilson et al., 2006). In turn, the combination of GPS and accelerometers allows us to simultaneously reconstruct birds' routes, speeds, wingbeat frequencies and amplitudes of dorsal body (DB) displacement. Although the precise relationship between the DB amplitude and the amplitude of wing motions is unclear, the former can nevertheless be used as an indirect measure of the latter (Hedrick et al., 2004; Usherwood et al., 2011). Together, wingbeat frequency and amplitude are related to the variation in power and speed of flapping flight, and thus can be used as a proxy for energy expenditure and/or work rate. By varying wingbeat frequency and amplitude, a bird is able to adjust the costs of flight. Reducing wingbeat frequency reduces the inertial power cost of the flight (i.e. power required to move the wings), as the power requirement of horizontal steady flight is proportional to the square of wingbeat amplitude but the cube of wingbeat frequency (Greenewalt, 1962; Lilienthal, 2001). By contrast, increasing wingbeat frequency and decreasing amplitude reduces the drag of the wings and body and increases lift, thereby optimising aerodynamic efficiency (i.e. optimising the forces acting on the bird relative to the air for efficient flight parameters) (Usherwood, 2009; Usherwood et al., 2011). Thus, analysing variation in wingbeat characteristics and speed in relation to navigational knowledge could shed new light on the costs of navigation and the energetic strategies employed by birds as they learn a route to a target.

MATERIALS AND METHODS

Subjects

Twenty-one homing pigeons aged either 1 or 3 years were used. All birds had prior homing experience, but had not been released at or near the sites used in the present study. The subjects were housed with ~120 other pigeons in two neighbouring lofts at the Oxford University Field Station, Wytham, UK (51°46'58.2"N, 1°19'2.7"W). Access to water, grit and a standard pigeon feed mix were available *ad libitum* at all times in the loft. All subjects were able to perform free flights around the loft on a daily basis throughout the year. In addition, in the month immediately preceding the start of the experiment, all subjects participated in a minimum of 24 solo or flock releases from four different release sites 1–3 km from home, as basic homing training, to familiarise the birds with the catch-and-release procedures and with being flown from an unfamiliar location. The protocols outlined in this paper were approved by the Local Ethical Review Committee of the University of Oxford's Department of Zoology.

Experimental protocols

Two release sites, both on a bearing of 282 deg from the lofts, were selected. The 'far' site (Barnard Gate; 51°47'48.1" N, 1°25'3.3"W) was 7.06 km from the lofts and the 'near' site (Mill Lane, Eynsham; 51°47'24.2"N, 1°22'19.5"W) was located 3.85 km from the lofts. Subjects were randomly assigned to two groups in an approximately even age distribution. Individuals in group 1 (10 pigeons; five 1-year-old and five 3-year-old birds; mean±s.d. body mass=471±39 g) were released 20 times individually from the 'far' site, and individuals in group 2 (11 pigeons; six 1-year-old and five 3-year-old birds; 471±20 g) were released 20 times individually from the

'near' site. Releases were conducted between May and July 2015, on days when the sun was visible and the wind speed was $<7 \text{ m s}^{-1}$ when measured 5.5 m above the ground. Subjects participated in a maximum of two releases per day, with a minimum of 3 h between each release. All birds were released individually. Initially, releases occurred at 10-min intervals; this was later reduced to a minimum of 4 min if it could be visually confirmed that the previously released bird had left the vicinity of the release site. If, at any point, a bird accidentally paired up with another subject, the release was excluded for both birds (18 flights). Four additional tracks were removed from the analysis. One bird failed to return home before the GPS battery ran out on its first release from the far site; a GPS fault occurred for two birds, one during the fifth release and one during the 14th release; and the devices could not be accurately synchronised for a bird on its 10th release. In addition, four birds landed during their first release. For these landings, the entire descent, stationary and ascent sections were removed from the track data from the point of first descent to the peak of ascent.

Data logging

The birds were tracked using 5 Hz GPS loggers (BT-Q1300ST, Qstarz International Co., Taipei, Taiwan; 15 g) and 200 Hz tri-axial accelerometers (AX3, Axivity, Newcastle upon Tyne, UK; ±16 g; 11 g). The loggers were attached to the pigeons using Velcro strips, which were glued to trimmed feathers on the back (Fig. 1; Biro et al., 2002). In total, the loggers and fastenings weighed 27 g (less than 7% of the subjects' mean body mass). Two weeks prior to the start of the experiment, clay weights (27 g) were attached to the birds' back via Velcro to accustom them to flying with the additional mass. These were exchanged for GPS devices and accelerometers immediately prior to each release. GPS and accelerometer data were downloaded using QTravel [Qstarz International Co.; version 1.48(T)] and Open Movement (Om) GUI Application (Newcastle University; version 1.0.0.28), respectively.

The weather, including mean wind speed per minute and a running mean of the wind bearing over the previous 10 min, was



Fig. 1. A homing pigeon with an Axivity AX3 accelerometer (front) and Qstarz BT-Q1300ST GPS logger (case removed; back) attached to the back via Velcro strip, which was glued to trimmed feathers.

recorded using a WS2083 Professional Wireless Weather Station with USB upload (Aercus Instruments, Doncaster, UK) situated 5.5 m above the pigeon lofts. Weather data was logged using Cumulus Weather Station Software (Sandaysoft, Sanday, Orkney, UK; version 1.9.4).

Data processing

GPS and accelerometer data were synchronised to an accuracy of ± 0.2 s (GPS frequency) using the point of take-off in both the GPS and accelerometer loggers, which were identified using the marked increases in GPS speed and dorsal acceleration peaks produced during take-off. The weather data were combined with the GPS and accelerometer data using the timestamps from the weather station and the GPS loggers. For each GPS point, the orthodromic (great-circular) distance travelled and birds' final bearing from the previous point were calculated using the haversine formula and forward azimuth, respectively. For each flight, route efficiency was calculated as the ratio between the total straight-line (great-circular) distance between release and home, divided by the sum of the direct (great-circular) distances between each successive GPS point (straightness index; Batschelet, 1981). Wind support and crosswind were calculated using the methods described in Safi et al. (2013): wind support represents the length of the wind vector in the direction of the bird's flight and crosswind represents the absolute speed of the wind vector perpendicular to the bird's direction of travel (Fig. S1). Airspeed, the speed of the bird relative to the wind, was then calculated using the speed derived from the GPS devices while taking into account wind support and crosswind (Safi et al., 2013).

The dorsal (Z-axis) accelerometer measurements were filtered by taking a running mean over five data points (0.025 s). Static acceleration (or gravity) was removed by subtracting a running mean over 15 wingbeat cycles (> 2 s). The running mean was calculated over wingbeat cycles rather than over specific time periods, because variation in wingbeat frequencies would have meant including varying quantities of partial wingbeat cycles in a time-based running mean. The dorsal acceleration signal was then used to detect each wingbeat using the upper reversal point in acceleration (Fig. S2) (Norberg, 1990; Portugal et al., 2014). The peak-to-peak DB acceleration (g) and wingbeat frequency (number of wingbeats per second; Hz) were calculated for each individual wingbeat. The amplitude of the DB displacement (mm), which is the amount the body is displaced per wingbeat, was then calculated by the double integration of dorsal accelerometer measurements (Usherwood et al., 2011). After the first integration, a running mean over 15 wingbeat cycles was removed from velocity to remove drift. The data were then filtered using a fourth-order high-pass Butterworth filter with a cut-off frequency of 1 Hz. The procedure was repeated after the integration for displacement but with a cut-off frequency of 2.5 Hz in the Butterworth filter. The cut-off frequencies were determined by visualising the data using fast Fourier transforms. A more conservative estimate of the amplitude of the DB displacement was also calculated by passing the raw accelerometer measurements through fourth-order Butterworth filters prior to integration instead of running means, but this led to no significant difference in the results (Fig. S3).

In order to only compare sections of steady flight, the data were trimmed in a 1000 m radius around the release site (start point) and the pigeon lofts (end point). The shortest straight-line distance of the entire steady flight therefore measured 5.08 km for the far site and 1.85 km for the near site. In addition to comparing the entire steady flight, the data were also trimmed to remove sections with lower

wingbeat frequencies (≤ 3.0 Hz) and sections of tortuous flight to remove any effect of gliding, idling or circling from the dataset. Tortuosity was calculated by taking a running mean of the change in the birds' bearing over every 1 s of data (five GPS points), with changes in direction of ≥ 3.0 deg removed in order to discard circling and keep only active straight-line powered flight.

Data analyses

Piecewise linear mixed effects (LME) models were used to investigate the effect of repeated releases on route efficiency, median peak-to-peak DB acceleration per wingbeat (g), median DB amplitude per wingbeat (mm), median wingbeat frequency (Hz) and median airspeed ($m s^{-1}$). Piecewise, or segmented, regression identifies an abrupt change of the dependent variable (or breakpoint) with respect to the independent variable, which allows one to fit pre- and post-event slopes (Naumova et al., 2001). We used this approach to determine whether changes in wingbeat characteristics corresponded to changes in route efficiency and to identify the trends in the data either side of this change. Breakpoints were objectively estimated using one-dimensional optimisation. Piecewise LME models were fitted using the fixed effects of release number less than the breakpoint (breakpoint – release number), release number greater than the breakpoint (release number – breakpoint), median wind support, median crosswind and group. Individual was also added as a random slope on both release number effects.

To establish the effect of wingbeat characteristics on airspeed, two LME models were used. Firstly, with median peak-to-peak DB acceleration and median wingbeat frequency as fixed effects, and secondly with median DB amplitude per wingbeat, which is dependent on peak-to-peak DB acceleration (force exerted on the dorsal body) and wingbeat frequency (duration of the wingbeat), as a fixed effect. Group was added as a fixed effect to both models but was insignificant. Individual was added as a random effect on the intercept. In addition, LME models were used to directly relate route efficiency with wingbeat characteristics and airspeed between releases 1 and 6 using the fixed effects of route efficiency, median wind support, median crosswind and group, and the random effect of individual.

Route efficiency was negatively skewed, and was therefore transformed before analysis by directly inverting values and taking the logarithm using the formula $\log_{10}(1-x)$. From the full models, simpler models were obtained by stepwise deletion of non-significant terms. Likelihood ratio tests were used to test the statistical significance of each fixed effect in the best-fitting model. LME models were calculated using maximum likelihood and the models were checked for assumptions of linearity, normality, homoskedasticity and autocorrelation by visual inspection of plotted residuals. Model fit was assessed by calculating conditional R -squared values ($R^2_{LME(c)}$) using the methods described in Nakagawa and Schielzeth (2013).

Data processing and analysis were conducted using MATLAB (MathWorks, Natick, MA, USA; version R2015a) and the open-source software R (version 3.2.3; R Foundation for Statistical Computing, Vienna, Austria) using the packages lme4 (Bates et al., 2015; version 1.1-8) and MuMIn (version 1.15.1; <https://cran.r-project.org/package=MuMIn>).

RESULTS

Route efficiency improved as the birds became more experienced (Fig. 2). Over the first five releases, route efficiency increased significantly from 0.46 ± 0.27 (mean $\pm$ s.d.) for release 1 to 0.82 ± 0.18

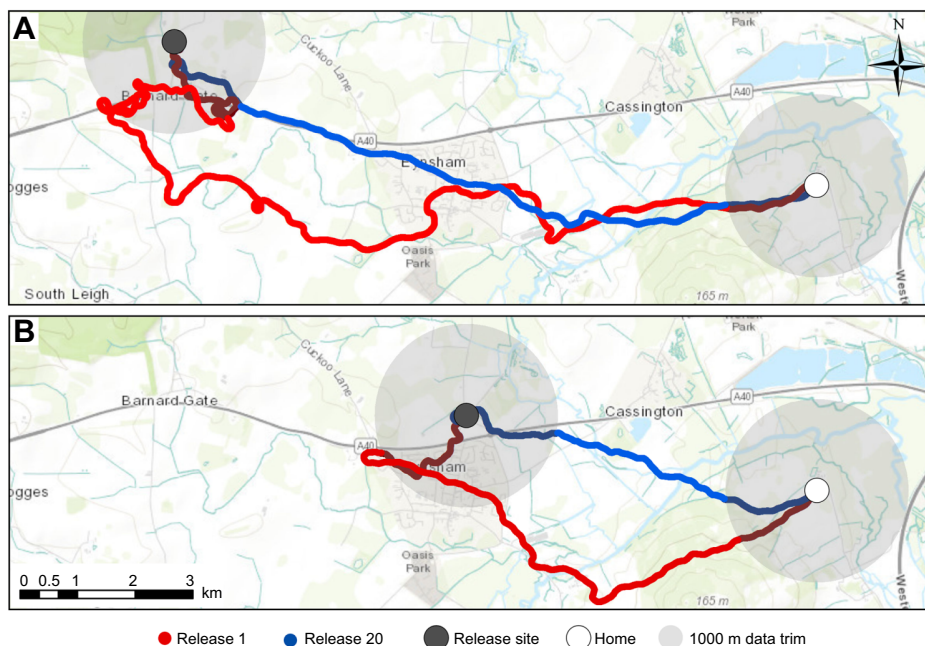


Fig. 2. Examples of routes flown during the first (red; release 1) and last release (blue; release 20). (A) From the far site; (B) from the near site. Note the increase in route efficiency at both sites. Map designed using ArcGIS 10.4.1 using the World Topographic Map (http://services.arcgisonline.com/ArcGIS/rest/services/World_Topo_Map/MapServer).

for release 5 (piecewise linear mixed model parameter estimate=0.287; likelihood ratio test for the model without release number: $\chi^2_1=32.9$, $P<0.001$). A breakpoint, which denotes a change of the dependent variable (route efficiency) in respect to the independent variable (release number), was then automatically detected between releases 5 and 6 {5.5, 95% confidence interval (CI)=[4.3, 6.2]; Fig. 3}. No significant difference in route efficiency was detected among releases ranging from release 6 (0.88 ± 0.10) to release 20 (0.87 ± 0.10 ; $\chi^2_1=0.7$, $P=0.390$). Group (i.e. release distance) also had a significant effect on route efficiency, with

birds released at the nearer site (group 2) flying significantly more efficient routes than those released at the far site (group 1; estimate=0.316, $\chi^2_1=4.8$, $P=0.029$). However, group had no significant effect on wingbeat characteristics or speed, thus the results from the two groups were pooled for the remainder of the analyses (Table 1). Route efficiency was also significantly affected by both median wind support (estimate=-0.05, $\chi^2_1=14.8$, $P<0.001$) and median crosswind (estimate=0.10, $\chi^2_1=7.9$, $P=0.005$), with greater wind support and lower crosswinds associated with higher route efficiency.

A breakpoint was detected in the median peak-to-peak DB acceleration (5.6, 95% CI [4.1, 6.8]) and in the median DB amplitude (5.99, 95% CI [4.6, 6.9]) between the same release numbers (5 and 6) as route efficiency (5.5, 95% CI [4.3, 6.2]). Both the DB acceleration and amplitude significantly increased prior to the breakpoint (acceleration: estimate=0.038, $\chi^2_1=7.4$, $P=0.007$; amplitude: estimate=0.295, $\chi^2_1=8.5$, $P=0.004$) before decreasing (acceleration: estimate=-0.006, $\chi^2_1=8.5$, $P=0.004$; amplitude: estimate=-0.123, $\chi^2_1=16.4$, $P<0.001$; Fig. 4A,B). By contrast, the breakpoint for median wingbeat frequency appeared later, between releases 9 and 10 (9.6, 95% CI [4.5, 12.6]), with no significant change prior to the breakpoint ($\chi^2_1=2.0$, $P=0.159$). Upon visual inspection, one might argue that there is a breakpoint in the median wingbeat frequency around release 6 (Fig. 4C). Indeed, manually moving the breakpoint to the breakpoints of DB acceleration (5.6) and amplitude (5.99) revealed that wingbeat frequency significantly decreased during the early releases (breakpoint 5.6: estimate=-0.03, $\chi^2_1=2.83$, $P=0.007$; breakpoint 5.99: estimate=-0.02, $\chi^2_1=6.89$, $P=0.009$). However, the resultant models were weaker and accounted for less of the variability, which is why the objective breakpoint is situated slightly later between releases 9 and 10. The visual ambiguity in the breakpoint is reflected in the confidence interval, which is large for median wingbeat frequency (95% CI [4.5, 12.6]). After the objective breakpoint, wingbeat frequency increased significantly (estimate=0.02, $\chi^2_1=18.6$, $P<0.001$).

Median wind support also had a significant effect on both median wingbeat frequency and median DB amplitude, with higher wind support associated with lower wingbeat frequencies

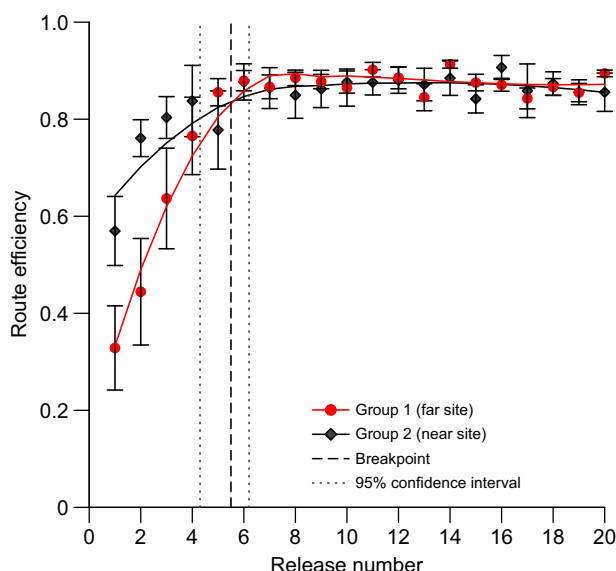


Fig. 3. Route efficiency (mean±s.e.m.) as a function of release number for group 1 (far site, $n=10$) and group 2 (near site, $n=11$). The dashed line indicates a computationally optimised piecewise linear mixed model breakpoint ($\pm 95\%$ CI indicated by dotted lines) denoting a change in response function in respect to release number. Solid lines correspond to local polynomial regression fitting.

Table 1. Comparison of the piecewise linear mixed effects models for efficiency, wingbeat characteristics and airspeed for releases 1–20

	Breakpoint (95% CI)	Release number<breakpoint		Release number>breakpoint		Wind support		Crosswind		Group		$R^2_{LME(c)}$
		<i>P</i>	Est.	<i>P</i>	Est.	<i>P</i>	Est.	<i>P</i>	Est.	<i>P</i>	Est.	
Efficiency (transformed)	5.5 (4.3, 6.2)	<0.001	0.287	0.390	–	<0.001	–0.049	<0.001	0.099	0.029	0.316	0.69
Median peak-to-peak DB acceleration (g)	5.6 (4.1, 6.8)	0.007	0.038	0.007	–0.006	0.487	–	0.679	–	0.286	–	0.65
Median DB amplitude per wingbeat (mm)	5.99 (4.6, 6.9)	0.004	0.294	<0.001	–0.123	<0.001	0.195	0.430	–	0.288	–	0.70
Median wingbeat frequency (Hz)*	9.6 (4.5, 12.6)	0.159	–	<0.001	0.016	<0.001	–0.025	0.302	–	0.735	–	0.68
Median airspeed (m s ^{–1})	5.2 (3.9, 7.8)	<0.001	0.527	0.001	–0.065	N/A	–	N/A	–	0.281	–	0.22

Fixed effects with *P*-values and parameter estimates (Est.) denoted in **bold** are included in the final model. Conditional *R*-squared values ($R^2_{LME(c)}$) are calculated using the methods described in Nakagawa and Schielzeth (2013).
*Note: manually moving the breakpoint for wingbeat frequency revealed a significant decrease in this variable during the early releases (breakpoint 5.6: estimate=–0.03, $\chi^2_1=2.83$, *P*=0.007; breakpoint 6.0: estimate=–0.002, $\chi^2_1=6.88$, *P*=0.009).

(estimate=–0.02, $\chi^2_1=26.5$, *P*<0.001) and increased DB amplitude (estimate=0.20, $\chi^2_1=25.3$, *P*<0.001). By contrast, median wind support had no effect on peak-to-peak DB acceleration, and median crosswind had no effect on any of the wingbeat characteristics.
Median airspeed (m s^{–1}) increased during the first five releases (breakpoint 5.2, 95% CI [3.9, 7.8]; estimate=0.53, $\chi^2_1=32.5$, *P*<0.001) and thereafter decreased slightly (estimate=–0.07, $\chi^2_1=10.6$, *P*<0.001; Fig. 4D). The means of the median flight airspeeds for the first three releases were particularly low (release 1: 20.1±1.6 m s^{–1}; release 2: 19.2±1.4 m s^{–1}; release 3: 19.7±1.0 m s^{–1}). However, the coefficient of determination for the relationship between median airspeed and release number was low, even when accounting for individual variation ($R^2_{LME(c)}$ =0.22). By analysing all 20 releases in an LME model with median peak-to-

peak acceleration and median wingbeat frequency as fixed effects, we found that higher airspeeds were associated with higher peak-to-peak DB accelerations (estimate=1.57, $\chi^2_1=10.3$, *P*=0.001) and lower wingbeat frequencies (estimate=–0.78, $\chi^2_1=3.9$, *P*=0.048). Furthermore, in a model with DB amplitude (displacement) as a fixed effect, which is dependent on peak-to-peak DB acceleration (force exerted on the DB) and wingbeat frequency (duration of the wingbeat), DB amplitude was positively associated with airspeed (estimate=–0.24, $\chi^2_1=23.3$, *P*<0.001).
The results thus far indicate that changes in wingbeat characteristics and airspeed correspond to changes in our route familiarity variable (i.e. route efficiency). To directly relate these findings, LME models were used with route efficiency as a fixed effect between releases 1 and 6. The results of these analyses

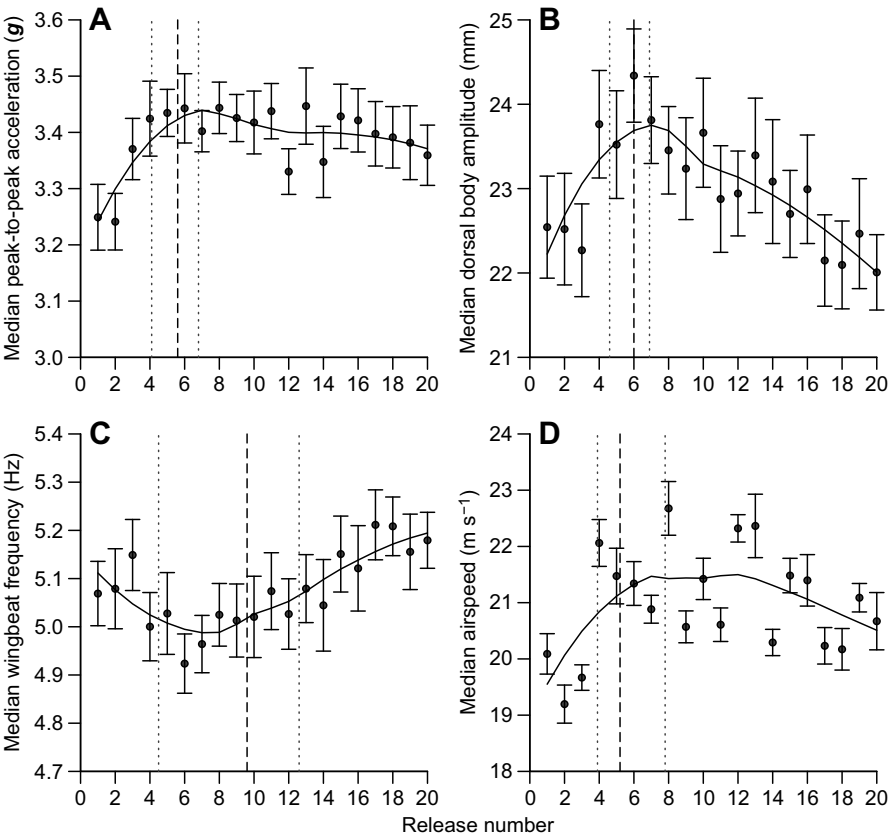


Fig. 4. Wingbeat characteristics and airspeed (mean±s.e.m., *n*=21) as a function of release number. (A) Median peak-to-peak acceleration, (B) median dorsal body amplitude, (C) median wingbeat frequency and (D) median airspeed. Dashed lines indicate computationally optimised piecewise linear mixed model breakpoints (±95% CI indicated by dotted lines) denoting a change in response function in respect to release number. Solid lines correspond to local polynomial regression fitting.

corroborate these findings, with median peak-to-peak DB acceleration (estimate = -0.11 , $\chi^2_1 = 30.0$, $P < 0.001$), median DB amplitude per wingbeat (estimate = -0.86 , $\chi^2_1 = 20.9$, $P < 0.001$) and median airspeed (estimate = -0.84 , $\chi^2_1 = 20.2$, $P < 0.001$) all positively related to route efficiency (negatively related to the transformed route efficiency; Table S1, Fig. S4). As with release number, median peak-to-peak acceleration was only influenced by route efficiency, with no significant effect of median wind support, median crosswind or group ($P > 0.1$). By contrast to DB acceleration, DB amplitude and airspeed, higher median wingbeat frequencies were associated with lower route efficiencies in releases 1–6 (estimate = 0.06 , $\chi^2_1 = 8.1$, $P = 0.004$). Although there was a significant difference between groups in route efficiency in the piecewise LME model (estimate = 0.318 , $\chi^2_1 = 4.8$, $P = 0.029$), there was no significant difference between groups when relating wingbeat characteristics and airspeed to route efficiency ($P > 0.1$).

We hypothesised that one potential explanation for differences in wingbeat characteristics could be changes in wingbeat modes with navigational experience, such as additional circling behaviour and gliding in the early releases. Analysing only data with flap frequencies > 3 Hz and tortuosity < 3 deg (i.e. without gliding and circling segments, respectively) resulted in a shift in the breakpoint in wingbeat frequency from release 9.6 (95% CI [4.5, 12.6]) to release 6.2 (95% CI [4.6, 12.5]). In addition, the wingbeat frequencies significantly decreased prior to the breakpoint (estimate = 0.02 , $\chi^2_1 = 4.6$, $P = 0.03$). However, aside from the slight changes to median wingbeat frequency, removing circling and gliding had no other significant effect on the results other than decreasing median wingbeat frequency and median peak-to-peak DB acceleration, and increasing median DB amplitude and median airspeed (Fig. S5). Furthermore, it is important to note that the confidence interval in the breakpoint for wingbeat frequency remains approximately the same and that on visual inspection, one could place a breakpoint in the whole flight data at around release 6, as discussed above.

DISCUSSION

We investigated the effect of navigational experience in relation to wingbeat characteristics and airspeed in homing pigeons. The results indicate, for the first time, that gradual increases in the birds' route efficiency, observed as birds become more experienced with a given terrain, are also accompanied by changes in wingbeat characteristics and airspeed. As the birds' route efficiency improved during the first six releases, the median peak-to-peak DB acceleration, median DB amplitude and, consequently, median airspeed also increased. By contrast, after route efficiency stabilised, the birds' median DB acceleration and amplitude decreased, whereas median wingbeat frequency increased. However, decreasing DB amplitude, and hence wingbeat amplitude, in favour of increasing wingbeat frequency did not result in a higher airspeed. Taken together, our results suggest that birds may be modulating their flight characteristics as a function of navigational familiarity with the area through which they are travelling.

