Fine-scale changes in flight effort revealed by animal-borne loggers

Baptiste Garde

Submitted to Swansea University in fulfilment of the requirements for the Degree of Doctor of Philosophy in Biological Sciences.

Department of Biosciences

Swansea University

2021

Abstract

The movements of the air are central to the life of flying birds, because they can determine whether the costs of flight are closer to resting or sprinting, and whether birds are able to reach their destination. Yet for species relying mainly on flapping flight, studies about the effects of weather on flight effort have mainly focussed on wind, with other atmospheric factors receiving less attention. In addition, with the development of new technologies to measure flight effort, it has become clear that some methods need standardisation and further verification. The goal of this PhD is to provide insight into how atmospheric conditions affect flight costs more broadly and study the extent to which birds prioritise energy expenditure over other currencies, such as time and risk. I used high-frequency data-loggers to explore the combined effects of wind and thermals, as well as air density, on flight effort over fine scales, as well as how birds adjust their behaviour to these factors. Results showed that pigeons (*Columba livia*), which are not limited by energy expenditure, prioritise speed over energy savings, and use a very costly flight style which could serve as a predator-avoidance strategy. I also found that wind support was a strong predictor of whether chick-rearing tropicbirds (*Phaethon rubricauda*) use thermal soaring to save energy during foraging trips, suggesting that birds were weighing up the trade-off between energy and time, and chose to save energy only when this would not cost them too much time. Comparison of air density between seasons also revealed that the flapping flight of tropicbirds was more costly during summer, when air density was lower. This finding shows that the effect of seasonal changes in air density on flight costs is significant, outweighing the influence of both wind and thermal availability. It also sheds new light on how flight costs (particularly those in tropical birds) might be affected by global change. Finally, the analysis of the accelerometer data showed that the type of tag used, as well as differences in the longitudinal position and attachment method, affected the amplitude of the signal, which has implications for the robustness of acceleration-based proxies for flight effort. Nonetheless, the adoption of standardized calibrations should facilitate the comparison of these metrics between study sites and through time, improving the prospect that they can be used to study the effect of a changing climate on flight costs and avian ecology.

Declarations and Statements

Declaration

This work has not previously been accepted in substance for any degree and is not being concurrently submitted in candidature for any degree.

Signed ..... [redacted]... (candidate)

Date: 17/09/2021

Statement 1

This thesis is the result of my own investigations, except where otherwise stated. Where correction services have been used, the extent and nature of the correction is clearly marked in a footnote(s).

Other sources are acknowledged by footnotes giving explicit references. A bibliography is appended.

Signed ......[redacted].. (candidate)

Date: 17/09/2021

Statement 2

I hereby give consent for my thesis, if accepted, to be available for photocopying and for inter-library loan, and for the title and summary to be made available to outside organisations.

Signed ......[redacted]... (candidate)

Date: 17/09/2021

Table of Contents

CONTENTS

Ethics Statements and Approvals

Personal

Ethical permission for the handling and use of biologgers on domestic homing pigeons (*Columba livia*) in Rome, Italy (preliminary study) was granted by Swansea University AWERB, permit SU-Ethics-Student-200618/460 (reference number: STU_BIOL_71255_090118115314_1).

The permits for tagging and handling of domestic homing pigeons (*Columba livia*) used in Chapter 1 and 5 were granted by Swansea University AWERB, issue number IP-1718-23 and the Regierungspräsidium Freiburg, Baden-Württemberg, Germany, permit number G-17/92.

Ethical permission for the capture and use of biologgers on wild red-tailed tropicbirds (*Phaethon rubricauda*) (Chapter 2, 3, 4 and 5) was granted by Swansea University AWERB, permit 040118/39.

Ethical permissions for the capture and use of biologgers black-legged kittiwakes (*Rissa tridactyla*) (Chapter 4 and 5) was granted by Swansea University AWERB, permit 110619/1590 (IP-1819-18).

Deployment of tags on 12 people for Chapter 4 was approved under code: PG201416A. All human participants were healthy adults and gave informed consent.

Contributors

Pigeons wind tunnel (*Columba livia*)

The tagging of pigeons and the procedure of flight in a wind tunnel (Chapter 4 and 5) was approved by the government of Upper Bavaria, "Sachgebiet 54 – Verbraucherschutz, Veterinärwesen, 80538 München" with the record number: Gz.: 55.2-1-54-2532-86-2015.

Dunlin wind tunnel (*Calidris alpina*)

Ethical permission for the tagging and wind tunnel flight of a dunlin (Chapter 5) was obtained from Swansea University AWERB, permit number 030718/66.

Common guillemot (*Uria aalge*) and Razorbills (*Alca torda*)

Ethical permission for the capture and use of biologgers on wild common guillemots and razorbills (Chapter 5) was granted by Swansea University AWERB, permit SU-Ethics-Staff-050619/150 (reference number: STAFF_BIOL_25956_280519125243_1).

Brünnich's guillemot (*Uria lomvia*)

The capture and tagging of Brünnich's guillemots (Chapter 5) was approved under Environment Canada Animal Care permits 1000-AG01a, 11-AG02, EC-PN-12-0, Migratory Bird Research Permits NUN-MBS-09-01, NUN-SCI-11-07 and NUN-SCI-12-01 and Nunavut and Nunavik Wildlife Research permits (WL-2010-038; WL-2011-019, WL-2012-04-06).

Barn owl (*Tyto alba*)

Barn owls (Chapter 5) were captured and tagged under legal authorisations VD 2844, VD 3213 and VD 3571.

Great Frigatebird (*Frigata magnificens*)

Field procedures and manipulations concerning Great Frigatebirds (Chapter 5) were approved by the Préfet des Terres Australes et Antarctiques Françaises and Comité National de la Protection de la Nature.

Northern fulmar (*Fulmarus glacialis*)

Tagging of Northern fulmars (Chapter 5) was conducted under licences from the British Trust for Ornithology (BTO) and Irish National Parks and Wildlife Service (NPWS).

Imperial cormorant (*Phalancrocorax atriceps*)

The tagging of Imperial cormorant (Chapter 5) was approved by the Consejo Nacional de Investigaciones Científicas y Técnicas de la República Argentina and the Organismo Provincial de Turismo.

Wandering albatrosses

Tagging of albatrosses (Chapter 5) was approved by the University of Cape Town's Science Faculty Animal Ethics Committee (2017/V10REV/PRyan).

Streaked shearwater (*Calonectris leucomelas*)

Tagging of streaked shearwaters (Chapter 5) was approved by the Animal Experimental Committee of the University of Tokyo and was carried out with permits from the Ministry of the Environment and Agency for Cultural Affairs.

Chapter 1 – The role of wingbeat frequency and amplitude in flight power

Chapter 2 – Fine-scale changes in speed and altitude suggest protean movements in homing pigeon flights

Chapter 3 – Cheap versus quick flight: the wind vector determines the profitability of thermal soaring of a chick-rearing bird

Chapter 4 – High costs in low flying birds: Changing air density matters at sea level

Chapter 5 – Ecological inference using data from accelerometers needs careful protocols

Supplementary Information

Acknowledgements

Writing this thesis was without question the hardest thing I happened to do in my life, and I don't think I could have achieved any of that without the support and encouragements of many people. Overall, I feel extremely privileged to have been able to do my PhD in such an environment of genuine kindness, where helping others is such a natural thing.

My first thanks obviously go to Emily, without whom none of this would have been possible. I feel extremely lucky to have been her student, and I hope I have learned from her expertise. Her enthusiasm and positivity towards my work was really something that kept me going, as it is not always easy to see the bright side when things don't go as expected! This PhD had all the experiences I could have hoped for: field work, collaborations with the Max Planck, as well as with other people, and I know that Emily really moved mountains to ensure I had the best possible experience, while pursuing our goals throughout this PhD, so genuine thanks to her.

I also address some particular thanks to Rory, who also contributed to a lot in this thesis. I see his experience and wisdom as a key to many doors, and his suggestions really helped bring forward my work when I found myself confronted to inexplicable results so many times. I also need to thank him for his consistent positivity and enthusiasm, his sense of humour, and especially for enquiring of my wellbeing with a "Ça gazouille ?" in the morning, which can only turn a day into a good day.

Special thanks to KiKi without whom I would never have been able to complete the first chapter of this thesis. But more than anything, my thanks to him for his daily good mood and optimism that meant a great deal to go through the last difficult months! Special thanks to Manos, James and Rich as well, who did so much for me that I will not take the risk to offend them by omitting some… Just to mention a few, thanks to Manos for figuring out the effects of air density and simply for being such a good friend (and housemate!), especially during our time in Germany. Thanks to James for the tropicbird photos (credits to him for the front-page picture) and for helping me with the thesis.

I would also like to thank Luca and Steve for their help throughout the PhD, in particular with the stats and the interpretation of the data. It's a shame we didn't get to work more together, but maybe in the future!

Thanks to Mark, for always being so prompt to help when tags start having their own free will and to turn against us. Thanks to Will for the very technical and interesting chats about R and headwinds… And in general, thanks to all the people from the Vislab who contributed to such a nice work environment.

Before I wrap up, I would like to thank my family for believing in me, because we never say it enough, but this matters a lot. Thanks also to Giacomo and Giulia who made Rome feel like home, to all the people on Middleton, to Kami’s team in Konstanz for such a good time there, as well as all the other people who helped me during those four years.

Finally, I would like to address some special words to my little Laure, who supported me relentlessly during the ups and downs. Thanks for always being there for me, no matter the distance and the situation. I know I wouldn’t have gone far without her.

Funding

This PhD was funded by the European Research Council under the European Union’s Horizon 2020 research and innovation program Grant 715874 (to E. L. C. Shepard) and a Max Planck Sabbatical Fellowship to E. L. C. Shepard.

Disclaimer

Chapter 2 has been published as “Garde, B., Wilson, R. P., Lempidakis, E., Börger, L., Portugal, S. J., Hedenström, A., Dell'Omo, G., Quetting, M., Wikelski, M. & Shepard, E. L. C. (2021). Fine-scale changes in speed and altitude suggest protean movements in homing pigeon flights. *Royal Society open science 8: 210130. https://doi.org/10.1098/rsos.210130*”.

Chapter 5 is currently in review at Methods in Ecology and Evolution as “Garde B., Wilson R. P., Fell A., Cole N., Tatayah V., Holton M. D., Rose K. A. R., Metcalfe R. S., Robotka H., Wikelski M., Tremblay F., Whelan S., Elliott K. H., Shepard E. L. C. Ecological inference using data from accelerometers needs careful protocols”.

Contributing authors

Chapter 1 – The role of wingbeat frequency and amplitude in flight power

Contributing authors: B Garde, K Krishnan, A Fell, A Roulin, A Prudor, E Cole, E Lempidakis, F Quintana, F Tremblay, H Weimerskirch, K Yoda, K Schalcher, K H Elliott, N Cole, P Ryan, S Whelan, S de Grissac, S Schoombie, V Tatayah, E Shepard

BG and KK analysed the data and wrote the first draft. The intention is to submit this work for publication with BG and KK as joint lead authors. Wind tunnel data was collected by ELCS, red-tailed tropicbird data by AF, VT, NC, black-legged kittiwake data by BG, FT, SW and KHE, great frigatebird data by AP, HW, northern fulmar data by SG, common guillemot data by EC, Brünnich’s guillemot data by SW and KHE, imperial cormorant data by FQ, albatross data by PR and SS, barn owl data by KS and AR, streaked shearwater data by KY and pigeon homing data by EL and BG. Data analysis was carried out by BG and KK. The whole study was supervised by ELCS.

Chapter 2 – Fine-scale changes in speed and altitude suggest protean movements in homing pigeon flights

Contributing authors: B Garde, R P Wilson, E Lempidakis, L Börger, S J Portugal, A Hedenström, G Dell'Omo, M Quetting, M Wikelski, E L C Shepard.

The experiment was conceived by BG, ELCS, MW, MQ, and GD, and conducted by BG, EL, and MQ. Statistical analysis was carried out by BG and overseen by LB. Interpretation of the results was undertaken by BG, ELCS, RPW, SJP and AH, and BG, wrote the first draft with contributions from all authors.

Chapter 3 – Cheap versus quick flight: the wind vector determines the profitability of thermal soaring of a chick-rearing bird

Contributing authors: B Garde, A Fell, V Tatayah, N Cole, E L C Shepard

The first draft of this chapter was written by BG, with input from ELCS. Red-tailed tropicbird data were collected by AF, NC and VT and analysed by BG.

Chapter 4 – High costs in low flying birds: Changing air density matters at sea level

Contributing authors: B Garde, A Fell, E Lempidakis, S de Grissac, R Gunner, V Tatayah, N Cole, E L C Shepard

BG wrote the first draft and analysed the data. Red-tailed tropicbird data were collected by AF, NC and VT, and weather data was provided by SG. EL provided valuable insight about air density and produced Figure 5. RG produced Figure 3 and assisted with data processing (notably the identification of soaring).

Chapter 5 – Ecological inference using data from accelerometers needs careful protocols

Contributing authors: B Garde, R P Wilson, A Fell, N Cole, V Tatayah, M D Holton, K A R Rose, R S Metcalfe, H Robotka, M Wikelski, F Tremblay, S Whelan, K H Elliott, E L C Shepard.

The chapter was written by BG, RPW and ELCS. Data analysis was carried out by BG with input from RPW. Calibrations were designed by RPW and MDH. Red-tailed tropicbird data were collected by AF, NC and VT. Human data were collected by KARR, RPW and RSM. Pigeon data were collected by HR, ELCS and MW. Black-legged kittiwake data were collected by BG, FT, SW and KHE. MDH contributed technical insight about accelerometers. All authors contributed to the revision of this chapter.

List of abbreviations

6-O	6-orientations (calibration method)
a	Vectorial sum of acceleration
ANOVA	Analysis of variance
ASL	Above sea level (Altitude)
AWERB	Animal Welfare and Ethical Review Body
BMR	Basal metabolic rate
COT	Cost of transport
DBA	Dynamic body acceleration
DDMT	Daily Diary Multiple Trace software
DDMT	Daily Diary
GLM	Generalised linear model
GLMM	Generalised linear mixed-effect model
GPS	Global positioning system
HWC	Headwind component
ISA	International standard atmosphere
A	Wingbeat amplitude
f	Wingbeat frequency
LMM	Linear mixed-effect model
R^2_c	Conditional coefficient of determination (R^2)
R^2_m	Marginal coefficient of determination (R^2)
s.d.	Standard deviation
Std.	Standard
Stdd.	Standardised

sVeDBA	Smoothed vector of dynamic body acceleration
TWC	Tailwind component
Unstdd.	Unstandardised
V_a	Airspeed
V_e	Equivalent airspeed
VeDBA	Vector of dynamic body acceleration
V_g	Groundspeed
VIF	Variance inflation factor
V_{mp}	Minimum power speed
V_{mr}	Maximum range speed
V_w	Wind speed
V_x	Horizontal airspeed
V_z	Rate of change of altitude (= Climb rate if $V_z > 0$)
WBA	Wingbeat amplitude
WBF	Wingbeat frequency
x	x axis of the accelerometer
x_D	dynamic acceleration in the x axis
y	y axis of the accelerometer
y_D	dynamic acceleration in the y axis
z	z axis of the accelerometer
z_D	dynamic acceleration in the z axis
ΔT	Difference between sea surface and air temperature
θ	the angle between the bird heading

General Introduction

The energetic costs of flight are something of a paradox: Flapping flight is considered to be the most costly form of locomotion, requiring around nine times the costs of resting (Butler, 2016), yet soaring flight is among the cheapest forms of locomotion (Schmidt-Nielsen, 1972), being around twice resting costs (Baudinette & Schmidt-Nielsen, 1974; Duriez *et al.*, 2014). This is made possible by the energy that is available in the air (Shepard *et al.* , 2016), which allows animals to subsidize the costs of flapping flight. The diverse strategies that animals employ to achieve this, from gaining altitude in thermal updrafts, to exploiting wind gradients or gusts, are all considered as forms of soaring (Hedenström, 1993). Incredibly, this allows some animals to fly at airspeeds up to ~ 20 m s^{-1} at close to resting costs (Richardson, 2011). The ability to extract energy from the air and cover ground so cheaply, has driven the evolution of morphologies and life histories adapted to different forms of soaring flight. In extreme cases this has enabled animals to occupy ecological niches that would not be available without the aerial environment subsidizing the metabolic costs of flight. For instance, soaring enables scavenging birds to fly hundreds to thousands of kilometres to exploit sparse food sources, whilst barely flapping (Sato *et al.*, 2009; Williams *et al.*, 2020) and may explain how common swifts (*Apus apus*), can remain airborne for almost the entire annual cycle (Hedenström *et al.*, 2016).

Obligate soaring fliers represent excellent model organisms to understand this mode of flight, and a range of studies have used them to understand the precise manoeuvres, bank angles and speeds that birds adopt to remain in updrafts (Harel *et al.*, 2016; Sherub *et al.*, 2016; Williams *et al.*, 2018), the mechanisms by which birds detect rising air (Williams *et al.*, 2018), as well as the link between environmental conditions and both flight effort (Furness & Bryant, 1996; Shamoun-Baranes *et al.*, 2016) and space use (Weimerskirch *et al.*, 2016).

Nonetheless, soaring is often presented in a way that implies it is confined to specialist fliers, which tend to be relatively large birds, such as raptors in the terrestrial environment, and many procellariiformes in the marine realm (e.g. Sato *et al.*, 2009; Williams *et al.*, 2020). Yet there are widespread examples of non-soaring birds adapting their behaviour to reduce their flight costs. For instance 55-g European bee-eaters (M*erops apiaster*), have been shown to use thermal updrafts to reduce the costs of their migration (Sapir *et al.*, 2010), barn swallows (*Hirundo rustica*) exploit wind gradients close to ground (Warrick *et al.*, 2016) and red-footed boobies (*Sula sula*) spend 68% of their foraging trips in gliding flight (Weimerskirch *et al.*, 2005). There is even evidence that some geese extract energy from the air in flight (Bishop *et al.*, 2015). This shows that there is not necessarily a black and white distinction between birds that do soar and birds that do not, and even suggests that all birds may be capable of some form of soaring. Indeed, bats and even insects have been shown to extract energy from tailwinds and/ or updrafts (O'Mara *et al.*, 2021), demonstrating that the ability to soar is not limited by morphology. Yet while the use of strategies like soaring has been studied a lot for obligate soarers, the extent to which other species adapt their behaviour to the movements of the air, and the energetic consequences, has received far less attention.

The aerial environment

While obligate flapping fliers adapt their movements to maximise the energy they can extract from these features, other flying animals cannot ignore them (although some animals, notably those that operate under forest canopies, experience air that is essentially still). The behaviour of the aerial environment should impact almost all flying animals because it is so changeable, with both wind speeds and updrafts being the same order of magnitude as animal flight speeds (Liechti, 2006; Shepard *et al.*, 2016). Flight costs and decisions should therefore vary in relation to the changing aerial conditions, even in the absence of soaring.

Various aspects of the flying environment influence flight effort, with the effects of wind being the most well studied (Alerstam *et al.*, 2019; Elliott *et al.*, 2014). Wind is crucial in the ecology of all flying animals: extreme wind conditions can lead to mortality during the migration of certain species (Loonstra *et al.*, 2019), while other species rely entirely on it to fly (Richardson, 2011). The reason wind is so important is related to its magnitude: flight speeds are generally equal to only 0.7 to 1.6 times those of typical wind speeds (Chapman *et al.*, 2011; Pennycuick *et al.*, 2013). To compensate for the drift caused by wind, birds must adjust their heading to avoid being drifted away from their destination (Liechti, 2006). Headwinds also increase the costs of flight when considered per unit time and per unit distance (i.e. the cost of transport), despite birds increasing their airspeed in response (Hedenström *et al.*, 2002; Spear & Ainley, 1997). As a result, this has shaped the migratory routes of billions of migrating birds (Kranstauber *et al.*, 2015; Mandel *et al.*, 2011), as well as the flight altitude (Liechti, 2006), and possibly departure times (Åkesson & Hedenström, 2000). Wind also influences soaring flight, as while some species rely on wind for dynamic soaring (Sachs, 2005) or the exploitation of orographic lift (Bohrer *et al.*, 2012; Duerr *et al.*, 2012), strong winds also alter the structure of thermals, reducing the efficiency of thermal soaring flight (Bohrer *et al.*, 2012; Kerlinger, 1989; Woodcock, 1940).

The impact of other parameters on the costs of flight in flapping fliers is less well known. This includes thermal updrafts, turbulence and air density. Thermals are driven by the uneven heating of the substrate, which causes air to rise when it is becomes warmer and less dense than the surrounding air. While the availability of thermals is patchy in space and time, being linked to the combination of the solar radiation and the substrate characteristics (Scacco *et al.*, 2019), it is also a source of energy that is regularly available, and in a range of seasons, increasing in strength up to around midday (Shamoun-Baranes *et al.*, 2016). The study on migrating bee-eaters showed that flapping fliers can benefit from thermals, experiencing a reduction in the energy required to produce lift even without switching to passive flight and circling within these features, as thermal soaring specialists do. Yet thermal updrafts are also a form of turbulence and birds flying through and near these features will experience both gusts and downdrafts (Shannon *et al.*, 2002; Williams *et al.*, 2018) and the effects of these on flight effort are unknown (cf. Bowlin & Wikelski, 2008).

Another facet of the aerial environment that varies substantially is the air density. The effect of air density on flight effort is well established (Bishop *et al.*, 2015; Pennycuick, 2008; Schmaljohann & Liechti, 2009), with lift decreasing with increasing altitude/ decreasing density (Pennycuick, 2008; Rayner, 1988), whereas weight remains essentially unchanged. Birds flying at lower air densities must therefore increase their wingbeat frequency and associated lift production for the same airspeed. Birds migrating at several kilometres altitude, either to cross mountain barriers or benefit from lower temperatures (Bishop *et al.*, 2015; Sjöberg *et al.*, 2021), therefore experience a substantial increase in flight costs. However, variation in air density is not confined to differences in altitude, as density also changes with temperature (Clapeyron, 1834), which shows marked seasonal variation, suggesting a dimension of flight effort that has been largely overlooked at low altitudes.

Flight currencies

Minimisation of the gross energy expenditure is not always the main currency for moving animals (Ydenberg & Hurd, 1998). Animals must consider energy expended in relation to the energy gained, with foraging locations being primarily determined by the availability of food resources, as well as the costs of accessing them. For instance, frigatebirds need to fly relatively close to the sea to search for food, considerably reducing their ability to soar, which causes foraging to be much more costly than travelling (Weimerskirch *et al.*, 2016). The other critical factor is the time available, as birds vary in the extent to which they are time-limited according to the season and the demands of chick-rearing (Norberg, 1981). For instance, the speed and costs of migration vary between spring and summer for many northern species, with birds migrating faster in the spring to secure the high-quality breeding sites (Kokko, 1999). Furthermore, birds can maximise their reproductive success by flying faster when provisioning chicks (Norberg, 1981), leading to costly flight during the breeding season than other periods of the year.

There are also other currencies beyond energy that influence flight decisions. Risk, including that from potential predators, governs many of the movement decisions made by animals, including space use, flight speed and timing (Cresswell, 1994; Laundré *et al.*, 2010; Shepard *et al.*, 2016; Usherwood *et al.*, 2011). Weather itself can constitute a risk, as storms can kill inexperienced birds (Nicoll *et al.*, 2017), while the absence of favourable winds during the crossing of a large water bodies can result in the exhaustion and ultimately drowning of larger species with limited capacity for powered flight or for taking off from the water (Bildstein *et al.*, 2009).

The main currencies that influence animal movement decisions are energy, time and risk (Gallagher *et al.*, 2017), as well as the information they have available to them, which is strongly influenced by factors such as ontogeny (Collet *et al.*, 2020) and the movements of conspecifics, particularly for social species (Krause *et al.*, 2002; Williams *et al.*, 2018). For instance, the flocking behaviour of pigeons requires them to adjust their speed to match that of the group (Sankey *et al.*, 2019). Overall, this highlights that to interpret the decisions of a bird in response to particular weather conditions, and in turn understand how environmental conditions can affect flight costs, it is necessary to look at the ecological context in which decisions are made, both at the large scale (e.g. seasonal patterns) and the fine scale (solo flight versus group flight).

Technology for the study of flight

The physical environment experienced by birds in flight will be determined by the weather and time of day, in combination with the substrate they are flying over. Given that the substrate and the weather can change rapidly, high-frequency data are required to assess the behavioural responses to these changing conditions, in terms of flight speed and trajectory, as well as their energetic consequences. Technological developments in the last 20 years mean that researchers now routinely equip animals with sophisticated biotelemetry devices that can reconstruct movement paths at fine scales and in all 3 dimensions (Gunner *et al.*, 2021). For instance, the use of Global Positioning Systems (GPS) allows scientist to follow the flight paths of individual birds for years (Flack *et al.*, 2016), measure flight speed (e.g. Mellone *et al.*, 2012; Sankey *et al.*, 2019) and identify different flight styles, including the use of thermal soaring (Bohrer *et al.*, 2012). More recently, the use of GPS units in association with very fine-scale barometric sensors and magnetometers have opened up new avenues in the study of flight, enabling accurate estimation of climb rates as well as highly-resolved movement trajectories (Gunner *et al.*, 2021).