As with previous studies (reviewed in Guilford and Biro, 2014), route efficiency improved over consecutive releases. It increased significantly over the first five releases, with a breakpoint detected between releases 5 and 6. The breakpoint denotes a change in route efficiency (dependent variable) with respect to release number (independent variable), with the position of the breakpoint determined by where the slopes of the two segments join. We chose the piecewise linear mixed model approach to objectively identify a change of state because, as these results demonstrate,

wingbeat characteristics and airspeed continue to change long after route efficiency stabilises. Whilst we could manually divide the data into segments, an automated approach enables us to objectively identify changes in wingbeat characteristics and airspeed as a function of release number and to identify whether these changes correspond to changes in route efficiency. In this study, we identified that route efficiency increases up to a breakpoint of 5.5 and thereafter stabilises. As expected, the near-site group (straight-line distance: 3.85 km) flew significantly more efficient routes home in the early stages of route learning than the far-site group (7.06 km), owing to the proximity of the near release site to the familiar area surrounding the pigeons' home lofts. However, despite these differences, no significant difference was found between groups in wingbeat characteristics and speed, and route efficiency still significantly increased over the first five releases for both groups. These results reinforce the idea that birds modulate their wingbeat characteristics in response to navigating an unfamiliar route, and that this effect is detectable even at short distances from home.

The aforementioned changes in route efficiency did correspond to changes in wingbeat characteristics, both in terms of the positioning of the breakpoint and when directly relating these factors during the first six releases. As route efficiency increased, the peak-to-peak DB acceleration and DB amplitude also increased, which indicates that the acceleration, or force, the dorsal body experienced increased over the first few releases. The median peak-to-peak DB acceleration per wingbeat was especially low during the first few releases. Although DB acceleration did decrease again after route efficiency stabilised, the DB accelerations the birds experienced during the first few releases were still much lower than in the last few releases, which could suggest that the overall flapping force was lower during the first few releases. Correspondingly, the airspeeds of the first three flights were also particularly low. By analysing the influence of peak-to-peak DB acceleration and wingbeat frequency on airspeed, we established that higher airspeeds were associated with higher peak-to-peak accelerations and lower wingbeat frequencies, with peak-to-peak acceleration having a slightly larger effect than wingbeat frequency. However, the amplitude of the DB displacement, which is dependent on the peak-to-peak acceleration (force exerted on the DB) and the wingbeat frequency (duration of the wingbeat), had the greatest overall effect on airspeed. For example, a wingbeat which is both high in force (peak-to-peak acceleration) and long in time (low wingbeat frequency) will result in a greater displacement, and hence higher airspeed, than one that is low in force or short in time. It should be noted, however, that this negative relationship between wingbeat frequency and airspeed is within the subtleties of active flight parameters, and may not represent the relationship over the entire range of the pigeons' wingbeat characteristics. Although DB amplitude is an indirect measure of wing amplitude, the two measures are likely to be related (Hedrick et al., 2004). An alternative explanation for the changes in wingbeat characteristics and airspeed could be changes in flight behaviour, such as increased circling and/or gliding. However, removing both wingbeat frequencies below 3 Hz and tortuous flight made no substantial difference to the results other than shifting the breakpoint of median wingbeat frequency, suggesting that the changes in wingbeat characteristics are occurring during straight-line powered flight. Flying at a slower speed from an unfamiliar location may be an advantage as it may enable the bird to gather more local ambient information.

Breakpoints in the median peak-to-peak acceleration (release: 5.7) and the median DB amplitude (5.99), which occur between the

same release number as route efficiency (5.5), along with the fact that higher peak-to-peak acceleration and DB amplitude were associated with higher route efficiency in releases 1–6, indicate that DB movements change as a function of navigational knowledge. By contrast, during the first six releases, higher wingbeat frequencies were associated with lower route efficiencies. The large confidence interval and slightly later breakpoint in wingbeat frequency (9.6) suggest that it is likely that birds continue to learn routes home even after route efficiency initially plateaus. Indeed, removing circling and gliding behaviour resulted in a breakpoint in wingbeat frequencies being detected at release 6.2. Thus, changes in wingbeat characteristics shortly after the route efficiency breakpoint could still be related to the acquisition of navigational knowledge. An alternative explanation could be increases in the birds' physical fitness, or acclimatisation to the sensor mass or to the capture and release procedure. However, given the substantial number of releases immediately prior to the start of the experiment (≥ 24), the daily free flights around the loft and the fact that the birds were fitted with clay weights equal to the size and mass of the devices 2 weeks prior to the start of the experiment, this is unlikely to have been a factor. Furthermore, migratory species, such as barnacle geese (*Branta leucopsis*) undertaking 2500 km journeys, do not increase flight behaviour prior to migratory departure (Portugal et al., 2012), suggesting exercise is not a prerequisite for extended flight.

Shortly after route efficiency stabilised, changes in the birds' flight characteristics consisted largely of increases in wingbeat frequency as the birds' DB acceleration and amplitude decreased. The inertial power requirement, or cost, of horizontal steady flight is proportional to the square of wingbeat amplitude but the cube of wingbeat frequency (Greenewalt, 1962; Lilienthal, 2001), which means increasing wingbeat frequency would result in a higher inertial power cost. If this higher wingbeat frequency translated into higher airspeeds, then this strategy could be beneficial as the bird would then reach its destination in less time (Hedenström and Ålerstam, 1995). However, as already highlighted, higher wingbeat frequencies were associated with lower airspeeds. Indeed, airspeed did decrease significantly from release 6, although variability in this was high and the effect size small. Albeit increasing wingbeat frequency would increase the inertial power costs, a higher wingbeat frequency would also result in a higher aerodynamic efficiency by reducing the drag from the wings and body and increasing lift (Greenewalt, 1962; Lilienthal, 2001), which may be advantageous once the total length of the journey is known. The median wingbeat frequency increased in this study from 4.9 (release 6) to 5.2 (release 18), i.e. by 5.8%. However, these wingbeat frequencies are still considerably lower than those reported for homing pigeons participating in flight that may require a higher degree of aerodynamic efficiency or stability, such as flock flight (~6.6–7.0 Hz; Usherwood et al., 2011) and during ascending and descending flight (6.1–9.6 Hz; Berg and Biewener, 2008). Thus, the increases in wingbeat frequency exhibited in the present study are more likely to be related to birds optimising their flight patterns between inertial power requirements and aerodynamic efficiency.

Increasing aerodynamic efficiency, by increasing wingbeat frequency, could help conserve energy, particularly as the results of this study also indicate a strong effect of the wind on route efficiency and flight characteristics. The effect of wind on flight is well documented, particularly in relation to the timing and distance travelled during migration (Ålerstam, 1979; Liechti and Bruderer, 1998). Liechti (2006) highlighted that wind speed can easily double or halve the bird's speed and thereby affect the overall cost of the

flight. Weather data used in this study (mean wind speed and bearing) were recorded 5.5 m above the pigeon lofts, 7.06 km from the 'far' release site. Therefore, the accuracy of the readings decreased the further away the bird was from the lofts, which could explain some of the variation, particularly in airspeed, found in this study. Nevertheless, the results indicate that wind support, in particular, was a consistent and significant factor contributing to the work rate, with a higher wind support (tail wind) associated with a lower wingbeat frequency, which would decrease the inertial power costs. By contrast, the birds' peak-to-peak DB acceleration was not affected by the wind, which suggests that in winds under 7 m s^{-1} , birds compensate for the wind by modulating wingbeat frequency rather than the amplitude. Indeed, the change in breakpoint in the wingbeat frequency from the whole flight data to the active straight-line data from release 9.6 to release 6.2 could also be a reflection of the birds utilising circling and gliding behaviour to compensate for the effects of the wind. Furthermore, higher route efficiency was associated with higher wind support and lower crosswinds, which suggests that the birds may modify their route (and hence their route efficiency) depending on the wind conditions.

Regardless of the underlying cause for the changes in wingbeat characteristics, the results of this study indicate, for the first time, that pigeons modulate their wingbeat characteristics as a function of navigational knowledge, which suggests that navigation and the learning process may have physical manifestations in birds. In particular, peak-to-peak DB acceleration was especially low during the first few releases, which was unaffected by wind characteristics, and related to a lower airspeed. Thus, measuring flight characteristics could provide new insights into the cognitive state of the bird. For example, wingbeat characteristics may be used as 'signatures' of birds' route familiarity, which could be utilised in navigation research to identify how familiar a bird is with a given navigational task. Furthermore, the results of this study lead us to speculate that birds may be able to orient and learn more effectively at lower speeds, in which case the flight would then become a trade-off, or compromise, between optimal navigation and learning (accuracy), and vulnerability to predators and the total flight time (speed). Moreover, these results suggest that the cost of the first flight, such as the first migration or first route out in search of a novel foraging site, may be higher than that of subsequent flights, because of both inefficiencies in the route, which increase the total distance flown, and the increased flight time, owing to lower airspeeds. This, in turn, could impact on the total time available for foraging and reproduction, and other decisions, such as whether to fly with other individuals. For example, despite the additional energetic cost of flying in a close cluster flock (Usherwood et al., 2011), a naive individual may be able to conserve energy by flying with experienced individuals to reduce the total flight time, as well as gain protection from predators. Thus, studying intra-individual modulations of wingbeat characteristics and airspeed could provide new insights into the decision-making and navigational strategies of birds.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: L.A.T., S.J.P., D.B.; Methodology: L.A.T., S.J.P., D.B.; Formal analysis: L.A.T.; Investigation: L.A.T.; Resources: L.A.T., D.B.; Data curation: L.A.T.; Writing - original draft: L.A.T.; Writing - review & editing: L.A.T., S.J.P., D.B.; Visualization: L.A.T.; Supervision: S.J.P., D.B.; Project administration: L.A.T., D.B.; Funding acquisition: L.A.T., D.B.

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Data availability

Data are available from the Dryad Digital Repository (Taylor et al., 2017): <http://dx.doi.org/10.5061/dryad.37d5m>

Supplementary information

Supplementary information available online at <http://jeb.biologists.org/lookup/doi/10.1242/jeb.154039.supplemental>

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B

Supplementary material for Chapter 2

Supplementary material for Chapter 2: Homing pigeons (*Columba livia*) modulate wingbeat characteristics as a function of route familiarity.

B.1 Supplementary figures

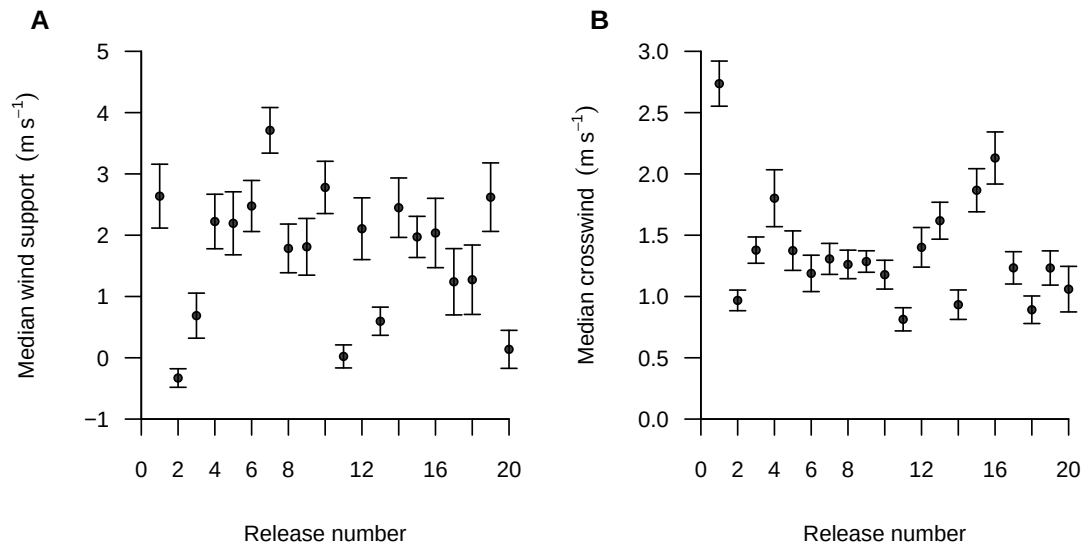


Figure B.1: (A) Median wind support (mean $\pm$ s.e.m.) and (B) median crosswind (mean $\pm$ s.e.m.) as a function of release number.

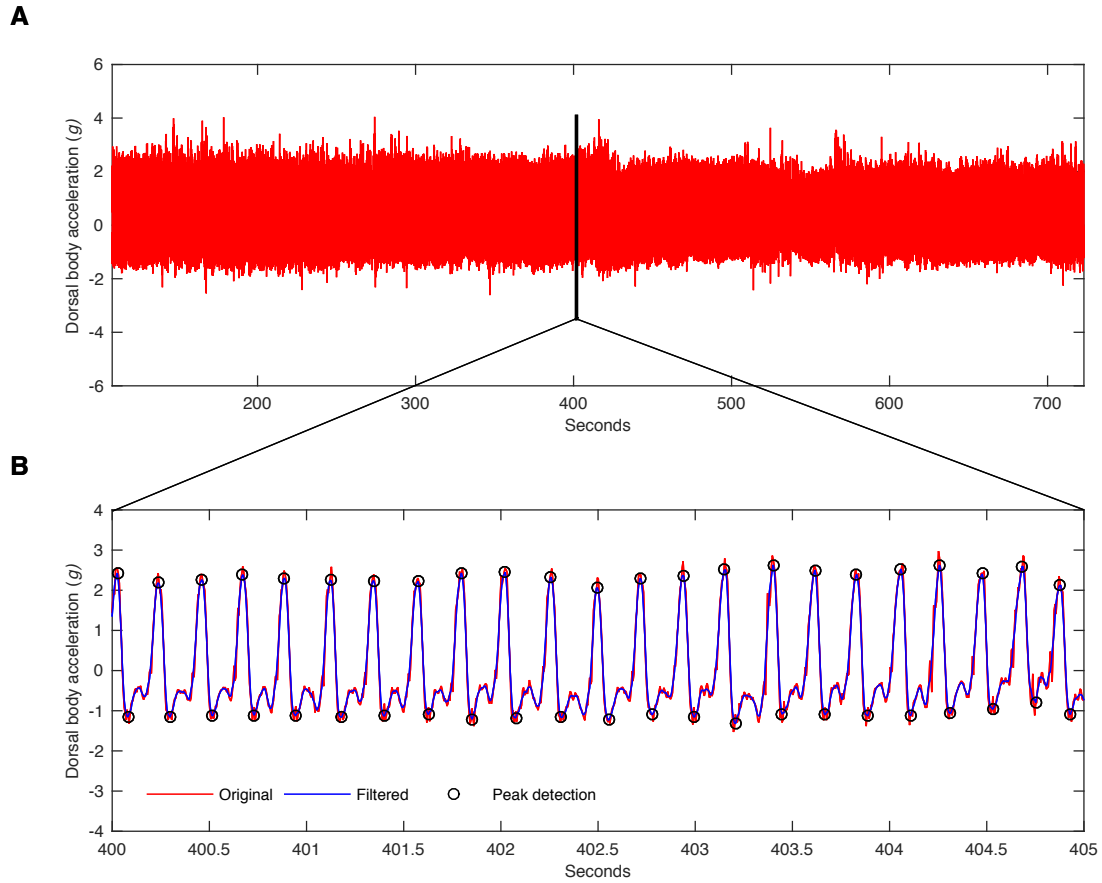


Figure B.2: Example of a dorsal acceleration trace for the first flight of bird B67 recorded on an Axivity AX3 accelerometer logging at 200 Hz (route can be seen in Fig. 1; panel (A); red line). The black rectangle positioned at 400 s refers to the zoomed section displayed in (A), which shows the original data (red) and the data filtered using a running mean over five data points (blue). The circles highlight the position of the maximum and minimum peaks identified using our peak detection analysis (see Methods). Gravity, which is calculated by a running mean over 15 wingbeat cycles, is removed from all data.

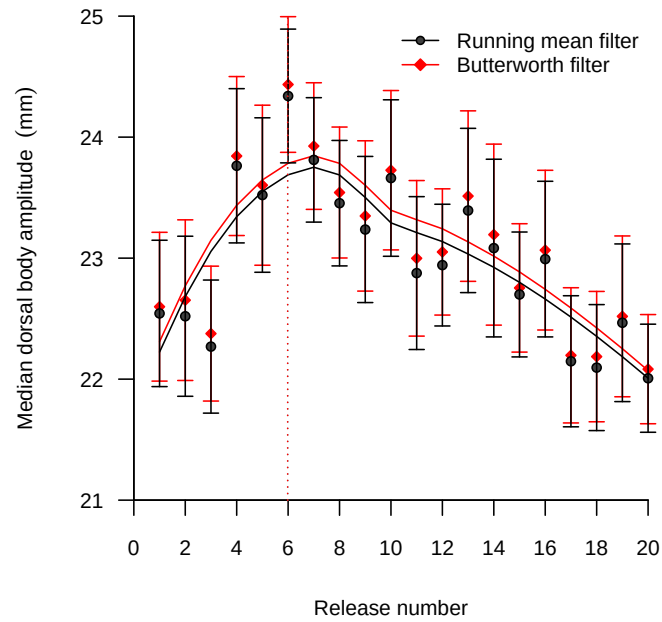


Figure B.3: Comparison of the running mean and Butterworth filter for the calculation of dorsal body amplitude (mean $\pm$ s.e.m.). Dotted lines indicate computationally optimised piecewise linear mixed model breakpoints denoting a change in response function in respect to release number, with the running mean breakpoint at 5.99 and the Butterworth filter at 5.98.

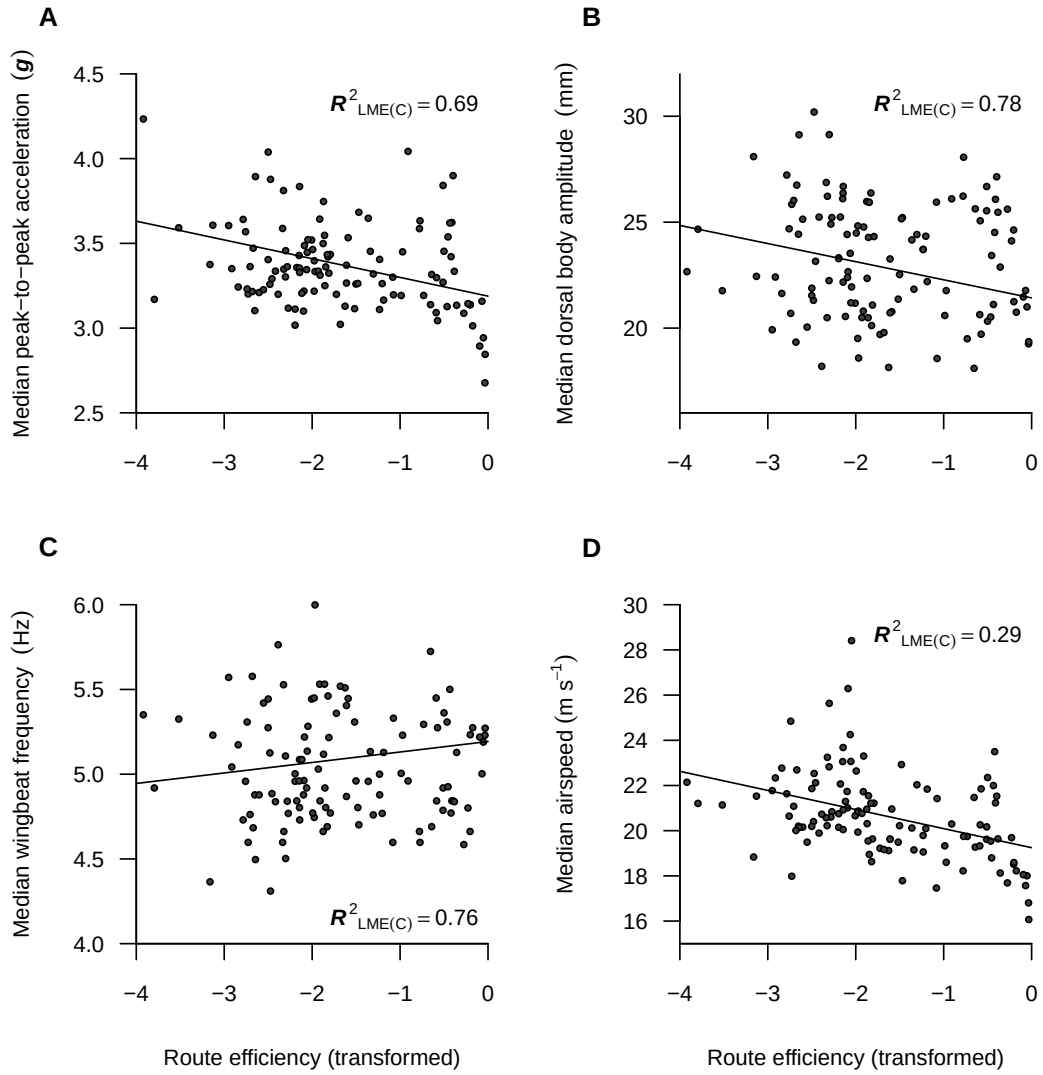


Figure B.4: Relationship between (A-C) Wingbeat characteristics and (D) airspeed and route efficiency. Solid lines correspond to linear mixed effects model fit. Conditional R-squared values ($R^2_{\text{LME}(C)}$) are calculated using the methods described in Nakagawa and Schielzeth (2013). Note: negative transformed route efficiency corresponds to higher actual route efficiency.

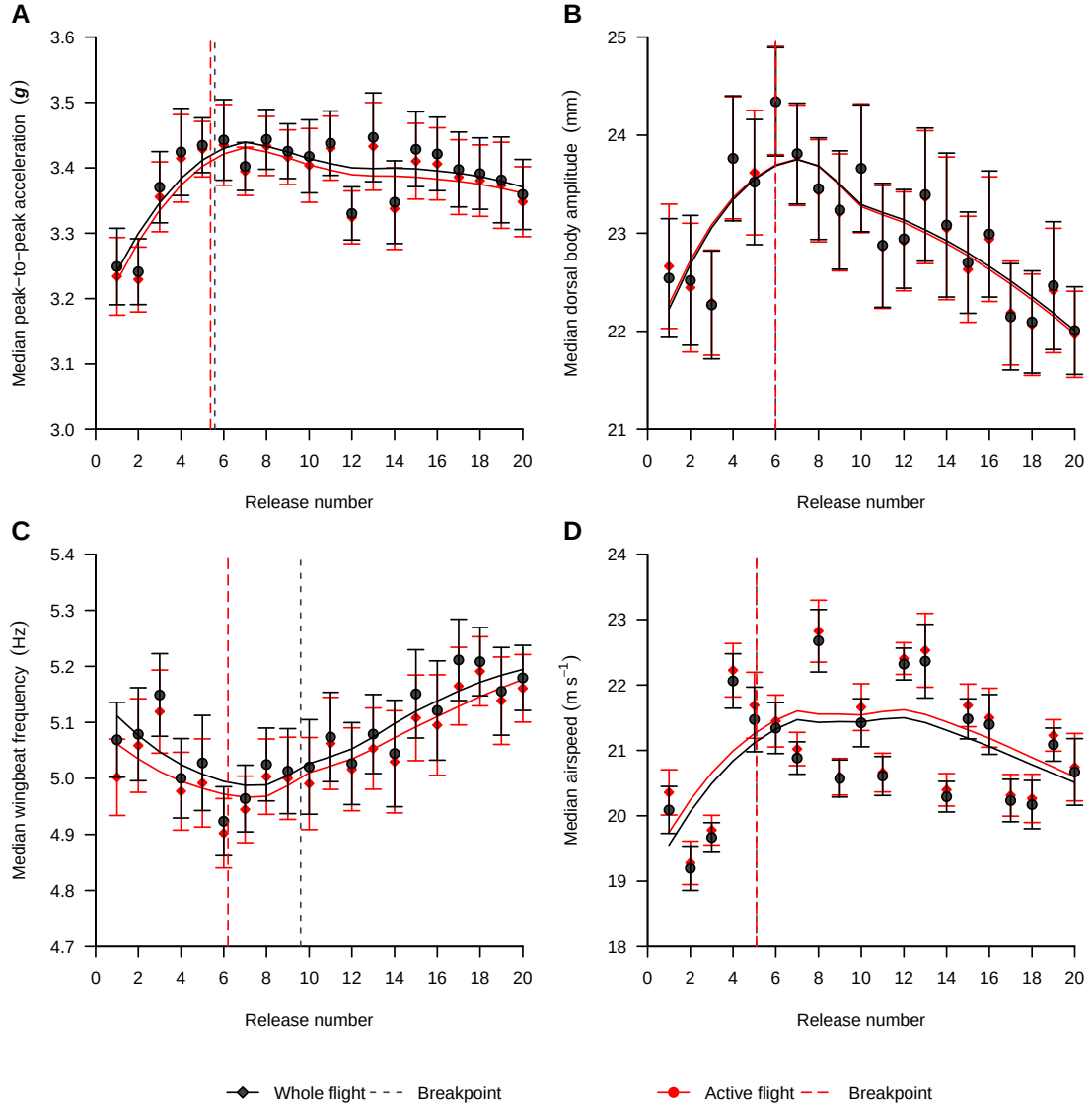


Figure B.5: Comparison of the (A-C) wingbeat characteristics and (D) airspeed (mean $\pm$ s.e.m.) as a function of release number for the whole flight and for the active straight-line flight. Dotted lines indicate computationally optimised piecewise linear mixed model breakpoints denoting a change in response function in respect to release number. Solid lines correspond to local polynomial regression fitting.

B.2 Supplementary tables

Table B.1: Comparison of the linear mixed effects models directly relating route efficiency to wingbeat characteristics and airspeed for releases 1-6. The fixed-effects with p -values and parameter estimates (Est.) denoted in **bold** are included in the final model. Conditional R-squared values ($R^2_{\text{LME}(C)}$) are calculated using the methods described in Nakagawa and Schielzeth (2013).

Variable	Route efficiency (transformed)		Wind support		Crosswind		Group		$R^2_{\text{LME}(C)}$
	p -value	Est.	p -value	Est.	p -value	Est.	p -value	Est.	
Median peak-to-peak DB acceleration (g)	<0.001	-0.111	0.184	-	0.201	-	0.472	-	0.69
Median DB amplitude per wingbeat (mm)	<0.001	-0.855	<0.001	0.240	0.266	-	0.877	-	0.78
Median wingbeat frequency (Hz)	0.004	0.062	<0.001	-0.040	0.211	-	0.966	-	0.76
Median airspeed (m s^{-1})	<0.001	-0.845	N/A	-	N/A	-	0.652	-	0.29

C

Supplementary material for Chapter 3

Supplementary material for Chapter 2: Birds invest wingbeats to reap the ultimate benefits of flocking.

C.1 Supplementary figures

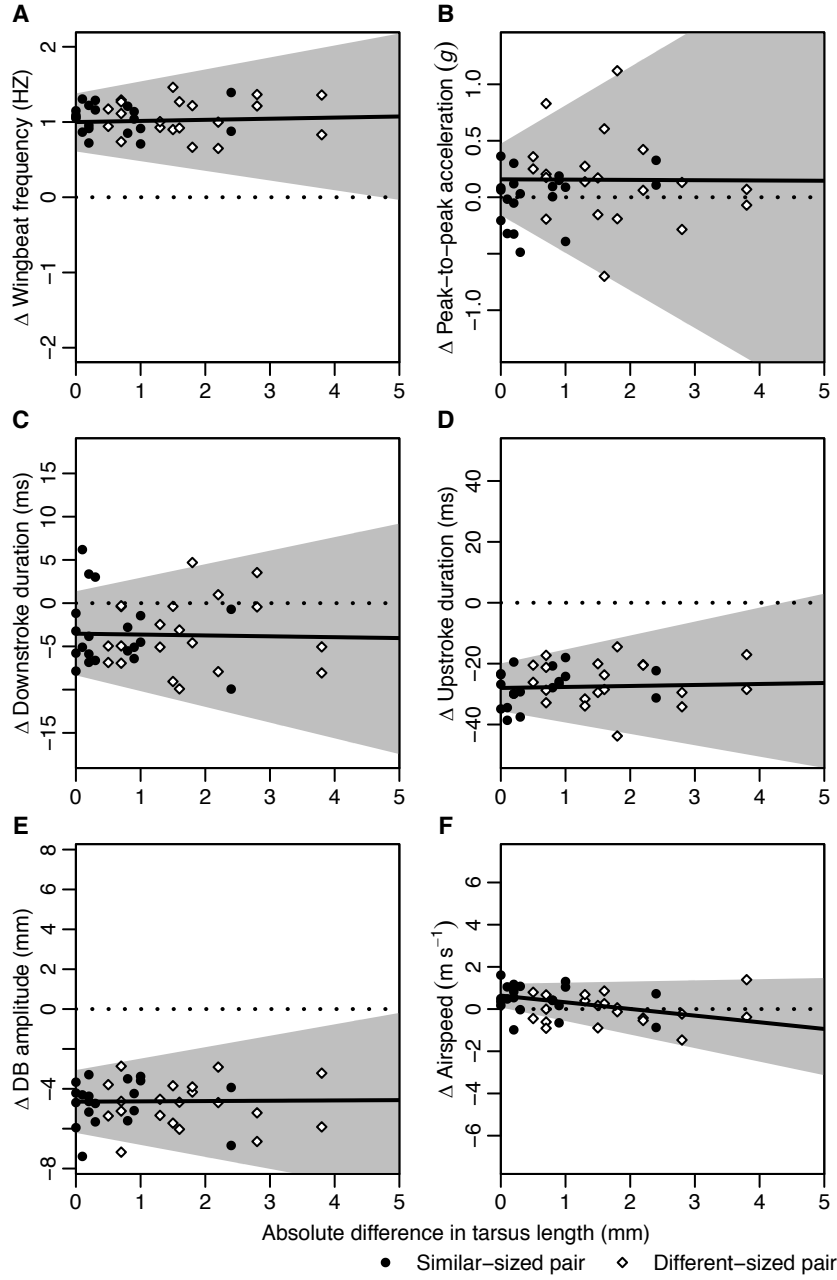


Figure C.1: Graphs show the difference (Δ) in (A) wingbeat frequency, (B) peak-to-peak dorsal body acceleration, (C) downstroke phase duration, (D) upstroke phase duration, (E) dorsal body (DB) amplitude and (F) airspeed between solo and paired flight per mm difference in tarsus length. Black line corresponds to the mean model fit which represents the difference between solo and paired flight per mm difference in tarsus length. Grey shaded area corresponds to the 95% credible interval of both the difference between solo and paired flight and the difference per mm difference in tarsus length. Points correspond to the difference between the median value for the paired flight and the median value for the solo flight, after accounting for the effects of weather, day and, in case of the a-c airspeed. Dotted line shows the solo value. All axes scaled to show $\pm 40\%$ of mean solo value.

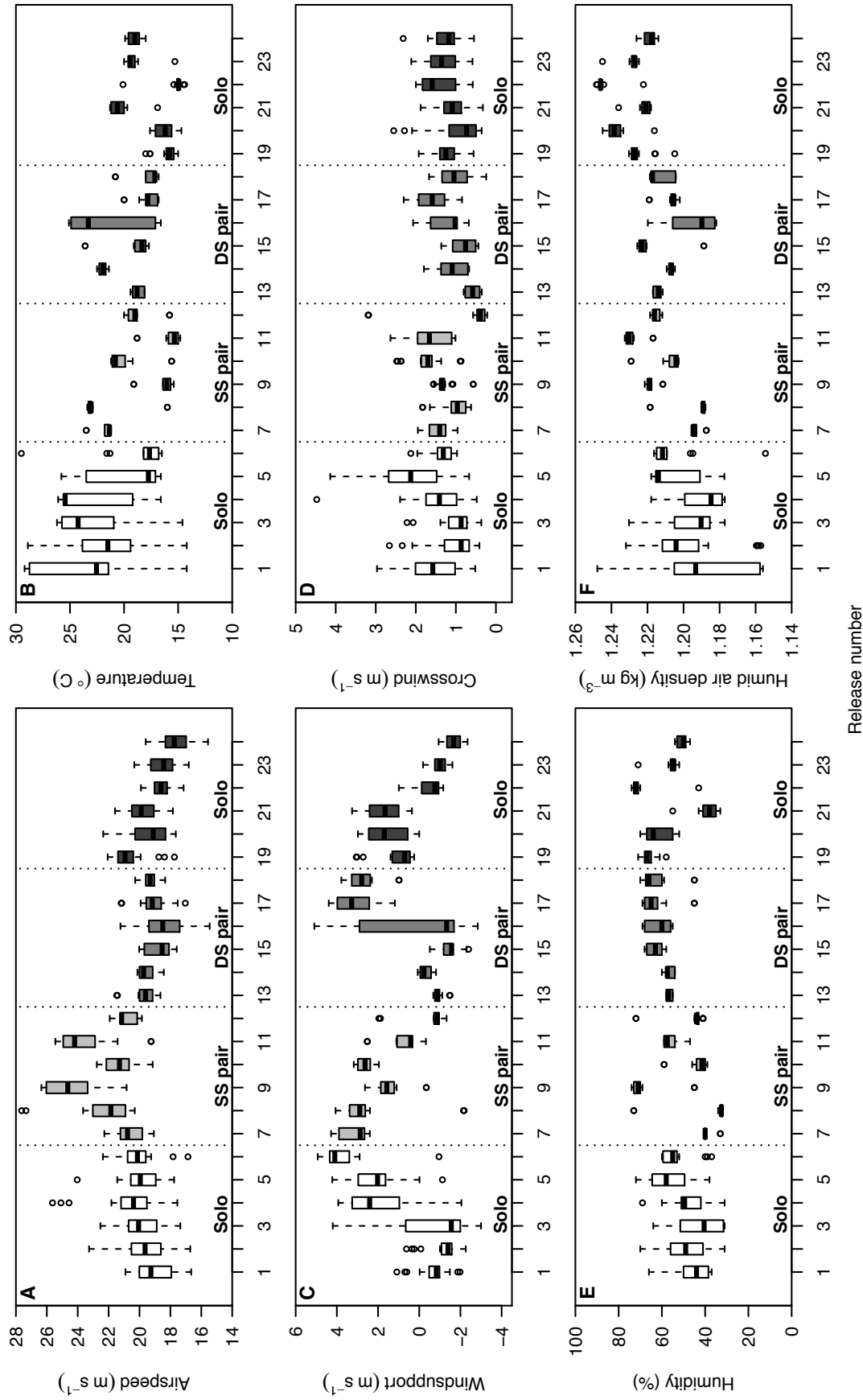


Figure C.2: Raw data showing the results per release for the Bayesian hierarchical model covariates: (A) median airspeed (m s^{-1}), (B) median temperature ($^{\circ}\text{C}$), (C) median wind support (m s^{-1}), (D) median crosswind, (E) median humidity (%), and median humid air density (kg m^{-3}).

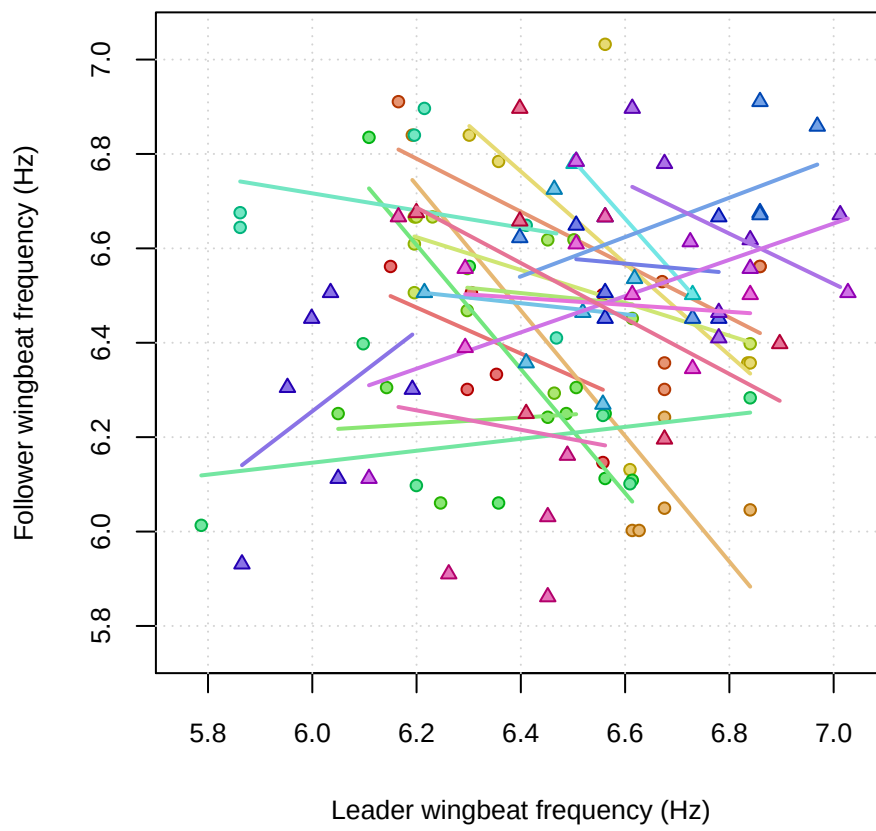


Figure C.3: Relationship between the leader and follower's median wingbeat frequency during each flight. A direct correlation between the leader and follower's wingbeat frequency would be indicative of the birds being in phase. The different coloured lines correspond to least squares regression lines fitted to the data from each pair.

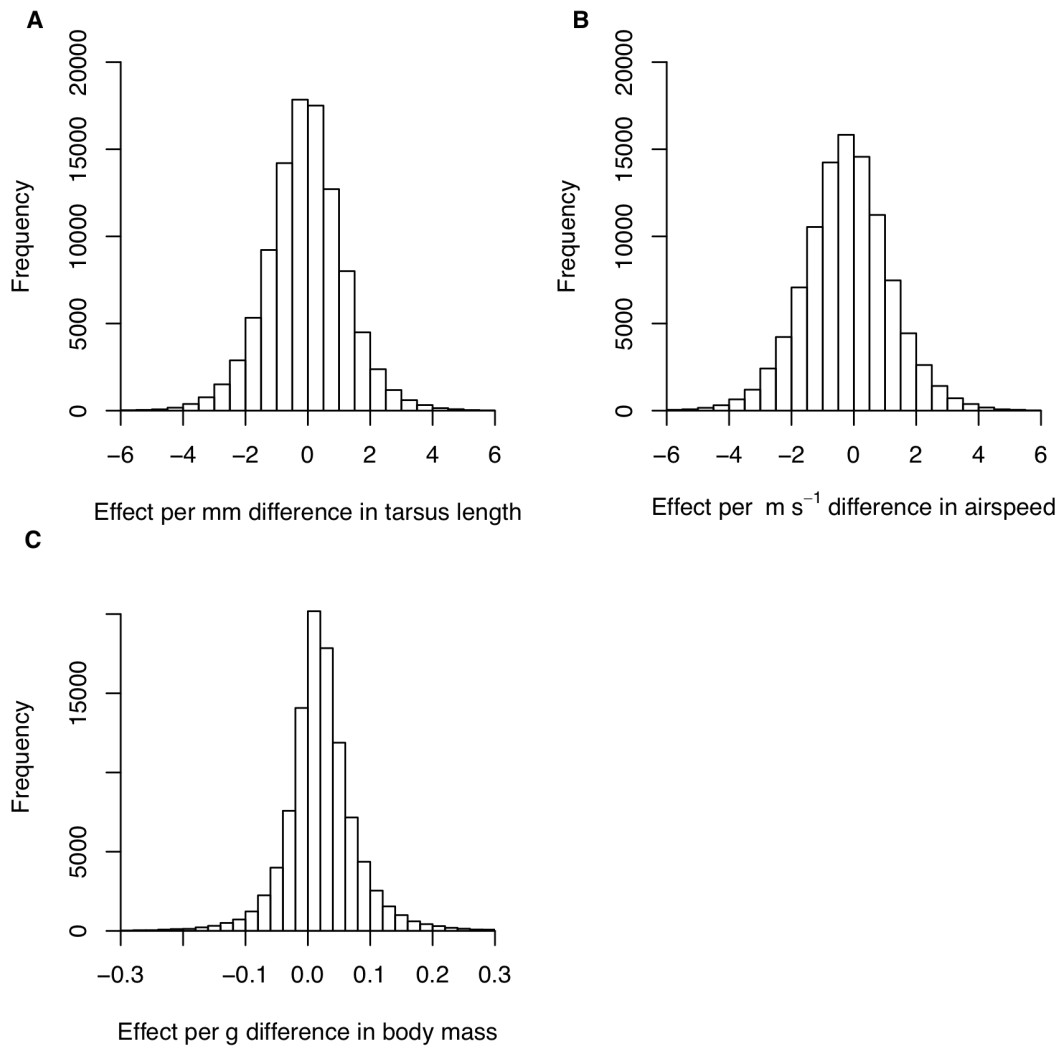


Figure C.4: Probability of a bird leading per unit difference in (A) tarsus length, (B) median solo airspeed and (C) body mass.

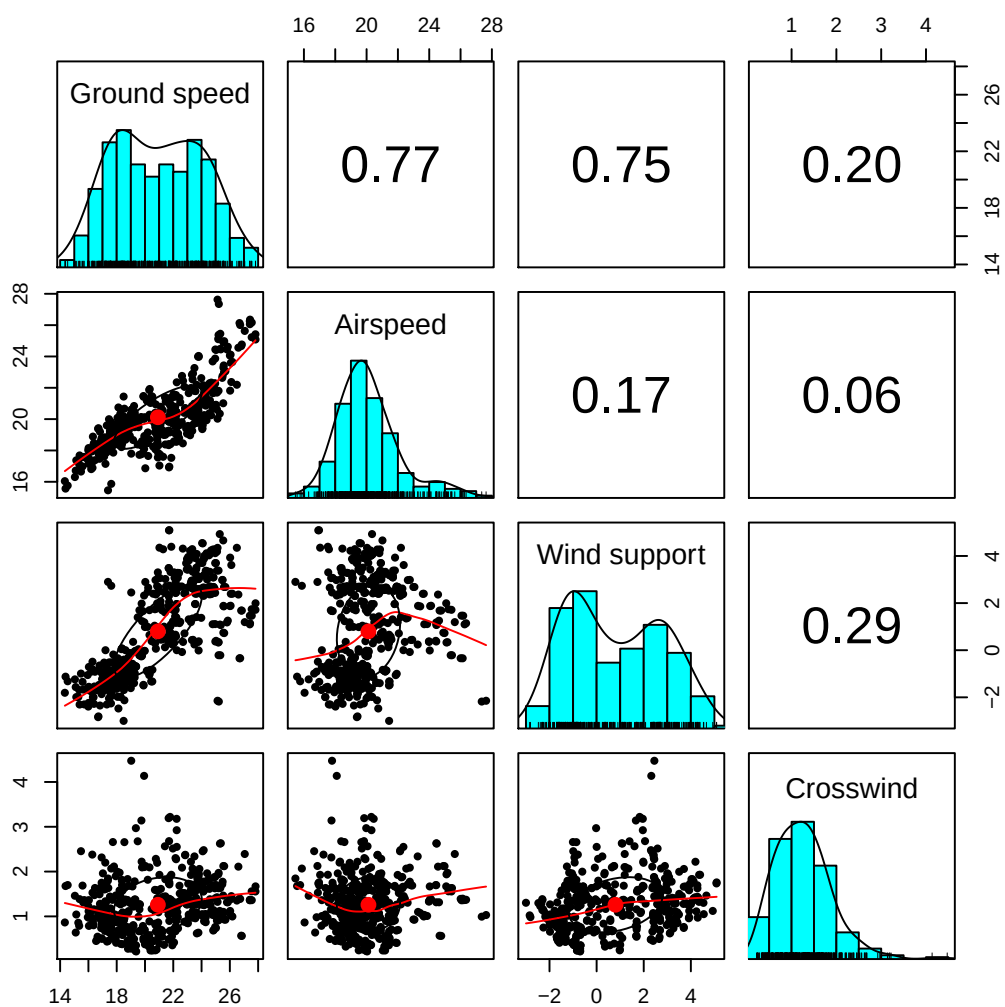


Figure C.5: Relationship between ground speed, airspeed, wind support and crosswind.

C.2 Supplementary tables

Table C.1: Results of the Bayesian hierarchical models. Corrected solo mean values refer to the mean of the median value from each individual, which has been corrected for the effects of airspeed, wind support, crosswind, temperature, humidity and air density according to the results of the model. Note: the covariates in this table are the difference per unit difference in the covariate.

Variable	Corrected solo mean	Difference from solo for birds of the same tarsus length		Difference per mm difference in tarsus length		Covariates: Difference per unit difference in						
		Mean Δ [95% CrI]	%	Mean Δ [95% CrI]	%	Wind support (m s ⁻¹) [95% CrI] min = 3.00 m s ⁻¹ max = 5.10 m s ⁻¹	Crosswind (m s ⁻¹) [95% CrI] min = 0.31 m s ⁻¹ max = 4.47 m s ⁻¹	Temperature (°C) [95% CrI] min = 29.4 °C max = 14.2 °C	Humidity (%) [95% CrI] min = 74 % max = 31 %	Air density (kg m ⁻³) [95% CrI] min = 1.25 kg m ⁻³ max = 1.15 kg m ⁻³	Airspeed (m s ⁻¹) [95% CrI] min = 27.63 m s ⁻¹ max = 15.46 m s ⁻¹	Date of release
Median wingbeat frequency (Hz)	5.48	1.00 [0.61, 1.38]	18.24	0.01 [-0.13, 0.16]	0.27	0.03 [-0.02, 0.07]	0.02 [-0.01, 0.05]	0.01 [-0.02, 0.04]	0.00 [-0.01, 0.01]	-0.40 [-1.16, 0.36]	0.01 [-0.01, 0.03]	Min: -0.40 Max: 0.43
Standard deviation of wingbeat frequency (Hz)	0.60	-0.01 [-0.11, 0.09]	-2.16	0.02 [-0.15, 0.18]	3.54	-0.01 [-0.04, 0.01]	0.00 [-0.01, 0.02]	0.02 [0.00, 0.03]	0.00 [0.00, 0.01]	-0.55 [-0.99, -0.11]	0.02 [0.00, 0.03]	Min: -0.19 Max: 0.20
Median downstroke phase duration (ms)	47.67	-3.53 [-8.35, 1.38]	-7.41	-0.1 [-1.82, 1.56]	-0.21	-0.07 [-0.69, 0.55]	0.13 [-0.19, 0.44]	0.01 [-0.17, 0.19]	0 [-0.05, 0.04]	0.87 [-2.83, 4.56]	-0.07 [-0.29, 0.15]	Min: -2.56 Max: 1.62
Median upstroke phase duration (ms)	135.76	-27.99 [-35.61, -19.92]	-20.62	0.33 [-3.73, 4.58]	0.24	-0.16 [-1.39, 1.09]	0.61 [0.04, 1.19]	-0.29 [-0.62, 0.03]	0.01 [-0.08, 0.09]	-0.63 [-6.58, 5.32]	0.4 [-0.02, 0.82]	Min: -7.47 Max: 7.53
Median peak-to-peak DB acceleration (g)	3.65	0.16 [-0.16, 0.47]	4.35	0 [-0.33, 0.34]	-0.07	0.01 [-0.07, 0.09]	-0.02 [-0.07, 0.03]	-0.01 [-0.06, 0.03]	0.00 [-0.01, 0.01]	-0.32 [-1.35, 0.71]	0.03 [0.00, 0.07]	Min: -0.36 Max: 0.47
Median DB amplitude (mm)	20.68	-4.65 [-6.21, -3.06]	-22.47	0.02 [-0.60, 0.57]	0.08	-0.09 [-0.34, 0.16]	0.09 [-0.06, 0.24]	-0.09 [-0.20, 0.01]	0 [-0.02, 0.02]	-0.33 [-2.77, 2.10]	0.14 [0.04, 0.25]	Min: -1.61 Max: 2.29
Airspeed (m s ⁻¹)	19.54	0.64 [0.08, 1.20]	3.26	-0.32 [-0.64, 0.05]	-1.62	-0.11 [-0.31, 0.09]	-0.76 [-0.87, -0.65]	-0.03 [-0.11, 0.05]	0.01 [0.00, 0.03]	0.75 [-1.24, 2.75]	N/A	Min: -4.26 Max: 4.92
Route accuracy	0.80	0.06 [0.01, 0.10]	6.93	0 [-0.02, 0.03]	0.07	-0.01 [-0.02, 0.00]	0.02 [0.01, 0.03]	0 [-0.01, 0.01]	0.00 [0.00, 0.00]	-0.23 [-0.50, 0.04]	0.01 [0.01, 0.02]	Min: -0.17 Max: 0.10

Table C.2: A calculation of the total number of wingbeats that would have been used during solo and paired flight had the birds flown with the stated wingbeat frequency, mean route accuracy and at the stated mean airspeed in the absence of any wind support. We calculated the difference using the results of the Bayesian hierarchical models combined with the means of the solo flights after accounting for the effects of covariates as not all birds completed 100% of the paired flights together with one leader.

		Solo	Pair
Variables	Straight-line distance (m; excluding 200m take-off and landing)	6660.58	6660.58
	Mean corrected route accuracy	0.8	0.86
	Mean corrected airspeed (m s^{-1})	19.54	20.17
	Mean corrected wingbeat frequency (Hz)	5.48	6.48
Calculations	Total flight distance (m)	8295	7759
	Total flight time (s)	425	385
	Total number of wingbeats	2325	2490
	Number of wingbeats difference		165.47
	Percentage wingbeats difference (%)		7.12

Table C.3: Bird and pairing information, including tarsus length (mm), body mass (g) and median solo airspeed (m s^{-1})

Bird ID	Individual information			Similar-sized pairs			Different-sized pairs			
	Tarsus length (mm)	Body mass (g)	Median solo airspeed (m s^{-1})	Partner ID	Δ Tarsus length (mm)	Δ Body mass (g)	Δ Tarsus length (mm)	Partner ID	Δ Body mass (g)	Δ Median solo airspeed (m s^{-1})
B01	32.4	452	19.0	B82	-0.9	21	-0.1	B07	-39	-1.0
B07	35.2	491	20.0	B87	0.3	-28	0.6	B01	39	1.0
B61	35.2	478	19.5	S25	-0.8	15	0.5	S87	48	1.9
B65	35.5	454	18.3	S84	1.0	-31	-0.5	S13	-75	-1.4
B67	36.0	474	20.7	B80	0.0	3	0.6	S05	7	0.4
B75	35.4	461	18.9	S06	-0.2	17	-1.5	S30	-33	-1.5
B80	36.0	471	20.1	B67	0.0	-3	-0.6	S12	2	1.0
B82	33.3	431	19.1	B01	0.9	-21	0.1	B87	-88	-0.3
B84	33.8	425	20.0	S87	2.4	-5	2.5	S25	-38	1.0
B87	34.9	519	19.5	B07	-0.3	28	-0.6	B82	88	0.3
S03	36.1	493	19.3	S30	0.0	-1	-1.1	S06	49	-1.1
S05	34.7	467	20.3	S12	0.2	-2	1.1	B67	-7	-0.4
S06	35.6	444	20.4	B75	0.2	-17	1.5	S03	-49	1.1
S12	34.5	469	19.1	S05	-0.2	2	-1.1	B80	-2	-1.0
S13	36.2	529	19.7	S27	-0.1	6	-0.5	B65	75	1.4
S25	36.0	463	19.0	B61	0.8	-15	-0.5	B84	38	-1.0
S27	36.3	523	20.2	S13	0.1	-6	0.5	S84	38	1.4
S30	36.1	494	20.4	S03	0.0	1	1.1	B75	33	1.5
S84	34.5	485	18.8	B65	-1.0	31	0.5	S27	-38	-1.4
S87	31.4	430	17.6	B84	-2.4	5	-2.5	B61	-48	-1.9

Table C.4: Model priors for the hyper-parameters of the Bayesian hierarchical model. The width of the prior distributions was chosen to be similar to that of the observed quantities. The hyper-parameters represent the population (i.e. across all birds) averages. The bird-level parameters are obtained by sampling from a normal distribution conditional on the hyper-parameters. See the Stan model for further information.

Variable	δ, η	χ	μ	γ	σ
Median wingbeat frequency (Hz)	normal(0,0.3)	normal(0,2)	normal(5.5,0.3)	normal(0,0.6)	cauchy(0,0.6)
Standard deviation of wingbeat frequency (Hz)	normal(0,0.1)	normal(0,2)	normal(0.6,0.1)	normal(0,0.4)	cauchy(0,0.4)
Median downstroke phase duration (ms)	normal(0,4.6)	normal(0,2)	normal(47.5,4.6)	normal(0,2.1)	cauchy(0,2.1)
Median upstroke phase duration (ms)	normal(0,11.1)	normal(0,2)	normal(135.9,11.1)	normal(0,3.3)	cauchy(0,3.3)
Median peak-to-peak DB acceleration (g)	normal(0,0.4)	normal(0,2)	normal(3.7,0.4)	normal(0,0.7)	cauchy(0,0.7)
Median DB amplitude (mm)	normal(0,2.2)	normal(0,2)	normal(20.7,2.2)	normal(0,1.5)	cauchy(0,1.5)
Airspeed (m s^{-1})	normal(0,1.6)	normal(0,2)	normal(19.5,1.6)	normal(0,1.3)	cauchy(0,1.3)
Route accuracy	normal(0,0.1)	normal(0,2)	normal(0.8,0.1)	normal(0,0.3)	cauchy(0,0.3)

C.3 Supplementary material

Stan code for the Bayesian hierarchical model of wingbeat frequency. In the model, the bird-level parameters are sampled from a normal distribution conditional on the hyper-parameters, which represent the population averages. For example, $\text{delta}_i \sim N(\text{delta}^{\{\text{top}\}}, \text{sigma_delta}^{\{\text{top}\}})$, where delta_i is the uplift for bird i of being in a pair, and $\text{delta}^{\{\text{top}\}}$ and $\text{sigma_delta}^{\{\text{top}\}}$ represent the population mean uplift and the standard deviation of the individual birds' effects about this mean. Note that in the Stan model, we use a non-centred parameterisation to implement this model (Carpenter *et al.*, 2017), which helps with sampling.