Furthermore, there is now a real prospect of measuring the costs of flight in wild birds over fine scales, using accelerometry. This technique has developed rapidly since the first demonstration that acceleration metrics (such as dynamic body acceleration, DBA), recorded using animal-attached loggers, are a powerful proxy for movement-related energy expenditure, even over scales of several seconds for terrestrial locomotion (Green *et al.*, 2009; Halsey *et al.*, 2011; Wilson *et al.*, 2006). There is also evidence that acceleration metrics can be powerful proxies for flight costs, as DBA was a good predictor of overall energy expenditure, as estimated with doubly labelled water, and better than flight time or wingbeat frequency in auks (Elliott *et al.*, 2013; Elliott *et al.*, 2014, see also Halsey *et al.*, 2009). This therefore presents an opportunity for information on flight effort to be coupled with detailed information on environmental conditions and individual responses to them. Nonetheless, studies assessing the relationship between acceleration metrics and other parameters related to flight costs, namely airspeed, are lacking, with examples being studies that have shown an increase in DBA and wingbeat frequency in relation to food loading (Sato *et al.*, 2008; Wilson *et al.*, 2006), flying in a cluster flock (Usherwood *et al.*, 2011) and at high altitudes (Bishop *et al.*, 2015). Overall therefore, there is a need for further examination of how acceleration-based metrics vary with flight effort at fine scales and understanding of how acceleration metrics relate to kinematic parameters, namely wingbeat amplitude.

The power of accelerometry in providing insight into behavioural patterns (Yoda *et al.*, 2001) and their energetic consequences has led to a rapid expansion in the use of this technique over the last 20 years, which has resulted in the collection of an incredible amount of data across taxa and study sites (Williams, *et al.*, 2020). This represents a potentially valuable resource that could enable researchers to assess how species respond to changing conditions over timescales of years, and ultimately decades (Davidson *et al.*, 2020). However, the rapid uptake of the method has outpaced the development of standards to ensure that data can be compared between seasons and sites. Standardising these measurements would open new doors to researchers in terms of meta-analyses, and should therefore be a priority for researchers to be able to maximize the use of these data in the future (*cf.* Sequeira *et al.*, 2021).

Biological models

In order to study the role of different atmospheric parameters and currencies in the flight behaviour, and look at its variation at different scales, this work will mainly focus on two different species of birds: homing pigeons (*Columba livia*) and red-tailed tropicbirds (*Phaethon rubricauda*).

Pigeons are medium-sized (400 g) obligate flappers that can be trained to return to their loft from a release site, allowing for standardised trajectories during an experiment, which makes them an excellent species model to study how flight effort and kinematics vary at fine-scales while largely controlling for the effect of route choice. Pigeons can also be trained to fly in a wind tunnel, allowing for biomechanical measurements in consistent conditions. Flight in a wind tunnel, however, does not reflect natural flight behaviour and decisions, for instance, in response to predation risk, which are better studied in free flight. In natural conditions, pigeons usually flock, as a predation avoidance mechanism, at the cost of increased energy expenditure (Usherwood *et al.,* 2011). They can be trained to fly solo, to standardise their flight effort, and to return to their loft from a release site, to control for route familiarity (which affects performance, Taylor *et al.*, 2017).

In contrast, the breeding ecology of red-tailed tropicbirds makes them ideal to understand how their flight is impacted by a wide range of atmospheric conditions. Red-tailed tropicbirds are medium sized birds (around 800 g) using flapping as their main flight mode, but occasionally using thermal soaring to gain altitude. Tropicbirds nesting on Round Island breed throughout the year, exposing them to seasonal variation in atmospheric conditions including wind, temperature and air density. This therefore provides a valuable opportunity to quantify the role of these parameters on flight effort and behaviour during their foraging flights, Which can be wide-ranging (80 km on average, see Sommerfeld *et al.*, 2010). Together, the two main study systems allowed me to study how two different flapping fliers respond to a range of flight conditions when flying over land (which is typified by variable substrate characteristics) and sea, and over fine and seasonal scales. **Summary**

The thesis starts by recognising that researchers are using different metrics as proxies for flight effort, including wingbeat frequency, and dynamic body acceleration. There is therefore a need to consider which would be more robust, in terms of the species and scenarios under which different metrics and kinematic parameters would vary. Chapter 1 addresses this, using data from flight in controlled and wild conditions. Specifically, I (i) assess the relationship between wingbeat amplitude and the amplitude of the acceleration signal, as derived from body-mounted accelerometers, (ii) evaluate the extent that birds vary their wingbeat frequency and amplitude to increase their power output, and (iii) examine whether the likelihood of using either parameter varies with flight morphology. Overall, the results provide strong evidence that the body acceleration varies with wingbeat amplitude, as well as frequency, and that a wide range of birds use both kinematic parameters to increase their power output, although wingbeat amplitude might be more important in producing the power required for more costly forms of flight, including climbing. This is supported by tagging data from 13 species and a review of the literature, where these issues tend to have been addressed in controlled conditions. I therefore highlight some of the complexities in moving from controlled to wild conditions where behaviour is also affected by biotic influences (see chapter 2). Nonetheless, data from free-ranging birds enables us to gain insight into how species such as albatrosses modify their kinematics, which would clearly be difficult in controlled conditions.

In chapter 2, I explore the role of energy, time and risk in the selection of flight speed in a flapping flier: the homing pigeon. While the power curve can be used to predict the speed at which birds should fly to minimise their cost of transport (Pennycuick, 2008), the "right" speed also depends on whether birds are prioritising energy saving over speed or predator avoidance, and the relative importance of these factors may vary in space and time, in particular in relation to the landscape birds are flying over (Gallagher *et al.*, 2017). Using data from solo homing pigeons equipped with high-frequency loggers, I investigate whether flight speeds are consistent with energy saving, both in climbing and descending flight. The results showed that although pigeons avoided steep (and costly) climbs, they flew faster than would be expected for energy optimisation, even when climbing. This alone makes for a very costly flight style. Furthermore, the very high variability in speed and altitude over fine scales is a source of substantial energetic inefficiency. This demonstrates how even within a single trip, an individual bird can combine examples of energy-efficient and energy-inefficient behaviour, which reflects the multiple currencies that influence movement decisions for animals in the wild. In this instance the variable flight style, with all its associated costs, could be driven by the need to reduce predation risk, with a less predictable movement path used as a strategy to reduce predation risk when flocking, which usually serves this purpose in pigeons (Krause & Ruxton, 2002), is not possible.

Chapter 3 focuses on the red-tailed tropicbirds (*Phaethon rubricauda*). The morphology of these birds does not suggest any adaptations to thermal soaring flight, so it was surprising to discover this behaviour in high-frequency movement data from their foraging flights. Because facultative soaring birds can choose between soaring and powered flight depending on the flight conditions, species such as tropicbirds provide a means to identify the range of conditions in which soaring is profitable. High-frequency loggers allowed me to quantify the soaring frequency and duration in relation to wind support and thermal strength, as well as the phase of the foraging trip i.e. commuting versus search. A key constraint in the use of soaring flight is that it is typically slower than flapping flight. The use of soaring should therefore depend on how fast birds can climb during the soaring phase, as well as the wind direction relative to their own heading. Tropicbirds mainly initiated soaring when they had wind support and thermal strength was higher, showing that they only switch to soaring when it allows them to save energy while still progressing at a reasonable speed. This confirms the importance of time over energy for birds provisioning young chicks, and also suggests that soaring could be much more widely used than morphology or biologging data suggest, given that most seabirds are instrumented in the breeding season.

Chapter 4 takes a step back to look at the importance of weather on the flight effort of tropical seabirds at seasonal scales. Birds are predicted to breed during the most efficient season for foraging, which is generally the season characterised by higher food availability (Lack, 1968). In the region of the Mascarenes, in the Indian Ocean, ocean productivity is relatively low year-round (Behrenfeld *et al.*, 2005). In these conditions, other factors, such as flight effort, could have a greater influence on foraging efficiency and ultimately, the costs and benefits of breeding. we examine the effects of wind, thermal availability and air density on the speed selection and wingbeat frequency of red-tailed tropicbirds. Despite their importance in the use of soaring, wind and thermal availability do not influence flight costs over seasonal scales due to the low seasonal variability in both parameters. However, large differences in air density, driven by changes in temperature, were found to drive seasonal variation in wingbeat frequency. This highlights a previously undocumented effect of increasing temperatures on flight effort, which could ultimately influence the balance of costs and benefits that birds experience when breeding in different seasons.

In my analysis of the tropicbird data in the previous chapters, I discovered large, unexpected differences in the amplitude of the acceleration signal, which, after a lot of detective work, seemed to be linked to slight differences in tagging methods between seasons. The popularity of accelerometers prompts an urgent need to standardise the methods of data collection in order to ensure that differences in data outputs can be correctly assigned to biological drivers. Chapter 5 illustrates the effect of tag position, attachment method and logger used on the signal recorded by the accelerometer across three species of birds as well as humans. Results show that longitudinal differences in the position of the loggers influence the amplitude of the signal in both pigeons and humans. In addition, differences in the attachment method and the type of accelerometer can lead to large differences in the acceleration signal. The results highlight the importance of standardising attachment methods within study systems and the role of simple calibrations (as presented in this chapter) in controlling for tag-specific differences.

Overall objectives

Studies about the effects of weather on the flight of birds that predominantly use flapping flight have largely been limited to the influence of wind, and methods used to estimate effort would benefit from standardisation and further validation. The goal of this PhD is to understand how atmospheric conditions, such as the combined effects of wind and thermals, as well as air density, affect flight costs, acknowledging that birds may not always be aiming to minimise energy expenditure. I investigate this using pigeons (*Columba livia*) as an archetypical example of a bird using powered flight that is not limited by energy use, and which can be manipulated to fly in a range of conditions due to its habit of returning to the loft from remote release sites. I go on to assess the environmental factors that determine the costs of flapping flight as well as the use of soaring in chick-rearing red-tailed tropicbirds (*Phaethon rubricauda*). These birds were tagged during chick-rearing, and were predicted to be limited by time. However, the fact that these birds breed year-round allowed me to compare the impact of changing flight conditions on the costs of chick-rearing. Finally, I propose a way to standardise accelerometer data in the hope that the widespread adoption of standard calibrations will facilitate the comparison of flight costs in current and changing climatic conditions.

References

Åkesson, S., & Hedenström, A. (2000). Wind selectivity of migratory flight departures in birds. *Behavioral Ecology and Sociobiology*, *47*(3), 140–144. doi: 10.1007/s002650050004

Alerstam, T., Bäckman, J., & Evans, T. J. (2019). Optimal central place foraging flights in relation to wind. *Journal of Ornithology*, *160*(4), 1065–1076. doi: 10.1007/s10336-019-01677-4

Baudinette, R. V, & Schmidt-Nielsen, K. (1974). Energy cost of gliding flight in herring gulls. *Nature*, *248*(5443), 83–84.

Behrenfeld, M. J., Boss, E., Siegel, D. A., & Shea, D. M. (2005). Carbon-based ocean productivity and phytoplankton physiology from space. *Global Biogeochemical Cycles*, *19*(1), 1–14. doi: 10.1029/2004GB002299

Bildstein, K. L., Bechard, M. J., Farmer, C., & Newcomb, L. (2009). Narrow sea crossings present major obstacles to migrating Griffon Vultures *Gyps fulvus*. *Ibis*, *151*(2), 382–391.

Bishop, C. M., Spivey, R. J., Hawkes, L. A., Batbayar, N., Chua, B., Frappell, P. B., … Butler, P. J. (2015). The roller coaster flight strategy of bar-headed geese conserves energy during Himalayan migrations. *Science*, *347*(6219), 250–254. doi: 10.1126/science.1258732

Bohrer, G., Brandes, D., Mandel, J. T., Bildstein, K. L., Miller, T. A., Lanzone, M., … Tremblay, J. A. (2012). Estimating updraft velocity components over large spatial scales: Contrasting migration strategies of golden eagles and turkey vultures. *Ecology Letters*, *15*(2), 96–103. doi: 10.1111/j.1461-0248.2011.01713.x

Bowlin, M. S., & Wikelski, M. (2008). Pointed wings, low wingloading and calm air reduce migratory flight costs in songbirds. *PloS One*, *3*(5), e2154.

Butler, P. J. (2016). The physiological basis of bird flight. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*(1704), 20150384. doi: 10.1098/rstb.2015.0384

Chapman, J. W., Klaassen, R. H. G., Drake, V. A., Fossette, S., Hays, G. C., Metcalfe, J. D., … Alerstam, T. (2011). Animal orientation strategies for movement in flows. *Current Biology*, *21*(20), R861–R870. doi: 10.1016/j.cub.2011.08.014

Clapeyron, É. (1834). Mémoire sur la puissance motrice de la chaleur. *Journal de l'École Polytechnique*, *14*, 153–190.

Collet, J., Prudor, A., Corbeau, A., Mendez, L., & Weimerskirch, H. (2020). First explorations: Ontogeny of central place foraging directions in two tropical seabirds. *Behavioral Ecology*, *31*(3), 815–825. doi: 10.1093/beheco/araa028

Cresswell, W. (1994). Song as a pursuit-deterrent signal, and its occurrence relative to other anti-predation behaviours of skylark (*Alauda arvensis*) on attack by merlins (*Falco columbarius*). *Behavioral Ecology and Sociobiology*, *34*(3), 217–223.

Davidson, S. C., Bohrer, G., Gurarie, E., LaPoint, S., Mahoney, P. J., Boelman, N. T., … Hebblewhite, M. (2020). Ecological insights from three decades of animal movement tracking across a changing Arctic. *Science*, *370*(6517), 712–715. doi: 10.1126/science.abb7080

Duerr, A. E., Miller, T. A., Lanzone, M., Brandes, D., Cooper, J., O'Malley, K., … Katzner, T. (2012). Testing an emerging paradigm in migration ecology shows surprising differences in efficiency between flight modes. *PloS One*, *7*(4), 1–7. doi: 10.1371/journal.pone.0035548

Duriez, O., Kato, A., Tromp, C., Dell'Omo, G., Vyssotski, A. L., Sarrazin, F., & Ropert-Coudert, Y. (2014). How cheap is soaring flight in raptors? A preliminary investigation in freely-flying vultures. *PLoS ONE*, *9*(1). doi: 10.1371/journal.pone.0084887

Elliott, Kyle H, Le Vaillant, M., Kato, A., Speakman, J. R., & Ropert-Coudert, Y. (2013). Accelerometry predicts daily energy expenditure in a bird with high activity levels. *Biology Letters*, *9*(1), 20120919.

Elliott, Kyle Hamish, Chivers, L. S., Bessey, L., Gaston, A. J., Hatch, S. A., Kato, A., … Hare, J. F. (2014). Windscapes shape seabird instantaneous energy costs but adult behavior buffers impact on offspring. *Movement Ecology*, *2*(1), 1–15.

Flack, A., Fiedler, W., Blas, J., Pokrovsky, I., Kaatz, M., Mitropolsky, M., … Jerzak, L. (2016). Costs of migratory decisions: a comparison across eight white stork populations. *Science Advances*, *2*(1), e1500931.

Furness, R. W., & Bryant, D. M. (1996). Effect of Wind on Field Metabolic Rates of Breeding Northern Fulmars. *Ecology*, *77*(4), 1181–1188. doi: 10.2307/2265587

Gallagher, A. J., Creel, S., Wilson, R. P., & Cooke, S. J. (2017). Energy landscapes and the landscape of fear. *Trends in Ecology & Evolution*, *32*(2), 88–96.

Green, J. A., Halsey, L. G., Wilson, R. P., & Frappell, P. B. (2009). Estimating energy expenditure of animals using the accelerometry technique: activity, inactivity and comparison with the heart-rate technique. *Journal of Experimental Biology*, *212*(4), 471–482.

Gunner, R. M., Holton, M. D., Scantlebury, M. D., van Schalkwyk, L., English, H. M., Williams, H. J., …

Börger, L. (2021). *Dead-Reckoning Animal Movements in R–A Reappraisal Using Gundog. Tracks*.

Halsey, L.G., Shepard, E. L. C., Quintana, F., Gomez Laich, A., Green, J. A., & Wilson, R. P. (2009). The relationship between oxygen consumption and body acceleration in a range of species. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, *152*(2), 197–202. doi: 10.1016/j.cbpa.2008.09.021

Halsey, Lewis G., Shepard, E. L. C., & Wilson, R. P. (2011). Assessing the development and application of the accelerometry technique for estimating energy expenditure. *Comparative Biochemistry and Physiology - A Molecular and Integrative Physiology*, *158*(3), 305–314. doi: 10.1016/j.cbpa.2010.09.002

Harel, R., Horvitz, N., & Nathan, R. (2016). Adult vultures outperform juveniles in challenging thermal soaring conditions. *Scientific Reports*, *6*(1), 1–8.

Hedenström, A. (1993). Migration by soaring or flapping flight in birds: the relative importance of energy cost and speed. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *342*(1302), 353–361. doi: 10.1098/rstb.1993.0164

Hedenström, A., Alerstam, T., Green, M., & Gudmundsson, G. A. (2002). Adaptive variation of airspeed in relation to wind, altitude and climb rate by migrating birds in the Arctic. *Behavioral Ecology and Sociobiology*, *52*(4), 308–317. doi: 10.1007/s00265-002-0504-0

Hedenström, A., Norevik, G., Warfvinge, K., Andersson, A., Bäckman, J., & Åkesson, S. (2016). Annual 10-month aerial life phase in the common swift Apus apus. *Current Biology*, *26*(22), 3066–3070.

Kerlinger, P. (1989). *Flight strategies of migrating hawks*. University of Chicago Press.

Kokko, H. (1999). Competition for early arrival in migratory birds. *Journal of Animal Ecology*, *68*(5), 940–950. doi: 10.1046/j.1365-2656.1999.00343.x

Kranstauber, B., Weinzierl, R., Wikelski, M., & Safi, K. (2015). Global aerial flyways allow efficient travelling. *Ecology Letters*, *18*(12), 1338–1345. doi: 10.1111/ele.12528

Krause, J., & Ruxton, G. D. (2002). *Living in groups*. Oxford University Press.

Lack, D. L. (1968). *Ecological adaptations for breeding in birds*.

Laundré, J. W., Hernández, L., & Ripple, W. J. (2010). The landscape of fear: ecological implications of being afraid. *The Open Ecology Journal*, *3*(1).

Le Corre, M. (2001). Breeding seasons of seabirds at Europa Island (southern Mozambique Channel) in relation to seasonal changes in the marine environment. *Journal of Zoology*, 254(2), 239–249. doi: 10.1017/S0952836901000759

Le Corre, M., Cherel, Y., Lagarde, F., Lormée, H., & Jouventin, P. (2003). Seasonal and inter-annual variation in the feeding ecology of a tropical oceanic seabird, the red-tailed tropicbird *Phaethon rubricauda. Marine Ecology Progress Series*, 255, 289–301. doi: 10.3354/meps255289

Liechti, F. (2006). Birds: Blowin' by the wind? *Journal of Ornithology*, *147*(2), 202–211. doi: 10.1007/s10336-006-0061-9

Loonstra, A. H. J., Verhoeven, M. A., Senner, N. R., Both, C., & Piersma, T. (2019). Adverse wind conditions during northward Sahara crossings increase the in-flight mortality of Black-tailed Godwits. *Ecology Letters*, *22*(12), 2060–2066. doi: 10.1111/ele.13387

Mandel, J. T., Bohrer, G., Winkler, D. W., Barber, D. R., Houston, C. S., & Bildstein, K. L. (2011). Migration path annotation: cross-continental study of migration-flight response to environmental conditions. *Ecological Applications*, *21*(6), 2258–2268.

Mellone, U., Klaassen, R. H. G., García-Ripollés, C., Limiñana, R., López-López, P., Pavón, D., … Alerstam, T. (2012). Interspecific comparison of the performance of soaring migrants in relation to morphology, meteorological conditions and migration strategies. *PLoS ONE*, *7*(7). doi: 10.1371/journal.pone.0039833

Nicoll, M. A. C., Nevoux, M., Jones, C. G., Ratcliffe, N., Ruhomaun, K., Tatayah, V., & Norris, K. (2017). Contrasting effects of tropical cyclones on the annual survival of a pelagic seabird in the Indian Ocean. *Global Change Biology*, *23*(2), 550–565. doi: 10.1111/gcb.13324

Norberg, R. A. (1981). Optimal Flight Speed in Birds when Feeding Young. *The Journal of Animal Ecology*, *50*(2), 473. doi: 10.2307/4068

O'Mara, M. T., Amorim, F., Scacco, M., McCracken, G. F., Safi, K., Mata, V., … Beja, P. (2021). Bats use topography and nocturnal updrafts to fly high and fast. *Current Biology*, *31*(6), 1311–1316.

Pennycuick, C. J., Akesson, S., & Hedenström, A. (2013). Air speeds of migrating birds observed by ornithodolite and compared with predictions from flight theory. *Journal of the Royal Society Interface*, *10*(86). doi: 10.1098/rsif.2013.0419

Pennycuick, C. J. (2008). *Modelling the flying bird*. Elsevier.

Rayner, J. M. V. (1988). Form and function in avian flight. In *Current ornithology* (pp. 1–66). Springer.

Richardson, P. L. (2011). How do albatrosses fly around the world without flapping their wings? *Progress in Oceanography*, *88*(1–4), 46–58.

Sachs, G. (2005). Minimum shear wind strength required for dynamic soaring of albatrosses. *Ibis*, *147*(1), 1–10.

Sankey, D. W. E., Shepard, E. L. C., Biro, D., & Portugal, S. J. (2019). Speed consensus and the 'Goldilocks principle' in flocking birds (*Columba livia*). *Animal Behaviour*, *157*, 105–119. doi: 10.1016/j.anbehav.2019.09.001

Sapir, N., Wikelski, M., Mccue, M. D., Pinshow, B., & Nathan, R. (2010). Flight modes in migrating European bee-eaters: Heart rate may indicate low metabolic rate during soaring and gliding. *PLoS ONE*, *5*(11), 1–13. doi: 10.1371/journal.pone.0013956

Sato, K., Daunt, F., Watanuki, Y., Takahashi, A., & Wanless, S. (2008). A new method to quantify prey acquisition in diving seabirds using wing stroke frequency. *Journal of Experimental Biology*, *211*(1), 58–65. doi: 10.1242/jeb.009811

Sato, K., Sakamoto, K. Q., Watanuki, Y., Takahashi, A., Katsumata, N., Bost, C. A., & Weimerskirch, H. (2009). Scaling of soaring seabirds and implications for flight abilities of giant pterosaurs. *PLoS ONE*, *4*(4), 1–6. doi: 10.1371/journal.pone.0005400

Scacco, M., Flack, A., Duriez, O., Wikelski, M., & Safi, K. (2019). Static landscape features predict uplift locations for soaring birds across Europe. *Royal Society Open Science*, *6*(1). doi: 10.1098/rsos.181440

Schmaljohann, H., & Liechti, F. (2009). Adjustments of wingbeat frequency and air speed to air density in free-flying migratory birds. *Journal of Experimental Biology*, *212*(22), 3633–3642. doi: 10.1242/jeb.031435

Schmidt-Nielsen, K. (1972). Locomotion: Energy cost of swimming, flying, and running. *Science*, *177*(4045), 222–228. doi: 10.1126/science.177.4045.222

Sequeira, A. M. M., O'Toole, M., Keates, T. R., McDonnell, L. H., Braun, C. D., Hoenner, X., … Weise, M. (2021). A standardisation framework for bio-logging data to advance ecological research and conservation. *Methods in Ecology and Evolution*, *12*(6), 996–1007. doi: 10.1111/2041-210X.13593

Shamoun-Baranes, J., Bouten, W., Van Loon, E. E., Meijer, C., & Camphuysen, C. J. (2016). Flap or soar? How a flight generalist responds to its aerial environment. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*(1704). doi: 10.1098/rstb.2015.0395

Shannon, H. D., Young, G. S., Yates, M. A., Fuller, M. R., & Seegar, W. S. (2002). Measurements of thermal updraft intensity over complex terrain using American white pelicans and a simple boundary-layer forecast model. *Boundary-Layer Meteorology*, *104*(2), 167–199.

Shepard, E. L. C., Ross, A. N., & Portugal, S. J. (2016). Moving in a moving medium: New perspectives on flight. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*(1704). doi: 10.1098/rstb.2015.0382

Sherub, S., Bohrer, G., Wikelski, M., & Weinzierl, R. (2016). Behavioural adaptations to flight into thin air. *Biology Letters*, *12*(10), 20160432.

Sjöberg, S., Malmiga, G., Nord, A., Andersson, A., Bäckman, J., Tarka, M., … Hasselquist, D. (2021). Extreme altitudes during diurnal flights in a nocturnal songbird migrant. *Science*, *372*(6542), 646–648. doi: 10.1126/science.abe7291

Spear, L. B., & Ainley, D. G. (1997). Flight behaviour of seabirds in relation to wind direction and wing morphology. *Ibis*, *139*(2), 221–233. doi: 10.1111/j.1474-919x.1997.tb04620.x

Usherwood, J. R., Stavrou, M., Lowe, J. C., Roskilly, K., & Wilson, A. M. (2011). Flying in a flock comes at a cost in pigeons. *Nature*, *474*(7352), 494–497. doi: 10.1038/nature10164

Warrick, D. R., Hedrick, T. L., Biewener, A. A., Crandell, K. E., & Tobalske, B. W. (2016). Foraging at the edge of the world: low-altitude, high-speed manoeuvering in barn swallows. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*(1704), 20150391.