C.3.1 Stan code for the Bayesian hierarchical model of wingbeat frequency

```
functions{
  real weighting(int aBird, int bBird, real[] chi_0, real[] chi, real[] tarsus){
    real aOmega;
    aOmega = inv_logit(chi_0[aBird] + chi[aBird] * fabs(tarsus[aBird]-tarsus[bBird]));
    return(aOmega);
  }
}

data{
  int N; // length of data
  real W[N]; // wingbeat frequency
  int nBirds; // number of birds

  // indices
  int bird1[N]; // identity of first bird in pair
  int bird2[N]; // identity of second bird in pair -- can be same as first

  // covariates
  real wind1[N];
  real wind2[N];
  real temp[N];
  real density[N];
  real humidity[N];
  real airspeed[N];

  // Matrix covariate
  int<lower=1> K;
  matrix[N,K] date;

  // Size covariates
  real tarsus[nBirds];
}
```

```

transformed data{
  real tarsusMean;
  tarsusMean = mean(tarsus);
}

parameters{
  // bird-specific
  real mu[nBirds]; // mean wingbeat for each bird
  real delta_0_raw[nBirds]; // Uplift from being in a pair
  real eta_raw[nBirds]; // Effect of size difference on wingbeat

  // Top-level
  real delta_0_top;
  real eta_top;
  real<lower=0> sigma_delta_0_top;
  real<lower=0> sigma_eta_top;

  // covariate specific
  real gamma1;
  real gamma2;
  real gamma3;
  real gamma4;
  real gamma5;
  real gamma6;

  // Matrix covariate
  vector[K] beta;

  // other
  real<lower=0> sigma;

  // Leading parameter
  real chi_raw[nBirds];
  real chi_0_raw[nBirds];
  real chi_top;
  real chi_0_top;
  real<lower=0> chi_sigma_top;
  real<lower=0> chi_0_sigma_top;
}

transformed parameters{
  real chi[nBirds];
  real chi_0[nBirds];
  real delta_0[nBirds]; // Uplift from being in a pair
  real eta[nBirds]; // Effect of size difference on wingbeat

  for(i in 1:nBirds){
    chi_0[i] = chi_0_top + chi_0_raw[i] * chi_0_sigma_top;
    chi[i] = chi_top + chi_raw[i] * chi_sigma_top;
    delta_0[i] = delta_0_top + delta_0_raw[i] * sigma_delta_0_top;
    eta[i] = eta_top + eta_raw[i] * sigma_eta_top;
  }
}

```

```

model{
  real omega;
  // likelihood
  for(i in 1:N){
    real aMean;
    if(bird1[i]==bird2[i]){ // solo
      aMean = 0.0;
    }else{
      aMean = delta_0[bird1[i]] + eta[bird1[i]] * fabs(tarsus[bird1[i]] - tarsus[bird2[i]]);
    }

    omega = weighting(bird1[i],bird2[i],chi_0,chi,tarsus);
    W[i] ~ normal(aMean + omega*mu[bird1[i]] + (1-omega)*mu[bird2[i]] + wind1[i] *
gamma1 + wind2[i] * gamma2 + temp[i] * gamma3 + density[i] * gamma4 + humidity[i] *
gamma5 + airspeed[i] * gamma6 + date[i] * beta, sigma);
  }

  // priors
  chi_0_raw ~ normal(0,1);
  chi_raw ~ normal(0,1);
  delta_0_raw ~ normal(0,1);
  eta_raw ~ normal(0,1);
  mu ~ normal(20.7,2.2); // change mean to be similar to that observed + sd change
  gamma1 ~ normal(0,1.5);
  gamma2 ~ normal(0,1.5);
  gamma3 ~ normal(0,1.5);
  gamma4 ~ normal(0,1.5);
  gamma5 ~ normal(0,1.5);
  gamma6 ~ normal(0,1.5);
  beta ~ normal(0,1.5);
  sigma ~ cauchy(0,1.5);

  // hyper-priors
  chi_0_top ~ normal(0,2);
  chi_top ~ normal(0,2);
  chi_sigma_top ~ cauchy(0,2);
  chi_0_sigma_top ~ cauchy(0,2);
  delta_0_top ~ normal(0,2.2);
  eta_top ~ normal(0,2.2);
  sigma_delta_0_top ~ cauchy(0,1.5);
  sigma_eta_top ~ cauchy(0,1.5);
}

generated quantities{
  real delta_0_av;
  real eta_av;
  real chi_av;
  real chi_0_av;

  delta_0_av = normal_rng(delta_0_top,sigma_delta_0_top);
  eta_av = normal_rng(eta_top,sigma_eta_top);
  chi_av = normal_rng(chi_top,chi_sigma_top);
  chi_0_av = normal_rng(chi_0_top,chi_0_sigma_top);
}

```

C.3.2 Model output of the Bayesian hierarchical model of wingbeat frequency

Inference for Stan model: wingbeat_continuous_pred_MEDIAN_FPS_wDate.
 8 chains, each with iter=25000; warmup=12500; thin=1;
 post-warmup draws per chain=12500, total post-warmup draws=1e+05.

	mean	se_mean	sd	2.5%	25%	50%	75%	97.5%	n_eff	Rhat
mu[1]	5.48	0.00	0.08	5.32	5.42	5.48	5.54	5.64	12695	1
mu[2]	5.33	0.00	0.08	5.16	5.27	5.33	5.38	5.49	13119	1
mu[3]	5.50	0.00	0.08	5.33	5.44	5.50	5.55	5.67	12531	1
mu[4]	5.69	0.00	0.09	5.52	5.63	5.69	5.74	5.86	13599	1
mu[5]	5.09	0.00	0.09	4.92	5.03	5.09	5.14	5.25	13127	1
mu[6]	5.43	0.00	0.08	5.26	5.37	5.43	5.49	5.60	13183	1
mu[7]	5.77	0.00	0.08	5.60	5.71	5.77	5.82	5.93	13079	1
mu[8]	5.18	0.00	0.08	5.01	5.12	5.18	5.23	5.34	12837	1
mu[9]	5.47	0.00	0.09	5.30	5.41	5.47	5.53	5.64	13580	1
mu[10]	5.65	0.00	0.08	5.49	5.60	5.65	5.71	5.82	13129	1
mu[11]	5.40	0.00	0.08	5.23	5.34	5.40	5.46	5.57	12668	1
mu[12]	5.37	0.00	0.09	5.20	5.31	5.37	5.43	5.55	13877	1
mu[13]	5.63	0.00	0.09	5.46	5.58	5.63	5.69	5.81	13688	1
mu[14]	5.45	0.00	0.08	5.28	5.39	5.45	5.51	5.61	12893	1
mu[15]	5.35	0.00	0.09	5.17	5.29	5.35	5.42	5.53	15439	1
mu[16]	5.65	0.00	0.09	5.48	5.59	5.65	5.71	5.82	13871	1
mu[17]	5.52	0.00	0.10	5.33	5.45	5.52	5.58	5.71	16426	1
mu[18]	5.76	0.00	0.08	5.60	5.70	5.76	5.82	5.92	12997	1
mu[19]	5.73	0.00	0.08	5.57	5.68	5.73	5.79	5.90	12928	1
mu[20]	5.48	0.00	0.09	5.30	5.42	5.48	5.54	5.65	14507	1
delta_0_raw[1]	0.63	0.00	0.72	-0.80	0.15	0.63	1.10	2.02	39555	1
delta_0_raw[2]	0.29	0.00	0.57	-0.88	-0.08	0.29	0.66	1.40	60260	1
delta_0_raw[3]	-0.98	0.00	0.58	-2.16	-1.35	-0.96	-0.59	0.14	61267	1
delta_0_raw[4]	-0.48	0.00	0.55	-1.61	-0.82	-0.46	-0.12	0.57	54396	1
delta_0_raw[5]	-0.20	0.00	0.61	-1.49	-0.58	-0.17	0.21	0.94	50238	1
delta_0_raw[6]	-0.10	0.00	0.55	-1.21	-0.46	-0.09	0.26	0.97	55738	1
delta_0_raw[7]	0.37	0.00	0.58	-0.79	-0.01	0.37	0.75	1.49	53970	1
delta_0_raw[8]	-0.48	0.00	0.69	-1.81	-0.94	-0.49	-0.02	0.90	61057	1
delta_0_raw[9]	-1.18	0.00	0.73	-2.54	-1.66	-1.21	-0.74	0.40	48195	1
delta_0_raw[10]	1.48	0.00	0.59	0.35	1.09	1.48	1.86	2.67	61922	1
delta_0_raw[11]	0.58	0.00	0.55	-0.51	0.23	0.58	0.94	1.65	56837	1
delta_0_raw[12]	-0.50	0.00	0.53	-1.61	-0.84	-0.48	-0.14	0.48	55758	1
delta_0_raw[13]	-0.65	0.00	0.57	-1.80	-1.01	-0.63	-0.27	0.44	46209	1
delta_0_raw[14]	1.23	0.00	0.53	0.24	0.87	1.21	1.57	2.31	66061	1
delta_0_raw[15]	0.81	0.00	0.57	-0.31	0.44	0.81	1.18	1.94	57962	1
delta_0_raw[16]	0.50	0.00	0.58	-0.61	0.13	0.49	0.86	1.70	59497	1
delta_0_raw[17]	-0.17	0.00	0.54	-1.27	-0.52	-0.16	0.19	0.87	62711	1
delta_0_raw[18]	0.72	0.00	0.53	-0.29	0.37	0.71	1.06	1.79	61395	1
delta_0_raw[19]	-1.10	0.00	0.59	-2.30	-1.48	-1.10	-0.72	0.05	61094	1
delta_0_raw[20]	1.11	0.00	0.71	-0.35	0.66	1.12	1.57	2.49	64988	1
eta_raw[1]	0.68	0.00	0.85	-1.11	0.15	0.70	1.24	2.30	65991	1
eta_raw[2]	0.15	0.00	0.81	-1.51	-0.36	0.16	0.68	1.75	79650	1
eta_raw[3]	-0.21	0.00	0.77	-1.73	-0.70	-0.22	0.26	1.36	67529	1
eta_raw[4]	-0.07	0.00	0.96	-1.94	-0.72	-0.07	0.58	1.84	100000	1
eta_raw[5]	-0.42	0.00	0.92	-2.20	-1.04	-0.44	0.18	1.44	100000	1
eta_raw[6]	0.31	0.00	1.01	-1.68	-0.37	0.31	0.99	2.27	100000	1
eta_raw[7]	-0.22	0.00	0.94	-2.03	-0.86	-0.23	0.41	1.67	100000	1

eta_raw[8]	0.10	0.00	0.97	-1.80	-0.56	0.09	0.75	2.01	100000	1
eta_raw[9]	-0.56	0.00	0.93	-2.29	-1.19	-0.60	0.04	1.37	56750	1
eta_raw[10]	-0.12	0.00	1.00	-2.07	-0.80	-0.11	0.56	1.81	100000	1
eta_raw[11]	0.24	0.00	0.99	-1.72	-0.43	0.24	0.90	2.18	100000	1
eta_raw[12]	0.14	0.00	0.92	-1.66	-0.48	0.14	0.75	1.96	100000	1
eta_raw[13]	0.16	0.00	1.00	-1.80	-0.51	0.17	0.83	2.11	100000	1
eta_raw[14]	0.16	0.00	0.96	-1.76	-0.48	0.18	0.82	2.00	100000	1
eta_raw[15]	0.02	0.00	0.97	-1.89	-0.63	0.02	0.68	1.92	100000	1
eta_raw[16]	-0.47	0.00	0.90	-2.18	-1.07	-0.50	0.10	1.37	73506	1
eta_raw[17]	0.23	0.00	0.91	-1.60	-0.37	0.24	0.84	1.99	100000	1
eta_raw[18]	-0.01	0.00	0.95	-1.88	-0.65	-0.01	0.63	1.88	100000	1
eta_raw[19]	-0.29	0.00	0.95	-2.12	-0.94	-0.31	0.33	1.63	100000	1
eta_raw[20]	0.20	0.00	0.82	-1.49	-0.33	0.21	0.73	1.80	65524	1
delta_0_top	1.00	0.00	0.08	0.85	0.95	1.00	1.05	1.14	37710	1
eta_top	0.02	0.00	0.04	-0.06	-0.01	0.01	0.04	0.09	43410	1
sigma_delta_0_top	0.17	0.00	0.04	0.10	0.14	0.17	0.20	0.27	28315	1
sigma_eta_top	0.05	0.00	0.03	0.00	0.02	0.04	0.07	0.13	19474	1
gamma1	0.02	0.00	0.02	-0.01	0.01	0.02	0.03	0.05	32409	1
gamma2	0.03	0.00	0.02	-0.02	0.01	0.03	0.04	0.07	83371	1
gamma3	0.01	0.00	0.02	-0.02	0.00	0.01	0.02	0.04	21735	1
gamma4	-0.40	0.00	0.38	-1.16	-0.66	-0.40	-0.14	0.36	24497	1
gamma5	0.00	0.00	0.00	-0.01	0.00	0.00	0.00	0.01	23728	1
gamma6	0.01	0.00	0.01	-0.01	0.00	0.01	0.01	0.03	34661	1
beta[1]	-0.18	0.00	0.22	-0.61	-0.33	-0.18	-0.03	0.26	23083	1
beta[2]	-0.07	0.00	0.17	-0.41	-0.19	-0.07	0.05	0.27	14841	1
beta[3]	-0.04	0.00	0.17	-0.36	-0.15	-0.04	0.07	0.28	12868	1
beta[4]	-0.11	0.00	0.15	-0.40	-0.21	-0.11	-0.01	0.19	10082	1
beta[5]	-0.37	0.00	0.14	-0.65	-0.46	-0.37	-0.27	-0.09	9383	1
beta[6]	-0.30	0.00	0.15	-0.58	-0.39	-0.30	-0.20	-0.01	9556	1
beta[7]	-0.40	0.00	0.16	-0.73	-0.51	-0.40	-0.29	-0.08	11510	1
beta[8]	-0.15	0.00	0.15	-0.45	-0.25	-0.15	-0.05	0.15	10360	1
beta[9]	0.06	0.00	0.15	-0.23	-0.04	0.06	0.16	0.35	9876	1
beta[10]	0.16	0.00	0.18	-0.20	0.04	0.16	0.28	0.52	11046	1
beta[11]	0.10	0.00	0.14	-0.17	0.01	0.10	0.20	0.37	8260	1
beta[12]	-0.18	0.00	0.17	-0.50	-0.29	-0.18	-0.06	0.15	9976	1
beta[13]	-0.14	0.00	0.13	-0.41	-0.23	-0.14	-0.05	0.12	8407	1
beta[14]	-0.16	0.00	0.13	-0.41	-0.24	-0.16	-0.07	0.09	7335	1
beta[15]	-0.08	0.00	0.14	-0.34	-0.17	-0.08	0.02	0.20	8157	1
beta[16]	-0.07	0.00	0.13	-0.32	-0.16	-0.07	0.02	0.19	7647	1
beta[17]	-0.02	0.00	0.15	-0.31	-0.12	-0.02	0.08	0.27	9042	1
beta[18]	0.13	0.00	0.13	-0.13	0.03	0.12	0.21	0.38	8155	1
beta[19]	0.01	0.00	0.19	-0.35	-0.11	0.01	0.14	0.38	15475	1
beta[20]	0.21	0.00	0.13	-0.04	0.13	0.21	0.30	0.47	7874	1
beta[21]	0.13	0.00	0.14	-0.14	0.03	0.13	0.22	0.40	8036	1
beta[22]	0.29	0.00	0.13	0.03	0.20	0.29	0.38	0.55	8156	1
beta[23]	0.05	0.00	0.17	-0.29	-0.07	0.05	0.16	0.38	10427	1
beta[24]	-0.06	0.00	0.13	-0.31	-0.15	-0.06	0.03	0.20	7775	1
beta[25]	-0.08	0.00	0.13	-0.33	-0.16	-0.08	0.01	0.18	7561	1
beta[26]	0.14	0.00	0.13	-0.10	0.06	0.14	0.23	0.38	7379	1
beta[27]	0.11	0.00	0.12	-0.13	0.03	0.11	0.19	0.35	6950	1
beta[28]	0.23	0.00	0.13	-0.01	0.15	0.23	0.32	0.48	7322	1
beta[29]	0.43	0.00	0.14	0.16	0.34	0.43	0.52	0.70	8657	1
sigma	0.18	0.00	0.01	0.17	0.18	0.18	0.19	0.20	100000	1
chi_raw[1]	0.23	0.00	1.00	-1.80	-0.43	0.28	0.90	2.12	61955	1
chi_raw[2]	-0.02	0.00	0.98	-1.93	-0.68	-0.03	0.63	1.93	100000	1

chi_raw[3]	0.19	0.00	0.95	-1.72	-0.43	0.20	0.82	2.06	100000	1
chi_raw[4]	-0.32	0.00	0.95	-2.11	-0.95	-0.36	0.29	1.66	78330	1
chi_raw[5]	0.53	0.00	0.86	-1.26	0.00	0.53	1.07	2.22	65970	1
chi_raw[6]	-0.81	0.00	0.95	-2.52	-1.44	-0.88	-0.25	1.30	58717	1
chi_raw[7]	-0.32	0.00	0.93	-2.10	-0.92	-0.36	0.24	1.66	58195	1
chi_raw[8]	-0.48	0.00	0.81	-2.05	-0.97	-0.50	-0.04	1.31	54191	1
chi_raw[9]	0.71	0.00	0.86	-1.15	0.20	0.72	1.26	2.38	65672	1
chi_raw[10]	-0.53	0.00	0.81	-2.07	-1.02	-0.56	-0.10	1.28	43879	1
chi_raw[11]	-0.29	0.00	1.01	-2.19	-0.99	-0.33	0.38	1.75	100000	1
chi_raw[12]	0.46	0.00	0.86	-1.30	-0.08	0.45	1.01	2.18	100000	1
chi_raw[13]	0.24	0.00	0.94	-1.66	-0.38	0.25	0.86	2.06	100000	1
chi_raw[14]	0.04	0.00	0.93	-1.79	-0.56	0.02	0.63	1.91	72609	1
chi_raw[15]	0.16	0.00	0.92	-1.65	-0.44	0.15	0.77	2.00	100000	1
chi_raw[16]	-0.19	0.00	0.92	-1.93	-0.79	-0.26	0.37	1.77	70294	1
chi_raw[17]	-0.27	0.00	0.96	-2.11	-0.91	-0.31	0.35	1.72	100000	1
chi_raw[18]	0.14	0.00	0.91	-1.63	-0.46	0.12	0.73	1.98	100000	1
chi_raw[19]	0.02	0.00	1.00	-1.97	-0.65	0.03	0.69	1.98	100000	1
chi_raw[20]	0.13	0.00	1.01	-1.89	-0.55	0.16	0.81	2.04	100000	1
chi_0_raw[1]	-0.02	0.00	1.00	-1.95	-0.69	-0.03	0.66	1.94	100000	1
chi_0_raw[2]	0.04	0.00	0.97	-1.86	-0.61	0.04	0.69	1.97	100000	1
chi_0_raw[3]	0.11	0.00	0.98	-1.82	-0.55	0.11	0.77	2.03	100000	1
chi_0_raw[4]	-0.20	0.00	0.98	-2.10	-0.86	-0.22	0.45	1.76	100000	1
chi_0_raw[5]	0.05	0.00	0.98	-1.85	-0.62	0.03	0.70	2.01	100000	1
chi_0_raw[6]	-0.25	0.00	0.97	-2.13	-0.90	-0.26	0.40	1.71	100000	1
chi_0_raw[7]	0.23	0.00	0.92	-1.58	-0.37	0.23	0.84	2.05	100000	1
chi_0_raw[8]	-0.01	0.00	0.96	-1.90	-0.65	-0.01	0.63	1.88	100000	1
chi_0_raw[9]	0.21	0.00	1.01	-1.80	-0.47	0.21	0.90	2.18	100000	1
chi_0_raw[10]	0.17	0.00	0.92	-1.66	-0.43	0.17	0.77	1.97	100000	1
chi_0_raw[11]	0.00	0.00	0.97	-1.89	-0.65	-0.01	0.64	1.92	100000	1
chi_0_raw[12]	0.23	0.00	0.97	-1.70	-0.42	0.24	0.89	2.12	100000	1
chi_0_raw[13]	-0.02	0.00	1.03	-2.04	-0.72	-0.01	0.69	1.99	100000	1
chi_0_raw[14]	0.06	0.00	0.97	-1.85	-0.58	0.07	0.71	1.96	100000	1
chi_0_raw[15]	0.00	0.00	1.01	-1.97	-0.69	0.00	0.68	1.97	100000	1
chi_0_raw[16]	0.10	0.00	0.97	-1.83	-0.55	0.11	0.76	2.00	100000	1
chi_0_raw[17]	-0.14	0.00	0.99	-2.05	-0.80	-0.15	0.52	1.82	100000	1
chi_0_raw[18]	0.22	0.00	0.95	-1.66	-0.40	0.22	0.85	2.08	100000	1
chi_0_raw[19]	-0.01	0.00	1.00	-1.98	-0.69	-0.01	0.66	1.97	100000	1
chi_0_raw[20]	0.02	0.00	1.01	-1.96	-0.66	0.02	0.71	1.98	100000	1
chi_top	-0.91	0.01	1.30	-3.22	-1.72	-1.03	-0.23	2.11	37663	1
chi_0_top	2.46	0.01	1.08	0.62	1.74	2.36	3.10	4.85	44115	1
chi_sigma_top	3.31	0.05	5.45	0.17	1.25	2.28	3.98	12.03	14355	1
chi_0_sigma_top	1.38	0.03	3.73	0.04	0.41	0.88	1.63	5.11	16724	1
chi[1]	-0.08	0.05	7.55	-7.95	-2.02	-0.49	1.28	10.20	20061	1
chi[2]	-0.81	0.04	6.21	-8.84	-2.64	-1.19	0.43	9.19	20667	1
chi[3]	-0.10	0.03	5.59	-6.91	-2.06	-0.73	1.15	10.28	38546	1
chi[4]	-1.95	0.05	6.48	-10.28	-3.46	-1.83	-0.51	6.17	20327	1
chi[5]	1.02	0.04	5.80	-3.89	-1.16	0.04	1.91	11.55	25381	1
chi[6]	-3.84	0.04	6.19	-13.51	-5.45	-3.11	-1.52	2.30	19263	1
chi[7]	-1.98	0.04	5.88	-10.62	-3.23	-1.86	-0.72	6.93	27718	1
chi[8]	-2.59	0.03	4.95	-9.96	-3.45	-2.20	-1.26	3.52	30293	1
chi[9]	1.44	0.03	5.26	-3.52	-0.73	0.49	2.37	12.07	29082	1
chi[10]	-2.48	0.03	4.30	-9.01	-3.58	-2.30	-1.39	4.14	28444	1
chi[11]	-2.12	0.03	6.17	-11.88	-3.62	-1.78	-0.33	6.41	32610	1
chi[12]	0.90	0.04	6.42	-4.01	-1.35	-0.14	1.82	11.49	26833	1
chi[13]	0.01	0.03	5.85	-6.33	-1.94	-0.63	1.35	10.10	34712	1

chi[14]	-0.76	0.04	6.04	-8.17	-2.35	-1.11	0.38	8.88	22827	1
chi[15]	-0.19	0.07	8.43	-6.31	-2.09	-0.82	0.92	9.83	13526	1
chi[16]	-1.40	0.05	7.00	-8.57	-2.93	-1.68	-0.43	7.97	17139	1
chi[17]	-1.97	0.03	5.61	-11.42	-3.37	-1.75	-0.41	6.49	37852	1
chi[18]	-0.13	0.03	6.11	-5.70	-2.09	-0.88	0.85	10.34	33396	1
chi[19]	-0.86	0.08	8.93	-9.55	-2.51	-1.08	0.58	9.14	14181	1
chi[20]	-0.49	0.04	6.21	-8.70	-2.30	-0.79	1.04	9.80	27651	1
chi_0[1]	2.44	0.05	6.92	-1.26	1.47	2.33	3.36	7.07	18596	1
chi_0[2]	2.66	0.02	3.17	-0.42	1.57	2.39	3.41	7.05	38581	1
chi_0[3]	2.71	0.02	3.16	-0.67	1.63	2.48	3.54	7.30	40346	1
chi_0[4]	2.11	0.01	3.17	-1.94	1.26	2.12	3.06	5.96	46298	1
chi_0[5]	2.81	0.03	4.71	0.00	1.53	2.36	3.45	7.63	19683	1
chi_0[6]	1.99	0.03	3.88	-2.01	1.25	2.08	2.99	5.56	20733	1
chi_0[7]	3.06	0.03	4.53	0.74	1.84	2.61	3.62	7.46	18147	1
chi_0[8]	2.38	0.02	3.83	-1.27	1.52	2.35	3.34	6.28	27529	1
chi_0[9]	2.96	0.02	3.74	-0.45	1.71	2.59	3.74	8.17	32897	1
chi_0[10]	2.84	0.02	2.84	0.33	1.78	2.55	3.53	6.77	33529	1
chi_0[11]	2.61	0.02	3.17	-0.31	1.53	2.34	3.34	6.81	30020	1
chi_0[12]	3.02	0.03	4.15	-0.02	1.77	2.61	3.72	7.83	23182	1
chi_0[13]	2.44	0.02	3.87	-2.03	1.42	2.33	3.41	6.88	35963	1
chi_0[14]	2.59	0.02	3.76	-0.78	1.59	2.43	3.45	6.90	43349	1
chi_0[15]	2.52	0.05	6.45	-1.55	1.48	2.36	3.40	6.93	15002	1
chi_0[16]	2.66	0.01	3.24	-0.76	1.64	2.48	3.53	6.99	53450	1
chi_0[17]	2.16	0.02	3.26	-1.95	1.31	2.19	3.18	6.16	40786	1
chi_0[18]	3.03	0.03	4.20	0.30	1.79	2.61	3.68	7.70	23585	1
chi_0[19]	2.43	0.02	3.83	-1.58	1.47	2.34	3.37	6.81	36946	1
chi_0[20]	2.55	0.02	3.94	-1.46	1.52	2.38	3.43	7.05	30406	1
delta_0[1]	1.11	0.00	0.14	0.85	1.02	1.11	1.20	1.39	38926	1
delta_0[2]	1.05	0.00	0.11	0.83	0.98	1.05	1.12	1.26	66376	1
delta_0[3]	0.84	0.00	0.11	0.61	0.76	0.84	0.91	1.06	53594	1
delta_0[4]	0.92	0.00	0.10	0.72	0.85	0.92	0.99	1.12	58054	1
delta_0[5]	0.97	0.00	0.12	0.72	0.90	0.97	1.04	1.17	46625	1
delta_0[6]	0.98	0.00	0.10	0.79	0.92	0.98	1.05	1.18	65330	1
delta_0[7]	1.07	0.00	0.10	0.86	0.99	1.06	1.13	1.27	67533	1
delta_0[8]	0.92	0.00	0.13	0.66	0.83	0.92	1.01	1.18	49771	1
delta_0[9]	0.80	0.00	0.15	0.52	0.70	0.79	0.89	1.10	35432	1
delta_0[10]	1.25	0.00	0.11	1.03	1.18	1.25	1.33	1.47	55695	1
delta_0[11]	1.10	0.00	0.10	0.90	1.04	1.10	1.16	1.28	70168	1
delta_0[12]	0.92	0.00	0.10	0.73	0.85	0.92	0.98	1.11	71403	1
delta_0[13]	0.89	0.00	0.10	0.70	0.83	0.89	0.96	1.09	56016	1
delta_0[14]	1.21	0.00	0.10	1.02	1.14	1.21	1.27	1.40	74389	1
delta_0[15]	1.14	0.00	0.10	0.93	1.07	1.14	1.21	1.33	69998	1
delta_0[16]	1.08	0.00	0.11	0.87	1.01	1.08	1.16	1.30	63736	1
delta_0[17]	0.97	0.00	0.10	0.78	0.91	0.97	1.04	1.17	80936	1
delta_0[18]	1.12	0.00	0.10	0.94	1.06	1.12	1.19	1.32	67174	1
delta_0[19]	0.81	0.00	0.12	0.59	0.74	0.81	0.89	1.04	52180	1
delta_0[20]	1.19	0.00	0.14	0.91	1.10	1.19	1.28	1.47	54676	1
eta[1]	0.05	0.00	0.05	-0.04	0.02	0.05	0.08	0.17	41428	1
eta[2]	0.02	0.00	0.04	-0.06	-0.01	0.02	0.05	0.11	71467	1
eta[3]	0.00	0.00	0.04	-0.07	-0.02	0.00	0.03	0.08	56256	1
eta[4]	0.01	0.00	0.06	-0.13	-0.03	0.01	0.05	0.14	58305	1
eta[5]	-0.01	0.00	0.06	-0.15	-0.04	0.00	0.03	0.09	46133	1
eta[6]	0.04	0.00	0.07	-0.09	-0.01	0.03	0.07	0.22	49301	1
eta[7]	0.00	0.00	0.06	-0.13	-0.03	0.00	0.04	0.12	49441	1
eta[8]	0.02	0.00	0.07	-0.11	-0.02	0.02	0.06	0.17	52793	1

eta[9]	-0.02	0.00	0.06	-0.15	-0.05	-0.01	0.02	0.08	30824	1
eta[10]	0.01	0.00	0.07	-0.15	-0.03	0.01	0.05	0.13	40411	1
eta[11]	0.03	0.00	0.07	-0.10	-0.01	0.03	0.07	0.20	61125	1
eta[12]	0.02	0.00	0.06	-0.09	-0.01	0.02	0.06	0.16	67106	1
eta[13]	0.03	0.00	0.07	-0.11	-0.01	0.02	0.06	0.19	65854	1
eta[14]	0.03	0.00	0.06	-0.10	-0.01	0.02	0.06	0.16	54079	1
eta[15]	0.02	0.00	0.07	-0.12	-0.02	0.02	0.05	0.16	73922	1
eta[16]	-0.01	0.00	0.06	-0.14	-0.05	-0.01	0.03	0.09	43406	1
eta[17]	0.03	0.00	0.06	-0.08	-0.01	0.03	0.06	0.16	60087	1
eta[18]	0.01	0.00	0.06	-0.12	-0.02	0.01	0.05	0.15	73311	1
eta[19]	0.00	0.00	0.06	-0.15	-0.04	0.00	0.04	0.11	42933	1
eta[20]	0.03	0.00	0.04	-0.06	0.00	0.03	0.05	0.11	55805	1
delta_0_av	1.00	0.00	0.19	0.61	0.88	1.00	1.12	1.38	80947	1
eta_av	0.01	0.00	0.07	-0.13	-0.02	0.01	0.05	0.16	70943	1
chi_av	-0.90	0.02	6.14	-9.46	-2.62	-1.14	0.59	9.09	100000	1
chi_0_av	2.48	0.02	4.49	-1.54	1.48	2.36	3.39	6.87	60077	1
lp_	485.14	0.06	10.18	464.37	478.46	485.47	492.15	504.15	25442	1

Samples were drawn using NUTS(diag_e) at Thu Oct 26 16:10:03 2017.
For each parameter, n_eff is a crude measure of effective sample size,
and Rhat is the potential scale reduction factor on split chains (at
convergence, Rhat=1).

D

Supplementary material for Chapter 4

Supplementary material for Chapter 4: Movement behaviour after birth demonstrates precocial abilities of African elephant (*Loxodonta africana*) calves.

D.1 Supplementary figures

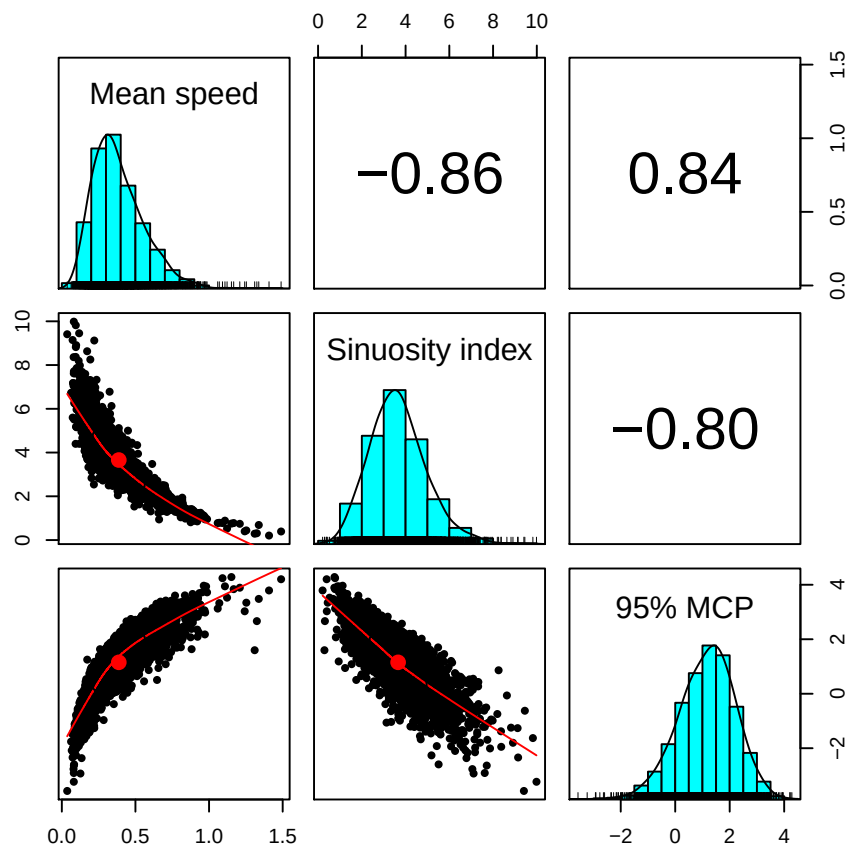


Figure D.1: Relationship between daily mean speed (km h⁻¹), sinuosity index and log-transformed 95% MCP for all individuals for -90 to 90 days after the estimated date of parturition.

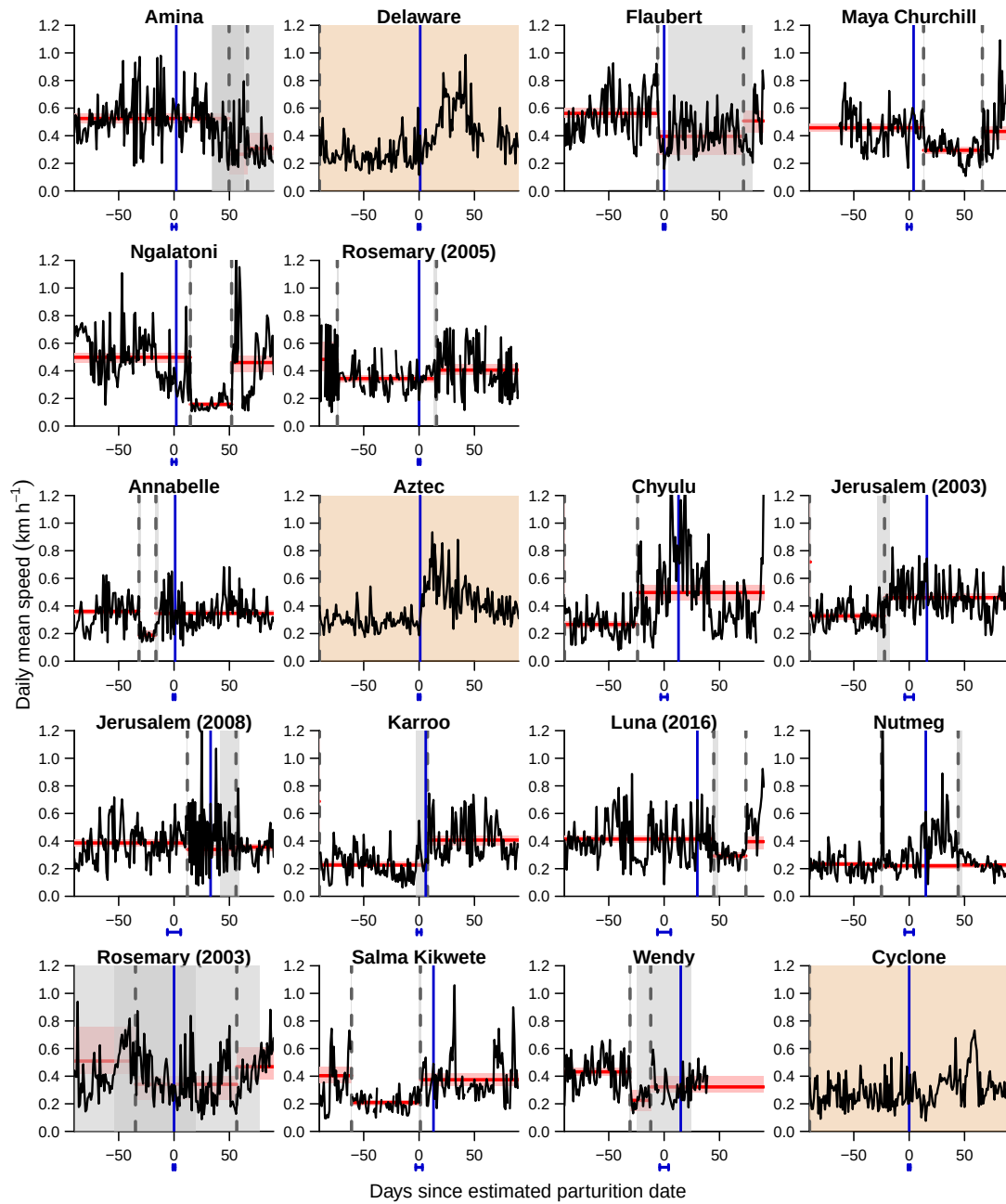


Figure D.2: Three-state hidden Markov model results for all multiparous subjects for daily mean speed (km h^{-1}) ± 90 days either side of the estimated date of parturition. Day 0 represents the estimated parturition date. Grey dashed lines denote the mean state change and grey shaded area indicates the credible interval ($\pm 95\%$). Red lines are the estimated mean speed during each state with the red shaded area corresponding to the 95% credible interval. Vertical blue line corresponds to the day the calf was first observed and the horizontal blue line indicates the potential error margin on the estimated parturition date (day 0). Orange backgrounds correspond to models which did not fully converge.

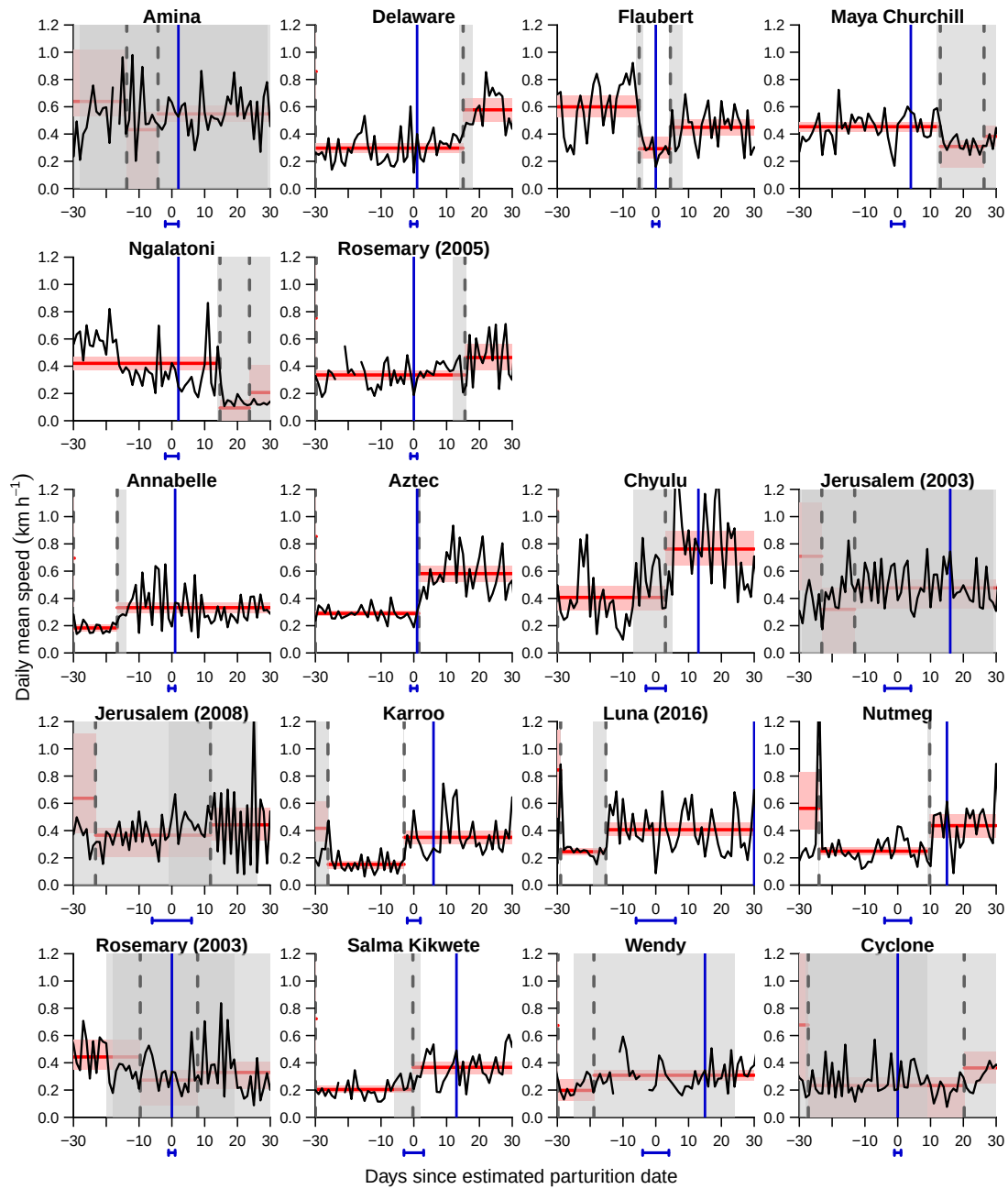


Figure D.3: Three-state hidden Markov model results for all multiparous subjects for daily mean speed (km h^{-1}) ± 30 days either side of the estimated date of parturition. Day 0 represents the estimated parturition date. Grey dashed lines denote the mean state change and grey shaded area indicates the credible interval ($\pm 95\%$). Red lines are the estimated mean speed during each state with the red shaded area corresponding to the 95% credible interval. Vertical blue line corresponds to the day the calf was first observed and the horizontal blue line indicates the potential error margin on the estimated parturition date (day 0). Orange backgrounds correspond to models which did not fully converge.

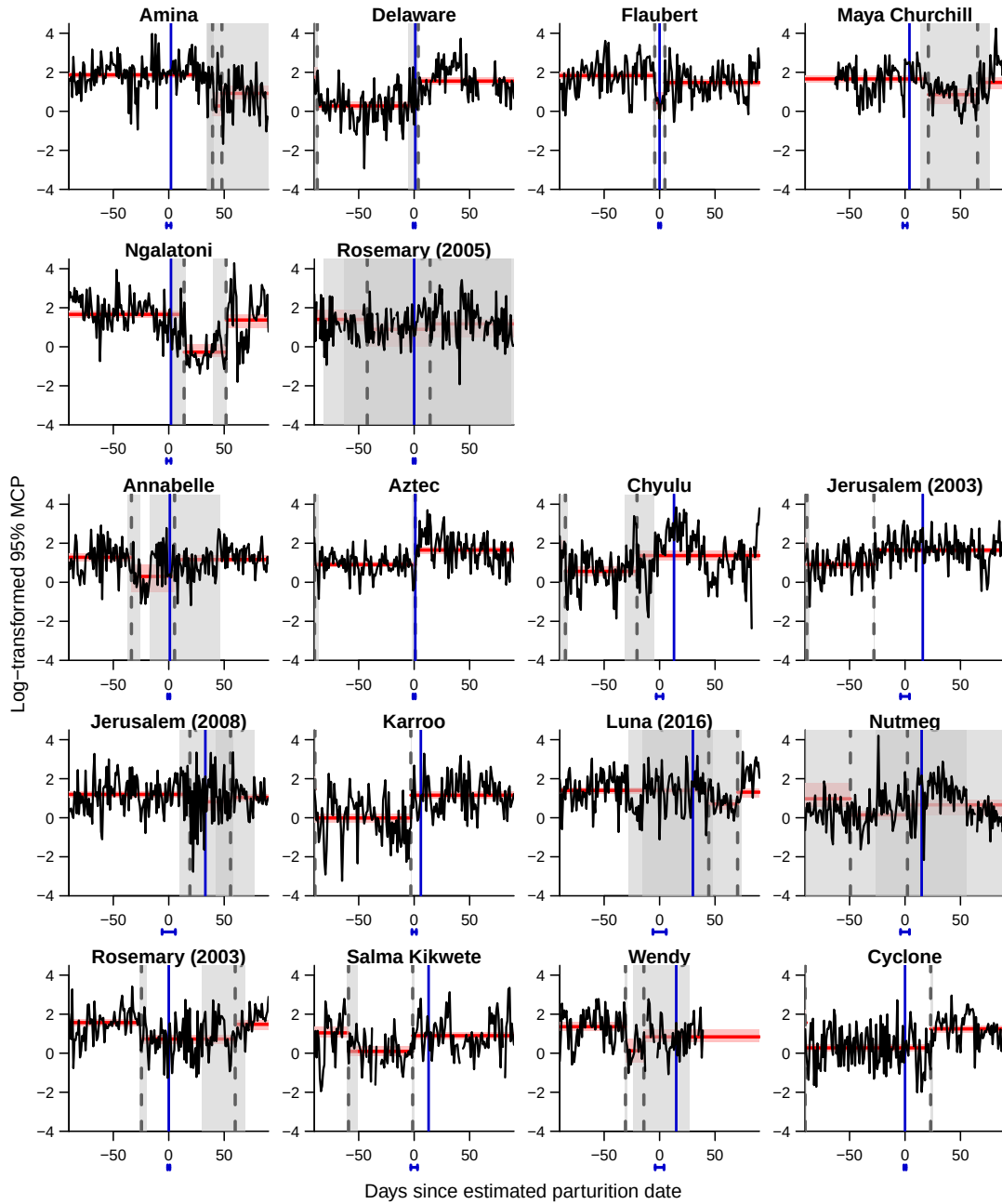


Figure D.4: Three-state hidden Markov model results for all multiparous subjects for **daily log-transformed 95% minimum convex polygon (MCP) ± 90 days** either side of the estimated date of parturition. Day 0 represents the estimated parturition date. Grey dashed lines denote the mean state change and grey shaded area indicates the credible interval ($\pm 95\%$). Red lines are the estimated mean speed during each state with the red shaded area corresponding to the 95% credible interval. Vertical blue line corresponds to the day the calf was first observed and the horizontal blue line indicates the potential error margin on the estimated parturition date (day 0). Orange backgrounds correspond to models which did not fully converge.

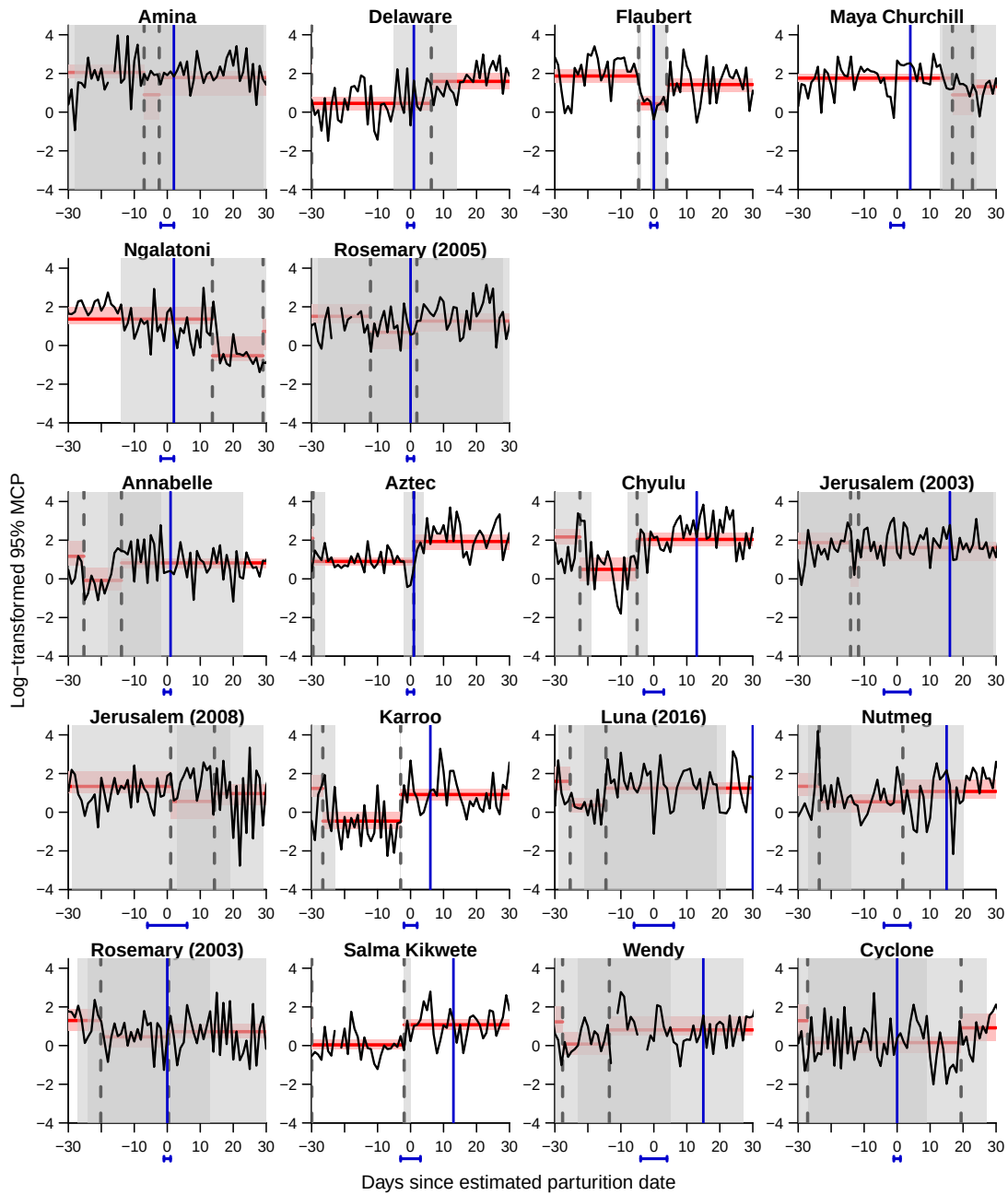


Figure D.5: Three-state hidden Markov model results for all multiparous subjects for **daily log-transformed 95% minimum convex polygon (MCP) ± 30 days** either side of the estimated date of parturition. Day 0 represents the estimated parturition date. Grey dashed lines denote the mean state change and grey shaded area indicates the credible interval ($\pm 95\%$). Red lines are the estimated mean speed during each state with the red shaded area corresponding to the 95% credible interval. Vertical blue line corresponds to the day the calf was first observed and the horizontal blue line indicates the potential error margin on the estimated parturition date (day 0). Orange backgrounds correspond to models which did not fully converge.

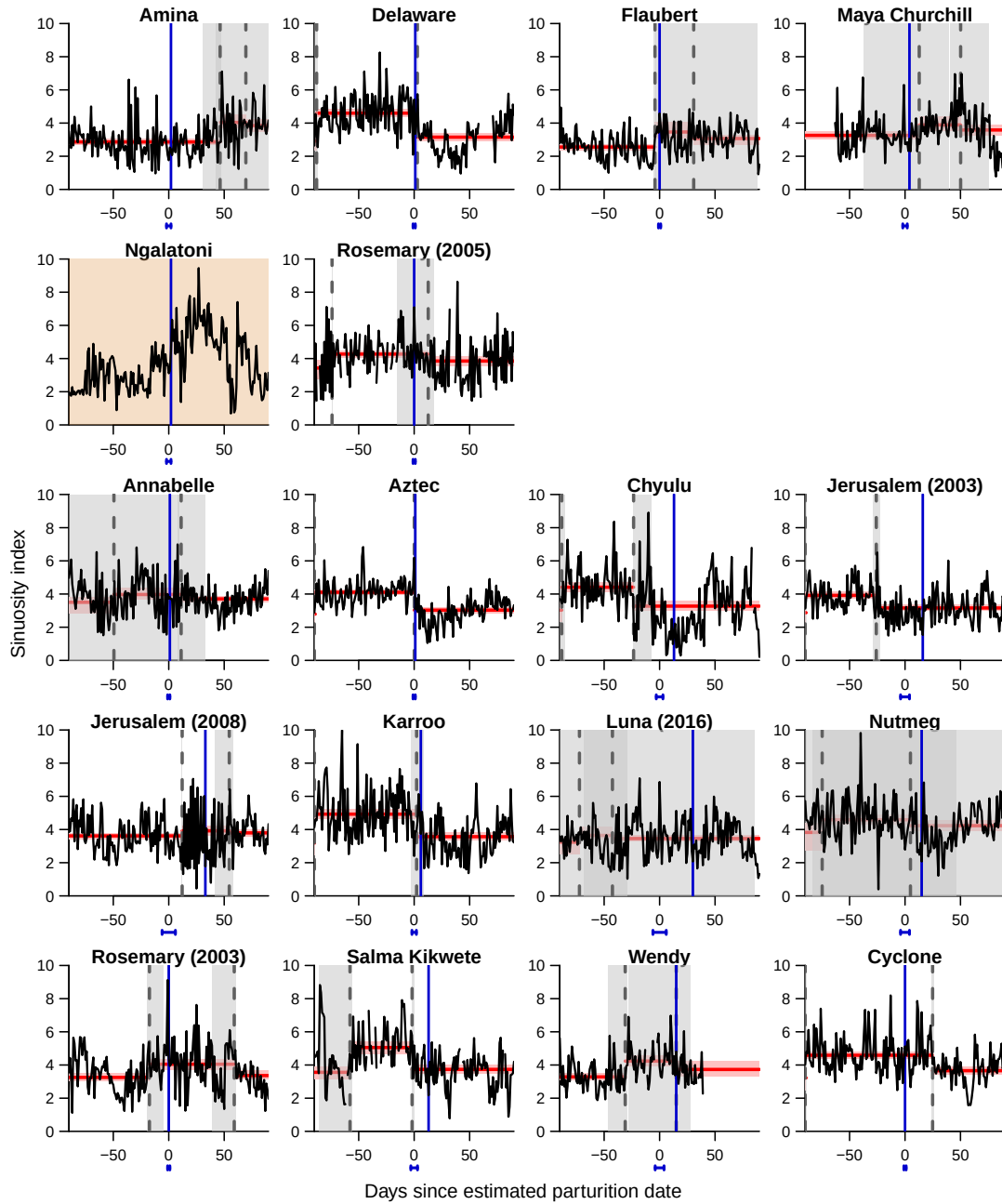


Figure D.6: Three-state hidden Markov model results for all multiparous subjects for daily sinuosity index ± 90 days either side of the estimated date of parturition. Day 0 represents the estimated parturition date. Grey dashed lines denote the mean state change and grey shaded area indicates the credible interval ($\pm 95\%$). Red lines are the estimated mean speed during each state with the red shaded area corresponding to the 95% credible interval. Vertical blue line corresponds to the day the calf was first observed and the horizontal blue line indicates the potential error margin on the estimated parturition date (day 0). Orange backgrounds correspond to models which did not fully converge.