Weimerskirch, H., Le Corre, M., Ropert-Coudert, Y., Kato, A., & Marsac, F. (2005). The three-dimensional flight of red-footed boobies: Adaptations to foraging in a tropical environment? *Proceedings of the Royal Society B: Biological Sciences*, *272*(1558), 53–61. doi: 10.1098/rspb.2004.2918

Weimerskirch, Henri, Bishop, C., Jeanniard-du-Dot, T., Prudor, A., & Sachs, G. (2016). Frigate birds track atmospheric conditions over months-long transoceanic flights. *Science*, *353*(6294), 74–78. doi: 10.1126/science.aaf4374

Williams, H. J., Duriez, O., Holton, M. D., Dell'Omo, G., Wilson, R. P., & Shepard, E. L. C. (2018). Vultures respond to challenges of near-ground thermal soaring by varying bank angle. *Journal of Experimental Biology*, *221*(23). doi: 10.1242/jeb.174995

Williams, H. J., King, A. J., Duriez, O., Börger, L., & Shepard, E. L. C. (2018). Social eavesdropping allows for a more risky gliding strategy by thermal-soaring birds. *Journal of the Royal Society Interface*, *15*(148). doi: 10.1098/rsif.2018.0578

Williams, H. J., Shepard, E. L. C., Holton, M. D., Alarcón, P. A. E., Wilson, R. P., & Lambertucci, S. A. (2020). Physical limits of flight performance in the heaviest soaring bird. *Proceedings of the National Academy of Sciences*, *117*(30), 17884–17890. doi: 10.1073/pnas.1907360117

Williams, H. J., Taylor, L. A., Benhamou, S., Bijleveld, A. I., Clay, T. A., de Grissac, S., … Börger, L. (2020). Optimizing the use of biologgers for movement ecology research. *Journal of Animal Ecology*, *89*(1), 186–206. doi: 10.1111/1365-2656.13094

Wilson, R. P., White, C. R., Quintana, F., Halsey, L. G., Liebsch, N., Martin, G. R., & Butler, P. J. (2006). Moving towards acceleration for estimates of activity-specific metabolic rate in free-living animals: The case of the cormorant. *Journal of Animal Ecology*, *75*(5), 1081–1090. doi: 10.1111/j.1365-2656.2006.01127.x

Woodcock, A. H. (1940). Convection and soaring over the open sea. *Journal of Marine Research*, (203), 248–253.

Ydenberg, R., & Hurd, P. (1998). Simple models of feeding with time and energy constraints. *Behavioral Ecology*, *9*(1), 49–53. doi: 10.1093/beheco/9.1.49

Yoda, K., Naito, Y., Sato, K., Takahashi, A., Nishikawa, J., Ropert-Coudert, Y., … Le Maho, Y. (2001). A new technique for monitoring the behaviour of free-ranging Adelie penguins. *Journal of Experimental Biology*, *204*(4), 685–690.

Chapter 1 – The role of wingbeat frequency and amplitude in flight power

Abstract

Metrics from body-mounted accelerometers, such as dynamic body acceleration, have been shown to be powerful proxies for movement-related energy expenditure in animals using terrestrial and aquatic locomotion. However, experimental validations of these metrics as proxies for the power produced in flight are lacking. In addition, the extent to which birds modulate their wingbeat kinematics to generate power, and therefore the need for a metric that varies with wingbeat amplitude as well as frequency, is unclear. To address this, we flew birds in a wind tunnel and showed that the dorsoventral body acceleration varies with wingbeat amplitude. We then assessed the extent to which birds modulate their wingbeat amplitude and frequency to increase their climb rate or airspeed, using two species flying in the wild (pigeons, *Columba livia*, and red-tailed tropicbirds, *Phaethon rubricauda*). Finally, accelerometer data from 13 species were used to assess whether birds were more likely to vary their wingbeat frequency or amplitude according to their morphology. We found that wingbeat amplitude and frequency were positively correlated, apart from species that use dynamic soaring and have a high aspect ratio and low wing loading. Nonetheless, positive relationships were characterised by very low R^2 values. We propose that this is due to wingbeat amplitude being used to increase power in more energetically demanding forms of flight, including climbing, and take-off. This is supported by data from the tropicbirds and the literature. Overall, this suggests that acceleration metrics that vary with wingbeat amplitude and frequency should be more robust proxies for power use than frequency alone. However, we caution that other kinematic parameters, such as stroke-plane angle, can also be used to increase power output, and there is therefore a need to assess the performance of acceleration metrics in relation to independent estimates of power.

Introduction

The energetic costs of flapping flight are notable for their magnitude, being the highest across all forms of locomotion when considered per unit time (Butler, 2016). They are also notable for their variability. Indeed, the costs of flight have been shown to vary with the animal's internal state (Hicks *et al.*, 2018), social context (Sankey & Portugal, 2019; Usherwood *et al.*, 2011), and the physical environment, including wind speed, turbulence and air density (Bishop *et al.*, 2015; Furness & Bryant, 1996; Sapir *et al.*, 2010). Disentangling the impact of the biological and physical environment on flight costs can therefore be challenging, given the number of factors that can vary simultaneously, and over fine time-scales e.g. depending on the substrate that birds are flying over and individual position within a flock (see Chapter 2, Portugal *et al.*, 2014).

High-frequency data from animal-attached loggers have proved powerful in this regard, with onboard accelerometers allowing the quantification of wingbeat frequency (Sato *et al.*, 2008; Van Walsum *et al.*, 2020). Power varies in a U-shaped curvilinear fashion with the flight speed for most flying birds (Norberg, 2012; Pennycuick, 2008; Tobalske *et al.*, 2003), and wingbeat frequency seems to follow the same trend, although it is not always pronounced (Ellerby & Askew, 2007; Hedrick *et al.* 2003; Pennycuick *et al.*, 1996; Schmidt-Wellenburg *et al.*, 2007; Tobalske *et al.*, 2003; Usherwood *et al.*, 2011). This explains why wingbeat frequency has been used as a proxy for flight costs in a range of ecological studies (Chapter 4, Taylor *et al.*, 2019; Usherwood *et al.*, 2011). For instance, Usherwood *et al.* (2011) observed that wingbeat frequency increased with all forms of aerodynamic power demand, particularly when individuals flew closely behind other birds in a cluster flock.

Yet there is a potential limitation in using wingbeat frequency as a proxy for power use, as while the minimum wingbeat frequency is assumed to occur at the minimum power speed (Pennycuick *et al.*, 1996), studies by Hedrick *et al.* (2003) and Tobalske *et al.* (2003) have shown that the minimum wingbeat frequency can occur at over twice the minimum power speed. This discrepancy, in addition to the unclear relationship between wingbeat frequency and airspeed, suggests that other kinematic parameters are also involved in the flight power output. Indeed, the aerodynamic power output of flapping flight can be modulated through wingbeat amplitude as well as wingbeat frequency. This follows from aerodynamic principles, which suggest that the aerodynamic forces exerted on the wings are proportional to the square of the velocity and the mechanical power output is proportional to the cube of the velocity. Assuming the two major flapping wing-kinematic parameters, wingbeat amplitude, A, and wingbeat frequency, f determine the aerodynamic power output of the flapping wings, the aerodynamic power output can be substituted for velocity and shown to vary with the cube of both amplitude and frequency:

$$\text{Power} \sim A^3 f^3$$

This likely explains why Tobalske *et al.* (2003) observed that the minimum wingbeat frequency recorded in several species did not coincide with the minimum power output.

Despite the importance of both wingbeat frequency and amplitude for overall power output, an overview of the scenarios under which birds are likely to increase one or the other is lacking. Indeed, examples from the literature suggest that the relationship is not straightforward (Table 5). Some studies show that birds can vary their power output with little to no variation in wingbeat frequency (Tobalske & Biewener, 2008; Torre-Bueno & Larochelle, 1978; Wang *et al.*, 2019). In other systems wingbeat frequency varies with the power output while the amplitude is unaltered (Ellerby & Askew, 2007). It is therefore unclear whether birds vary in how they increase power according to their flight mode (e.g. climbing versus level flight) or morphology.

What is clear is that a proxy for flight power should ideally integrate information on wingbeat frequency and amplitude in order to be most widely applicable. Two related acceleration proxies for energy expenditure have been proposed, both of which integrate information on stroke frequency and peak amplitude: Dynamic Body Acceleration (DBA) was proposed in 2006 as a metric that captures whole-body acceleration (Wilson *et al.*, 2020, 2006), and has been shown to vary with the energy expended by free-living auks in flight (Elliott *et al.*, 2013). However, the precise relationship between the DBA signal and wingbeat kinematics is unknown. Recently, Spivey and Bishop (2013) established a theoretical framework of how body acceleration can be related to the biomechanical power output of flapping flight, and used acceleration-based proxies such as root mean square values of heave and surge signals and wingbeat frequency to estimate the perceived body power. This assumes that the amplitude of the dorsoventral or “heave” accelerometer measurements varies with the wingbeat amplitude (Usherwood *et al.*, 2011). However, similarly to DBA, the exact relationship between body motions and wing motions, and how they vary together over a wingbeat cycle has not been established.

In this study, we examine the outlook for acceleration-based proxies for power use in flapping flight. Specifically, we (1) test whether the output of body-mounted accelerometers varies with wingbeat amplitude, using a novel methodology, (2) assess whether birds preferentially use wingbeat frequency or amplitude to increase their power output according to (a) their body mass or morphology, (b) whether power is required to increase their airspeed or climb rate. We address this by reviewing the experimental literature, where wingbeat kinematics have largely been quantified using high-speed video, and by conducting further trials, where we equip 13 species of bird with body-mounted accelerometers. Finally, we (3) examine these results within the broader theoretical framework underpinning our understanding of animal flight, to assess the prospect of acceleration-based metrics as proxies for flight costs across species and contexts.

Methods

Wind tunnel trials*:* Does the acceleration signal vary with wingbeat amplitude?

We quantified relative changes in wingbeat amplitude, using changes in magnetic field strength measured by the tri-axial magnetometer mounted on the bird's body, in relation to the movement of a small neodymium boron magnet attached to the leading edge of the wing (Wilson & Liebsch, 2003). The geomagnetic signal strength in each axis varied with both the angle to the magnet and the distance. We therefore calculated the vector sum from all three magnetometer channels, which varied solely with the distance to the magnet, giving a clear peak per wingbeat cycle when the magnet was closest to the sensor.

As the wing and body are coupled, the wing movement in the vertical (heave) results in body movement in the same axis. Furthermore, greater wingbeat amplitudes should result in greater vertical accelerations of the body. We examined the relationship between these events, comparing the maximum vector sum from the magnetometer with the body accelerations in the same wingbeat cycle.

Data were collected from two pigeons (*Columba livia*) and a dunlin (*Calidris alpina*), flying at a range of speeds in large, low turbulence wind tunnels. Pigeons were equipped with Daily Diary (DD) data loggers (Wildbyte Technologies, Swansea University, UK), sampling acceleration at 150 Hz and magnetic field strength at 13 Hz. Loggers had the following dimensions: 22 x 15 x 9 mm and a total tag mass that was less than 3% of the bird body mass. A small neodymium magnet (8 × 2 mm, 0.19 g) was taped to the leading edge of the wing, close to the wing root (Figure 1 A). Each bird was equipped with two units; one on the upper back and another on the lower back. The logger at the top of the back was positioned close to the magnet, whereas the logger on the lower back was sufficiently far from the magnet not to be influenced by it. The second logger allowed us to control for the potential influence of changing geomagnetic field strength (due to changes in bird trajectory) on the magnetometer output. The loggers and the magnet were attached with micropore tape. Experiments were performed between 25/01/2019 and 01/02/2019 in the wind tunnel of the Max Planck Institute for Ornithology, Germany, under ethical approval Gz.: 55.2-1-54-2532-86-2015 granted by the government of Upper Bavaria, “Sachgebiet 54 – Verbraucherschutz, Veterinärwesen, 80538 München”.

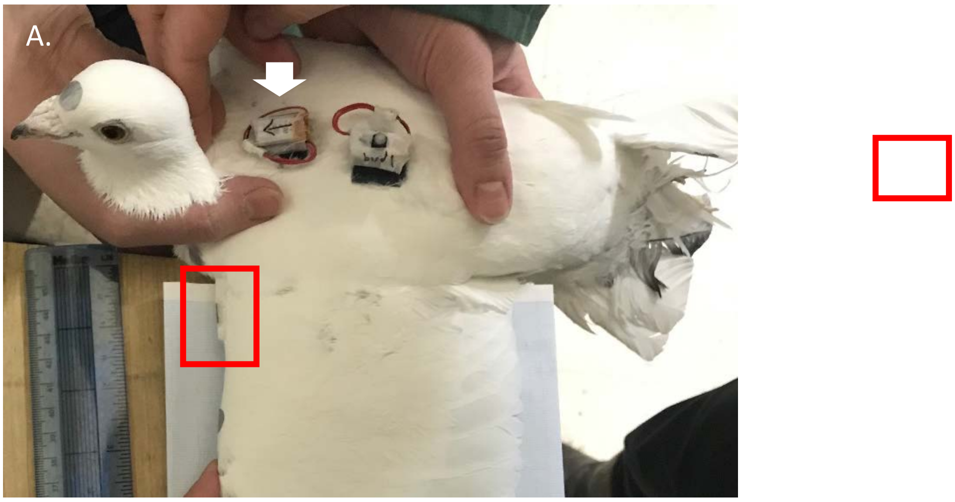

Figure 1. Setup of the Daily Diary (DD)and magnet (highlighted by the red rectangle) on (A) a pigeon and (B) the dunlin. The arrow indicates the DD used in the analysis

The dunlin flight trials were conducted in 2017 in the avian wind tunnel in Lund University, Sweden. Similarly to the wind tunnel used for pigeon flights, this wind tunnel is designed for bird flight studies, with comparable performance characteristics (Pennycuick *et al.*, 1997). A small neodymium magnet (4 × 2 mm, 0.02 g) was attached to the wing of the dunlin following the same procedure as pigeons. A single logger (Technosmart Europe, Guidonia-Montecelio, Italy; 16 × 24 × 12 mm, 2.6 g including battery, equivalent to 4.8% of the bird’s body mass) was attached to the back of the dunlin using micropore tape (Figure 1 B). This logger recorded acceleration and magnetometer data at 100 Hz. Ethical permission was obtained from Swansea University AWERB, permit number 030718/66.

Assessing the relationship between wingbeat amplitude and frequency

Accelerometers were attached to 13 species of birds (Table 1) to examine the relationship between wingbeat frequency and amplitude and whether birds are more likely to vary one parameter or the other to increase their power output, according to their mass and morphology.

To calculate wing loading and aspect ratio, wingspan, area, and body mass were either measured directly (following Pennycuick, 2008) or taken from the literature (Table 1). In order to assess the role of wing loading independently from body mass, we calculated the residual wing loading as the residuals of the linear regression between log(wing loading) and log(body Mass) (Lee *et al.*, 2008). A high residual wing loading indicates a species characterised by a higher wing loading for any given mass.

All species were tagged with accelerometers recording tri-axial acceleration at 40 Hz (except common guillemots and barn owls, where the sampling rate was 50 Hz) (Table 1). An examination of accelerometer data revealed some slight variation in sampling rate between logger types (up to 3 Hz), which was accounted for in the calculation of wingbeat frequency. Tags were attached to the back feathers using Tesa tape (Wilson *et al.*, 1997) in all species apart from pigeons, where tags were attached via Velcro strips glued to the back feathers (Chapter 2, Biro *et al.*, 2002). The total mass of the tag, including housing and attachments was kept under 5% of bird body mass in most cases. Ethical permissions are detailed on p.5 of the thesis.

Flapping flight was identified visually from the acceleration data (Shepard *et al.*, 2008) for both wind tunnel and free flight data. Only periods of consistent flapping, with no interruption or progressive changes in amplitude, were selected for the analysis of wind tunnel data.

Wingbeat frequency and heave amplitude (amplitude of the vertical body acceleration within a wingbeat) were quantified as follows: Peaks in heave acceleration resulting from the downstroke of the wingbeat (Figure 2) were identified by smoothing the heave signal over 3-5 events. A second-order derivative was applied to identify the positive-to-negative turning points. Peaks were marked when the differential channel exceeded a threshold within 5 points of the turning point. Thresholds were selected so that they only captured wingbeat peaks, as characterised by a high heave acceleration (around 2 *g*). The section between each marked peak was considered as one wingbeat. We measured the duration of each wingbeat based on the number of points from one peak to the other. The heave amplitude was calculated as the difference between the highest and lowest values of raw heave recorded during the wingbeat. It was not necessary to smooth the heave acceleration data to aid peak identification in guillemots, due to their high wingbeat frequency, which resulted in a relatively clean signal. Peak identification was conducted in R version 4.0.2 (R Core Team, 2020) for thick-billed murres, common guillemots, pigeons (homing flights only), and tropicbirds, all other data were processed using DDMT.

Table 1. Datasets in the study, along with the source of body mass and wing morphology data, where these were taken from the literature.

Species	**Location**	**N**	**Tag type**	**Data from literature**	**Source**
Brünnich's guillemot *Uria lomvia*	Coats Island, Nunavut, Canada	13	Daily Diary	Wings	Orben *et al.*, 2015, aspect ratio from Spear & Ainley, 1997
Common guillemot *Uria aalge*	Puffin Island, UK	6	AxyTrek	Mass, Wings	Spear & Ainley, 1997
Northern fulmar *Fulmarus glacialis*	Saltee Islands, Ireland	3	Daily Diary	Wings	Warham, 1977
Pigeon *Columba livia*	Radolfzell, Germany	9	Daily Diary	None	NA
Red-tailed tropicbird *Phaethon rubricauda*	Round Island, Mauritius	10	Daily Diary	None	NA
Great frigatebird *Frigata magnificens*	Europa Island	3	Daily Diary	None	NA
Black-legged kittiwake *Rissa tridactyla*	Middleton Island, Alaska, USA	3	Daily Diary	Wings	Pennycuick, 1997, aspect ratio from Spear & Ainley, 1997 (n = 2)
Imperial cormorant *Phalancrocorax atriceps*	Punta Leon, Argentina	5	Daily Diary	Mass, Wings	Quintana *et al.*, 2011, Spear & Ainley, 1997 (n = 1)
Barn owl *Tyto alba*	Switzerland	10	AxyTrek	None	NA
Grey-headed albatross *Thalassarche chrysostoma*	Marion Island, South Africa	5	Daily Diary	Mass, Wings	Phillips *et al.*, 2004, aspect ratio from Spear & Ainley, 1997 (n = 1)
Wandering albatross *Diomedea exulans*	Marion Island, South Africa	6	Daily Diary	Mass, Wings	Pennycuick, 1997; Pennycuick, 2008
Streaked shearwater *Calonectris leucomelas*	Awashima Island, Japan	5	Daily Diary	Wings	Shirai *et al.*, 2013
Dunlin *Calidris alpina*	Sweden	1	Axy XS	Mass, Wings	Hentze, 2012

Wingbeat frequency and heave amplitude (amplitude of the vertical body acceleration within a wingbeat) were quantified as follows: Peaks in heave acceleration resulting from the downstroke of the wingbeat (Figure 2) were identified by smoothing the heave signal over 3-5 events. A second-order derivative was applied to identify the positive-to-negative turning points. Peaks were marked when the differential channel exceeded a threshold within 5 points of the turning point. Thresholds were selected so that they only captured wingbeat peaks, as characterised by a high heave acceleration (around 2 *g*). The section between each marked peak was considered as one wingbeat. We measured the duration of each wingbeat based on the number of points from one peak to the other. The heave amplitude was calculated as the difference between the highest and lowest values of raw heave recorded during the wingbeat. It was not necessary to smooth the heave acceleration data to aid peak identification in guillemots, due to their high wingbeat frequency, which resulted in a relatively clean signal. Peak identification was conducted in R version 4.0.2 (R Core Team, 2020) for thick-billed murres, common guillemots, pigeons (homing flights only), and tropicbirds, all other data were processed using DDMT.

Some low outliers were recorded during short sections of non-flapping flight that were not excluded during the previous steps. High outliers were also recorded and were probably caused by false peak identification due to noise, take-offs, landings or shaking behaviours. Because each species presented a different range of wingbeat frequency and heave amplitudes, individual filtering was applied to each species individually (see Table S1) to exclude those outliers. Using filtered data, wingbeat frequency was calculated as the mean wingbeat duration divided by the total duration of 10 consecutive wingbeats for wild data and 5 wingbeats for wind tunnel data. Heave amplitude was also averaged over the same interval.

Modulation of wingbeat kinematics with climb rate and airspeed

The free flight of pigeons and tropicbirds was used to examine how birds vary their wingbeat kinematics (i.e. frequency and amplitude) to increase their speed and climb rate. GPS fixes were taken once per second for pigeons, and once per minute for tropicbirds (see Chapters 2, 3 and 4 for details). To estimate the airspeed (i.e. the speed relative to the air, see Pennycuick (2008)) GPS data were coupled with wind speed and direction, as recorded by a portable weather station (Kestrel 5500L, Kestrel instruments, USA) mounted on a 5 m pole. The weather station was stationed at the pigeons’ release site, and at the highest point of Round Island (265 m) where tropicbirds were nesting (see Chapters 2, 3 and 4 for details).

Airspeed was calculated using the formulas described in Chapter 2, and altitude was calculated from the pressure recorded by the Daily Diary (at 4 Hz), following the same procedure as in Chapter 2. Climb rate was calculated as the difference between consecutive values of altitude smoothed over 2 s.

To study how birds modulated their wingbeat kinematics with airspeed, we selected periods of level flapping flight, where the rate of change of altitude > -0.2 and < 0.2 m s^{-1}. In order to minimise the variability of airspeed in the climb rate analysis, points with speeds higher or lower than the overall mean airspeed ± standard deviation were excluded.

Airspeed and climb rates were averaged over 10 wingbeats for the pigeons. As the tropicbirds' airspeed was estimated every minute, wingbeat frequency and heave amplitude were averaged over 1-minute intervals instead. For each interval (10 wingbeats or 1 minute) the proportion of level flapping flight was calculated, and only intervals with $\geq$ 80% level flapping flight were included in the analysis. In addition, any interval including non-flapping flight was excluded.

Statistical analysis

We used linear models to examine whether the peak heave acceleration increased with the peak magnetometer vectorial sum (as a proxy for wingbeat amplitude) in both dunlin and pigeon wind tunnel flights. We also used linear models to assess whether the heave amplitude varied with wingbeat frequency, using separate models for wind tunnel and wild flights.

To test whether birds modulate their wingbeat amplitude more than their wingbeat frequency to increase their climb rate and airspeed, we ran two linear mixed-effects models (LMM) per species (tropicbirds and pigeons). These models included wingbeat amplitude as the response variable, expressed as a function of wingbeat frequency and the effect of either airspeed or climb rate on the slope of this relationship (i.e. the interaction between wingbeat frequency and either climb rate or airspeed). A positive interaction would indicate that birds increase their amplitude more than frequency to generate speed/climb rate, while a negative relationship would indicate that birds modulate wingbeat frequency more than amplitude. Individual was included as random intercept to account for uncontrolled variation related to morphology and motivation (only one trip per bird was included). We examined the distribution of residuals against fitted values using the function "plot.lme" from the R package “nlme” (Pinheiro et al., 2017, version 3.1-151) to verify that there was no pattern in the distribution of residuals, which would suggest a non-linear relationship. The function “simulateResiduals” from the R package DHARMa (Hartig & Hartig, 2017, version 0.4.5) was used to obtain QQ plots of the models and identify whether assumptions made to create the models were correct.

To investigate the effect of morphology on the way birds modulate wingbeat frequency and amplitude in flight, we calculated the standard deviation of wingbeat frequency and heave amplitude for each species, with the prediction that species constrained in their ability to vary either frequency or amplitude would show lower variation in either parameter. We used Spearman’s rank correlation tests and Pearson's product-moment correlation tests to see how the species-specific standard deviation of wingbeat frequency and heave amplitude (respectively) varied with morphological parameters i.e., aspect ratio, body mass, wing loading. Note that pigeon flights recorded in the wind tunnel were not used in this analysis as free flight had been recorded for pigeons, but the dunlin flights were included.

All the statistical analyses were performed using R version 4.0.2. LMMs were performed using the package “nlme” (Pinheiro *et al.*, 2017, version 3.1-151). Coefficients of determination were estimated using the package “MuMIn” (Barton & Barton, 2015, version 1.43.17), and the distribution of residuals was tested using “fitdistrplus” (Delignette-Muller *et al.*, 2015, version 1.1-5).

Results

Wind tunnel trials*:* Does the acceleration signal vary with wingbeat amplitude?