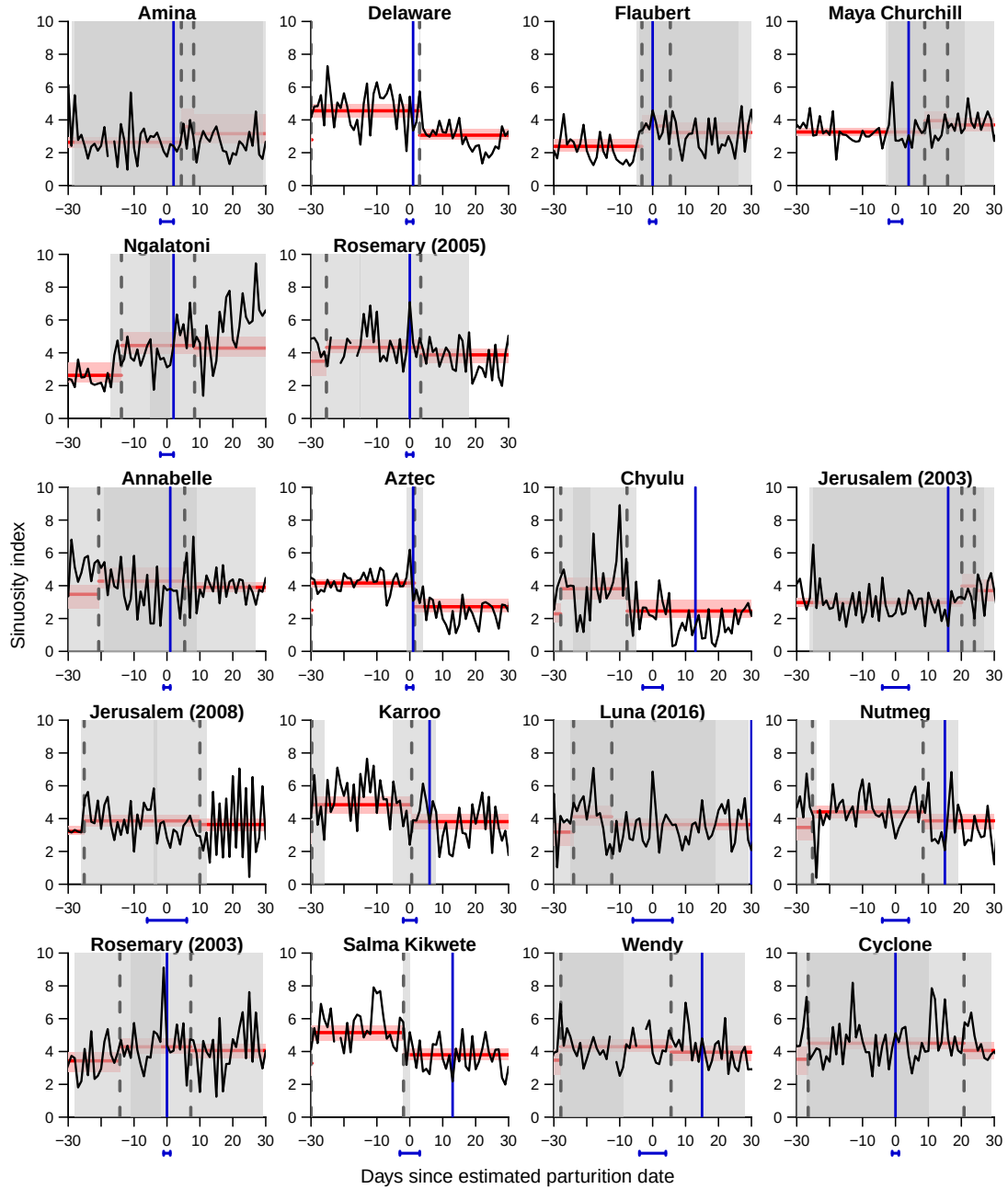


Figure D.7: Three-state hidden Markov model results for all multiparous subjects for daily sinuosity index ± 30 days either side of the estimated date of parturition. Day 0 represents the estimated parturition date. Grey dashed lines denote the mean state change and grey shaded area indicates the credible interval ($\pm 95\%$). Red lines are the estimated mean speed during each state with the red shaded area corresponding to the 95% credible interval. Vertical blue line corresponds to the day the calf was first observed and the horizontal blue line indicates the potential error margin on the estimated parturition date (day 0). Orange backgrounds correspond to models which did not fully converge.

D.2 Supplementary tables

Table D.1: Model priors for three state-hidden Markov models.

Model	Distribution	β (State 1, State 2, State 3)	σ (State 1, State 2, State 3)	γ
Daily mean speed (km h ⁻¹)	Normal	0.4, 0.2, 0.4	0.2, 0.2, 0.2	NA
Log-transformed 95% MCP	Normal	1.0, 0.5, 1.0	0.5, 0.5, 0.5	NA
Sinuosity index	Normal	3.5, 4.5, 3.5	1.0, 1.0, 1.0	NA
Hourly speed (km h ⁻¹)	Exponential	1.0, 1.0, 1.0	NA	Uniform ($-\infty, \infty$)

Table D.2: Results of the three-state hidden Markov models of hourly speed with the covariates of day-night, NDMI, slope and protected area for ± 30 days and ± 10 days each individual elephant. Day 0.00 was considered 12:00 on the estimated date of parturition. Missing data points are models which failed to converge ($\hat{R} > 1.1$).

Group	Name	± 30 days hourly speed with covariates					± 10 days hourly speed with covariates				
		Mean state change (days)		Mean speed during state (km h ⁻¹)			Mean state change (days)		Mean speed during state (km h ⁻¹)		
		[95% CrI]		State 1	State 2	State 3	[95% CrI]		State 1	State 2	State 3
Multiparous	Amina	-27.13	-25.57	0.94	0.30	0.91	3.79	6.91	0.92	0.31	0.83
		[-28.46, -11.71]	[-26.83, -10.96]	[0.82, 1]	[0.16, 0.46]	[0.78, 0.99]	[-9.08, 5.96]	[-1.92, 8.46]	[0.75, 1.00]	[0.19, 0.49]	[0.46, 0.98]
	Delaware	-14.16	13.95	0.38	0.18	0.37	-10.39	-2.60	0.78	0.29	0.60
		[-14.54, -14.04]	[12.17, 14.96]	[0.31, 0.46]	[0.15, 0.21]	[0.30, 0.45]	[-10.50, -10.38]	[-4.12, -1.71]	[0.47, 0.99]	[0.19, 0.41]	[0.35, 0.88]
	Flaubert	-5.12	6.90	0.97	0.43	0.66	-5.12	7.61	0.91	0.33	0.64
		[-5.12, -5.12]	[4.62, 8.21]	[0.91, 1.00]	[0.36, 0.51]	[0.58, 0.75]	[-5.12, -5.12]	[4.62, 8.21]	[0.73, 1.00]	[0.25, 0.42]	[0.43, 0.88]
	Maya Churchill	13.32	27.14	0.63	0.34	0.46					
		[13.33, 13.33]	[13.75, 29.71]	[0.45, 0.86]	[0.15, 0.46]	[0.31, 0.7]					
	Ngalatoni	-16.22	6.78	0.98	0.51	0.60	1.79	6.11	0.89	0.55	0.79
		[-17.04, -13.00]	[-16.79, 30.25]	[0.93, 1.00]	[0.19, 0.60]	[0.50, 0.77]	[-4.00, 6.21]	[-2.79, 9.21]	[0.67, 1.00]	[0.08, 0.86]	[0.57, 0.96]
Expanded	Rosemary (2005)	-30.50	10.89	0.83	0.49	0.77	-1.67	-0.10	0.62	0.18	0.51
		[-30.50, -30.50]	[-30.46, 18.71]	[0.13, 1.00]	[0.01, 0.65]	[0.07, 0.98]	[-5.17, -1.17]	[-3.83, 0.79]	[0.32, 0.96]	[0.06, 0.35]	[0.25, 0.86]
	Annabelle	-30.07	-14.52	0.40	0.14	0.25	-1.58	2.14	0.82	0.42	0.6
		[-30.50, -29.46]	[-16.25, -13.12]	[0.20, 0.88]	[0.10, 0.19]	[0.18, 0.33]	[-1.62, -0.62]	[-1.12, 8.38]	[0.51, 0.99]	[0.19, 0.66]	[0.36, 0.85]
	Aztec	-30.50	3.20	0.85	0.35	0.73	-10.50	2.93	0.81	0.38	0.67
		[-30.50, -30.50]	[2.92, 4.25]	[0.62, 0.99]	[0.25, 0.44]	[0.53, 0.93]	[-10.50, -10.42]	[2.92, 4.25]	[0.49, 0.99]	[0.22, 0.57]	[0.37, 0.93]
	Chyulu	-30.12	0.75	0.97	0.49	0.94					
		[-30.12, -30.12]	[-5.71, 6.46]	[0.89, 1.00]	[0.42, 0.55]	[0.84, 0.99]					
Jerusalem (2003)		-30.50	-16.83	0.93	0.48	0.87					
		[-30.50, -30.50]	[-16.83, -16.83]	[0.79, 1.00]	[0.41, 0.55]	[0.72, 0.98]					
Jerusalem (2008)		21.48	22.84	0.93	0.15	0.88	-5.16	-2.18	0.82	0.50	0.72
		[21.5, 21.54]	[22.88, 22.88]	[0.79, 1.00]	[0.10, 0.23]	[0.74, 0.98]	[-9.92, 6.83]	[-10.38, 8.75]	[0.56, 0.99]	[0.11, 0.81]	[0.48, 0.93]

Group	Name	±30 days hourly speed with covariates						±10 days hourly speed with covariates					
		Mean state change (days)			Mean speed during state (km h ⁻¹)			Mean state change (days)			Mean speed during state (km h ⁻¹)		
		[95% CrI]			[95% CrI]			[95% CrI]			[95% CrI]		
		1	2		State 1	State 2	State 3	1	2		State 1	State 2	State 3
Multiparous	Karoo	-25.38	-2.79		0.41	0.17	0.40	-10.46	8.89		0.93	0.31	0.86
		[-25.38, -25.38]	[-3.04, -2.75]		[0.32, 0.52]	[0.14, 0.20]	[0.31, 0.51]	[-10.46, -10.46]	[8.83, 9.00]		[0.75, 1.00]	[0.24, 0.40]	[0.66, 0.98]
	Luna (2016)	-0.49	0.18		0.50	0.05	0.48	-0.53	0.17		0.42	0.04	0.39
		[-0.54, 0.83]	[0.12, 1.17]		[0.38, 0.64]	[0.02, 0.09]	[0.37, 0.62]	[-0.54, -0.54]	[0.12, 0.25]		[0.28, 0.60]	[0.02, 0.07]	[0.25, 0.56]
	Nutmeg	-23.57	-5.62		0.86	0.24	0.43	-10.46	-6.96		0.66	0.17	0.36
		[-23.58, -23.58]	[-5.67, -5.62]		[0.64, 0.99]	[0.20, 0.28]	[0.33, 0.52]	[-10.46, -10.46]	[-7.25, -5.79]		[0.32, 0.98]	[0.11, 0.26]	[0.24, 0.53]
	Rosemary (2003)	-20.05	3.31		0.95	0.42	0.71	-10.45	0.62		0.93	0.40	0.86
		[-23.08, -19.62]	[0.71, 5.88]		[0.83, 1.00]	[0.33, 0.51]	[0.6, 0.83]	[-10.50, -10.50]	[0.17, 0.71]		[0.76, 1.00]	[0.26, 0.58]	[0.66, 0.98]
	Salma Kikwete	-30.44	-6.74		0.66	0.23	0.45	-10.46	-5.63		0.83	0.36	0.68
		[-30.50, -30.21]	[-6.75, -6.75]		[0.40, 0.98]	[0.18, 0.28]	[0.34, 0.58]	[-10.46, -10.46]	[-8.62, -2.25]		[0.54, 0.99]	[0.18, 0.55]	[0.41, 0.93]
Primiparous	Wendy							2.55	5.13		0.68	0.29	0.39
								[1.92, 5.08]	[-10.46, 10.08]		[0.41, 0.96]	[0.08, 0.46]	[0.22, 0.66]
	Cyclone							-6.67	-1.84		0.37	0.19	0.29
								[-10.42, -6.42]	[-8.79, 3.79]		[0.23, 0.72]	[0.10, 0.36]	[0.18, 0.55]
	Habiba	-11.46	-7.88		0.37	0.09	0.35	-10.50	-7.88		0.72	0.12	0.45
		[-11.46, -11.46]	[-7.88, -7.88]		[0.29, 0.47]	[0.06, 0.13]	[0.27, 0.46]	[-10.50, -10.50]	[-7.88, -7.88]		[0.36, 0.99]	[0.06, 0.22]	[0.24, 0.73]
	Luna (2014)	-0.46	0.70		0.56	0.03	0.44	-0.29	0.83		0.89	0.06	0.38
		[-0.50, -0.46]	[0.67, 0.71]		[0.45, 0.69]	[0.02, 0.05]	[0.37, 0.53]	[-0.29, -0.29]	[0.79, 0.88]		[0.65, 1.00]	[0.04, 0.10]	[0.27, 0.49]
	Soutine	-3.02	2.98		0.90	0.33	0.81	-2.69	-1.40		0.84	0.09	0.65
		[-3.08, -2.71]	[2.79, 3.17]		[0.71, 1.00]	[0.24, 0.42]	[0.63, 0.95]	[-3.04, -2.67]	[-1.83, 3.17]		[0.55, 0.99]	[0.03, 0.38]	[0.42, 0.86]

Table D.3: Results of the linear mixed-effects models of daily mean speed (km h^{-1}), daily standard deviation of hourly speed (km h^{-1}), log-transformed 95% MCP and sinusity index for the all 18 multiparous births. Each row corresponds to a different model with a different day range. Covariates were standardised across the entire dataset. Missing values correspond to variables which were removed from the final model and therefore do not have a significant effect on the results. Marginal ($R^2_{\text{LME}(M)}$) and conditional R-squared values ($R^2_{\text{LME}(C)}$) were calculated using the methods described in Nakagawa and Schielzeth (2013).

Variable	Model day range		All individuals						
	Min day	Max day	R^2_{LME}	Estimated change per unit [95% CI]					
	m	c	Day difference	Day difference ²	Mean NDVI	Mean NDVI ²	Mean slope	Mean slope ²	Protected area
Daily mean speed (km h^{-1})	-90	-1	0.19	0.32	0.05 [0.03, 0.06]	-0.02 [-0.03, -0.02]	-0.04 [-0.05, -0.03]	0.08 [0.06, 0.10]	
	-30	-1	0.17	0.32	0.04 [0.01, 0.07]	-0.03 [-0.04, -0.01]	-0.04 [-0.06, -0.03]	0.09 [0.05, 0.12]	
	1	30	0.11	0.43	0.50 [0.13, 0.88]	-0.70 [-1.28, -0.12]	-0.06 [-0.08, -0.04]	0.00 [0.00, 0.01]	0.07 [0.04, 0.10]
	1	90	0.13	0.22	0.04 [0.02, 0.06]	-0.03 [-0.04, -0.01]	-0.04 [-0.05, -0.03]	0.08 [0.06, 0.10]	
Daily standard deviation of speed (km h^{-1})	-90	-1	0.15	0.22	0.03 [0.01, 0.05]	-0.02 [-0.03, -0.01]	-0.03 [-0.04, -0.02]	0.11 [0.08, 0.13]	0.03 [0.01, 0.05]
	-30	-1	0.13	0.24	0.03 [0.00, 0.07]	-0.02 [-0.04, 0.00]	-0.03 [-0.05, -0.01]	0.10 [0.06, 0.14]	0.03 [0.00, 0.07]
	1	30	0.08	0.35	0.67 [0.19, 1.16]	-0.92 [-1.67, -0.17]	-0.03 [-0.05, -0.01]	0.10 [0.05, 0.14]	
	1	90	0.07	0.16	0.02 [0, 0.04]	-0.02 [-0.04, -0.01]	-0.04 [-0.05, -0.02]	0.08 [0.06, 0.11]	0.02 [0.00, 0.04]

Variable	Model day range		All individuals								
			R ² _{LME}	Estimated change per unit [95% CI]							
	Min day	Max day	<i>m</i>	<i>c</i>	Day difference	Day difference ²	Mean NDVI	Mean NDVI ²	Mean slope	Mean slope ²	Protected area
Log-transformed 95% MCP	-90	-1	0.12	0.25			0.15 [0.06, 0.24]	-0.06 [-0.11, 0.00]	-0.17 [-0.26, -0.08]	-0.02 [-0.05, 0.00]	0.39 [0.26, 0.52]
	-30	-1	0.09	0.29					-0.23 [-0.34, -0.13]		0.43 [0.21, 0.65]
	1	30	0.14	0.32			0.2 [0.00, 0.39]	-0.14 [-0.25, -0.03]	-0.32 [-0.39, -0.24]		0.33 [0.14, 0.53]
	1	90	0.14	0.19			0.26 [0.16, 0.36]	-0.14 [-0.20, -0.08]	-0.25 [-0.33, -0.17]	-0.01 [-0.03, 0.00]	0.32 [0.21, 0.44]
Sinosity index	-90	-1	0.14	0.24			-0.34 [-0.45, -0.23]	0.16 [0.09, 0.23]	0.3 [0.23, 0.38]		-0.39 [-0.56, -0.23]
	-30	-1	0.12	0.27			-0.29 [-0.52, -0.06]	0.19 [0.07, 0.32]	0.31 [0.17, 0.44]		-0.45 [-0.73, -0.18]
	1	30	0.11	0.37	-2.81 [-5.24, -0.39]	4.19 [0.44, 7.93]	-0.25 [-0.48, -0.03]	0.17 [0.04, 0.30]	0.35 [0.26, 0.44]		-0.34 [-0.56, -0.11]
	1	90	0.12	0.2			-0.32 [-0.44, -0.2]	0.18 [0.11, 0.25]	0.35 [0.28, 0.41]		-0.32 [-0.47, -0.18]

Table D.4: Results of the linear mixed-effects models of daily mean speed (km h^{-1}), daily standard deviation of hourly speed (km h^{-1}), log-transformed 95% MCP and sinuosity index for the six individuals with accurate birth estimates. Each row corresponds to a different model with a different day range. Covariates were standardised across the entire dataset. Missing values correspond to variables which were removed from the final model and therefore do not have a significant effect on the results. Marginal ($R^2_{\text{LME}(M)}$) and conditional R-squared values ($R^2_{\text{LME}(C)}$) were calculated using the methods described in Nakagawa and Schielzeth (2013).

Variable	Model day range		Accurate individuals								
			R ² _{LME}	Estimated change per unit [95% CI]							
	Min day	Max day	m	c	Day difference	Day difference ²	Mean NDVI	Mean NDVI ²	Mean slope	Mean slope ²	Protected area
Daily mean speed (km h ⁻¹)	-90	-1	0.2	0.28			0.07 [0.04, 0.11]	-0.03 [-0.05, -0.02]	-0.05 [-0.07, -0.03]		0.08 [0.04, 0.11]
	-30	-1	0.34	0.35	-0.73 [-1.39, -0.07]	-1.34 [-2.45, -0.23]	0.10 [0.05, 0.16]	-0.05 [-0.08, -0.02]	-0.05 [-0.1, -0.01]		0.08 [0.02, 0.15]
	1	30	0.13	0.31	0.13 [-0.05, 0.31]				-0.04 [-0.07, -0.01]		0.14 [0.07, 0.20]
	1	90	0.18	0.18							
Daily standard deviation of speed (km h ⁻¹)	-90	-1	0.14	0.2		0.01 [0, 0.03]	0.05 [0.01, 0.1]	-0.02 [-0.04, 0.00]	-0.03 [-0.06, 0.00]		0.09 [0.05, 0.13]
	-30	-1	0.21	0.28	-0.60 [-1.3, 0.09]	-1.35 [-2.51, -0.19]	0.11 [0.04, 0.18]	-0.05 [-0.08, -0.02]	-0.04 [-0.09, 0.01]		
	1	30	0.09	0.29	0.16 [-0.03, 0.34]			-0.03 [-0.05, -0.01]			0.10 [0.02, 0.18]
	1	90	0.12	0.12	0.06 [0.01, 0.11]		0.06 [0.02, 0.11]	-0.04 [-0.06, -0.02]	-0.04 [-0.06, -0.01]		0.11 [0.06, 0.15]

Variable	Model day range		Accurate individuals								
			R ² _{LME}	Estimated change per unit [95% CI]							
	Min day	Max day	<i>m</i>	<i>c</i>	Day difference	Day difference ²	Mean NDVI	Mean NDVI ²	Mean slope	Mean slope ²	Protected area
Daily mean speed (km h ⁻¹)	-90	-1	0.05	0.28						-0.08 [-0.14, -0.03]	0.40 [0.21, 0.59]
	-30	-1	0.28	0.31	-5.7 [-8.92, -2.47]	-10.62 [-16.06, -5.17]	0.43 [0.14, 0.72]	-0.14 [-0.3, 0.01]	-0.30 [-0.54, -0.06]		0.39 [0.04, 0.74]
	1	30	0.1	0.37				-0.14 [-0.24, -0.03]			0.69 [0.31, 1.08]
	1	90	0.18	0.19		0.14 [0.01, 0.26]	0.37 [0.16, 0.57]	-0.19 [-0.3, -0.09]	-0.29 [-0.39, -0.18]		0.53 [0.31, 0.74]
Daily standard deviation of speed (km h ⁻¹)	-90	-1	0.12	0.26		-0.09 [-0.19, 0.02]	-0.40 [-0.66, -0.14]	0.18 [0.06, 0.29]	0.35 [0.18, 0.51]		-0.24 [-0.47, -0.01]
	-30	-1	0.31	0.38	2.90 [-0.91, 6.7]	6.35 [-0.05, 12.74]	-0.75 [-1.14, -0.35]	0.33 [0.14, 0.51]	0.52 [0.23, 0.80]		
	1	30	0.11	0.39	-4.51 [-8.84, -0.18]	6.94 [0.23, 13.64]			0.38 [0.17, 0.58]		
	1	90	0.16	0.19	-0.43 [-0.72, -0.14]		-0.54 [-0.82, -0.25]	0.28 [0.14, 0.41]	0.36 [0.23, 0.50]		-0.52 [-0.79, -0.24]

D.3 Supplementary material

Stan code for the Bayesian hierarchical model of wingbeat frequency. In the model, the bird-level parameters are sampled from a normal distribution conditional on the hyper-parameters, which represent the population averages. For example, $\text{delta}_i \sim N(\text{delta}^{\{\text{top}\}}, \text{sigma_delta}^{\{\text{top}\}})$, where delta_i is the uplift for bird i of being in a pair, and $\text{delta}^{\{\text{top}\}}$ and $\text{sigma_delta}^{\{\text{top}\}}$ represent the population mean uplift and the standard deviation of the individual birds' effects about this mean. Note that in the Stan model, we use a non-centred parameterisation to implement this model (Carpenter *et al.*, 2017), which helps with sampling.

D.3.1 Stan code for the three state hidden Markov model

Stan code for the Bayesian three-state hidden Markov model of daily mean speed. See methods section for details.

```
data{
  int T;
  int K;
  real Speed[T];
  int aMinDayDiff;

  // priors
  vector[3] Speed_mean_prior;
  vector[3] Speed_sigma_prior;
}

transformed data {
  real log_unif;
  vector[3] alpha_prior_reordered;
  alpha_prior_reordered[1] = -Speed_mean_prior[1];
  alpha_prior_reordered[2] = -Speed_mean_prior[3];
  alpha_prior_reordered[3] = -Speed_mean_prior[2];
  log_unif = -log(T);
}

parameters{
  ordered[K] alpha;
  real<lower=0> sigma[K];
}

transformed parameters{
  matrix[T,K] lp;
  vector[K] alphaReordered;
```

```

alphaReordered[1] = alpha[1];
alphaReordered[2] = alpha[3];
alphaReordered[3] = alpha[2];

lp[1] = rep_row_vector(-log(K),K);

for(t in 2:T){

  for(k in 1:K){
    if(Speed[t] == -99){
      lp[t,k] = lp[t-1,k];
    }else{
      if(k==1) // early (long)
        lp[t,k] = lp[t-1,k] + gamma_lpdf(Speed[t] | -alphaReordered[k],
sigma[k]);
      else if(k==2) // mid (short)
        lp[t,k] = log_sum_exp(lp[t-1,1:2]) + gamma_lpdf(Speed[t] |
-alphaReordered[k],sigma[k]);
      else // late (medium)
        lp[t,k] = log_sum_exp(lp[t-1,2:3]) + gamma_lpdf(Speed[t] |
-alphaReordered[k],sigma[k]);
    }
  }
}

model{
  target += log_sum_exp(lp[T]);
  alpha ~ gamma(alpha_prior_reordered,0.5);
  sigma ~ gamma(0,Speed_sigma_prior);
}

generated quantities{
  int path[T];
  int changePoint1 = T-1;
  int changePoint2 = T;
  vector[3] meanSpeed = -alphaReordered;

  {
    matrix[T,K] mLogProb;
    int mBestIndex[T-1,K];
    real aLogProbTemp;
    int aBestFinal;

    for(t in 1:T){

      for(k in 1:K){
        if(Speed[t] == -99){
          mLogProb[t,k] = mLogProb[t-1,k];
          mBestIndex[t-1,k] = mBestIndex[t-2,k];
        } else{
          if(t==1){
            if(k==1)
              mLogProb[t,k] = gamma_lpdf(Speed[t] | -alphaReordered[k]
,sigma[k]);

```

```

else
    mLogProb[t,k] = negative_infinity();
}else if(t==2){
    if(k==1){
        mLogProb[t,k] = mLogProb[t-1,1] + gamma_lpdf(Speed[t] |
-alphaReordered[k],sigma[k]);
        mBestIndex[t-1,k] = 1;
    }
    else if(k==2){
        mLogProb[t,k] = mLogProb[t-1,1] + gamma_lpdf(Speed[t] |
-alphaReordered[k],sigma[k]);
        mBestIndex[t-1,k] = 1;
    }
    else{
        mLogProb[t,k] = negative_infinity();
        mBestIndex[t-1,k] = 0;
    }
}else if(t==3){
    if(k==1){
        mLogProb[t,k] = mLogProb[t-1,1] + gamma_lpdf(Speed[t] |
-alphaReordered[k],sigma[k]);
        mBestIndex[t-1,k] = 1;
    }
    else if(k==2){
        mLogProb[t,k] = max(mLogProb[t-1,1:2]) + gamma_lpdf(Speed[t] |
-alphaReordered[k],sigma[k]);
        aLogProbTemp = negative_infinity();
        for(i in 1:2){
            if(mLogProb[t-1,i]>aLogProbTemp){
                aLogProbTemp = mLogProb[t-1,i];
                mBestIndex[t-1,k] = i;
            }
        }
    }
    else{
        mLogProb[t,k] = mLogProb[t-1,2] + gamma_lpdf(Speed[t] |
-alphaReordered[k],sigma[k]);
        mBestIndex[t-1,k] = 2;
    }
}else{
    if(k==1){
        mLogProb[t,k] = mLogProb[t-1,1] + gamma_lpdf(Speed[t] |
-alphaReordered[k],sigma[k]);
        mBestIndex[t-1,k] = 1;
    }
    else if(k==2){
        mLogProb[t,k] = max(mLogProb[t-1,1:2]) + gamma_lpdf(Speed[t] |
-alphaReordered[k],sigma[k]);
        aLogProbTemp = negative_infinity();
        for(i in 1:2){
            if(mLogProb[t-1,i]>aLogProbTemp){
                aLogProbTemp = mLogProb[t-1,i];
                mBestIndex[t-1,k] = i;
            }
        }
    }
}

```

```

    }
    else{
        mLogProb[t,k] = max(mLogProb[t-1,2:3]) + gamma_lpdf(Speed[t] |
-alphaReordered[k],sigma[k]);
        aLogProbTemp = negative_infinity();
        for(i in 2:3){
            if(mLogProb[t-1,i]>aLogProbTemp){
                aLogProbTemp = mLogProb[t-1,i];
                mBestIndex[t-1,k] = i;
            }
        }
    }
}
}
}

aLogProbTemp = negative_infinity();
for(k in 1:K){
    if(mLogProb[T,k]>aLogProbTemp){
        aLogProbTemp = mLogProb[T,k];
        aBestFinal = k;
    }
}

for(t in 1:T){
    int aIndex;
    aIndex = T - t + 1;
    if(aIndex == T){
        path[aIndex] = aBestFinal;
    }else if(aIndex==1){
        path[aIndex] = 1;
    }else{
        path[aIndex] = mBestIndex[aIndex,path[aIndex+1]];
    }
}

for(t in 2:T){
    if(path[t-1]==1){
        if(path[t]-path[t-1]>0)
            changePoint1 = t-1;
    }
    else{
        if(path[t]-path[t-1]>0)
            changePoint2 = t-1;
    }
}
changePoint1 = changePoint1 + aMinDayDiff - 1;
changePoint2 = changePoint2 + aMinDayDiff - 1;
}
c

```

D.3.2 Example model output

Example model output for Flaubert (Figure 4.2e) for the Bayesian three-state hidden Markov model of daily mean speed.