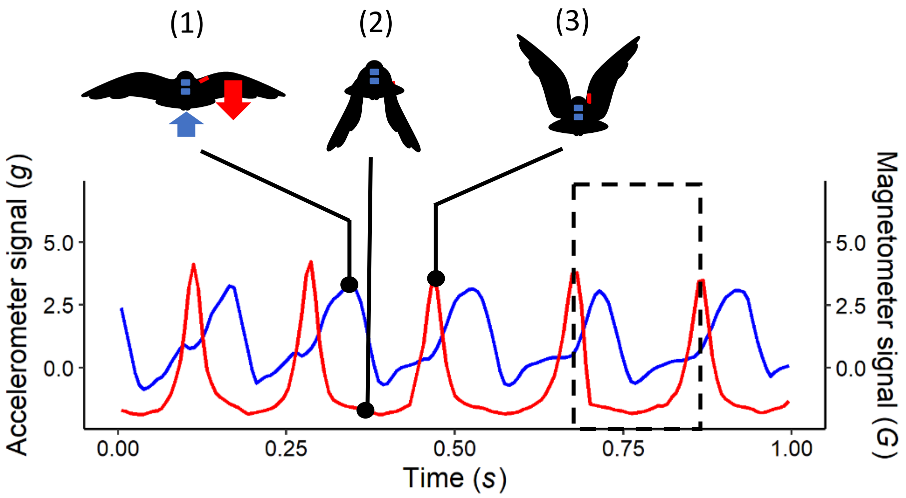

Figure 2. Comparison of the accelerometer (blue) and magnetometer (red) signals in the heave axis for 22 wingbeats of a pigeon flying in a wind tunnel. Peaks in heave occur in the middle of the downstroke (1) when the lift generation is at its maximum, troughs in the magnetometer signal correspond to the end of the downstroke (2) and peaks in the magnetometer signal correspond to the end of the upstroke (3). The dashed line represents one wingbeat cycle.

Pronounced cyclic changes in the magnetometer signal were evident through the wingbeat cycle (Figure 2) due to the changing magnetic field strength driven by the small neodymium boron magnet attached to the leading edge of the wing. The magnetometer signal was highest when the bird completed the upstroke, when the distance between the magnet and the transducer was at a minimum, and the signal decreased during the downstroke (Figure 2). The maximum heave acceleration occurred mid-downstroke when the wing traversed the body, corresponding to the point of maximal lift generation. This causes an obvious offset between the peak in magnetic and acceleration signals.

Nonetheless, we found a positive relationship between heave amplitude and the peak magnetometer vectorial sum in both species (Pigeons: estimate = 1.253, std. error = 1.02, t-value = 5.151, $p < 0.001$; Dunlin: estimate = 2.639, std. error = 0.085, t-value = 31.01, $p < 0.001$), showing that the rate of vertical displacement of the body increases with the wingbeat amplitude, even though the signals are offset within the wingbeat cycle. This was evident during periods of change in both signals (Figure 2) and when values were considered across a range of flight speeds for both the dunlin (Figure 3 A) and pigeons (Figure 3 B and C).

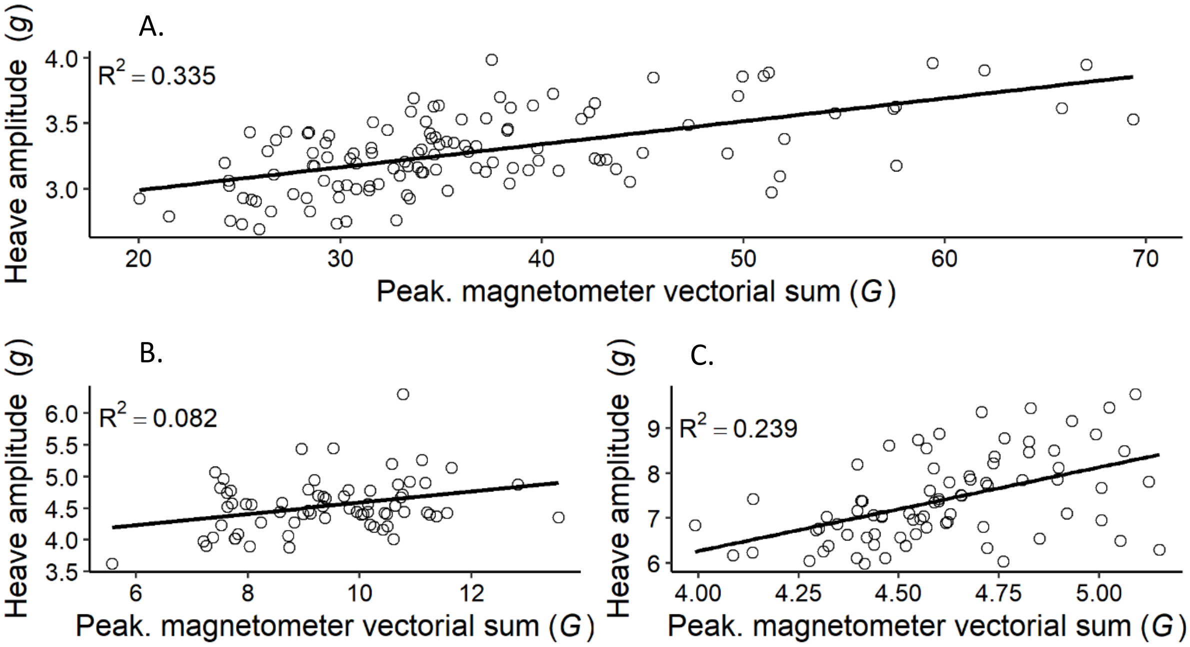

Figure 3. Comparison between the amplitude of the acceleration signal and the maximum of magnetometer vectorial sum during each wingbeat cycle for A. a dunlin, B. and C. two pigeons flying in wind tunnels across a range of flight speeds. The variation in absolute values from the magnetometer will vary due to the position of the magnet on the wing and its distance to the body-mounted magnetometer.

Assessing the relationship between wingbeat amplitude and frequency

There was a positive, linear relationship between wingbeat frequency and amplitude in all species apart from three of the four birds that use dynamic soaring: the northern fulmar, grey-headed albatross, and wandering albatross (Table 2). The R^2 values were low, although they were slightly higher for birds flying in the wind tunnel, where data were filtered and variation in both frequency and amplitude occurred primarily in relation to changes in flight speed (Table 2).

Species	**Signal amplitude (*g*)**	**Wingbeat frequency (Hz)**	**Slope**	**Intercept**	**p-value**	**R^2**	**Total wingbeats**
Dunlin*	3.2 ± 0.3	13.2 ± 0.9	0.110	1.833	0.000	0.112	73
Pigeon*	6.0 ± 0.7	6.7 ± 0.4	0.893	1.337	0.000	0.309	147
Pigeon	3.7 ± 0.4	5.2 ± 0.5	0.189	2.713	0.000	0.048	4,858
Barn Owl	2.4 ± 0.4	3.5 ± 0.3	0.518	0.531	0.000	0.162	134,919
Common Guillemot	2.5 ± 0.3	9.7 ± 0.6	0.206	0.541	0.000	0.170	31,349
Thick-billed Murre	1.3 ± 0.2	7.7 ± 0.5	0.180	-0.076	0.000	0.195	122,598
Imperial Cormorant	1.1 ± 0.2	5.7 ± 0.2	0.190	0.044	0.000	0.062	11,068
Red-tailed Tropicbird	1.8 ± 0.3	4.0 ± 0.3	0.527	-0.341	0.000	0.151	174,190
Black-legged Kittiwake	2.0 ± 0.4	4.0 ± 0.2	0.998	-1.915	0.000	0.383	21,767
Great Frigatebird	1.7 ± 0.3	2.6 ± 0.2	0.757	-0.213	0.000	0.256	2,805
Streaked shearwater	1.4 ± 0.1	4.1 ± 0.3	0.018	1.315	0.000	0.001	18,036
Northern Fulmar	1.3 ± 0.1	4.7 ± 0.3	-0.003	1.354	0.437	0.000	8,505
Grey-headed Albatross	1.4 ± 0.1	3.1 ± 0.2	0.016	1.325	0.500	-0.001	590
Wandering Albatross	1.1 ± 0.1	2.8 ± 0.2	0.043	0.952	0.207	0.001	533

Table 2: The relationship between the heave amplitude and wingbeat frequency for 12 species flying in the wild and 2 species flying in controlled conditions. An asterisk indicates where data were collected from birds flying in the wind tunnel. All other data were collected from birds operating in the wild.

We examined the standard deviation (s.d.) in wingbeat frequency and heave amplitude (as a proxy for wingbeat amplitude), in order to assess which birds were more likely to vary one or other kinematic parameter. The only significant correlation was between the residual wing loading and the s.d. of wingbeat frequency, which were positively correlated (Spearman's correlation: S = 202, $R^2 = 0.678$, $p = 0.042$) (Figure 4), showing that birds with higher wing loading than predicted by allometry had a relatively higher range in wingbeat frequencies.

There was some suggestion that the variation in wingbeat frequency was negatively correlated with aspect ratio and body mass (Figure 4), although neither trend was significant (Spearman's correlation with aspect ratio: S = 677.24, $R^2 = 0.187$, $p = 0.076$; Body mass: S = 686, $R^2 = 0.213$, $p = 0.067$). The same non-significant tendencies were found between heave amplitude and aspect ratio (Pearson's correlation: $\rho = -0.472$, $R^2 = 0.152$, $p = 0.10$) and body mass (Pearson's correlation: $\rho = -0.494$, $R^2 = 0.175$, $p = 0.08$).

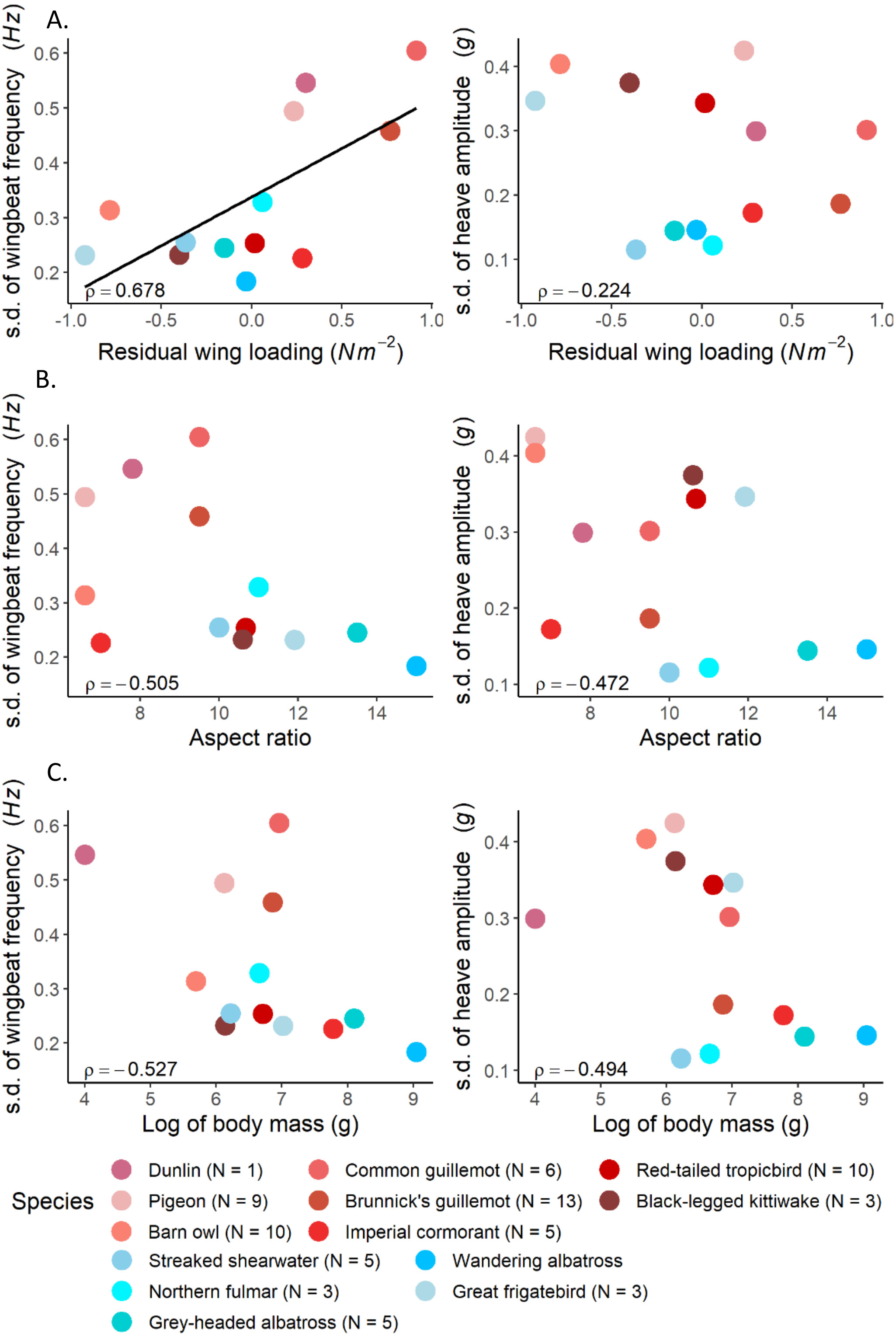

Figure 4. Variation in wingbeat frequency and amplitude as a function of the following morphological parameters for 13 bird species: A. residual wing loading, B. aspect ratio, and C. log of body mass.

Do birds modulate different kinematic parameters to increase speed and climb rate?

We found a positive effect of climb rate on the relationship between wingbeat frequency and amplitude for tropicbirds, demonstrating that they varied their wingbeat amplitude more to increase their climb rate (Table 3). However, we were not able to make any meaningful conclusion concerning pigeons as the fixed effects in the model explained only 1% of the variance of the response variable ($R^2_m = 0.01$, see Table 3).

We did not find any effect of airspeed on the relationship between wingbeat frequency and amplitude in tropicbirds ($p = 0.164$), nor in pigeons, as the model explained only 3% of the variability of the response variable ($R^2_m = 0.03$, see Table 4).

Table 3. Output of the model of amplitude as a function of wingbeat frequency and the interaction between wingbeat frequency and climb rate for red-tailed tropicbirds (n = 10) and pigeons (n = 9), using individual as a random factor.

Formula: Amplitude ~ WBF + WBF: V_z

A. Tropicbirds ($R^2_m = 0.50$, $R^2_c = 0.66$)				
	Estimate	**Std. Error**	**t-value**	**p**
(Intercept)	-2.275	0.056	-40.622	< 0.001
WBF	1.014	0.011	91.817	< 0.001
WBF: V_z	0.018	0.001	13.301	< 0.001
B. Pigeons ($R^2_m = 0.01$, $R^2_c = 0.42$)				
(Intercept)	3.882	0.132	29.524	< 0.001
WBF	-0.053	0.018	-3.013	0.003
WBF: V_z	-0.008	0.003	-3.256	0.001

Table 4. Output of the model of amplitude as a function of wingbeat frequency and the interaction between wingbeat frequency and airspeed in level flapping flight for red-tailed tropicbirds (n = 10) and pigeons (n = 9), using individual as a random factor.

Formula: Amplitude ~ WBF + WBF: Airspeed

A. Tropicbirds ($R^2_m = 0.11$, $R^2_c = 0.14$)				
	Estimate	**Std. Error**	**t-value**	**p**
(Intercept)	1.137	0.377	3.016	0.004

WBF	0.273	0.095	2.876	0.006
WBF: Airspeed	-0.003	0.002	-1.41	0.164
B. Pigeons ($R^2_m = 0.03$, $R^2_c = 0.42$)				
(Intercept)	3.714	0.229	16.198	< 0.001
WBF	-0.143	0.053	-2.688	0.008
WBF: Airspeed	0.006	0.002	3.95	< 0.001

Table 5. Summary of experimental evidence of the relationship between frequency, amplitude, power and other morphological data from the literature

Species	**Method**	**Flight mode**	**Speed (m s^{-1})**	**Remarks**	**Source**
Pigeons *Columba livia*	Field data – GPS and accelerometer measurements	Level, ascending and descending flight	10-18	As speed increased WBF – varied approx. U shaped WBA – increased At constant speed, as power increases WBF – increased WBA – decreased At ascending flight WBF – increased WBA – increased At accelerating flight WBF – increased WBA – increased	(Usherwood *et al.*, 2011)
Pigeon *Columba livia*	Platform – muscle force measurements and kinematics analysis with high-speed cameras	Take-off, level and landing	1.4-3.9	At different flight modes WBF – did not vary significantly WBA – decreased relatively before take-off and landing	(Tobalske & Biewener, 2008)
Swift *Apus apus*	Wind tunnel – PIV and kinematics analysis with high-speed cameras	Steady flight	8-9.2	As speed increased WBF – decreased WBA – increased	(Henningsson *et al.*, 2008)
European starling *Sturnus vulgaris*	Wind tunnel – kinematics analysis recorded on magnetic tape	Burst flapping and gliding	6-18	As speed increased WBF – constant WBA – decreased at lower speed and increased at higher speed Met. power – did not vary significantly	(Torre-Bueno & Larochelle, 1978)
European starling *Sturnus vulgaris*	Wind tunnel – respirometry masks and kinematics analysis with high-speed cameras	Steady flight	6-14	As speed increased WBF – increased (less significant) WBA – increased (less significant) Power – increased	(Ward *et al.*, 2001)
Cockatiel *Nymphicus hollandicus*	Wind tunnel – *in vivo* pectoralis muscle length change measurements	Steady flight	0-16	As speed increased Power – increased (approx. U shaped) WBF – reduced (highest at the lower range)	(Morris & Askew, 2010)
Cockatiels *Nymphicus hollandicus*	Wind tunnel – *in vivo* surgical procedures and kinematics analysis with high-speed cameras	Steady flight	0-14	As speed increased WBF – reduced at lower speed and increased at higher speed (approx. U shaped)	(Hedrick *et al.*, 2003; Tobalske *et al.*, 2003)

				Power – varied (approx. U shaped)	
Thrush nightingale *Luscinia luscinia*	Wind tunnel – PIV and kinematics analysis with high-speed cameras	Steady flight	5-10	As speed increased WBF – no significant variation WBA – no significant variation	(Rosén *et al.*, 2004)
Thrush nightingale *Luscinia luscinia* **Teal** *Anas crecca*	Wind tunnel – Wingbeat frequency measured using a shutter stroboscope and video recording	Level flight	5-16	As mass increased WBF – increased As speed increased WBF – varied in U shape (less significantly)	(Pennycuick *et al.*, 1996)
Barn Swallows *Hirundo rustica*	Wind tunnel – energetic costs measured by DLW, and kinematics analysis is by video recordings	Level flight	8-11.5	As speed increases WBF – varied as U shaped Intraspecific: As mass increased WBF – increased Power - increased	Schmidt-Wellenburg *et al.*, 2007
Zebra finch *Taeniopygia guttata*	Wind tunnel – kinematics analysis with high-speed cameras	Intermittent flap-bounding flight	0-14	As speed increased WBF – increased (less significant) WBA – decreased (significantly)	(Tobalske *et al.*, 1999)
Zebra finches *Taeniopygia guttata* **Budgerigars** *Melopsittacus undulates*	Wind tunnel – muscle *in vivo* pectoralis fascicle strain measurements, and kinematics by high-speed video recordings	Level flight	0-14 (ZF) 4-16 (Burg)	Zebra finch: As speed increased WBF – varied approx. U shaped WBA – increased only at hovering Budgerigars: As speed increased WBF – varied approx. U shaped WBA – did not vary significantly	(Ellerby & Askew, 2007)
Blue tits *Cyanistes caeruleus*	Flight inside a custom-built box – kinematics analysis with high-speed cameras	Take-off	3.4	Intraspecific: As wing loading increased WBF – decreased WBA – did not vary Power – decreased AR – increased	(McFarlane *et al.*, 2016)
Eurasian tree sparrow *Passer montanus*	Experiments in flight chamber – kinematics analysis with high-speed cameras	Vertical flight	-	Intraspecific: As maximum load-lifted WBF – no significant variation WBF – no significant variation	(Wang *et al.*, 2019)
Phasianidae family	Flight chamber – muscle force measurements and kinematics analysis with high-speed cameras	Take-off flight	4.9	Intraspecific: As mass increased WBF – decreased Power – decreased	(Askew *et al.*, 2001)
Passerines and woodpeckers	Field flight and data from other studies – kinematics analysis with high-speed cameras	Intermittent flight	4.7-12.7	Intraspecific: As mass increased WBF – decreased Speed – increased Flap % – increased	(Tobalske, 2001)
Corvidae family: gray jay *Perisoreus canadensis*, **black-billed magpie** *Pica hudsonia*, **American crow** *Corvus brachyrhynchos*, **and common raven** *Corvus corax*	Vertical flight chamber – flight muscle force measurements and kinematics analysis with high-speed cameras	Burst take-off and vertical flight	-	Interspecific: As mass increased Power – reduced WBF – reduced	(Jackson & Dial, 2011)

Fruit-eating bat *Cynopterus brachyotis*	Wind tunnel – experiments with robotic bat wing	Level flight	5	As power increased WBF – increased (cubic relationship) WBA – increased (linear relationship)	(Bahlman *et al.*, 2014)
Zebra finch *Taeniopygia guttata*	Surgical procedures to measure flight muscle activity	?	-	As power increased WBF – no significant effect WBA – increased effectively	(Bahlman *et al.*, 2020)
Ruby-throated hummingbird *Archilochus colubris*	Flight experiments in an airtight cube – varying air density treated with heliox	Hovering	-	As power increased WBF – increased (less significant) WBA – increased (significantly) As air density decreased Power – increased	(Chai & Dudley, 1995)
Ruby-throated hummingbird *Archilochus colubris*	Flight experiments in an airtight cube – varying air density treated with helium	Hovering	-	As power increased WBF – did not vary WBA – increased (significantly) As air density decreased Power – increased	(Chai & Dudley, 1996)
Ruby-throated hummingbird *Archilochus colubris*	Cubic testing arena - surgical procedures to measure flight muscle activity and kinematics analysis with high-speed cameras	Hovering	-	As load-lifted increased WBF – did not vary WBA – increased (significantly) As air density decreased WBF – did not vary WBA – increased (significantly)	(Mahalingam & Welch, 2013)
Rufous hummingbirds *Selasphorus rufus*	Wind tunnel – kinematics analysis with high-speed cameras	Hovering and level flight	0-12	As speed increased WBF – did not vary WBA – increased (approx. U shaped)	(Bret W Tobalske *et al.*, 2007)

Discussion

The total power output of bird flight varies between level flight, accelerating flight, ascending/descending, manoeuvring, and load carrying. Birds are expected to modulate the required power output predominantly through wingbeat frequency and/ or wingbeat amplitude changes, as first principles state that the power output of flapping flight is directly proportional to the cube of both the wingbeat frequency and amplitude. Metrics from onboard accelerometers should be able to provide insight into the relative importance of both parameters. Here we confirm this, by showing that the amplitude of the dorsoventral body acceleration (heave) and the wingbeat amplitude are positively related within a wingbeat cycle. The variance in the relationship between these two parameters is likely explained by the fact that birds did not always fly level in the wind tunnel and sometimes the flight style was closer to manoeuvring than steady level flight. It could also be affected by the stability of the magnet attachment, which could result in additional noise. The fact that the R^2 was lower for one pigeon than the other (0.08 versus 0.24) supports the idea that the variability is associated with individual behaviour and measurement error.

The question that follows is, to what extent do birds modify wingbeat frequency and/ or amplitude to increase their power output? Our finding that both wingbeat frequency and amplitude increased with flight speed for two species flying in a wind tunnel was consistent with other experimental studies, which tend to report a positive relationship between wingbeat frequency, amplitude and airspeed (Henningsson *et al.*, 2008; Torre-Bueno & Larochelle, 1978; Usherwood *et al.*, 2011; Ward *et al.*, 2001).

It was therefore surprising that we found no relationship between wingbeat frequency, amplitude and airspeed in pigeons undertaking homing flights. The discrepancy between our wind tunnel and "wild" flights may be related to the extremely variable nature of the pigeon flight when flying solo in the wild (Chapter 2). Indeed, the extreme (and costly) variation in speed and rate of change in altitude has been proposed as a predator avoidance strategy, which birds such as pigeons may adopt when flocking is not possible (Chapter 2). This variability is relevant in the current context as it could mask a relationship between wingbeat frequency, amplitude and airspeed in homing flights. There are also likely to be errors in the estimation of airspeed, as wind was collected near the release site and variation in space and with height, was not accounted for. These errors will be larger for the tropicbird study, where GPS locations were recorded once a minute and wind speeds were taken tens of kilometres from the bird locations, which likely explains the lack of a correlation between kinematic parameters and airspeed in this system. Nonetheless, the positive relationship between kinematic parameters and climb rates for tropicbirds in their foraging flights shows that expected relationships can be resolved using high frequency data from birds flying in the wild (as unlike wind, pressure was recorded with sub-second resolution).

Our finding that wingbeat frequency and amplitude were positively correlated in 10 of the 13 species examined, also suggests that both parameters tend to be involved in power production across a range of morphologies and body mass. However, the low R^2 values indicate that they are unlikely to covary in a straightforward manner. Bahlman *et al.*, (2020) demonstrate that in zebra finches (*Taeniopygia guttata*), variation in the net power output during a wingbeat cycle is most closely related to the wingbeat amplitude. Our findings that tropicbirds increase their wingbeat amplitude to a greater extent than frequency during climbing flight are in line with this, and a range of studies show that birds tend to increase their wingbeat amplitude more in the most energetically demanding forms of flight (Table 5).

For instance, while Usherwood *et al.* (2011) found that wingbeat frequency increased during all flight modes for pigeons flying in a flock, the wingbeat amplitude increased with induced power, climb rate, and accelerating flight. Parallels can be found in pigeons studied by Tobalske and Biewener (2008), which varied their wingbeat amplitude (but not frequency) during take-off and landing, and zebra finches increased their wingbeat amplitude substantially during hovering, but not in level flight (Ellerby & Askew, 2007). Other studies have shown that wingbeat amplitude increased to meet the power demand associated with increasing load in hovering/vertical flight, whereas the wingbeat frequency was flat (Mahalingam & Welch, 2013). Similarly, hummingbirds have been shown to increase their wingbeat amplitude when flying in low density air, both in the laboratory (Chai & Dudley, 1995; Chai & Dudley, 1996; Mahalingam & Welch, 2013) and in the field along natural elevational gradients (Altshuler & Dudley, 2006; Altshuler & Dudley, 2003), with wingbeat amplitudes up to 180° at flight failure densities.

There are also exceptions to the general trends that emerge in the literature. For instance, while a U-shaped relationship was found between wingbeat amplitude and flight speed in hummingbirds, with the highest amplitudes in hovering, but wingbeat frequency did not vary significantly (Tobalske *et al.*, 2007). It could be argued that hummingbirds have very particular kinematics, but zebra finches were also found to modulate wingbeat amplitude over wingbeat frequency for high power-demanding events (Bahlman *et al.*, 2020).

Overall there was no compelling evidence that body mass or morphology affect whether birds use wingbeat frequency or amplitude to increase their power output. There was a suggestion that flight style might be important, as the three species that did not show a significant relationship between wingbeat frequency and amplitude (northern fulmars, grey-headed- and wandering albatrosses) all use dynamic soaring. These species also have a lower residual wing loading and tended to vary their wingbeat frequency less than species such as common guillemot or pigeons. It may be that species with high aspect ratios and low wing loading are more constrained in terms of their wingbeat frequencies, however, a larger dataset would be needed to investigate how morphological factors combine to determine the best, or feasible, methods of increasing power output.

This study has focused on variation in wingbeat frequency and amplitude. However, birds can also vary the aerodynamic forces through changes in the wingbeat pattern and wing flexing and it is unclear whether and how these parameters could be captured by body-mounted accelerometers. The other kinematics parameters that have a significant role in power output include the upstroke-to-downstroke ratio, stroke-plane angle, span ratio, and angle of attack. In experiments with a house martin (*Delichon urbicum*) and a thrush nightingale (*Luscinia luscinia*), the upstroke-to-downstroke ratio and span ratio varied with increasing flight speed, whereas the wingbeat frequency and amplitude did not (Rosén *et al.*, 2004; Rosén *et al.*, 2007). Similarly, Ward *et al.* (2001) showed that for a European starling (*Sturnus vulgaris*), the wingbeat frequency and amplitude were the least important parameters associated with an increase in power, compared to variations in the stroke-plane angle and downstroke ratio. Finally, several species have been shown to vary the body angle and stroke-plane angle to support weight at low speeds and augment thrust at higher speeds, and frequency and amplitude varied to a lesser degree in these scenarios (Tobalske & Dial, 1996). The situation is potentially even more complex in intermittent flap-bounding flight, and indeed, cycle time spent flapping, flapping-and-bounding duration, and the number of flaps were more important than wingbeat frequency and amplitude for a zebra finch increasing its flight speed (Tobalske *et al.*, 1999).

In conclusion, body mounted accelerometers can provide information on wingbeat amplitude as well as frequency, both of which show substantial variation when considered across free-ranging flights of multiple species. Acceleration metrics that incorporate variation due to wingbeat frequency and amplitude, such as DBA and RMS (Spivey & Bishop, 2013; Wilson *et al.*, 2006) should therefore be more robust proxies for power use than wingbeat frequency alone. In support of this, DBA has been shown to be a better predictor of overall energy expenditure (estimated with doubly labelled water) than flight time or wingbeat frequency in auks (Elliott *et al.*, 2013; Elliott *et al.*, 2014). Nonetheless, wingbeat frequency and amplitude are only partial descriptors of the wingbeat kinematics associated with power, and other factors, such as stroke angle, play a substantial role in power production for certain flight types (Berg & Biewener, 2008). Further experimental work that provides independent estimates of the power output will provide insight into the extent that this can be approximated by metrics using body-mounted accelerometers.

References

Altshuler, D. L., & Dudley, R. (2006). The physiology and biomechanics of avian flight at high altitude. *Integrative and Comparative Biology*, *46*(1), 62–71. doi: 10.1093/icb/icj008

Altshuler, Douglas L, & Dudley, R. (2003). Kinematics of hovering hummingbird flight along simulated and natural elevational gradients. *Journal of Experimental Biology*, *206*(18), 3139–3147.

Askew, G. N., Marsh, R. L., & Ellington, C. P. (2001). The mechanical power output of the flight muscles of blue-breasted quail (*Coturnix chinensis*) during take-off. *Journal of Experimental Biology*, *204*(21), 3601–3619.

Bahlman, J. W., Baliga, V. B., & Altshuler, D. L. (2020). Flight muscle power increases with strain amplitude and decreases with cycle frequency in zebra finches (*Taeniopygia guttata*). *Journal of Experimental Biology*, *223*(21), jeb225839.

Bahlman, J. W., Swartz, S. M., & Breuer, K. S. (2014). How wing kinematics affect power requirements and aerodynamic force production in a robotic bat wing. *Bioinspiration & Biomimetics*, *9*(2), 25008.

Barton, K., & Barton, M. K. (2015). Package 'MuMIn.' *Version*, *1*, 18.

Berg, A. M., & Biewener, A. A. (2008). Kinematics and power requirements of ascending and descending flight in the pigeon (*Columba livia*). *Journal of Experimental Biology*, *211*(7), 1120–1130. doi: 10.1242/jeb.010413

Biro, D., Guilford, T., Dell'Omo, G., & Lipp, H. P. (2002). How the viewing of familiar landscapes prior to release allows pigeons to home faster: Evidence from GPS tracking. *Journal of Experimental Biology*, *205*(24), 3833–3844.

Bishop, C. M., Spivey, R. J., Hawkes, L. A., Batbayar, N., Chua, B., Frappell, P. B., … Butler, P. J. (2015). The roller coaster flight strategy of bar-headed geese conserves energy during Himalayan migrations. *Science*, *347*(6219), 250–254. doi: 10.1126/science.1258732

Butler, P. J. (2016). The physiological basis of bird flight. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*(1704), 20150384. doi: 10.1098/rstb.2015.0384

Chai, Peng, & Dudley, R. (1995). Limits to vertebrate locomotor energetics suggested by hummingbirds hovering in heliox. *Nature*, *377*(6551), 722–725.

Chai, PENG, & Dudley, R. (1996). Limits to flight energetics of hummingbirds hovering in hypodense and hypoxic gas mixtures. *The Journal of Experimental Biology*, *199*(10), 2285–2295.

Delignette-Muller, M. L., Dutang, C., Pouillot, R., Denis, J.-B., & Delignette-Muller, M. M. L. (2015). *Package 'fitdistrplus.'* R Foundation for Statistical Computing, Vienna, Austria. URL http://www. R ….

Ellerby, D. J., & Askew, G. N. (2007). Modulation of pectoralis muscle function in budgerigars Melopsitaccus undulatus and zebra finches *Taeniopygia guttata* in response to changing flight speed. *Journal of Experimental Biology*, *210*(21), 3789–3797.

Elliott, Kyle H, Le Vaillant, M., Kato, A., Speakman, J. R., & Ropert-Coudert, Y. (2013). Accelerometry predicts daily energy expenditure in a bird with high activity levels. *Biology Letters*, *9*(1), 20120919.

Elliott, Kyle Hamish, Chivers, L. S., Bessey, L., Gaston, A. J., Hatch, S. A., Kato, A., … Hare, J. F. (2014). Windscapes shape seabird instantaneous energy costs but adult behavior buffers impact on offspring. *Movement Ecology*, *2*(1), 1–15.

Furness, R. W., & Bryant, D. M. (1996). Effect of Wind on Field Metabolic Rates of Breeding Northern Fulmars. *Ecology*, *77*(4), 1181–1188. doi: 10.2307/2265587

Hedrick, T. L., Tobalske, B. W., & Biewener, A. A. (2003). How cockatiels (Nymphicus hollandicus) modulate pectoralis power output across flight speeds. *Journal of Experimental Biology*, *206*(8), 1363–1378.

Henningsson, P., Spedding, G. R., & Hedenstrom, A. (2008). Vortex wake and flight kinematics of a swift in cruising flight in a wind tunnel. *Journal of Experimental Biology*, *211*(5), 717–730.

Hentze, N. T. (2012). *Characteristics of over-ocean flocking by Pacific dunlins (Calidris alpina pacifica)*. Science: Biological Sciences Department.

Hicks, O., Burthe, S. J., Daunt, F., Newell, M., Butler, A., Ito, M., … Green, J. A. (2018). The energetic cost of parasitism in a wild population. *Proceedings of the Royal Society B:*

Biological Sciences, *285*(1879), 20180489.

Jackson, B. E., & Dial, K. P. (2011). Scaling of mechanical power output during burst escape flight in the Corvidae. *Journal of Experimental Biology*, *214*(3), 452–461.

Lee, S. Y., Scott, G. R., & Milsom, W. K. (2008). Have wing morphology or flight kinematics evolved for extreme high altitude migration in the bar-headed goose? *Comparative Biochemistry and Physiology Part C: Toxicology & Pharmacology*, *148*(4), 324–331.

Mahalingam, S., & Welch Jr, K. C. (2013). Neuromuscular control of hovering wingbeat kinematics in response to distinct flight challenges in the ruby-throated hummingbird, *Archilochus colubris*. *Journal of Experimental Biology*, *216*(22), 4161–4171.

McFarlane, L., Altringham, J. D., & Askew, G. N. (2016). Intra-specific variation in wing morphology and its impact on take-off performance in blue tits (*Cyanistes caeruleus*) during escape flights. *Journal of Experimental Biology*, *219*(9), 1369–1377.

Morris, C. R., & Askew, G. N. (2010). The mechanical power output of the pectoralis muscle of cockatiel (*Nymphicus hollandicus*): the in vivo muscle length trajectory and activity patterns and their implications for power modulation. *Journal of Experimental Biology*, *213*(16), 2770–2780.

Norberg, U. M. (2012). *Vertebrate flight: mechanics, physiology, morphology, ecology and evolution* (Vol. 27). Springer Science & Business Media.

Orben, R. A., Paredes, R., Roby, D. D., Irons, D. B., & Shaffer, S. A. (2015). Body size affects individual winter foraging strategies of thick-billed murres in the Bering Sea. *Journal of Animal Ecology*, *84*(6), 1589–1599.

Pennycuick, C. (1997). Actual and’optimum’flight speeds: field data reassessed. *The Journal of Experimental Biology*, *200*(17), 2355–2361.

Pennycuick, C. J., Alerstam, T., & Hedenström, A. (1997). A new low-turbulence wind tunnel for bird flight experiments at Lund University, Sweden. *Journal of Experimental Biology*, *200*(10), 1441–1449.

Pennycuick, C J, Klaassen, M., Kvist, A., & Lindström, Å. (1996). Wingbeat frequency and the body drag anomaly: wind-tunnel observations on a thrush nightingale (*Luscinia luscinia*) and a teal (*Anas crecca*). *The Journal of Experimental Biology*, *199*(12), 2757–2765.

Pennycuick, Colin J. (2008). *Modelling the flying bird*. Elsevier.

Phillips, R. A., Silk, J. R. D., Phalan, B., Catry, P., & Croxall, J. P. (2004). Seasonal sexual segregation in two *Thalassarche* albatross species: competitive exclusion, reproductive role specialization or foraging niche divergence? *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *271*(1545), 1283–1291.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., Heisterkamp, S., Van Willigen, B., & Maintainer, R. (2017). Package ‘nlme.’ *Linear and Nonlinear Mixed Effects Models, Version*, *3*(1).

Portugal, S. J., Hubel, T. Y., Fritz, J., Heese, S., Trobe, D., Voelkl, B., … Usherwood, J. R. (2014). Upwash exploitation and downwash avoidance by flap phasing in ibis formation flight. *Nature*, *505*(7483), 399–402. doi: 10.1038/nature12939

Quintana, F., Wilson, R., Dell’Arciprete, P., Shepard, E., & Laich, A. G. (2011). Women from Venus, men from Mars: inter-sex foraging differences in the imperial cormorant Phalacrocorax atriceps a colonial seabird. *Oikos*, *120*(3), 350–358.

R Core Team. (2020). *R: A language and environment for statistical computing*. Retrieved from https://www.r-project.org/

Rosén, M., Spedding, G. R., & Hedenstrom, A. (2004). The relationship between wingbeat kinematics and vortex wake of a thrush nightingale. *Journal of Experimental Biology*, *207*(24), 4255–4268.

Rosén, M., Spedding, G. R., & Hedenström, A. (2007). Wake structure and wingbeat kinematics of a house-martin *Delichon urbica*. *Journal of The Royal Society Interface*, *4*(15), 659–668.

Sankey, D. W. E., & Portugal, S. J. (2019). When flocking is costly: reduced cluster-flock density over long-duration flight in pigeons. *Science of Nature*, *106*(7–8). doi: 10.1007/s00114-019-1641-x

Sapir, N., Wikelski, M., Mccue, M. D., Pinshow, B., & Nathan, R. (2010). Flight modes in migrating European bee-eaters: Heart rate may indicate low metabolic rate during soaring and gliding. *PLoS ONE*, *5*(11), 1–13. doi: 10.1371/journal.pone.0013956

Sato, K., Daunt, F., Watanuki, Y., Takahashi, A., & Wanless, S. (2008). A new method to quantify prey acquisition in diving seabirds using wing stroke frequency. *Journal of Experimental Biology*, *211*(1), 58–65. doi: 10.1242/jeb.009811

Schmidt-Wellenburg, C. A., Biebach, H., Daan, S., & Visser, G. H. (2007). Energy expenditure and wing beat frequency in relation to body mass in free flying Barn Swallows (*Hirundo rustica*). *Journal of Comparative Physiology B*, *177*(3), 327–337.

Shepard, E., Wilson, R., Quintana, F., Gómez Laich, A., Liebsch, N., Albareda, D., … McDonald, D. (2008). Identification of animal movement patterns using tri-axial accelerometry. *Endangered Species Research*, *10*(1), 47–60. doi: 10.3354/esr00084

Shirai, M., Niizuma, Y., Tsuchiya, K., Yamamoto, M., & Oka, N. (2013). Sexual size dimorphism in Streaked Shearwaters *Calonectris leucomelas*. *Ornithological Science*, *12*(1), 57–62.

Spear, L. B., & Ainley, D. G. (1997). Flight behaviour of seabirds in relation to wind direction and wing morphology. *Ibis*, *139*(2), 221–233. doi: 10.1111/j.1474-919x.1997.tb04620.x

Spivey, R. J., & Bishop, C. M. (2013). Interpretation of body-mounted accelerometry in flying animals and estimation of biomechanical power. *Journal of the Royal Society Interface*, *10*(87). doi: 10.1098/rsif.2013.0404

Taylor, L. A., Taylor, G. K., Lambert, B., Walker, J. A., Biro, D., & Portugal, S. J. (2019). Birds invest wingbeats to keep a steady head and reap the ultimate benefits of flying together. *PLOS Biology*, *17*(6), e3000299. doi: 10.1371/journal.pbio.3000299

Tobalske, B. W., Hedrick, T. L., Dial, K. P., & Biewener, A. A. (2003). Comparative power curves in bird flight. *Nature*, *421*(6921), 363–366. doi: 10.1038/nature01284

Tobalske, Bret W., & Dial, K. P. (1996). Flight kinematics of black-billed magpies and pigeons over a wide range of speeds. *Journal of Experimental Biology*, *199*(2), 263–280.

Tobalske, Bret W., Peacock, W. L., & Dial, K. P. (1999). Kinematics of flap-bounding flight in the zebra finch over a wide range of speeds. *Journal of Experimental Biology*, *202*(13), 1725–1739.

Tobalske, B. W. (2001). Morphology, velocity, and intermittent flight in birds. *American Zoologist*, *41*(2), 177–187.

Tobalske, B. W., & Biewener, A. A. (2008). Contractile properties of the pigeon supracoracoideus during different modes of flight. *Journal of Experimental Biology*, *211*(2), 170–179.

Tobalske, B. W., Warrick, D. R., Clark, C. J., Powers, D. R., Hedrick, T. L., Hyder, G. A., & Biewener, A. A. (2007). Three-dimensional kinematics of hummingbird flight. *Journal of Experimental Biology*, *210*(13), 2368–2382.

Torre-Bueno, J. R., & Larochelle, J. (1978). The metabolic cost of flight in unrestrained birds. *Journal of Experimental Biology*, *75*(1), 223–229.

Usherwood, J. R., Stavrou, M., Lowe, J. C., Roskilly, K., & Wilson, A. M. (2011). Flying in a flock comes at a cost in pigeons. *Nature*, *474*(7352), 494–497. doi: 10.1038/nature10164

Van Walsum, T. A., Perna, A., Bishop, C. M., Murn, C. P., Collins, P. M., Wilson, R. P., & Halsey, L. G. (2020). Exploring the relationship between flapping behaviour and accelerometer signal during ascending flight, and a new approach to calibration. *Ibis*, *162*(1), 13–26. doi: 10.1111/ibi.12710

Wang, Y., Yin, Y., Ge, S., Li, M., Zhang, Q., Li, J., … Dudley, R. (2019). Limits to load-lifting performance in a passerine bird: the effects of intraspecific variation in morphological and kinematic parameters. *PeerJ*, *7*, e8048.

Ward, S., Moller, U., Rayner, J. M. V, Jackson, D. M., Bilo, D., Nachtigall, W., & Speakman, J. R. (2001). Metabolic power, mechanical power and efficiency during wind tunnel flight by the European starling *Sturnus vulgaris*. *Journal of Experimental Biology*, *204*(19), 3311–3322.

Warham, J. (1977). Wing loadings, wing shapes, and flight capabilities of Procellariiformes. *New Zealand Journal of Zoology*, *4*(1), 73–83.

Wilson, R., & Liebsch, N. (2003). Up-beat motion in swinging limbs: new insights into assessing movement in free-living aquatic vertebrates. *Marine Biology*, *142*(3), 537–547.

Wilson, R. P., Börger, L., Holton, M. D., Scantlebury, D. M., Gómez-Laich, A., Quintana, F., … Shepard, E. L. C. (2020). Estimates for energy expenditure in free-living animals using acceleration proxies: A reappraisal. *Journal of Animal Ecology*, *89*(1), 161–172. doi:

10.1111/1365-2656.13040

Wilson, R. P., Pütz, K., Peters, G., Culik, B., Scolaro, J. A., Charrassin, J.-B., & Ropert-Coudert, Y. (1997). Long-term attachment of transmitting and recording devices to penguins and other seabirds. *Wildlife Society Bulletin*, 101–106.

Wilson, R. P., White, C. R., Quintana, F., Halsey, L. G., Liebsch, N., Martin, G. R., & Butler, P. J. (2006). Moving towards acceleration for estimates of activity-specific metabolic rate in free-living animals: The case of the cormorant. *Journal of Animal Ecology*, *75*(5), 1081–1090. doi: 10.1111/j.1365-2656.2006.01127.x

Chapter 2 – Fine-scale changes in speed and altitude suggest protean movements in homing pigeon flights

Disclaimer

This work was published as:

Garde, B., Wilson, R. P., Lempidakis, E., Börger, L., Portugal, S. J., Hedenström, A., Dell'Omo, G., Quetting, M., Wikelski, M. & Shepard, E. L. C. (2021). Fine-scale changes in speed and altitude suggest protean movements in homing pigeon flights. *Royal Society open science*

Abstract

The power curve provides a basis for predicting adjustments that animals make in flight speed, for example in relation to wind, distance, habitat foraging quality, and objective. However, relatively few studies have examined how animals respond to the landscape below them, which could affect speed and power allocation through modifications in climb rate and perceived predation risk. We equipped homing pigeons (*Columba livia*) with high frequency loggers to examine how flight speed, and hence effort, varies in relation to topography and land cover. Pigeons showed mixed evidence for an energy saving strategy, as they minimised climb rates by starting their ascent ahead of hills, but selected rapid speeds in their ascents. Birds did not modify their speed substantially in relation to land cover, but used higher speeds during descending flight, highlighting the importance of considering the rate of change in altitude before estimating power use from speed. Finally, we document an unexpected variability in speed and altitude over fine scales; a source of substantial energetic inefficiency. We suggest this may be a form of protean behaviour adopted to reduce predation risk when flocking is not an option, and that such a strategy could be widespread.

Introduction

Time and energy are currencies that have a profound influence on animal movement, with the judicious use of energy being particularly pertinent for flying animals, due to the scale of the costs in flapping flight (Jodice *et al.*, 2003; Schmidt-Nielsen, 1972). Indeed, in-flight decisions such as route choice (Bishop *et al.*, 2015; Shepard *et al.*, 2016), flight altitude (Bishop *et al.*, 2015) or speed (Alerstam & Lindström, 1990; Hedenstrom & Alerstam, 1995; Pennycuick, 1968) can markedly affect power consumption on a second-by-second basis.

Flight speed is particularly relevant with regard to energy expenditure because the power required for flight is predicted to follow a U-shaped curve, from a high point during hovering, down through a minimum, to an exponentially increasing power load with increasing speed thereafter (Pennycuick, 1968). This power curve can be used to predict a range of optimal speeds including the minimum power speed (V_{mp}), which requires the least energy per unit time, and the maximum range speed (V_{mr}), which uses the least energy per unit distance travelled (Pennycuick, 1968). Observations indicate that most birds travel at speeds between V_{mp} and V_{mr} (Pennycuick *et al.*, 2013; Pennycuick, 2008), with the specific predictions often borne out according to the situation and the purpose of the flight (e.g. display flight versus foraging or migration, etc., Bäckman & Alerstam, 2001; Hedenström, 2003; Hedenstrom & Alerstam, 1995). Optimal flight speeds are also predicted to vary with head- and tailwinds (Hedenström, 2003), and a range of studies show that birds adjust their airspeeds accordingly (Hedenström *et al.*, 2002; Liechti, Hedenström, & Alerstam, 1994; Sankey & Portugal, 2019). Finally, birds should reduce their airspeed as they climb, in line with the increase in energy required to gain potential energy (Hedenström & Alerstam, 1994; Hedenström *et al.*, 2002).

There are however instances where birds fly at speeds above V_{mr}. Faster travel can be achieved for a minimal cost when birds fly at their minimum time speed (V_{mt}) (Hedenström, 2003; Hedenström *et al.*, 2002). Circumstances may also favour non-energy-efficient speeds, for instance, faster flight during foraging may increase the provisioning rate of hatchlings (Norberg, 1981; Ydenberg *et al.*, 1994; Ydenberg & Hurd, 1998) and speed can be advantageous during migration if birds then arrive at the breeding grounds before competitors, increasing the likelihood of reproductive success (Kokko, 1999). Birds can also vary their speed when flying in a group (Hedenström & Åkesson, 2017) compared to when they fly solo, if the benefits of maintaining group cohesion outweigh the costs of flying at speeds that are sub-optimal for energy use (Dell'Ariccia *et al.*, 2008; Sankey & Portugal, 2019).

Overall, flight speed seems therefore to vary with (i) the currency that is driving the movement, and (ii) the physical environment, which impacts the efficiency of any given speed. However, studies examining both of these factors tend to quantify speed at relatively large scales, averaging it over individual flights or large sections of the track (e.g. Hedenström *et al.*, 2002; Shamoun-Baranes *et al.*, 2006, though see Pennycuick *et al.*, 2013; Williams *et al.*, 2018). This means that factors impacting the choice of flight speed over fine scales, including changes in the substrate (mainly land cover and topography) that birds fly over, tend to be averaged out. Land cover could first affect birds directly, due to the way that the substrate affects the movement of air above it, with some land types more likely to generate rising air, for instance (Scacco *et al.*, 2019). Land cover might also affect flight indirectly, as different habitats present different predation risks. For instance, pigeons are more likely to be attacked by peregrine falcons (*Falco peregrinus*) swooping from above in open spaces, while woodlands can be associated with goshawks (*Accipiter gentilis*) attacking from below (Cramp & Brooks, 1992), or waiting for them next to their loft (Henderson *et al.*, 2004).