Inference for Stan model: threeStateFinal_normal_missing.

8 chains, each with iter=10000; warmup=5000; thin=1;

post-warmup draws per chain=5000, total post-warmup draws=40000.

	mean	se_mean	sd	2.5%	25%	50%	75%	97.5%	n_eff	Rhat
alpha[1]	-0.60	0.00	0.04	-0.68	-0.63	-0.60	-0.57	-0.52	17327	1
alpha[2]	-0.45	0.00	0.03	-0.51	-0.47	-0.45	-0.43	-0.39	40000	1
alpha[3]	-0.29	0.00	0.04	-0.38	-0.31	-0.29	-0.27	-0.22	20210	1
sigma[1]	0.20	0.00	0.03	0.15	0.18	0.20	0.22	0.27	26859	1
sigma[2]	0.09	0.00	0.04	0.05	0.07	0.08	0.11	0.18	17714	1
sigma[3]	0.15	0.00	0.02	0.11	0.13	0.14	0.16	0.20	23342	1
lp[1,1]	-1.10	0.00	0.00	-1.10	-1.10	-1.10	-1.10	-1.10	4	1
lp[1,2]	-1.10	0.00	0.00	-1.10	-1.10	-1.10	-1.10	-1.10	4	1
lp[1,3]	-1.10	0.00	0.00	-1.10	-1.10	-1.10	-1.10	-1.10	4	1
lp[2,1]	-0.58	0.00	0.15	-0.90	-0.68	-0.57	-0.47	-0.30	20233	1
lp[2,2]	-14.17	0.08	11.72	-41.50	-19.39	-11.33	-5.90	-1.63	22047	1
lp[2,3]	-1.12	0.00	0.52	-2.29	-1.42	-1.05	-0.74	-0.29	40000	1
lp[3,1]	-0.55	0.00	0.15	-0.92	-0.63	-0.52	-0.44	-0.35	20150	1
lp[3,2]	0.19	0.00	0.63	-1.32	-0.07	0.32	0.59	0.98	29417	1
lp[3,3]	-0.20	0.00	0.38	-1.10	-0.41	-0.14	0.07	0.35	40000	1
lp[4,1]	-1.31	0.00	0.53	-2.58	-1.60	-1.22	-0.93	-0.55	21494	1
lp[4,2]	2.05	0.00	0.39	1.23	1.82	2.10	2.33	2.64	18576	1
lp[4,3]	0.95	0.00	0.44	0.06	0.70	0.99	1.23	1.62	23798	1
lp[5,1]	-1.68	0.01	0.86	-3.73	-2.16	-1.55	-1.05	-0.39	21489	1
lp[5,2]	3.45	0.01	0.70	1.99	3.02	3.52	3.97	4.55	18679	1
lp[5,3]	2.93	0.00	0.41	2.08	2.68	2.95	3.20	3.61	22892	1
lp[6,1]	-2.62	0.01	1.34	-5.77	-3.37	-2.43	-1.64	-0.59	22386	1
lp[6,2]	4.80	0.01	0.96	2.67	4.22	4.96	5.54	6.12	15109	1
lp[6,3]	3.94	0.00	0.71	2.48	3.52	4.00	4.43	5.11	23413	1
lp[7,1]	-1.95	0.01	1.31	-5.06	-2.69	-1.76	-1.00	0.02	21407	1
lp[7,2]	-0.46	0.03	4.73	-11.92	-2.18	1.04	2.72	3.50	23399	1
lp[7,3]	5.85	0.01	0.78	4.18	5.34	5.95	6.46	7.03	15754	1
lp[8,1]	-1.36	0.01	1.19	-4.24	-2.02	-1.16	-0.49	0.37	21209	1
lp[8,2]	-11.03	0.08	11.92	-37.85	-17.50	-8.22	-1.88	2.22	22144	1
lp[8,3]	5.52	0.01	0.87	3.65	4.97	5.58	6.15	6.98	17727	1
lp[9,1]	-0.70	0.01	1.20	-3.57	-1.35	-0.50	0.18	1.03	20652	1
lp[9,2]	-5.75	0.04	5.62	-18.18	-8.60	-5.02	-2.00	2.48	20377	1
lp[9,3]	6.21	0.01	0.93	4.22	5.63	6.27	6.88	7.82	19458	1
lp[10,1]	-0.98	0.01	1.51	-4.58	-1.81	-0.74	0.12	1.24	20759	1
lp[10,2]	0.99	0.01	1.29	-1.91	0.25	1.12	1.84	3.44	18014	1
lp[10,3]	6.86	0.01	0.84	5.09	6.32	6.92	7.48	8.27	16957	1
lp[11,1]	-0.30	0.01	1.49	-3.83	-1.12	-0.06	0.78	1.88	20422	1
lp[11,2]	-5.49	0.05	6.63	-20.67	-8.60	-4.26	-1.06	3.38	20815	1
lp[11,3]	7.34	0.01	0.95	5.27	6.75	7.39	8.02	8.96	19433	1
lp[12,1]	0.01	0.01	1.33	-3.23	-0.69	0.26	0.99	1.84	20495	1
lp[12,2]	-18.05	0.11	15.62	-53.65	-25.36	-14.91	-7.37	1.27	20954	1
lp[12,3]	5.78	0.01	1.49	2.36	4.93	5.95	6.83	8.17	26190	1
lp[13,1]	-0.09	0.01	1.14	-2.98	-0.64	0.18	0.76	1.26	21106	1
lp[13,2]	-24.77	0.14	20.36	-71.75	-33.93	-20.11	-10.70	-1.45	21697	1

lp[13,3]	2.86	0.01	2.49	-2.92	1.43	3.20	4.65	6.73	32638	1
lp[14,1]	0.31	0.01	1.02	-2.30	-0.14	0.58	1.06	1.42	21356	1
lp[14,2]	-16.44	0.09	13.77	-48.35	-22.63	-13.22	-6.82	-1.16	21825	1
lp[14,3]	1.68	0.02	3.08	-5.43	-0.13	2.09	3.92	6.49	40000	1
lp[15,1]	0.74	0.01	1.14	-2.17	0.21	1.03	1.59	2.04	20959	1
lp[15,2]	-0.85	0.02	2.27	-6.22	-1.94	-0.40	0.74	1.99	22609	1
lp[15,3]	2.74	0.01	2.88	-3.79	0.98	3.09	4.86	7.32	40000	1
lp[16,1]	1.42	0.01	1.14	-1.47	0.89	1.70	2.27	2.73	20506	1
lp[16,2]	-5.87	0.05	6.82	-21.61	-9.09	-4.36	-1.05	2.06	21837	1
lp[16,3]	3.58	0.01	2.45	-1.24	1.85	3.61	5.42	8.00	40000	1
lp[17,1]	2.01	0.01	1.09	-0.78	1.51	2.29	2.81	3.22	19955	1
lp[17,2]	-10.51	0.07	10.53	-34.84	-15.26	-8.15	-3.20	1.57	21760	1
lp[17,3]	3.22	0.01	2.83	-2.44	1.27	3.29	5.33	8.25	40000	1
lp[18,1]	2.19	0.01	1.28	-1.02	1.59	2.50	3.13	3.69	20253	1
lp[18,2]	2.28	0.01	1.43	-1.15	1.55	2.54	3.30	4.22	21439	1
lp[18,3]	4.20	0.01	2.69	-1.26	2.38	4.28	6.19	8.95	40000	1
lp[19,1]	2.83	0.01	1.26	-0.36	2.23	3.13	3.76	4.29	19894	1
lp[19,2]	-7.24	0.06	9.37	-29.02	-11.50	-5.01	-0.63	3.30	21921	1
lp[19,3]	4.70	0.01	2.36	0.39	3.03	4.50	6.38	9.38	32499	1
lp[20,1]	3.18	0.01	1.16	0.17	2.65	3.48	4.03	4.45	19290	1
lp[20,2]	-14.58	0.10	14.66	-48.47	-21.16	-11.21	-4.38	1.96	21802	1
lp[20,3]	3.31	0.02	2.98	-2.24	1.17	3.19	5.49	9.03	33541	1
lp[21,1]	3.48	0.01	1.08	0.66	3.02	3.78	4.26	4.61	18494	1
lp[21,2]	-15.13	0.10	15.24	-50.45	-21.93	-11.53	-4.46	1.67	21895	1
lp[21,3]	1.76	0.02	3.66	-5.27	-0.84	1.71	4.46	8.62	40000	1
lp[22,1]	3.36	0.01	0.95	0.81	3.00	3.65	4.05	4.31	17250	1
lp[22,2]	-21.58	0.14	20.38	-68.73	-30.67	-16.77	-7.31	0.64	21914	1
lp[22,3]	-1.10	0.02	4.66	-10.33	-4.31	-1.06	2.31	7.42	40000	1
lp[23,1]	3.70	0.01	0.94	1.21	3.33	3.98	4.37	4.62	16383	1
lp[23,2]	-14.39	0.10	14.80	-48.68	-20.99	-10.85	-4.00	1.71	21949	1
lp[23,3]	-2.36	0.03	5.24	-13.06	-5.85	-2.21	1.41	7.11	34082	1
lp[24,1]	3.00	0.01	0.92	0.53	2.64	3.28	3.65	3.90	15913	1
lp[24,2]	-29.27	0.18	26.42	-90.36	-41.00	-23.03	-10.75	-0.59	21927	1
lp[24,3]	-6.41	0.04	6.36	-20.01	-10.40	-6.05	-1.99	5.01	32196	1
lp[25,1]	3.54	0.01	0.97	0.91	3.15	3.83	4.23	4.50	15411	1
lp[25,2]	-10.31	0.08	11.41	-36.78	-15.39	-7.56	-2.33	2.13	21997	1
lp[25,3]	-6.72	0.04	6.83	-21.52	-11.04	-6.14	-1.84	5.16	30818	1
lp[26,1]	4.05	0.01	1.01	1.33	3.65	4.36	4.77	5.05	15376	1
lp[26,2]	1.56	0.02	2.86	-5.20	0.24	2.19	3.56	4.94	21604	1
lp[26,3]	-3.21	0.04	5.82	-16.81	-6.61	-2.22	0.99	5.95	23733	1
lp[27,1]	3.97	0.01	1.06	1.15	3.57	4.29	4.71	5.00	16152	1
lp[27,2]	5.30	0.01	1.14	2.40	4.77	5.54	6.10	6.81	17459	1
lp[27,3]	2.90	0.02	2.56	-3.19	1.56	3.37	4.67	6.59	22226	1
lp[28,1]	3.29	0.01	1.21	0.07	2.84	3.67	4.15	4.46	18173	1
lp[28,2]	7.02	0.01	1.08	4.23	6.53	7.27	7.77	8.37	16167	1
lp[28,3]	5.83	0.01	1.22	2.92	5.23	6.02	6.63	7.63	18954	1
lp[29,1]	2.74	0.01	1.45	-1.13	2.20	3.19	3.77	4.15	19928	1
lp[29,2]	8.49	0.01	1.23	5.49	7.87	8.70	9.35	10.24	16130	1
lp[29,3]	7.73	0.01	1.10	4.98	7.23	7.96	8.49	9.19	17246	1
lp[30,1]	2.77	0.01	1.64	-1.58	2.14	3.27	3.93	4.38	20367	1
lp[30,2]	9.24	0.01	1.44	5.85	8.47	9.47	10.26	11.33	19009	1
lp[30,3]	9.78	0.01	1.16	6.95	9.21	9.99	10.59	11.41	16457	1
lp[31,1]	0.88	0.01	2.20	-4.90	-0.04	1.52	2.48	3.13	22634	1
lp[31,2]	9.32	0.01	1.44	5.97	8.70	9.63	10.29	10.94	15488	1
lp[31,3]	9.15	0.01	1.43	5.93	8.37	9.33	10.13	11.32	18780	1

lp[32,1]	-0.12	0.02	2.65	-7.03	-1.28	0.60	1.83	2.72	23209	1
lp[32,2]	10.62	0.01	1.45	7.05	9.94	10.95	11.66	12.38	13596	1
lp[32,3]	10.00	0.01	1.34	6.84	9.28	10.19	10.93	12.02	17295	1
lp[33,1]	-0.88	0.02	3.06	-8.80	-2.28	-0.11	1.38	2.53	23395	1
lp[33,2]	12.05	0.01	1.63	8.05	11.27	12.42	13.23	14.06	12893	1
lp[33,3]	11.33	0.01	1.35	8.10	10.62	11.57	12.30	13.25	15404	1
lp[34,1]	-1.29	0.02	3.39	-10.02	-2.89	-0.47	1.21	2.61	23344	1
lp[34,2]	13.44	0.02	1.83	8.96	12.54	13.86	14.78	15.72	12848	1
lp[34,3]	13.04	0.01	1.46	9.51	12.27	13.33	14.11	15.02	14052	1
lp[35,1]	-2.22	0.03	3.85	-12.04	-4.10	-1.33	0.63	2.36	23467	1
lp[35,2]	14.78	0.02	2.12	9.61	13.72	15.26	16.34	17.41	12686	1
lp[35,3]	14.02	0.01	1.67	10.04	13.12	14.34	15.24	16.31	14144	1
lp[36,1]	-1.55	0.03	3.81	-11.28	-3.39	-0.66	1.27	2.95	23189	1
lp[36,2]	9.07	0.03	5.23	-3.77	7.58	10.59	12.27	13.62	22458	1
lp[36,3]	15.83	0.02	1.84	11.38	14.82	16.22	17.23	18.25	12943	1
lp[37,1]	-2.29	0.03	4.23	-13.02	-4.36	-1.34	0.85	2.85	23238	1
lp[37,2]	10.81	0.02	3.63	1.80	9.15	11.90	13.52	14.86	26063	1
lp[37,3]	16.08	0.02	1.83	11.66	15.09	16.46	17.46	18.51	13194	1
lp[38,1]	-2.70	0.03	4.57	-14.23	-4.97	-1.72	0.69	2.97	23177	1
lp[38,2]	12.21	0.02	3.53	3.42	10.59	13.24	14.84	16.21	26048	1
lp[38,3]	16.68	0.02	1.81	12.31	15.70	17.03	18.02	19.15	13456	1
lp[39,1]	-2.32	0.03	4.68	-14.09	-4.66	-1.32	1.14	3.52	22954	1
lp[39,2]	11.40	0.03	5.03	-1.57	9.27	13.04	15.06	16.69	26498	1
lp[39,3]	17.80	0.02	1.74	13.54	16.89	18.15	19.06	20.16	13156	1
lp[40,1]	-1.76	0.03	4.56	-13.27	-4.01	-0.75	1.63	3.84	22900	1
lp[40,2]	-1.13	0.10	14.97	-38.39	-7.75	3.67	9.98	13.25	23681	1
lp[40,3]	17.35	0.01	1.69	13.15	16.48	17.72	18.59	19.60	12790	1
lp[41,1]	-1.25	0.03	4.62	-12.93	-3.55	-0.23	2.19	4.46	22677	1
lp[41,2]	2.59	0.05	8.00	-13.47	-3.24	2.65	9.91	13.77	22022	1
lp[41,3]	18.33	0.02	1.68	14.15	17.47	18.70	19.56	20.54	12512	1
lp[42,1]	-0.73	0.03	4.69	-12.55	-3.06	0.29	2.75	5.08	22470	1
lp[42,2]	2.52	0.05	8.04	-13.45	-3.19	2.17	9.83	14.36	21438	1
lp[42,3]	19.30	0.02	1.68	15.10	18.44	19.66	20.53	21.53	12321	1
lp[43,1]	-0.98	0.03	4.99	-13.50	-3.49	0.08	2.72	5.30	22436	1
lp[43,2]	5.81	0.04	6.05	-6.60	1.96	5.44	11.01	15.40	20674	1
lp[43,3]	19.97	0.02	1.69	15.77	19.12	20.32	21.20	22.22	12260	1
lp[44,1]	-2.18	0.04	5.51	-15.91	-4.98	-1.04	1.91	4.89	22617	1
lp[44,2]	7.03	0.04	5.77	-5.15	3.45	6.89	11.89	16.02	21179	1
lp[44,3]	19.69	0.02	1.75	15.45	18.77	20.02	20.95	22.07	12903	1
lp[45,1]	-1.72	0.04	5.60	-15.67	-4.58	-0.58	2.42	5.48	22455	1
lp[45,2]	5.62	0.05	7.29	-9.16	0.74	5.31	12.05	16.69	21462	1
lp[45,3]	20.69	0.02	1.71	16.49	19.79	21.02	21.94	23.06	12735	1
lp[46,1]	-1.07	0.04	5.60	-15.00	-3.94	0.09	3.08	6.13	21846	1
lp[46,2]	1.47	0.07	10.60	-20.22	-5.92	1.57	10.86	16.70	21438	1
lp[46,3]	21.44	0.02	1.70	17.26	20.55	21.76	22.68	23.77	12379	1
lp[47,1]	-0.42	0.04	5.51	-14.17	-3.22	0.74	3.67	6.61	21729	1
lp[47,2]	-4.80	0.10	14.14	-33.42	-14.33	-4.76	7.30	15.69	20813	1
lp[47,3]	21.45	0.02	1.70	17.28	20.55	21.78	22.69	23.78	12206	1
lp[48,1]	-0.43	0.04	5.76	-14.76	-3.38	0.76	3.83	6.99	21658	1
lp[48,2]	4.46	0.05	6.81	-9.76	0.46	4.45	8.49	16.72	18904	1
lp[48,3]	22.29	0.02	1.71	18.09	21.40	22.62	23.54	24.64	12087	1
lp[49,1]	0.17	0.04	5.79	-14.25	-2.80	1.37	4.45	7.65	21493	1
lp[49,2]	1.45	0.07	9.08	-16.96	-4.31	1.20	7.83	17.18	19218	1
lp[49,3]	23.16	0.02	1.72	18.93	22.26	23.49	24.42	25.55	12014	1
lp[50,1]	-0.29	0.04	6.14	-15.55	-3.46	0.96	4.25	7.74	21529	1

lp[50,2]	5.70	0.05	6.83	-8.82	1.75	5.89	9.60	18.08	18317	1
lp[50,3]	23.65	0.02	1.74	19.40	22.73	23.98	24.93	26.08	12011	1
lp[51,1]	0.37	0.04	6.07	-14.69	-2.74	1.61	4.85	8.25	21425	1
lp[51,2]	-3.57	0.09	12.92	-29.92	-11.67	-3.43	5.79	17.28	19465	1
lp[51,3]	23.71	0.02	1.75	19.46	22.78	24.04	24.99	26.15	12019	1
lp[52,1]	0.83	0.04	6.17	-14.48	-2.34	2.09	5.39	8.89	21295	1
lp[52,2]	2.39	0.06	8.22	-14.38	-2.49	2.28	7.18	18.03	17783	1
lp[52,3]	24.70	0.02	1.77	20.40	23.75	25.03	26.00	27.19	11963	1
lp[53,1]	1.41	0.04	6.22	-14.02	-1.77	2.67	6.01	9.56	21162	1
lp[53,2]	1.50	0.07	9.05	-16.86	-3.98	1.36	6.99	18.59	18147	1
lp[53,3]	25.60	0.02	1.82	21.21	24.63	25.94	26.94	28.16	12043	1
lp[54,1]	1.70	0.04	6.39	-14.08	-1.59	2.99	6.42	10.13	21076	1
lp[54,2]	4.43	0.06	7.73	-11.93	-0.05	4.58	8.81	19.52	17426	1
lp[54,3]	26.60	0.02	1.86	22.11	25.60	26.94	27.96	29.22	12100	1
lp[55,1]	2.38	0.04	6.34	-13.27	-0.87	3.67	7.07	10.71	20972	1
lp[55,2]	-2.59	0.09	12.22	-27.71	-10.01	-2.37	5.32	19.10	18498	1
lp[55,3]	26.86	0.02	1.91	22.28	25.82	27.20	28.26	29.58	12362	1
lp[56,1]	2.99	0.04	6.39	-12.75	-0.29	4.29	7.71	11.41	20858	1
lp[56,2]	1.68	0.07	9.05	-16.98	-3.64	1.82	7.01	19.57	17140	1
lp[56,3]	27.72	0.02	1.98	22.96	26.63	28.07	29.16	30.55	12659	1
lp[57,1]	3.44	0.05	6.50	-12.57	0.08	4.75	8.24	12.07	20770	1
lp[57,2]	4.22	0.06	7.99	-12.76	-0.35	4.54	8.86	20.37	16874	1
lp[57,3]	28.71	0.02	2.04	23.82	27.59	29.07	30.21	31.65	12871	1
lp[58,1]	2.23	0.05	6.98	-14.94	-1.38	3.61	7.39	11.56	20959	1
lp[58,2]	7.27	0.05	7.04	-8.58	3.39	7.99	11.61	20.78	17147	1
lp[58,3]	28.41	0.02	1.94	23.76	27.37	28.76	29.83	31.14	11914	1
lp[59,1]	2.91	0.05	6.98	-14.25	-0.70	4.29	8.06	12.22	20858	1
lp[59,2]	1.72	0.08	10.08	-19.40	-4.19	2.12	7.97	20.84	17796	1
lp[59,3]	29.02	0.02	1.99	24.23	27.94	29.37	30.48	31.84	12300	1
lp[60,1]	1.93	0.05	7.42	-16.33	-1.93	3.37	7.41	11.91	20994	1
lp[60,2]	7.05	0.06	7.51	-9.87	2.90	7.81	11.71	21.42	17193	1
lp[60,3]	28.97	0.02	1.95	24.28	27.92	29.33	30.40	31.71	11780	1
lp[61,1]	1.45	0.05	7.77	-17.64	-2.63	2.94	7.18	11.98	21041	1
lp[61,2]	8.54	0.06	7.37	-8.27	4.47	9.38	13.22	22.27	17523	1
lp[61,3]	29.44	0.02	1.95	24.73	28.38	29.79	30.87	32.19	11818	1
alphaReordered[1]	-0.60	0.00	0.04	-0.68	-0.63	-0.60	-0.57	-0.52	17327	1
alphaReordered[2]	-0.29	0.00	0.04	-0.38	-0.31	-0.29	-0.27	-0.22	20210	1
alphaReordered[3]	-0.45	0.00	0.03	-0.51	-0.47	-0.45	-0.43	-0.39	40000	1
path[1]	1.00	0.00	0.00	1.00	1.00	1.00	1.00	1.00	40000	NaN
path[2]	1.00	0.00	0.00	1.00	1.00	1.00	1.00	1.00	40000	NaN
path[3]	1.00	0.00	0.00	1.00	1.00	1.00	1.00	1.00	40000	NaN
path[4]	1.00	0.00	0.00	1.00	1.00	1.00	1.00	1.00	40000	NaN
path[5]	1.00	0.00	0.00	1.00	1.00	1.00	1.00	1.00	40000	NaN
path[6]	1.00	0.00	0.00	1.00	1.00	1.00	1.00	1.00	40000	NaN
path[7]	1.00	0.00	0.00	1.00	1.00	1.00	1.00	1.00	40000	NaN
path[8]	1.00	0.00	0.00	1.00	1.00	1.00	1.00	1.00	40000	NaN
path[9]	1.00	0.00	0.00	1.00	1.00	1.00	1.00	1.00	40000	NaN
path[10]	1.00	0.00	0.00	1.00	1.00	1.00	1.00	1.00	40000	NaN
path[11]	1.00	0.00	0.00	1.00	1.00	1.00	1.00	1.00	40000	NaN
path[12]	1.00	0.00	0.00	1.00	1.00	1.00	1.00	1.00	40000	NaN
path[13]	1.00	0.00	0.00	1.00	1.00	1.00	1.00	1.00	40000	NaN
path[14]	1.00	0.00	0.00	1.00	1.00	1.00	1.00	1.00	40000	NaN
path[15]	1.00	0.00	0.00	1.00	1.00	1.00	1.00	1.00	40000	NaN
path[16]	1.00	0.00	0.00	1.00	1.00	1.00	1.00	1.00	40000	NaN
path[17]	1.00	0.00	0.00	1.00	1.00	1.00	1.00	1.00	40000	NaN

path[18]	1.00	0.00	0.00	1.00	1.00	1.00	1.00	1.00	40000	NaN
path[19]	1.00	0.00	0.00	1.00	1.00	1.00	1.00	1.00	40000	NaN
path[20]	1.00	0.00	0.00	1.00	1.00	1.00	1.00	1.00	40000	NaN
path[21]	1.00	0.00	0.00	1.00	1.00	1.00	1.00	1.00	40000	1
path[22]	1.00	0.00	0.01	1.00	1.00	1.00	1.00	1.00	40000	1
path[23]	1.00	0.00	0.01	1.00	1.00	1.00	1.00	1.00	40000	1
path[24]	1.00	0.00	0.01	1.00	1.00	1.00	1.00	1.00	40000	1
path[25]	1.00	0.00	0.02	1.00	1.00	1.00	1.00	1.00	40000	1
path[26]	1.08	0.00	0.28	1.00	1.00	1.00	1.00	2.00	15136	1
path[27]	1.98	0.00	0.17	1.00	2.00	2.00	2.00	2.00	34938	1
path[28]	2.00	0.00	0.08	2.00	2.00	2.00	2.00	2.00	27913	1
path[29]	2.00	0.00	0.08	2.00	2.00	2.00	2.00	2.00	27767	1
path[30]	2.00	0.00	0.08	2.00	2.00	2.00	2.00	2.00	24536	1
path[31]	2.01	0.00	0.10	2.00	2.00	2.00	2.00	2.00	20202	1
path[32]	2.01	0.00	0.10	2.00	2.00	2.00	2.00	2.00	19681	1
path[33]	2.01	0.00	0.10	2.00	2.00	2.00	2.00	2.00	19569	1
path[34]	2.01	0.00	0.11	2.00	2.00	2.00	2.00	2.00	19841	1
path[35]	2.01	0.00	0.11	2.00	2.00	2.00	2.00	2.00	19841	1
path[36]	2.89	0.00	0.32	2.00	3.00	3.00	3.00	3.00	21713	1
path[37]	2.89	0.00	0.32	2.00	3.00	3.00	3.00	3.00	21713	1
path[38]	2.89	0.00	0.32	2.00	3.00	3.00	3.00	3.00	21713	1
path[39]	2.97	0.00	0.17	2.00	3.00	3.00	3.00	3.00	15260	1
path[40]	2.99	0.00	0.11	3.00	3.00	3.00	3.00	3.00	12612	1
path[41]	2.99	0.00	0.10	3.00	3.00	3.00	3.00	3.00	12880	1
path[42]	2.99	0.00	0.10	3.00	3.00	3.00	3.00	3.00	12880	1
path[43]	2.99	0.00	0.10	3.00	3.00	3.00	3.00	3.00	12880	1
path[44]	2.99	0.00	0.10	3.00	3.00	3.00	3.00	3.00	12880	1
path[45]	2.99	0.00	0.08	3.00	3.00	3.00	3.00	3.00	11375	1
path[46]	2.99	0.00	0.08	3.00	3.00	3.00	3.00	3.00	11125	1
path[47]	2.99	0.00	0.08	3.00	3.00	3.00	3.00	3.00	11125	1
path[48]	2.99	0.00	0.08	3.00	3.00	3.00	3.00	3.00	11125	1
path[49]	2.99	0.00	0.08	3.00	3.00	3.00	3.00	3.00	11125	1
path[50]	2.99	0.00	0.08	3.00	3.00	3.00	3.00	3.00	11125	1
path[51]	2.99	0.00	0.08	3.00	3.00	3.00	3.00	3.00	11125	1
path[52]	2.99	0.00	0.08	3.00	3.00	3.00	3.00	3.00	11125	1
path[53]	2.99	0.00	0.08	3.00	3.00	3.00	3.00	3.00	11125	1
path[54]	2.99	0.00	0.08	3.00	3.00	3.00	3.00	3.00	11125	1
path[55]	2.99	0.00	0.08	3.00	3.00	3.00	3.00	3.00	11163	1
path[56]	2.99	0.00	0.08	3.00	3.00	3.00	3.00	3.00	11163	1
path[57]	2.99	0.00	0.08	3.00	3.00	3.00	3.00	3.00	11163	1
path[58]	2.99	0.00	0.08	3.00	3.00	3.00	3.00	3.00	11134	1
path[59]	2.99	0.00	0.08	3.00	3.00	3.00	3.00	3.00	11134	1
path[60]	2.99	0.00	0.08	3.00	3.00	3.00	3.00	3.00	11134	1
path[61]	2.99	0.00	0.08	3.00	3.00	3.00	3.00	3.00	11571	1
changePoint1	-5.05	0.00	0.36	-6.00	-5.00	-5.00	-5.00	-4.00	19264	1
changePoint2	4.46	0.02	2.45	4.00	4.00	4.00	4.00	8.00	12153	1
meanSpeed[1]	0.60	0.00	0.04	0.52	0.57	0.60	0.63	0.68	17327	1
meanSpeed[2]	0.29	0.00	0.04	0.22	0.27	0.29	0.31	0.38	20210	1
meanSpeed[3]	0.45	0.00	0.03	0.39	0.43	0.45	0.47	0.51	40000	1
lp__	18.54	0.02	2.05	13.43	17.47	18.95	20.03	21.33	10476	1

Samples were drawn using NUTS(diag_e) at Sat Mar 10 12:48:46 2018.
For each parameter, n_eff is a crude measure of effective sample size,
and Rhat is the potential scale reduction factor on split chains (at
convergence, Rhat=1).