We released solo-flying homing pigeons (*Columba livia*), equipped with high frequency GPS and pressure sensors, to examine the extent to which a flapping flier modulates its airspeed within individual flights, and specifically in relation to the substrate. Pigeons have been the dominant model species used in studies examining navigation mechanisms, which are strongly linked to landscape features over fine scales (Biro *et al.*, 2004; Gagliardo *et al.*, 2011; Mann *et al.*, 2011; Wallraff & Wallraff, 2005). Nonetheless, there have been no studies assessing whether the landscape affects their speed, or the resulting implications for energy efficiency and predation avoidance. Homing pigeons have been selected for racing and are thus expected to invest primarily into speed during their homing flights. However, we expected birds to reduce speed when climbing (Hedenström *et al.*, 2002). We therefore predicted that the greatest changes in speed would depend on the topography, with individuals decreasing their airspeed with increased climb rate (*cf*. Berg & Biewener, 2008; Hedenström *et al.*, 2002). We also assessed whether birds minimise their climb rate by climbing gradually ahead of a high point, or whether they track the terrain beneath them (resulting in higher instantaneous climb rates). We also quantified variation in speed in relation to land cover, predicting that an increase in speed or altitude above a certain type of land cover would likely represent a response to greater perceived predation risk. Overall, this should provide insight into the fine-scale changes in effort and perceived risk driven by the landscape that could ultimately influence the costs associated with route choice when flight is considered in all three dimensions.

Materials and Methods

Homing pigeons (Rock doves, *Columba livia* Linnaeus) were equipped with high-frequency GPS loggers linked to barometric pressure sensors (see below) and released on solo homing flights from Bodman-Ludwigshafen in Germany (47.815°N, 8.999°E, Figure 1), between the 24th and the 31st of July 2018 and the 3rd and the 19th of April 2019. The release site was an open field 5.7 km north of their home loft. Releases were conducted during the morning, in weather ranging from sunny to cloudy and in a range of temperatures from 23 to 36°C in July, and from 7 to 19°C in April. Every day, six pigeons were brought to the release site by car, in a common transport box preventing them from seeing outside. Birds were taken out of the transport box 2 minutes before the release. Changes in homing efficiency in response to route familiarity can still be observed 20 flights after the first release (Taylor *et al.*, 2017). Pigeons were therefore flown with dummy loggers from the release site > 30 times prior to trials (Biro *et al.*, 2006; Dell'Ariccia *et al.*, 2008; Taylor *et al.*, 2017) to remove changes associated with route learning (a phase also associated with increased inter-individual variability linked to differences in learning and navigational capabilities, as well as personality, Portugal *et al.*, 2017; Sasaki *et al.*, 2018). The same birds were used in 2018 and 2019, with bird masses, wingspan and wing area taken once for each release session. Wing loading was calculated as the ratio of body mass to wing area, following Pennycuick (2008). R package "afpt" (Klein Heerenbrink *et al.*, 2015) was used to calculate the theoretical minimum power speed (V_{mp}) and maximum range speed (V_{mr}) based on those measurements and a body drag coefficient of 0.2 (Klein Heerenbrink *et al.*, 2015).

Birds were equipped with two data loggers: a Daily Diary (Wildbyte Technologies, Swansea University, UK) and a GPS (GiPSy 5, Technosmart Europe, Guidonia-Montecelio, Italy). The Daily Diaries recorded a range of parameters including pressure at 4 Hz (using Bosch pressure sensor BMP280 with a relative accuracy of ± 0.12 hPa, equivalent to ± 1 m), while the GPS was set to sample at 1 Hz for the July flights and 5 Hz for April flights (data were subsequently subsampled to 1 Hz). The two units were connected to each other and the Daily Diary was programmed to receive an initial timestamp from the GPS in order to synchronise the time between the two datasets. Loggers were combined in a lightweight, 3-d printed housing, producing a unit measuring 47 × 22 × 15 mm and weighing up to 18.0 g (Sankey & Portugal, 2019; Taylor *et al.*, 2017), and representing between 3.8 and 4.2 % of a bird's body mass. Loggers were attached to the back of the bird via Velcro strips, with the bottom strip being glued to the pigeon's back feathers (Biro *et al.*, 2002). All procedures were approved by the Swansea University AWERB (approval number: IP-1718-23) and by the Regierungspräsidium Freiburg (reference number: G-17/92).

An anemometer (Kestrel 5500L, Kestrel instruments, USA) was deployed in an open location at the release site on a 5 m pole and set to record wind speed and direction every 10 seconds. Flights with an average wind speed > 2 m s^{-1} were not used in the analysis in order to control for the influence of wind on the selection of flight speed, which is already well established (e.g. Hedenström, 2003; Sankey *et al.*, 2019). In addition, circling was identified in the GPS tracks and excluded from the analysis (Aldridge, 1987; Wilson *et al.*, 2013). Resting was also excluded from the flight, along with the descent before landing and the ascent after take-off.

The 2012 Corine Land Cover classification (100 m resolution, land.copernicus.eu) was used to determine two categories of land cover; open land (which mainly constituted fields in our study area, Figure 1) and woodland. Elevation data were obtained from a Digital Surface Model (DSM) (30 m resolution, source: https://opendem.info/index.html). The topography of the area between the release site and the loft included a valley, and flights were classified according to whether they were routed along the valley (where ground elevations were < 465 m) or over the hill (where flight altitudes exceeded 465 m, Figure 1).

Flight altitude above mean sea level (ASL) was calculated by smoothing the barometric pressure data over 5 s to reduce any potential noise caused by the wingbeats and the pressure sensor, and converting pressure to altitude adjusting for daily changes in pressure at the release site in the seconds preceding take-off. Barometric pressure was used to estimate altitude, due to greater within-flight accuracy (Péron *et al.*, 2020). Altitude above ground level was calculated as the difference between flight altitude and the elevation of the substrate.

Groundspeed and heading were calculated from consecutive GPS fixes, using the R package “move” version 3.1.0 (Kranstauber *et al.*, 2018), and smoothed over 5 s to reduce GPS error. The speed of the bird relative to the horizontal movement of the surrounding air, or horizontal airspeed V_x (m s^{-1}), was taken as:

$$(1)\ V_x = \sqrt{V_g^2 + V_w^2 + 2V_g V_w \cos\left(\frac{\theta \times \pi}{180}\right)}$$

where V_g is the groundspeed, V_w the wind speed and θ the angle between the bird heading and the wind direction (ranging between 0 and 180 degrees). These values were then adjusted to account for the climb rate, giving airspeed, V_a, as the vector sum of the horizontal airspeed V_x and the climb rate V_z:

$$(2)\ V_a = \sqrt{V_x^2 + V_z^2}$$

Finally, the rate of change of speed (i.e. forward acceleration and deceleration) and altitude (i.e. climb rate, V_z) were calculated as the difference between consecutive estimates of speed (at 1 Hz) or altitude (smoothed values) respectively.

We used a Linear Mixed Effects model (LMM) to examine which aspects of the physical environment drive the selection of airspeed, with climb rate, flight altitude and land cover as predictors. The interaction between climb rate and altitude was also included in the global model, to account for the influence of altitude on flight forces. A model comparison showed that the interaction between climb rate and land cover did not improve the model (AIC difference = 1, $\chi^2 = 3.333$, $p = 0.068$), so this interaction was removed from the model. Day of the flight and bird identity were compiled into one variable, as using a nested effect would prevent the model from converging, and was included as random intercept in this and subsequent LMMs. We examined the distribution of residuals against fitted values using the function “plot.lme” from the R package “nlme” (Pinheiro et al., 2017, version 3.1-151) to verify that there was no pattern in the distribution of residuals, which would suggest a non-linear relationship. The functions “qqnorm” and “simulateResiduals” from the R package DHARMa (Hartig & Hartig, 2017, version 0.4.5) were used to obtain QQ plots of the models and identify whether assumptions made to create the model were correct.

Statistical analyses were conducted in R-Studio, using R version 3.3.2 (R Core Team, 2020), using the packages “lme4” version 1.1-19 (Bates *et al.*, 2018), “car” version 3.0-3 (Fox *et al.*, 2012) and “MuMIn” version 1.43.6 (Barton & Barton, 2015). A visual representation of the GPS tracks was generated using the R package “ggmap” (Kahle & Wickham, 2013).

Results

Overall, 88 homing flights were recorded from eight male pigeons (mean mass ± s.d. = 455.0 ± 14.7 g). Once the flights with interruptions, missing data or average wind speeds > 2 m s^{-1} were excluded, 29 flights were available for further analysis (15 from 2018 and 14 from 2019, one pigeon was tested in 2019 only). The travelling section of the homing flight lasted an average of 6.1 ± 1.0 minutes (mean ± s.d.) and covered 7.2 ± 0.9 km (mean ± s.d.). No differences in individual wing loading were observed between the two field seasons (paired t-test: t = 1.456, p = 0.219) and neither was there a significant difference in the average airspeed recorded for each pigeon (paired t-test: t = 0.357, p = 0.739).

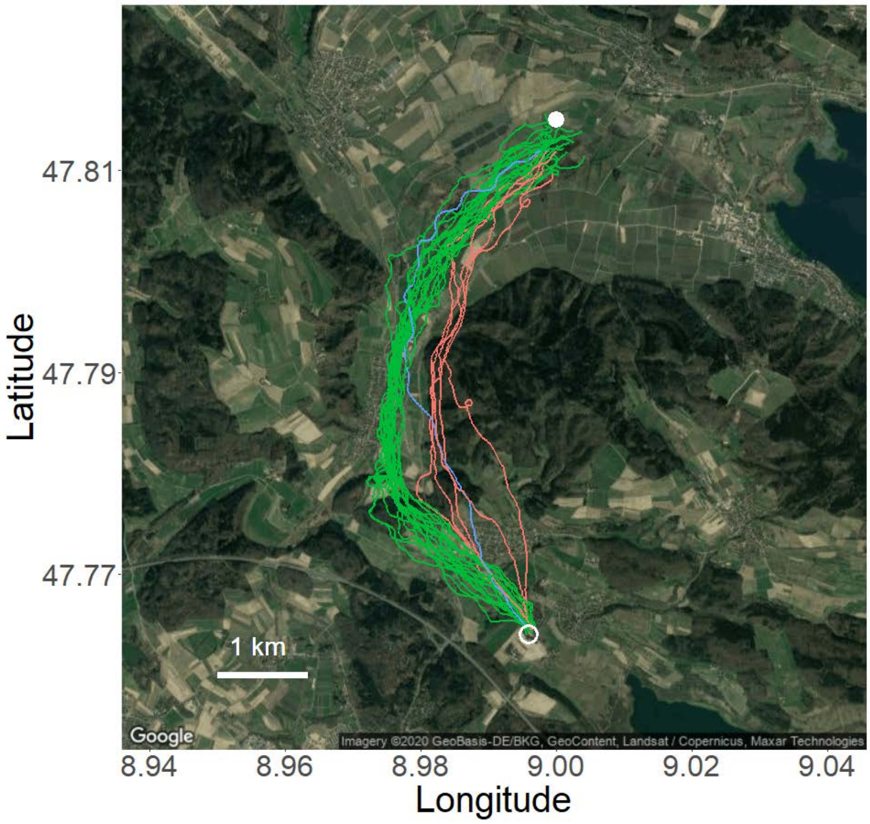

Figure 1: GPS tracks of 29 pigeon homing flights (7 individuals) from the release site (filled circle) to the loft (empty circle). Green tracks correspond to “Valley” flights (n = 20), red tracks

to "Hill" flights (n = 5) and the blue track corresponds to a flight that started over the valley but reached the hill towards the end.

Birds flew with a mean airspeed of 19.9 m s^{-1} (± 2.6 s.d.), with speed varying by 10.4 m s^{-1} on average within each flight, and an overall maximum of 23.0 m s^{-1} across individuals. The mean speed was therefore substantially higher than the theoretical maximum range speed (mean V_{mr} = 16.4 m s^{-1}). Nonetheless, V_{mp} (mean = 12.4 m s^{-1}) was a good predictor of minimum speeds, as birds rarely flew below V_{mp}, even during ascending flight, when speeds were lowest.

Climb rate was the strongest predictor of airspeed (V_a), with speed decreasing with increasing climb rate, V_z (Table 1, Figure 2). When airspeed was considered separately for climbing and descending flight, the relationship between V_a and V_z remained linear, but we observed a better fit and a steeper slope in descending flight compared to ascending flight (LMM model, climbing: estimate = -1.093, std. error = 0.043, χ^2 = 657.560, p-value < 0.001, R^2_m = 0.07, R^2_c = 0.53; Descending: estimate = -1.16, std. error = 0.031, χ^2 = 1394.3, p-value < 0.001, R^2_m = 0.14, R^2_c = 0.59) (see Figure 2). The effects of land cover, altitude and the interaction between V_z and altitude were also significant, but the difference in airspeed between land cover was minor (0.165 m s^{-1} slower over woodlands, see Table 1).

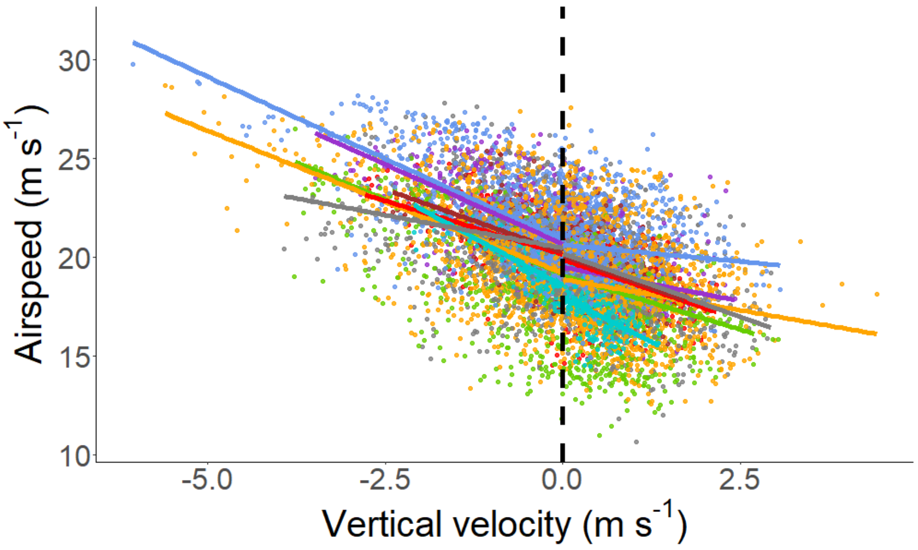

Figure 2: Relationship between airspeed and vertical velocity in seven homing pigeons. Each individual is represented in different colours. The dashed line shows the limit between descending (left) and climbing (right).

Table 1: Statistical results of the LMM model showing the effect on airspeed (V_a) of rate of change of altitude (V_z), land cover, altitude ASL and the interaction between V_z and altitude (LMM model: $R^2_m = 0.27$, $R^2_c = 0.62$). The model was executed with standardized (centred and scaled) variables to compare the magnitude of their effects. A higher estimate shows an effect of greater magnitude (V_z). Raw estimates (unstandardized) are given in the left column to allow quantitative interpretation of these effects.

	Estimate (Unstdd.)	**Estimate (Stdd.)**	**Std. Error**	**t value**	**χ^2**	**p**
(Intercept)	16.182	20.089	0.311	64.624	NA	NA
V_z	-1.239	-1.323	0.017	-77.579	5915.680	< 0.001
Land cover (woodlands)	-0.165	-0.165	0.046	-3.619	13.099	< 0.001
Altitude	0.008	0.310	0.028	10.908	116.953	< 0.001
V_z:Altitude	-0.004	-0.187	0.018	-10.544	111.185	< 0.001

Flight altitude varied between 401 and 630 m ASL (the highest topographical point in the area was 716 m). Birds climbed more rapidly when flying over steeper terrain, however, this explained only 1% of the variation in climb rate (LMM model: estimate = 0.06, $\chi^2 = 99.54$, $p < 0.001$, $R^2_m = 0.01$, $R^2_c = 0.01$) (Figure 2. C and D). A comparison of flight altitude over the plain before the hill showed a significant effect of the subsequent route on the flight altitude; birds that continued along the valley flew on average 51.6 m lower than the birds that flew over the hill (LMM model: estimate = -51.58, $\chi^2 = 18.56$, std. error = 11.98, $p < 0.001$, $R^2_m = 0.25$, $R^2_c = 0.62$).

One of the most striking and unanticipated features was the fine-scale variability in airspeed, as substantial and rapid changes in speed were exhibited during the flights (Figure 3A), with accelerations ranging from -4.5 m s^{-2} to 3.5 m s^{-2} (median: 0.0, IQR: 0.6 m s^{-2}). Altitude was also very variable, with a median climb rate of 0.6 m s^{-1} (IQR: 0.7 m s^{-1}), and a median descent rate of -0.7 m s^{-1} (IQR: 0.9 m s^{-1}) when climbing and descending was considered across flights

(Figure 3B). The maximum climb angle was 14°, with 90% of angles being between 0 and 5°. Variability in climb rate did not differ greatly between valley and hill flights (standard deviation: 1.0 and 1.2 m s^{-1} respectively), and both routes were associated with substantial variation in altitude (Figure 3C and D). An ultralight, equipped with the same tagging technology, simultaneously flew a section of the pigeon's flight path with the intention of

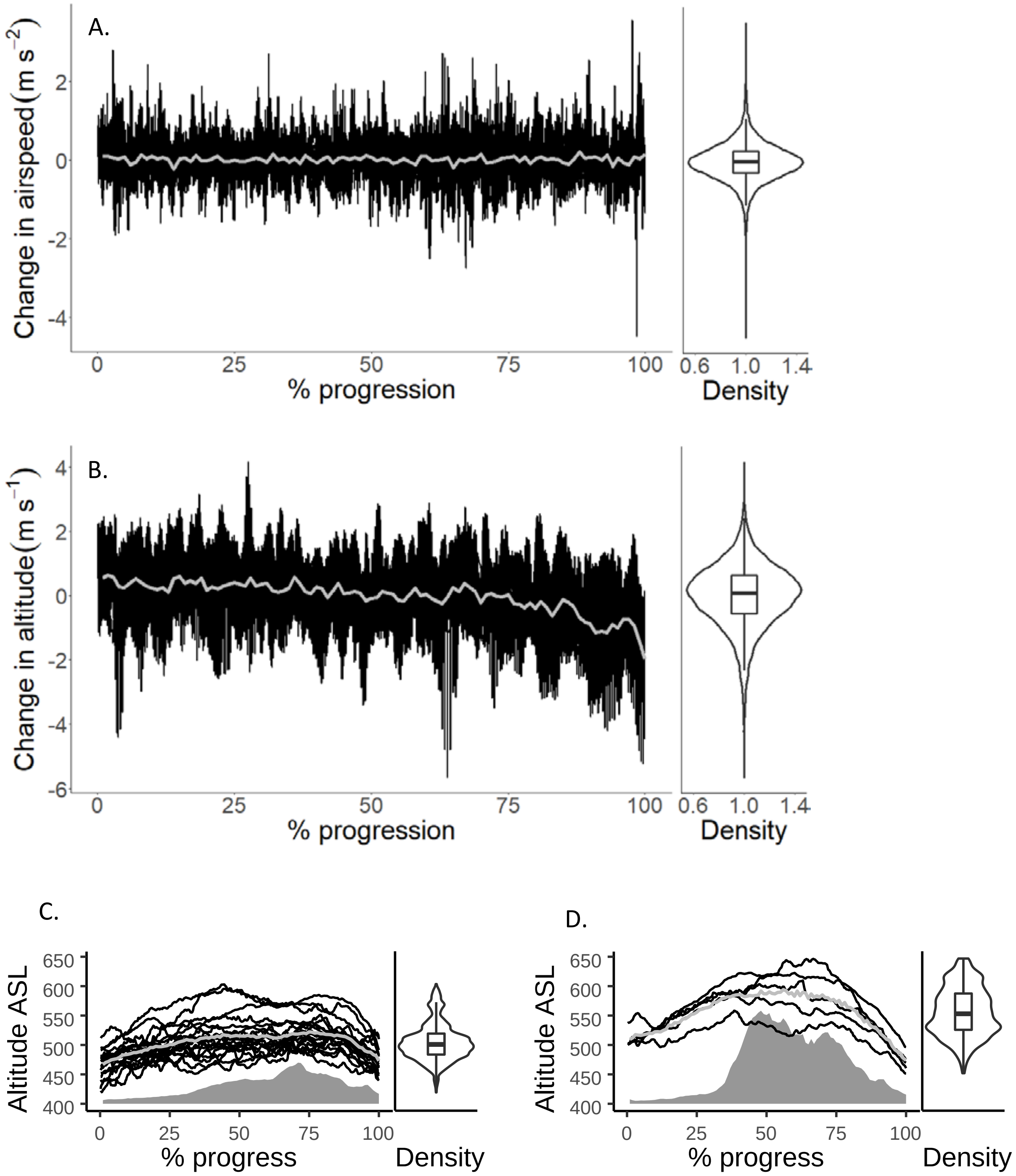

Figure 3. Change in (A) airspeed per second and (B) altitude per second, in relation to the proportion of time through 25 homing flights. (C) and (D) depict the elevation and altitude

profiles of birds flying over the valley (n = 20) and above the hill (n = 5), respectively. The grey line corresponds to the average value calculated for all tracks. The filled grey area represents the average ground elevation below the birds. Violin plots show the distribution of the data, while box plots show the median, upper and lower quartiles, and the distribution of the data excluding the outliers. The change in airspeed and altitude was calculated as the difference in airspeed or altitude over 1 second. Values were averaged over every % progress for each trip.

maintaining a fixed speed and altitude. Data from the ultralight flight showed markedly less variation in climb rate (Standard deviation of V_z: pigeon = 15.3 m s^{-1}, ultralight = 6.5 m s^{-1}, Bartlett test of homogeneity of variances: Bartlett's K-squared = 32261, $p > 0.001$), suggesting that the variability is a specific feature of pigeon flight (Figure S1). The variation in speed was however not significantly different between the pigeon and the ultralight (Bartlett's K-squared = 0.699, p = 0.403).

Discussion

Homing pigeons have been bred for their ability to return to the loft quickly, and the selective pressure to minimise the flight time is likely to outweigh that to minimise power (in relation to time or distance). In addition, pigeons know that the distance to their loft is short, and may thus be unlikely to employ an energy-efficient flight style. We therefore believe that many of our results can be interpreted within this high-performance context, as supported by the high mean flight speeds (some 3.5 m s^{-1} greater than predicted for V_{mr}), which are consistent with other studies on homing pigeons (Taylor *et al.*, 2017; Usherwood *et al.*, 2011). Furthermore, flight speeds in this study frequently exceeded V_{mr} even during climbing. These high speeds contrast with those recorded from wild species with a mass similar to pigeons, which migrate at a speed close to V_{mr} (Pennycuick *et al.*, 2013).

Our highest speeds occurred in descending flight (as observed, but not quantified, by Tucker, 1973), with speeds increasing with steeper descents. This is likely due to the conversion of some of the potential energy into aerodynamic power, enabling birds to accrue energy savings for the fastest speeds. The motivation for the extremely high speeds found at the end of some flights is likely due to goshawks waiting for pigeons in the vicinity of the loft (Santos *et al.*, 2015), causing them to descend faster. Nonetheless, the fact that the slope of the relationship between airspeed and vertical velocity varied between climbing and descending flight, demonstrates that average speeds taken over entire flights will be biased upwards by periods of descent. In the context of behavioural ecology, this means that estimates of power use, or the currency driving speed selection, cannot be extrapolated from measurements of speed without accounting for changes in altitude.

Despite operating within a high-power framework, pigeons did show some signs of judicious energy use, a prominent example being climbing at minimum rates to fly over high points. Specifically, birds started climbing shortly after the beginning of the flight and ~ 2 km ahead of hills on their route, indicating that they anticipated the topographic change. While gaining height early in the flight may also be advantageous for navigation and reducing predation risk, the distribution of climb rates, which was centred around 0°, with 90% of positive climb angles between 0 and 5° (*cf.* Hedenström & Alerstam, 1994; Pennycuick, 2008), constitutes a time and/or energy saving. Gradual climbs have also been observed in bar-headed geese (Bishop *et al.*, 2015), which are more limited by energy than our pigeons, suggesting that in general, birds may favour this strategy for energetic reasons.

Nonetheless, the remarkable variation in both altitude and speed observed in flights highlights a major source of energetic inefficiency. Barometric pressure provides the best estimates of relative changes in altitude at small spatial and temporal scales (Péron *et al.*, 2020) and both speed and altitude were smoothed over 5 s to remove the variability that could be caused by logger inaccuracy. This strongly suggests that pigeons willingly adopt a variable flight style, a behaviour that was not predicted at the outset. Whether animals aim to optimize their use of time or energy, they should maintain a constant speed and altitude (Pennycuick, 1968) and adopt a path with minimum tortuosity, because turns are energetically costly (Usherwood *et al.*, 2011), they increase the overall path length, and accelerations and decelerations will be more costly than simply maintaining a constant speed (Kramer & McLaughlin, 2001). In this respect, birds did not present profiles of animals maximizing power for overall homing speed. Specifically, our pigeons exhibited substantial fine-scale variability in speed and rate of change of altitude and took horizontal paths that deviated appreciably from that of a straight line (Figure 1), despite training prior to the experimental releases to control for changes in familiarity (Meade *et al.*, 2005). Future studies will need to consider changes in route familiarity or experience within and between flights, given that this affects estimates of speed and efficiency at the level of individual flights (Taylor *et al.*, 2017). While aspects of navigation, such as following landscape features (Mann *et al.*, 2011), can lead to horizontal track variation, this does not account for the observed variation in height nor for the effect on speed and increased path length that this may have. In our study, the fine-scale changes in altitude amounted to an additional 178.7 m per flight (compared to a vertical profile smoothed over 20 seconds).

We suggest that the marked, apparently inefficient, variability in pigeon flight patterns may be explained within the context of predator defence. Homing pigeons are common targets for raptors (Armstrong, 1991), most notably peregrine falcons *Falco peregrinus*, sparrowhawks *Accipiter nisus* and goshawks *Accipiter gentilis*, with sources quoting losses during races of up to 23% due to peregrine falcons alone (Parrott *et al.*, 2008). A study taking place in our study area recorded 15 attacks during 27 flights (Santos *et al.*, 2015). It is likely relevant that artificial selection by breeders can select for birds to fly faster, but cannot avoid selection pressures related to predators on their routes. Moving in a variable way is a strategy adopted by numerous taxa to avoid, and reduce the accuracy of, predator attacks (Jones *et al.*, 2011; Kane *et al.*, 2015; Richardson *et al.*, 2018). Such strategies are known as protean behaviours, and they work by preventing predators from predicting the future positions of prey engaging in unpredictable lateral movements and altitude and/or speed. These movements can occur specifically as a reaction to a defined attack (*cf*. examples in Kane *et al.*, 2015; Richardson *et al.*, 2018) or occur as constant changes in trajectory even when predators are not immediately apparent (Humphries & Driver, 1970; Richardson *et al.*, 2018). Well known examples include the common snipe (*Gallinago gallinago*) and jack snipe (*Lymnocryptes minimus*) (Humphries & Driver, 1970). While birds in this study did not adopt an erratic flight style that was obvious to observers, the variation in both speed and vertical velocity in the high-frequency logger data is notable. Our results suggest that, far from being a distinctive but relatively rare behaviour in birds, protean movement could be widespread, expressed in the form of fine-scale changes in trajectory.

The archetypal strategy for reducing individual predation risk during flight is flocking (Kenward, 1978; Ydenberg & Dill, 1986), which also leads to higher flight costs in pigeons (Usherwood *et al.*, 2011). However, flocking is not always possible, for instance, solitary breeders must make solo flights to and from the nest. Individuals therefore need a range of strategies to reduce predation risk, including for when they are forced to fly solo or in pairs, when the risk of being caught is higher (Kenward, 1978). While further testing is required to establish the effectiveness of this as an anti-predation strategy, the irregular flight style reported in this study may be a response to predation risk when flying in a large group is not possible. It is unlikely to be tenable or needed in large flocks, where the costs and risks of collision are already high (Usherwood *et al.*, 2011). Currencies and conditions between solo and group flight are very different, making the comparison of those two flight types challenging. The turbulence created by other birds (Usherwood *et al.*, 2011) and the need for birds to co-ordinate movements in relation to other flock members when flying together (Taylor *et al.*, 2019), may also lead to a very variable and costly flight style in flocks. This might explain why studies to date show that the variance in wingbeat frequency is similar between solo and group flying birds (Sankey *et al.*, 2019; Taylor *et al.*, 2019). Further high frequency data will provide insight into how widespread protean behaviours are, and how flight variability varies with the number of flock mates.

In conclusion, pigeons do not seem to primarily adopt energy-efficient strategies that minimize overall cost in returning to their loft. Rather, they use high power to return fast and exhibit ostensibly inefficient behaviour in the form of varying movement in terms of altitude, speed and overall trajectory. We propose that this corresponds to a previously unidentified form of protean behaviour allowing better predator avoidance, with birds offsetting the proximate costs of increased energy expenditure for the ultimate benefit of reducing predation risk. Estimating the cost of variable locomotion is notoriously difficult (Kramer & McLaughlin, 2001), given that protocols for measuring metabolic costs in controlled conditions are based on steady state movement. Nonetheless, this may prove an important element in understanding how risk affects flight costs in the wild.

References

Aldridge, H. D. (1987). Turning flight of bats. *Journal of Experimental Biology*, *128*(1), 419–425.

Alerstam, T., & Lindström, Å. (1990). Optimal bird migration: the relative importance of time, energy, and safety. In *Bird migration* (pp. 331–351). Springer.

Armstrong J. B. 1991 Raptors and racing pigeons: an analysis of avian predation on dome pigeons. Fifth Eastern Wildlife Damage Control Conference, Ithaca, USA.

Bäckman, J., & Alerstam, T. (2001). Confronting the winds: orientation and flight behaviour of roosting swifts, *Apus apus*. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *268*(1471), 1081–1087. doi: 10.1098/rspb.2001.1622

Barton, K., & Barton, M. K. (2015). Package 'MuMIn.' *Version*, *1*, 18.

Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R. H. B., Singmann, H., … Green, P. (2018). Package 'lme4.' *Version*, *1*, 17.

Berg, A. M., & Biewener, A. A. (2008). Kinematics and power requirements of ascending and descending flight in the pigeon (*Columba livia*). *Journal of Experimental Biology*, *211*(7), 1120–1130. doi: 10.1242/jeb.010413

Biro, D., Guilford, T., Dell'Omo, G., & Lipp, H. P. (2002). How the viewing of familiar landscapes prior to release allows pigeons to home faster: Evidence from GPS tracking. *Journal of Experimental Biology*, *205*(24), 3833–3844.

Biro, D., Meade, J., & Guilford, T. (2004). Familiar route loyalty implies visual pilotage in the homing pigeon. *Proceedings of the National Academy of Sciences of the United States of America*, *101*(50), 17440–17443. doi: 10.1073/pnas.0406984101

Biro, D., Sumpter, D. J. T., Meade, J., & Guilford, T. (2006). From Compromise to Leadership in Pigeon Homing. *Current Biology*, *16*(21), 2123–2128. doi: 10.1016/j.cub.2006.08.087

Bishop, C. M., Spivey, R. J., Hawkes, L. A., Batbayar, N., Chua, B., Frappell, P. B., … Butler, P. J. (2015). The roller coaster flight strategy of bar-headed geese conserves energy during Himalayan migrations. *Science*, *347*(6219), 250–254. doi: 10.1126/science.1258732

Cramp, S., & Brooks, D. J. (1992). *Handbook of the birds of Europe, the Middle East and North*

Africa. The birds of the western Palearctic, vol. VI. Warblers. oxford university Press, oxford.

Dell'Ariccia, G., Dell'Omo, G., Wolfer, D. P., & Lipp, H. P. (2008). Flock flying improves pigeons' homing: GPS track analysis of individual flyers versus small groups. *Animal Behaviour*, *76*(4), 1165–1172. doi: 10.1016/j.anbehav.2008.05.022

Fox, J., Weisberg, S., Adler, D., Bates, D., Baud-Bovy, G., Ellison, S., … Graves, S. (2012). Package 'car.' *Vienna: R Foundation for Statistical Computing*.

Gagliardo, A., Ioalè, P., Filannino, C., & Wikelski, M. (2011). Homing Pigeons Only Navigate in Air with Intact Environmental Odours: A Test of the Olfactory Activation Hypothesis with GPS Data Loggers. *PLoS ONE*, *6*(8), e22385. doi: 10.1371/journal.pone.0022385

Hedenström, A. (2003). Twenty-Three Testable Predictions About Bird Flight. In *Avian Migration* (pp. 563–582). Berlin, Heidelberg: Springer Berlin Heidelberg. doi: 10.1007/978-3-662-05957-9_38

Hedenström, A., & Åkesson, S. (2017). Flight speed adjustment by three wader species in relation to winds and flock size. *Animal Behaviour*, *134*, 209–215. doi: 10.1016/j.anbehav.2017.10.022

Hedenstrom, A., & Alerstam, T. (1995). Optimal flight speed of birds. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *348*(1326), 471–487. doi: 10.1098/rstb.1995.0082

Hedenström, A., & Alerstam, T. (1994). Optimal climbing flight in migrating birds: predictions and observations of knots and turnstones. *Animal Behaviour*, *48*(1), 47–54. doi: 10.1006/anbe.1994.1210

Hedenström, A., Alerstam, T., Green, M., & Gudmundsson, G. A. (2002). Adaptive variation of airspeed in relation to wind, altitude and climb rate by migrating birds in the Arctic. *Behavioral Ecology and Sociobiology*, *52*(4), 308–317. doi: 10.1007/s00265-002-0504-0

Henderson I., Parrott D. & Moore, N. 2004 Racing Pigeons: Impact of Raptor Predation. *Central Science Laboratory report to Scottish Natural Heritage & Scottish Homing Union*. Scottish Natural Heritage, Edinburgh, UK.

Humphries, D. A., & Driver, P. M. (1970). Protean defence by prey animals. *Oecologia*, *5*(4), 285–302. doi: 10.1007/BF00815496

Jodice, P. G. R., Roby, D. D., Suryan, R. M., Irons, D. B., Kaufman, A. M., Turco, K. R., & Visser, G. H. (2003). Variation in Energy Expenditure among Black-Legged Kittiwakes: Effects of Activity-Specific Metabolic Rates and Activity Budgets. *Physiological and Biochemical Zoology*, *76*(3), 375–388. doi: 10.1086/375431

Jones, K. A., Jackson, A. L., & Ruxton, G. D. (2011). Prey jitters; protean behaviour in grouped prey. *Behavioral Ecology*, *22*(4), 831–836. doi: 10.1093/beheco/arr062

Kahle, D., & Wickham, H. (2013). ggmap: Spatial Visualization with ggplot2. *The R Journal*, *5*(1), 144–161.

Kane, S. A., Fulton, A. H., & Rosenthal, L. J. (2015). When hawks attack: animal-borne video studies of goshawk pursuit and prey-evasion strategies. *Journal of Experimental Biology*, *218*(2), 212–222. doi: 10.1242/jeb.108597

Kenward, R. E. (1978). Hawks and Doves: Factors Affecting Success and Selection in Goshawk Attacks on Woodpigeons. *The Journal of Animal Ecology*, *47*(2), 449. doi: 10.2307/3793

Klein Heerenbrink, M., Johansson, L. C., & Hedenström, A. (2015). Power of the wingbeat: Modelling the effects of flapping wings in vertebrate flight. *Proceedings of the Royal Society A: Mathematical, Physical and Engineering Sciences*, *471*(2177). doi: 10.1098/rspa.2014.0952

Kokko, H. (1999). Competition for early arrival in migratory birds. *Journal of Animal Ecology*, *68*(5), 940–950. doi: 10.1046/j.1365-2656.1999.00343.x

Kramer, D. L., & McLaughlin, R. L. (2001). The behavioral ecology of intermittent locomotion1. *American Zoologist*, *41*(2), 137–153. doi: 10.1668/0003-1569(2001)041[0137:TBEOIL]2.0.CO;2

Kranstauber, B., Smolla, M., & Scharf, A. K. (2018). *move: visualizing and analyzing animal track data. R package version 3.1. 0.*

Liechti, F., Hedenström, A., & Alerstam, T. (1994). Effects of sidewinds on optimal flight speed of birds. *Journal of Theoretical Biology*, Vol. 170, pp. 219–225. doi:

10.1006/jtbi.1994.1181

Mann, R., Freeman, R., Osborne, M., Garnett, R., Armstrong, C., Meade, J., … Roberts, S. (2011). Objectively identifying landmark use and predicting flight trajectories of the homing pigeon using Gaussian processes. *Journal of the Royal Society Interface*, *8*(55), 210–219. doi: 10.1098/rsif.2010.0301

Meade, J., Biro, D., & Guilford, T. (2005). Homing pigeons develop local route stereotypy. *Proceedings of the Royal Society B: Biological Sciences*, *272*(1558), 17–23. doi: 10.1098/rspb.2004.2873

Norberg, R. A. (1981). Optimal Flight Speed in Birds when Feeding Young. *The Journal of Animal Ecology*, *50*(2), 473. doi: 10.2307/4068

Parrott, D., Henderson, I., Deppe, C., & Whitfield, P. (2008). Scottish racing pigeons killed by Peregrine Falcons Falco peregrinus: Estimation of numbers from ring recoveries and Peregrine daily food intake. *Bird Study*, *55*(1), 32–42. doi: 10.1080/00063650809461502

Pennycuick, C. J., Akesson, S., & Hedenström, A. (2013). Air speeds of migrating birds observed by ornithodolite and compared with predictions from flight theory. *Journal of the Royal Society Interface*, *10*(86). doi: 10.1098/rsif.2013.0419

Pennycuick, C. J. (1968). Power requirements for horizontal flight in the pigeon Columba livia. *Journal of Experimental Biology*, *49*(3), 527–555.

Pennycuick, C. J. (2008). *Modelling the flying bird*. Elsevier.

Péron, G., Calabrese, J. M., Duriez, O., Fleming, C. H., García-Jiménez, R., Johnston, A., … Shepard, E. L. C. (2020). The challenges of estimating the distribution of flight heights from telemetry or altimetry data. *Animal Biotelemetry*, *8*(1), 1–13. doi: 10.1186/s40317-020-00194-z

Portugal, S. J., Ricketts, R. L., Chappell, J., White, C. R., Shepard, E. L., & Biro, D. (2017). Boldness traits, not dominance, predict exploratory flight range and homing behaviour in homing pigeons. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *372*(1727), 20160234. doi: 10.1098/rstb.2016.0234

R Core Team. (2020). *R: A language and environment for statistical computing*. Retrieved from https://www.r-project.org/

Richardson, G., Dickinson, P., Burman, O. H. P., & Pike, T. W. (2018). Unpredictable movement as an anti-predator strategy. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1885). doi: 10.1098/rspb.2018.1112

Sankey, D. W. E., & Portugal, S. J. (2019). When flocking is costly: reduced cluster-flock density over long-duration flight in pigeons. *Science of Nature*, *106*(7–8). doi: 10.1007/s00114-019-1641-x

Sankey, D. W. E., Shepard, E. L. C., Biro, D., & Portugal, S. J. (2019). Speed consensus and the 'Goldilocks principle' in flocking birds (*Columba livia*). *Animal Behaviour*, *157*, 105–119. doi: 10.1016/j.anbehav.2019.09.001

Santos, C. D., Cramer, J. F., Pârâu, L. G., Miranda, A. C., Wikelski, M., & Dechmann, D. K. N. (2015). Personality and morphological traits affect pigeon survival from raptor attacks. *Scientific Reports*, *5*(1), 15490. doi: 10.1038/srep15490

Sasaki, T., Mann, R. P., Warren, K. N., Herbert, T., Wilson, T., & Biro, D. (2018). Personality and the collective: bold homing pigeons occupy higher leadership ranks in flocks. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *373*(1746), 20170038. doi: 10.1098/rstb.2017.0038

Scacco, M., Flack, A., Duriez, O., Wikelski, M., & Safi, K. (2019). Static landscape features predict uplift locations for soaring birds across Europe. *Royal Society Open Science*, *6*(1). doi: 10.1098/rsos.181440

Schmidt-Nielsen, K. (1972). Locomotion: Energy cost of swimming, flying, and running. *Science*, *177*(4045), 222–228. doi: 10.1126/science.177.4045.222

Shamoun-Baranes, J., van Loon, E., Alon, D., Alpert, P., Yom-Tov, Y., & Leshem, Y. (2006). Is there a connection between weather at departure sites, onset of migration and timing of soaring-bird autumn migration in Israel? *Global Ecology and Biogeography*, *15*(6), 541–552. doi: 10.1111/j.1466-822X.2006.00261.x

Shepard, E. L. C., Williamson, C., & Windsor, S. P. (2016). Fine-scale flight strategies of gulls in urban airflows indicate risk and reward in city living. *Philosophical Transactions of the*

Royal Society B: Biological Sciences, *371*(1704). doi: 10.1098/rstb.2015.0394

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*(16), 2908–2915. doi: 10.1242/jeb.154039

Taylor, L. A., Taylor, G. K., Lambert, B., Walker, J. A., Biro, D., & Portugal, S. J. (2019). Birds invest wingbeats to keep a steady head and reap the ultimate benefits of flying together. *PLOS Biology*, 17(6), e3000299. doi: 10.1371/journal.pbio.3000299

Tucker, V. A. (1973). Bird metabolism during flight: evaluation of a theory. *Journal of Experimental Biology*, *58*(3), 689–709.

Usherwood, J. R., Stavrou, M., Lowe, J. C., Roskilly, K., & Wilson, A. M. (2011). Flying in a flock comes at a cost in pigeons. *Nature*, *474*(7352), 494–497. doi: 10.1038/nature10164

Wallraff, H. G., & Wallraff, H. G. (2005). *Avian navigation: pigeon homing as a paradigm*. Berlin, Germany: Springer.

Williams, H. J., King, A. J., Duriez, O., Börger, L., & Shepard, E. L. C. (2018). Social eavesdropping allows for a more risky gliding strategy by thermal-soaring birds. *Journal of the Royal Society Interface*, *15*(148). doi: 10.1098/rsif.2018.0578

Wilson, R. P., Griffiths, I. W., Legg, P. A., Friswell, M. I., Bidder, O. R., Halsey, L. G., … Shepard, E. L. C. (2013). Turn costs change the value of animal search paths. *Ecology Letters*, *16*(9), 1145–1150. doi: 10.1111/ele.12149

Ydenberg, R. C., & Dill, L. M. (1986). The Economics of Fleeing from Predators. In *Advances in the Study of Behavior* (Vol. 16, pp. 229–249). Elsevier. doi: 10.1016/S0065-3454(08)60192-8

Ydenberg, R. C., Welham, C. V. J., Schmid-Hempel, R., Schmid-Hempel, P., & Beauchamp, G. (1994). Time and energy constraints and the relationships between currencies in foraging theory. *Behavioral Ecology*, *5*(1), 28–34. doi: 10.1093/beheco/5.1.28

Ydenberg, R., & Hurd, P. (1998). Simple models of feeding with time and energy constraints. *Behavioral Ecology*, *9*(1), 49–53. doi: 10.1093/beheco/9.1.49

Chapter 3 – Cheap versus quick flight: the wind vector determines the profitability of thermal soaring of a chick-rearing bird

Abstract

A wide range of bird species use thermal soaring to reduce their flight costs. This flight mode is well studied for large species, but smaller birds, which are generally facultative soarers, have received less attention. Because they can choose between soaring and powered flight depending on the flight conditions, such species provide a means to identify the range of weather conditions in which soaring is profitable. We use high-frequency data loggers on red-tailed tropicbirds (*Phaethon rubricauda*) as a facultative soaring seabird, to measure the extent of their use of thermal soaring, and identify the effect of wind conditions on the use of soaring flight. Tropicbirds were more likely to use thermal soaring when flying in tailwinds and in conditions of strong thermals. Estimations of flight speed and cost of transport revealed that soaring was cheaper than powered flight in all wind conditions, but also slower. By mainly soaring with tailwinds, tropicbirds are therefore able to save energy while minimising the time spent in flight, which is a critical element for a chick-rearing bird. This shows how wind can tip the balance in favour of an energy or time-efficient flight style in a non-obligatory soarer, and how soaring may be more common among generalist fliers than generally thought.

Introduction

Diverse species of birds from 11 kg Andean condors (*Vultur gryphus*) to 55 g bee-eaters (*Merops apiaster*) use thermal updrafts to reduce their flight costs (Sapir *et al.*, 2010; Williams *et al.*, 2020), with some species gaining hundreds, even thousands of kilometres of altitude in thermals and using this altitude to glide over long distances (Weimerskirch *et al.*, 2016). This low-cost form of transport (C J Pennycuick, 1975) is particularly advantageous when considered in relation to the high costs of flapping flight, which become proportionately more costly with increasing body mass (Pennycuick, 2008).

However, thermals are not always available. Thermal updrafts are driven by the heating of the air by the substrate, which rises when it is warmer, and hence less dense, than the surrounding air. On land, there is a strong diurnal change in thermal availability and strength, both of which tend to peak around midday due to the solar heating of the ground surface. This explains temporal patterns in the use of soaring flight over land (Shamoun-Baranes *et al.*, 2016) as well as the flight height of soaring birds (Shamoun-Baranes *et al.*, 2006). Thermal availability also varies in space, as thermals tend to develop over parts of the substrate that heat more rapidly or retain heat to a greater degree, including dark substrates and slopes orientated towards the sun (Bradbury, 1989). This has been shown to predict the use of soaring flight in vultures at regional scales (Scacco *et al.*, 2019). The difference in thermal availability over land and water is also what is responsible for a range of soaring birds migrating around, rather than across, the Mediterranean (Becciu *et al.*, 2020; Newton, 2010).

Thermal activity is much weaker over water than over land, nonetheless, sea thermals still form when the water is warmer than the air above it. This represents an important source of energy for birds including gulls and raptors (Duriez *et al.*, 2018; Shamoun-Baranes *et al.*, 2016; Woodcock, 1975), with the most extreme and specialist example being the frigatebirds, which have been shown to use thermal soaring for up 82% of their migratory trips (Weimerskirch *et al.*, 2016). There are fundamental differences in the factors that drive the availability of thermals over sea and land. The thermal inertia of water means that it does not heat the air above it to the same extent, explaining why sea thermals are weaker than their terrestrial counterparts. The sea surface temperature is also relatively constant throughout the day, leading to the expectation that there will be less of a diurnal signal in thermal availability. Finally, the relative homogeneity of the sea surface compared to the mosaic of terrestrial substrates means that sea thermals should be more widely available or evenly distributed, although surface temperatures may vary with water depth, as well as surface mixing (and hence wind and wave action).

In fact, the effect of wind on thermal development and soaring ability and efficiency remains little studied (but see Harel *et al.*, 2016). Nonetheless, the effects of the wind on thermal updrafts should be substantial: strong winds disrupt thermal structure (Bohrer *et al.*, 2012; Kerlinger, 1989; Woodcock, 1975). Even weak winds cause thermal drift (Vansteelant *et al.*, 2017; Weinzierl *et al.*, 2016). In order to stay in a thermal, birds must track it as it drifts, and therefore move horizontally as well as vertically. A study by Harel et al (2016) demonstrated how birds climb in one part of each turn in order to achieve this. At a more fundamental level, the energy savings that are possible from thermal soaring will depend on the direction that a bird is being drifted, relative to its direction of travel. While drift from a tailwind will move a bird towards its goal, soaring in a headwind will move the bird away from its destination, considerably reducing the speed of travel, to a point where flapping flight may even be required to make forward progress. This phenomenon is particularly relevant when thermals are weaker, as birds must soar for longer to gain the same amount of altitude (Pennycuick, 2008). The profitability of thermal soaring should therefore depend on thermal strength, wind strength, and the difference between the wind direction and bird’s direction of travel.

In order to understand how the physical environment affects flight costs, we therefore need to assess how weather conditions, including wind, affect the benefits and use of thermal soaring. This is particularly important in the context of global changes in wind speed as well as temperature (Solomon *et al.*, 2007; Young *et al.*, 2011). We used high-frequency data from multi-sensor tags to identify the flight mode (soaring, gliding and flapping), trajectory and speed of red-tailed tropicbirds (*Phaethon rubricauda*) breeding on Round Island, Mauritius. These facultative soaring birds breed throughout the year, offering an opportunity to quantify their flight behaviour across the seasonal spectrum of flight conditions. Specifically, we examined whether the use of soaring flight was driven by the type of activity (foraging versus travelling flight), prevailing environmental conditions (wind and thermal strength) or the tailwind component, which is determined by both the wind vector and the direction of travel. We then assessed the relative profitability of soaring flight by (i) quantifying the use of flapping flight during thermal soaring and (ii) modelling the speed and cost of transport of flapping and soaring flight modes in relation to wind support. Overall, this should provide insight into the use of thermal soaring and its energetic consequences in relation to changing environmental conditions.

Methods

We captured red-tailed tropicbirds nesting on Round Island, Mauritius (19.8486° S, 57.7885° E) (Gardner *et al.*, 1985) during chick rearing in February, March, September and October 2018. Birds were weighed and photographed to quantify their wing loading following Pennycuick (2008). They were then equipped with a Daily Diary (Wildbyte Technologies, Swansea University, UK) and a GPS logger (GiPSy 5, Technosmart Europe, Guidonia-Montecelio, Italy). The Daily Diary recorded acceleration and magnetic field strength in 3 axes at 40 and 13 Hz respectively, and barometric pressure and temperature at 4 Hz. The GPS was set to log one location per minute. Both loggers were placed in a zip-lock bag and fixed to the back feathers using Tesa tape (Wilson & Wilson, 1989). The loggers, housing and tape weighed 27.7 g, representing < 3% of the average body mass (mean body mass for tagged birds was 826 g), and 4.3% of the lowest body mass recorded during this study (650 g). After exclusion of the short flights generally following capture (therefore not associated with foraging), and incomplete trips due to tag failure, a total of 76 flights were recorded from 55 birds. Ethical permissions for the deployment of loggers on tropicbirds were granted by Swansea University AWERB, permit 040118/39.