E

Supplementary material for Chapter 5

Supplementary material for Chapter 4: Movement-related reproductive tactics alter with age in male African savannah elephants (*Loxodonta africana*)

E.1 Supplementary figures

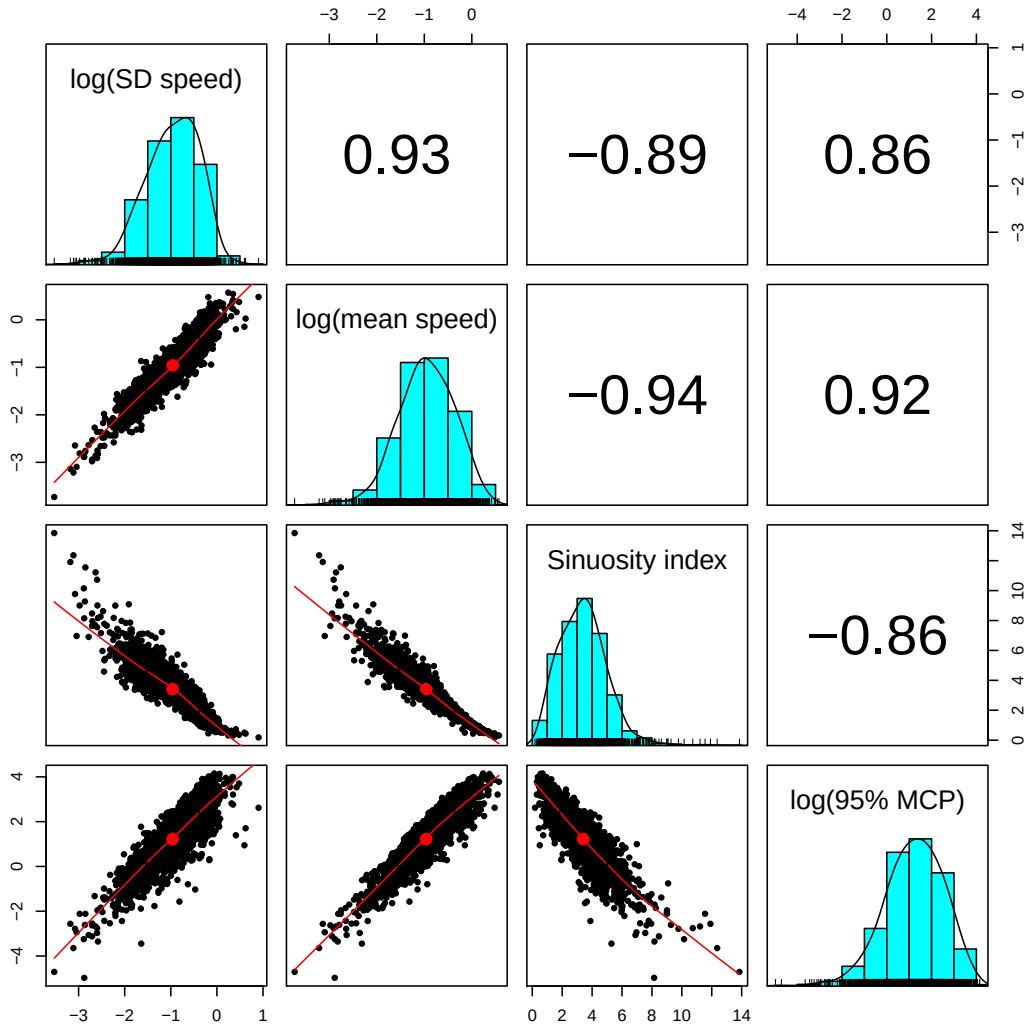


Figure E.1: Relationship between log-transformed daily standard deviation of speed, log-transformed daily mean speed, sinuosity index, log-transformed 95% minimum convex polygon (MCP) and proportion of exploratory behaviour for the all GPS tracked days used in the linear mixed-effects model analysis.

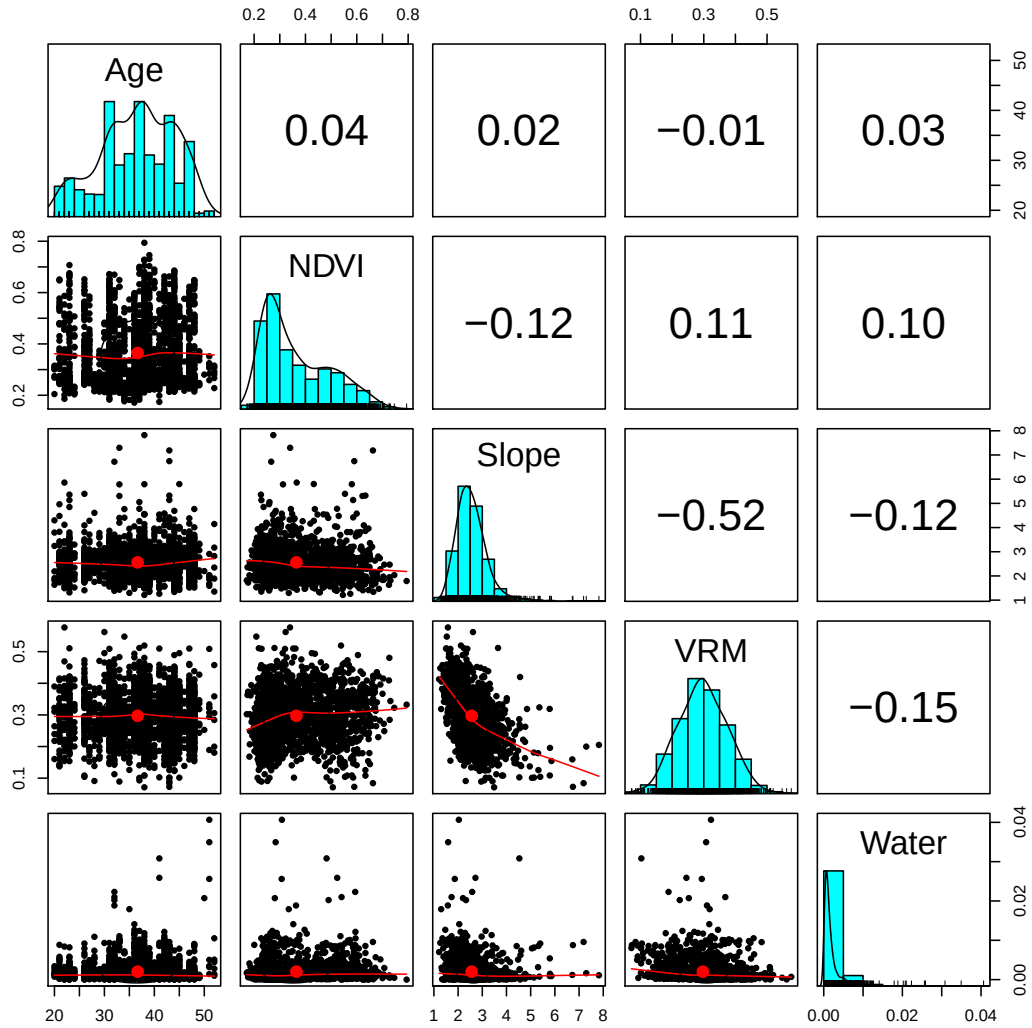


Figure E.2: Relationship between all of the continuous covariates for the all GPS tracked days used in the linear mixed-effects model analysis. Covariates include the age at observation (years), daily mean NDVI, daily mean slope (degrees), daily mean vector ruggedness measure (VRM) and daily mean distance to water (km).

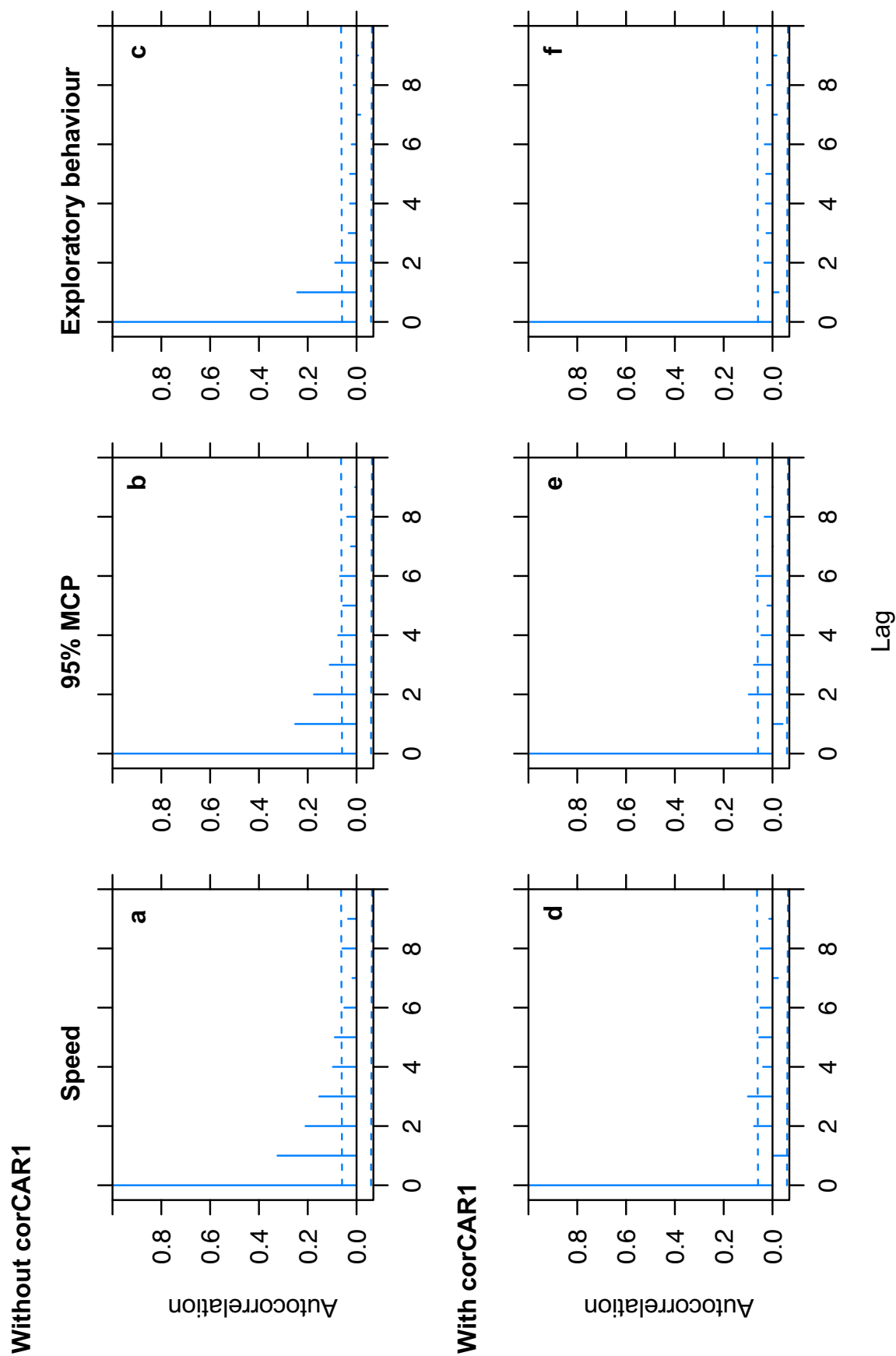


Figure E.3: Autocorrelation of residuals (a-c) without and (d-f) with a corCAR1 autocorrelation structure. Plots show the linear mixed-effects model of (a, d) log-transformed daily mean speed and (b, e) log-transformed 95% MCP, and the binominal generalised linear mixed-effects model of (c, f) proportion exploratory behaviour per day. Note in autocorrelation in plots a-c, which is resolved by adding the corCAR1 autocorrelation structure (d-f).

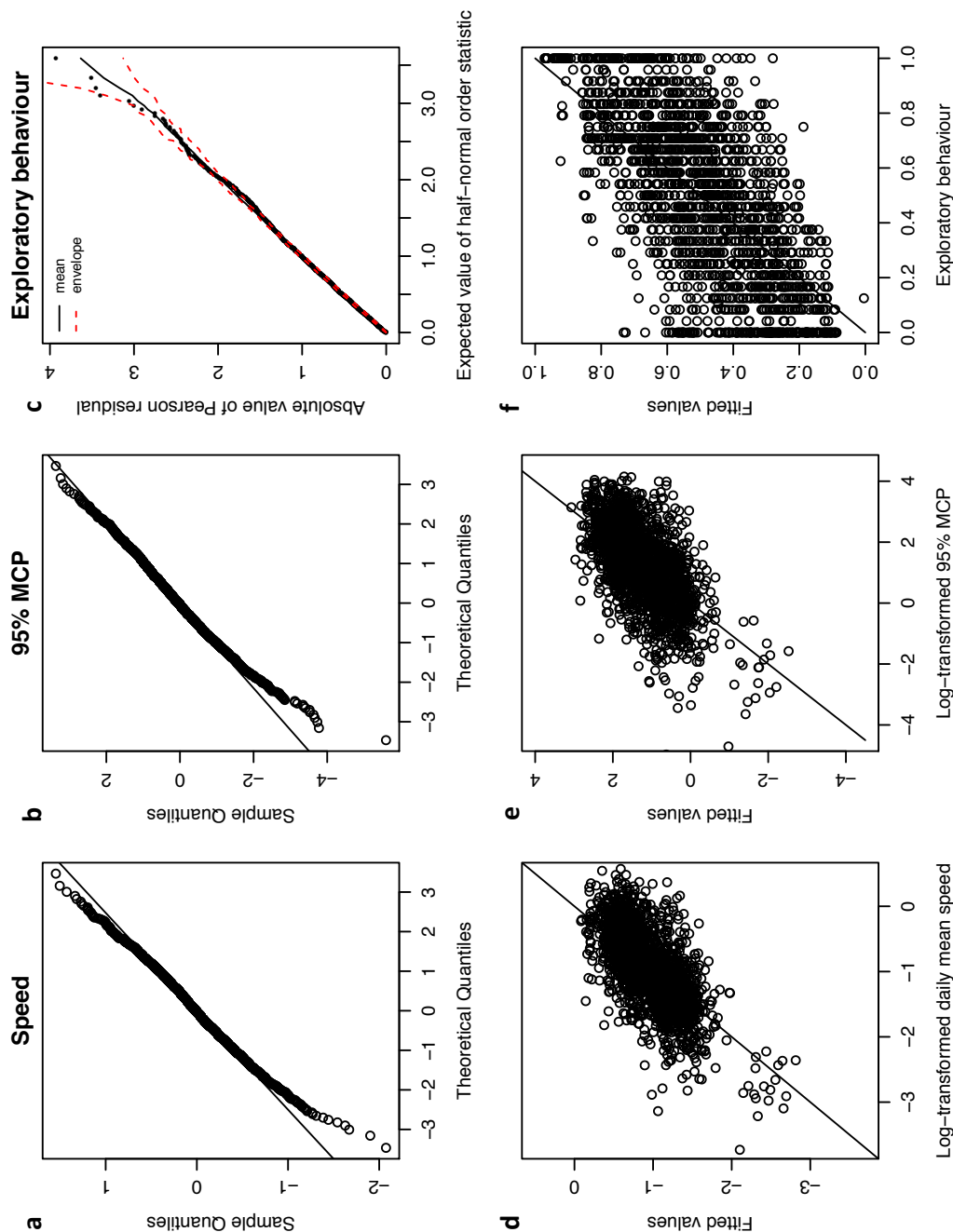


Figure E.4: Model fit of the linear mixed-effects models of (a,d) log-transformed daily mean speed and (b, e) log-transformed 95% MCP and (c, f) binomial generalised linear mixed-effects model of the proportion of exploratory behaviour. (a, b) Q-Q (quantile-quantile) plot of the linear mixed-effects models, which shows that the residuals of the log-transformed variables followed a normal distribution. (c) Half-normal plot of Pearson residuals, which produces a half normal plot of the residuals with simulated envelopes and shows that the proportion of exploratory variables fits a binomial distribution (Collett, 2002). (d-f) Fitted values plotted against the raw data to show the model fit.

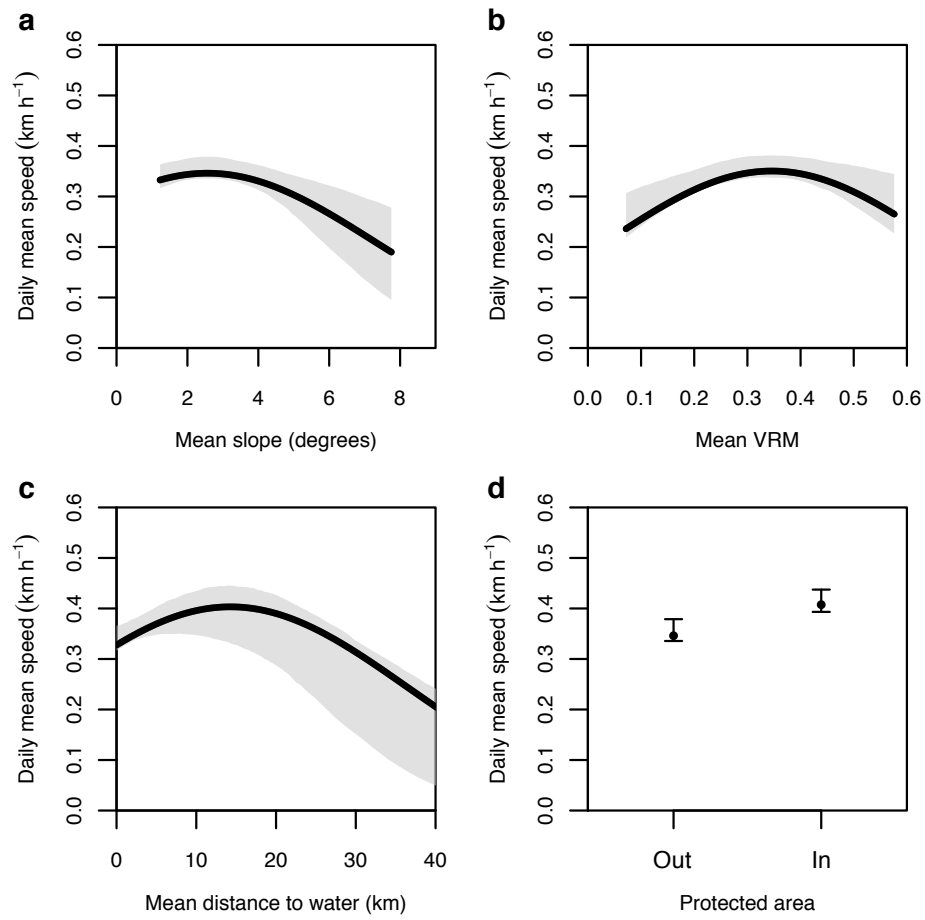


Figure E.5: Linear mixed-effects model results of the daily mean speed for the fixed-effects of daily mean slope, mean vector ruggedness measure (VRM), mean distance to water and protected area. Grey shaded area and error bar correspond to the 95% confidence interval from a non-parametric bootstrap of 1,000 resampled data points.

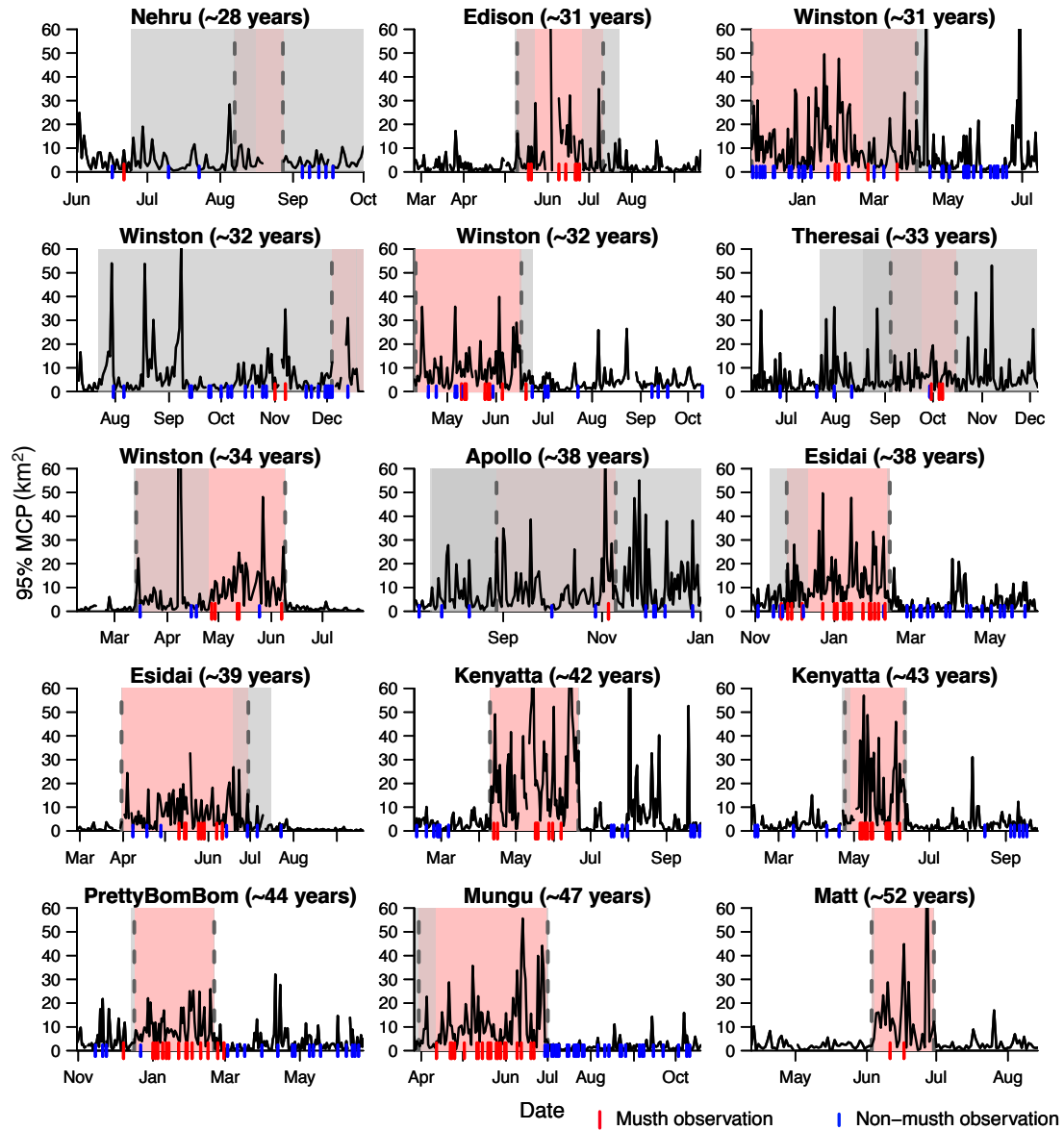


Figure E.6: Three-state hidden Markov model results of the model for log-transformed 95% MCP aiming to detect musth periods in bull elephants. Plots show the untransformed 95% MCP (km²) with the detected musth periods shaded in red. Grey shaded area indicates the corresponding credible interval ($\pm 95\%$). Visual observations of the bull in musth or non-musth are denoted by the red and blue lines at the base of the plot. Plots are ordered by age from youngest to oldest.

E.2 Supplementary tables

Table E.1: Total GPS tracking non-musth and musth days by month. Note the low number of musth observations between July and October.

Month	Total GPS tracking days	
	Non-musth	Musth
January	83	73
February	131	44
March	128	19
April	87	51
May	147	119
June	102	91
July	140	3
August	83	3
September	108	7
October	129	7
November	148	32
December	117	33
Total	1,403	482

Table E.2: Model priors for three state-hidden Markov models

Model	β (State 1, State 2, State 3)	σ (State 1, State 2, State 3)
Log-transformed daily mean speed	-1.0, 0.0, -1.0	0.75, 1.5, 0.75
Log-transformed 95% MCP	1.0, 2.0, 1.0	0.75, 1.5, 0.75

Table E.3: Results of the three-state hidden Markov model of log-transformed 95% MCP aiming to detect musth in male elephants. The number of observations corresponds to the number of visual observations correctly or incorrectly assigned by the three-state HMM.

Name	Age (years)	Change point SD	Non-musth			Musth		Total % correct
			Correct	Incorrect	% Correct	Correct	% Correct	
Nehru	28	21.0	9	0	100	0	0	90
Edison	31	15.1	0	0		7	100	100
Theresai	33	37.5	4	1	80	3	100	88
Winston	31	20.0	16	18	47	4	100	53
	32	38.1	20	2	91	0	0	83
	32	4.3	8	6	57	7	88	68
	34	8.6	0	4	0	5	100	56
Apollo	38	64.4	8	2	80	1	100	82
Esidai	38	8.3	20	2	91	16	94	92
	39	7.3	2	5	29	8	100	67
Kenyatta	42	0.0	15	0	100	8	100	100
	43	3.5	11	0	100	13	100	100
PrettyBomBom	44	1.1	18	1	95	12	80	88
Mungu	47	4.3	28	1	97	20	100	98
Matt	52	1.4	0	0		2	100	100
Total count/ mean value		17.2*	159	42	82*	106	85*	89*
Under 35		22.8*	57	31	76*	26	68*	86*
Over 35		13.5*	102	11	86*	80	96*	91*