Flight altitude above sea level was calculated using the barometric pressure recorded by the Daily Diary, and the mean sea-level pressure from Earth (https://earth.nullschool.net/) with a resolution of 3 hours and 0.5 x 0.5 degrees. Raw pressure values were smoothed over 2 s and the rate of change of altitude (V_z) was calculated over 1 second intervals. The air density at flight altitude was estimated using the ideal gas law, using pressure measured by the Daily Diary, as well as the temperature and relative humidity (Schmaljohann & Liechti, 2009) recorded every 5 minutes by a portable weather station (Kestrel 5500L, Kestrel instruments, USA) mounted on a 5 m pole and stationed at the highest point of Round island (265 m ASL). Wind speed and direction were also recorded by the weather station but measurements were interrupted due to battery failure between 09/02 and 20/02, during which 7 flights were recorded. These values were replaced by hourly wind records from Sir Seewoosagur

Ramgoolam International Airport in Mauritius, approximately 65 km from Round Island (http://www.wunderground.com).

The difference between the sea surface temperature (obtained from Earth, https://earth.nullschool.net/) and air temperature (measured by the weather station) (ΔT) was used as a proxy for thermal strength. Higher values of ΔT indicate that sea surface temperature was higher than air temperature, which is associated with stronger sea thermals (Duriez et al 2018 Ospreys sea thermals or Woodcock 1975).

Categorization of flight type

Periods of flight were evident from associated changes in altitude. Flight data was categorized as flapping, gliding and soaring as follows: The Vectorial sum of the Dynamic Body Acceleration (VeDBA) was calculated according to Wilson (2020), using smoothed raw acceleration values over two seconds to derive the static component. VeDBA values were smoothed again over two seconds, in order to produce a metric that varied between high and low levels of activity. Any point in flight with VeDBA $\geq 0.3\ g$ was labelled as flapping, and any point with VeDBA $< 0.3\ g$ and a negative rate of change of altitude was labelled as gliding. Level flapping flight was taken as sections of flapping flight where the absolute rate of change of altitude was < 0.1 m s^{-1}. Soaring was defined as periods where birds were circling and gaining altitude. Circling was identified using one of the horizontal channels of the magnetometer, where circling is evident as highly repetitive sine-waves with a maximum when the sensor faces magnetic north and a minimum when it faces south (Williams *et al.*, 2017). Each turn is therefore represented by a positive and a negative turning point, which were identified automatically using the custom-written animal movement analysis software DDMT (Wildbyte Technologies, http://wildbytetechnologies.com/software.html). As the time taken to complete one circle was between 10 and 20 s, we labelled 5 s either side of each turn point (1/4 of a circle) (Wilson *et al.*, 2018) and excluded periods with less than 2 turns. The labelling of the different flight modes was done in R Studio (R Core Team, 2020 version 4.0.0).

Speed and cost of transport

Bird groundspeed (V_g) was taken as the haversine distance between GPS fixes divided by the time. For soaring/ gliding flight this represented the cross-country speed that results from alternating periods of altitude gain (where little ground is covered) and gliding. The resulting underestimation of actual distance flown by birds during the circling behaviour meant that airspeed could not be estimated for this flight mode. Nonetheless, airspeeds were not necessary to estimate the power used during passive flight, as this is thought to be a constant multiple of resting costs (Baudinette & Schmidt-Nielsen, 1974; Duriez *et al.*, 2014; Hedenström, 1993).

Airspeeds (V_a) during flapping flight were calculated as the magnitude of the resulting vector of groundspeed and wind speed (see Chapter 2, Pennycuick, 1983). True airspeeds were converted to equivalent airspeeds in order to remove the effect of air density, which varied between seasons and with altitude. Equivalent airspeed corresponds to the airspeed at sea level that would produce the same dynamic pressure that a bird experienced at the true airspeed and altitude/ air density at which it flew (Pennycuick 2008). Equivalent airspeeds were used in all subsequent analyses. The wind support was calculated as the projection of the wind vector on the airspeed vector (see Chapter 2), with positive values indicating a tailwind and negative values a headwind.

The chemical power requirements of level flapping flight were estimated from airspeed values using the r package “afpt” (Klein Heerenbrink *et al.*, 2015) for each bird where body mass, wingspan and wing area were known (N = 35). The average chemical power for soaring-gliding (assuming no wingbeats) was taken as 3 × BMR, using the average body mass to determine BMR, according to Pennycuick (2008). The cost of transport was estimated for level flapping and soaring-gliding flight by dividing their respective power by the groundspeed (Schmidt-Nielsen, 1972).

Our estimates of airspeed produced some unfeasibly low values (Pennycuick, 2008), most probably because the GPS sampling frequency (1 fix per minute) underestimated the true distance travelled in periods of more tortuous flight. We therefore excluded sections of level flapping flight with V_g or $V_a < 4$ m s^{-1} for estimations of power use. Likewise, as the resolution of the GPS did not allow us to estimate the speed achieved by soaring and gliding (i.e. the cross-country speed) reliably as soaring and gliding bouts were often shorter than 1 minute, we assumed that cross-country speed was equivalent to V_g for any section of flight with > 80% of soaring and gliding, and included only those data in estimates of the cost of transport.

Statistical analysis

We used a GLMM with Poisson distribution to model the effect of ΔT and wind support on the presence/absence of passive flight, scoring the presence of soaring/gliding between successive GPS fixes as a binary variable with 0 corresponding to absence and 1 to presence. We expected a stronger effect of wind in poor thermal conditions, and the interaction between ΔT and wind support was therefore included in the model to test this assumption. Trip ID was included as random intercept to account for individual differences, route choice as well as non-measured flight conditions. An autocorrelation function (ACF) revealed an autocorrelation in the residuals of the model. For that reason, an autocorrelation factor of order 1 was also included in the model, using the function corAR1 from package "nlme" (Pinheiro et al. 2017). To verify whether this accounted for all the autocorrelation of the data, another ACF was used on the residuals of the final model.

Inspection of the data revealed that tropicbirds sometimes flapped while circling. We categorised soaring bouts according to whether they included flapping and used a binomial GLM to see if this was predicted by the wind support or ΔT values. Body mass was also included in the model as a factor to account for individual variation. We also compared the climb rates (the total altitude gained during a soaring bout divided by its duration) of soaring bouts with and without flapping using a Wilcoxon test.

To understand the consequences of soaring and wind support on the flight, we classified the data into two different flight styles: level flapping flight and soaring/gliding (when at least 80% of the flight section was passive flight). We used a Linear Mixed-Effects model to examine the effects of wind support on equivalent airspeed, as airspeed is the main determinant of power in level flapping flight (Pennycuick, 1968). Altitude was included as a fixed factor, as we expected birds flying higher to fly faster because they were less likely to be looking for prey than birds flying close to the sea surface. We included the number of prey pursuits as a fixed factor to account for the changes in mass due to feeding during the trip, and trip ID was included (containing the bird ID) as a random factor. Another Linear Mixed-Effects model was used to model the effect of wind support on the power required for level flapping flight, with trip ID as random intercept.

To examine how groundspeed varied between flight modes, we used a GLMM (with gamma distribution) that included wind support, flight mode as well as their interaction. An autocorrelation of factor 1 was included in the model, as residuals were autocorrelated, and the ID of the trip was used as random intercept to account for uncontrolled differences between trips, such as local conditions, foraging route or chances to catch a prey. To understand the energetic consequences of the difference in speed between flight modes while accounting for the difference in power between them, we used another GLMM with gamma distribution modelling the effect of wind support, flight style and their interaction on the cost of transport. Autocorrelation of factor 1 was also included in the model and trip ID included as random intercept. For all models, we examined the distribution of residuals against fitted values using the function “plot.lme” from the R package “nlme” (Pinheiro et al., 2017, version 3.1-151) to verify that there was no pattern in the distribution of residuals, which would suggest a non-linear relationship. The functions “qqnorm” and “simulateResiduals” from the R package DHARMa (Hartig & Hartig, 2017, version 0.4.5) were used to obtain QQ plots of the models and identify whether assumptions made to create the models were correct.

Data analysis was conducted in R Studio, the distribution of the models’ residuals was estimated using the R package “fitdistrplus” (Delignette-Muller *et al.*, 2015), mixed-effect models were made using “nlme” (Pinheiro *et al.*, 2017), R^2 were computed using the package “MuMIn” (Barton & Barton, 2015) and models were tested using “MASS” (Ripley *et al.*, 2013), “lme4” (Bates *et al.*, 2018) and “DHARMa” (Hartig & Hartig, 2017).

Results

Wind conditions were consistent between the two study seasons, with prevailing south-easterly winds. There was a seasonal difference in air temperature, with higher temperatures during the austral summer (February-March, mean = 24.9°C) than the winter (September-October, mean = 20.6°C). Sea surface temperature followed the same trend (28.7°C in February-March and 24.2°C in September-October), leading to very little variation in the difference in temperature between sea and air (ΔT) (Wilcoxon test: $W = 827$, $p = 0.174$).

Predicting the use of soaring

Tropicbirds spent on average 13% of their foraging trips either soaring or gliding (inter-quartile range 7 to 18%, Figure S2 A), for an average duration of 31.6 ± 22.9 s (mean ± s.d.). Thermal soaring was mostly composed of passive circling, but birds flapped during 16 ± 33%

(mean ± s.d., S2 B) of the time spent circling. The climb rate varied according to whether or not birds flapped in soaring bouts, with flapping increasing the climb rate from 0.57 to 0.84 m s^{-1} on average (Wilcoxon test: W = 7349, p < 0.001, n = 309).

Birds flew in different directions away from Round Island according to the nest location (see Chapter 4) and therefore varied in terms of whether they experienced a tailwind on the outbound or return leg of the trip. Soaring appeared most likely when birds experienced tailwinds, independently of whether this was in the beginning or the end of the flight (Figure 1 A and B) and when foraging activity occurred. However, birds tagged at the main study colony, which constituted the majority of the dataset, experienced the strongest tailwinds in the last 20% of the trip, once they had finished most of their foraging.

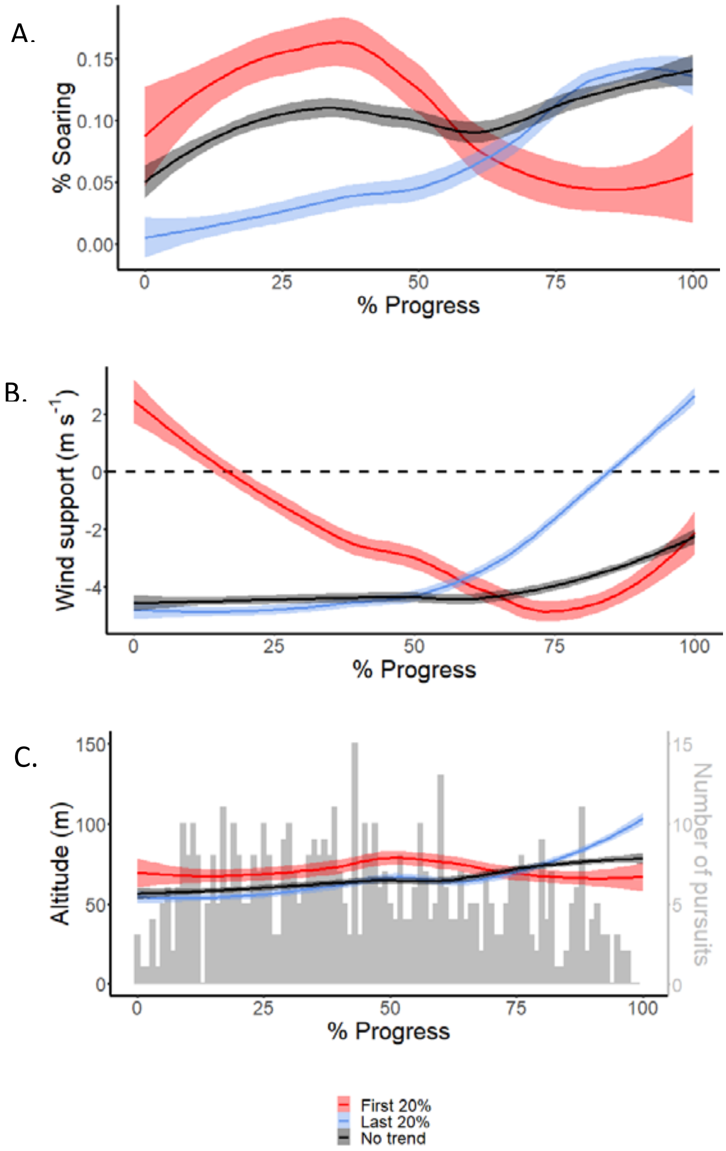

Figure 1. The occurrence of different flight and behavioural parameters throughout the foraging trips. Lines and filled areas (95% confidence intervals) show the local polynomial regressions of flight variables in relation to the proportion of progress, for each of the following categories: birds that experienced a tailwind (TWC > 0) during the first 20% of their flight (blue line), birds that experienced a tailwind during the last 20% of their flight (red line), and birds that did not experience a particular pattern of tailwind during their trip (black line). A. Proportion of time spent soaring (%); B. Wind support, the horizontal dashed line indicates a tailwind of 0 m s^{-1}*, values above 0 correspond to a tailwind and values below 0 a headwind; C. Flight altitude (lines) and total number of pursuits (grey bars).*

A GLMM confirmed that birds were more likely to switch to soaring-gliding flight with higher ΔT and wind support (Table 1). However, the marginal r-squared of the model was very low ($R^2_m = 0.03$), showing that ΔT and wind support did not explain a lot of variability compared to the random factors ($R^2_c = 0.24$).

Table 1: Summary statistics of the binomial GLMM showing the effect of the wind support (tailwind component, TWC), thermal strength (ΔT) and their interaction on the presence/absence of soaring sampled for each GPS fix across the 76 foraging trips. $R^2_m = 0.03$, $R^2_c = 0.24$

	Value	**Std. Error**	**t-value**	**p**
(Intercept)	-0.833	0.220	-3.782	< 0.001
ΔT (°C)	0.259	0.049	5.288	< 0.001
TWC (m s^{-1})	0.070	0.030	2.358	0.018
ΔT: TWC	-0.015	0.008	-1.940	0.052

Birds were less likely to flap during a soaring bout with increasing wind support (estimate = -0.1, Figure 2 A and C). Heavier birds were also more likely to flap during a soaring bout (Table 2). There was no relationship between the likelihood of flapping within circling and ΔT (Table 2, Figure 2 B).

*Table 2: Summary statistics of the binomial GLM showing the effect of tailwind component (TWC), thermal strength (*ΔT*), and body mass on the presence/absence of flapping during a soaring bout.*

	Estimate	Std. Error	z value	p	
(Intercept)	5.861	1.553	3.775	< 0.001	***
TWC (m s^{-1})	-0.109	0.034	-3.171	0.002	**
ΔT (°C)	-0.221	0.201	-1.102	0.271	
Mass (g)	-0.008	0.002	-3.482	< 0.001	***

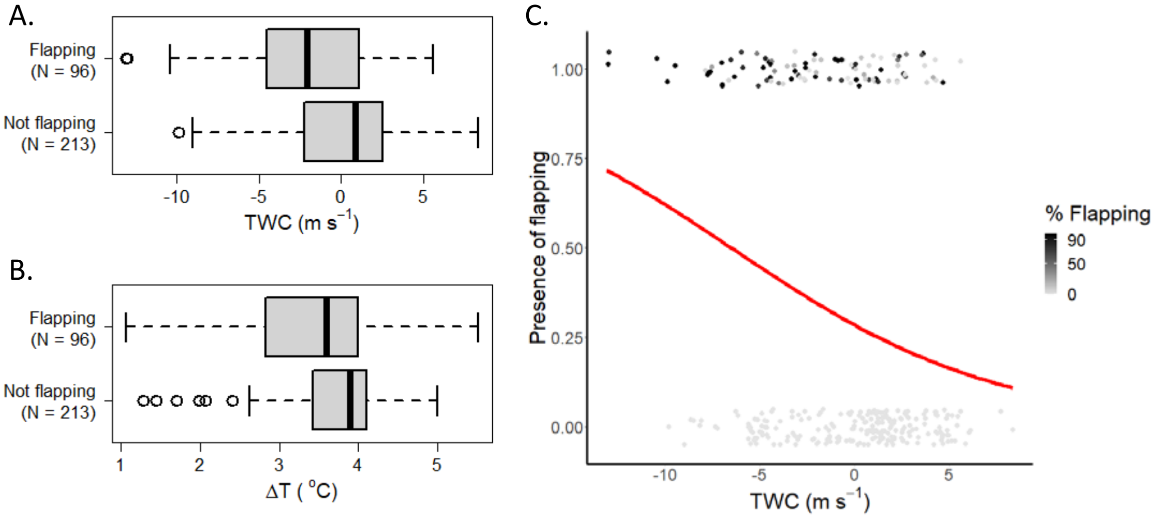

Figure 2. Effect of wind support (tailwind component, TWC, A.) and thermal strength (ΔT, B.) on the presence/absence of flapping in a soaring bout. Whiskers indicate the total distribution of the data in each group excluding outliers (points), edges of the box indicate the upper and lower quartiles and the thick black line the median. C. Logistic (binomial) regression of the probability of observing flapping during a soaring bout as a function of wind support (TWC). Darker points correspond to higher proportions of flapping.

Implications of soaring/gliding for flight speed and cost of transport

As expected, groundspeed increased and the cost of transport decreased with increasing wind support, this was true for both level flapping flight and soaring-gliding flight (Table 3 A., Figure 3 A, Table 3 B). The relationship between the COT and wind support was driven by the relationship between groundspeed and wind support, as the power requirements for flapping flight did not vary with wind support (Linear Mixed-Effects model: t-value = -0.50, p = 0.62, Figure S3 B), despite the fact that birds decreased their airspeed in relation to increasing wind support (Table 4, Figure S3 A). We did not find any effect of altitude or the number of prey pursuits on the equivalent airspeed (Table 4). Overall, the cost of transport (COT) was estimated to be 4 to 5 times lower in soaring-gliding flight (median = 1.4, IQR = 0.8 W kg^{-1})

than level flapping flight (median = 6.5, IQR = 4.4 W kg^{-1}) across the range of wind support values.

Table 3. A. Output for the model of groundspeed (m s^{-1}) in relation to wind support (tailwind component, abbreviated TWC, m s^{-1}) for level flapping flight (intercept) and soaring-gliding. The relationship between TWC and V_g *would be* $V_g = 12.51 \times TWC^{0.11}$ *for level flapping flight, and* $V_g = 8.30 \times TWC^{0.06}$ *for soaring-gliding.* $R^2_m = 0.40$, $R^2_c = 0.54$. *B. Output for the cost of transport model (COT, J m^{-1} kg^{-1}). The relationship between TWC and COT would be* $COT = 5.37 \times TWC^{-0.09}$ *for level flapping flight, and* $COT = 1.81 \times TWC^{-0.09}$ *for soaring-gliding. Delta* $R^2_m = 0.66$, $R^2_c = 0.76$.

A. Groundspeed (V_g)	**Value**	**Standard error**	**t-value**	**P**
(Intercept)	2.527	0.023	111.806	< 0.001
TWC	0.109	0.005	19.742	< 0.001
Soaring-gliding	-0.411	0.027	-15.502	< 0.001
TWC: Soaring-gliding	-0.045	0.006	-8.005	< 0.001
B. Cost of transport				
(Intercept)	1.681	0.036	46.587	< 0.001
TWC	-0.085	0.007	-11.961	< 0.001
Soaring-gliding	-1.086	0.039	-27.545	< 0.001
TWC: Soaring-gliding	-0.007	0.008	-0.882	0.378

Table 4. Summary of the Linear Mixed-Effects model of airspeed (m s^{-1}) in relation to wind support (tailwind component, TWC, m s^{-1}), number of prey pursuits and flight altitude for level flapping flight. $R^2_m = 0.05$, $R^2_c = 0.14$.

	Value	**Standard error**	**t-value**	**p**	**Significance**
(Intercept)	9.728	0.299	32.519	< 0.001	***
TWC (m s^{-1})	-0.252	0.024	-10.419	< 0.001	***
Number of prey pursuits	0.060	0.167	0.358	0.721	NS
Altitude (m)	0.002	0.002	0.799	0.425	NS

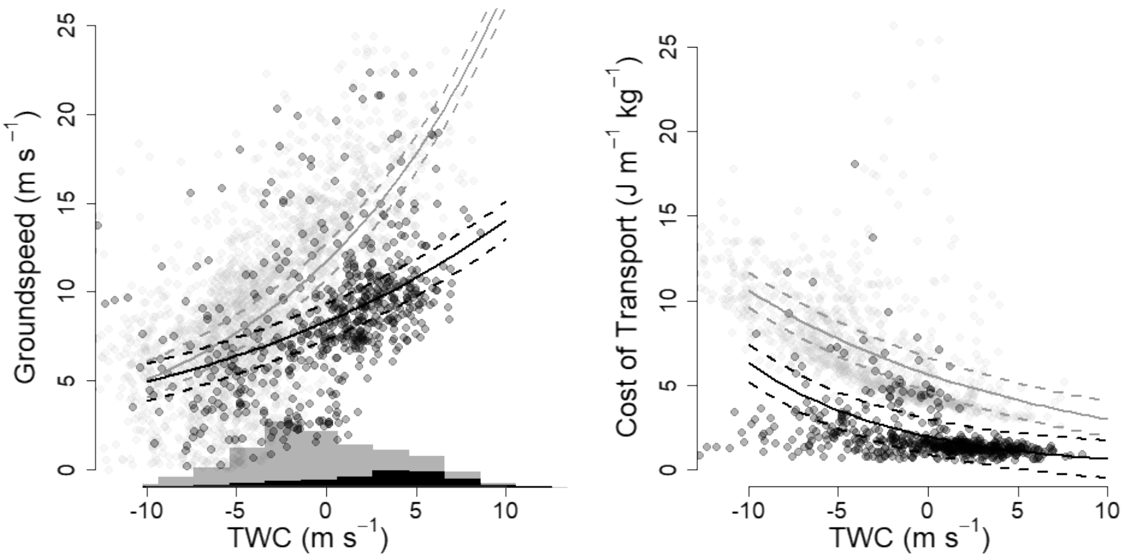

Figure 3. A. Groundspeed in relation to the tailwind component (TWC) for level flapping flight (light grey) and soaring-gliding (black). B. The cost of transport (COT) against TWC for level flapping flight (light grey) and soaring-gliding (black). Standard errors of the regressions are represented by the dashed lines.

Discussion

We show that the probability that a facultative soaring bird will switch to thermal soaring flight is predicted by the wind support, with soaring being more likely in tailwinds. Importantly therefore, it is the combination of wind and thermal strength that affects the viability of this strategy, rather than thermal strength alone. Curiously, birds were more likely to flap when they were soaring with a headwind than a tailwind. This suggests that the effect of wind on the ability to turn and gain altitude within a thermal, depends not only on wind strength but also the birds' direction of travel (*cf*. Harel *et al.*, 2016). While the mechanism underpinning this is not clear, the upshot is that headwinds not only make soaring less viable, but also more costly.

Thermal soaring is most commonly considered as a form of low-cost transport (though see reports of insectivores feeding in thermals: de Margerie *et al.*, 2018), but our results suggest that soaring is a flexible behaviour, used during commuting and prey searching, with its use predicted by the wind vector in relation to travel, rather than a particular behaviour. The relatively high costs of climbing flight (Berg & Biewener, 2008) mean that gaining altitude passively offers a notable energy saving for birds that search for and pursue prey at height. Tropicbirds in this study climbed 328 m per trip on average in association with feeding behaviour, as the mean altitude of tropicbirds in the minute before a pursuit was 41 m (± 26 m, s.d.), and birds undertook 8 prey-pursuits per trip on average. It seemed that birds foraging in a tailwind used soaring to climb between prey pursuits, while birds returning to the colony with a tailwind used thermals to climb to high altitudes and glide to their destination. These savings may be capitalised on to gain height for prey-searching or to cover distance cheaply by gliding, the latter being particularly advantageous on the return leg, as flight costs are increased by the additional mass of the prey carried (Sato *et al.*, 2008).

Given that tropicbirds do soar in thermals, and have the flexibility to use this during commuting or prey searching (Figure 1 C), the question is then why they do not use passive flight more? The proportion of soaring-gliding was low on average (13% of trip duration) and several trips barely included any soaring, despite featuring tailwinds and relatively high thermal strength. Given that the cost of transport is predicted to be lower during soaring irrespective of whether birds fly with a head or tailwind, the reason that birds are more likely to switch to flapping flight with increasing headwinds, and use powered flight in general, suggests that they are time limited. This is in line with the finding that tropicbirds favour short trips and reduce their resting time during the chick-feeding period (Sommerfeld & Hennicke, 2010) to optimise the rate of food delivery for chicks, and that, in general, birds fly faster when feeding young for the same reasons (Norberg, 1981).

Nonetheless, in conditions of headwind, the groundspeeds in soaring/ gliding flight were similar to the speeds for flapping flight, when flapping flight should be much faster in this scenario. This is most likely the result of the low number of observations of birds soaring/ gliding into headwinds causing an inflated intercept, possibly exacerbated by errors in the estimation of the wind at the bird locations (Safi *et al.*, 2013). A consequence of this is that the COT estimates for soaring/ gliding into headwinds are too low. Nonetheless, it still seems likely that birds stop soaring when flying into headwinds because of the penalty in speed, rather than COT, as the groundspeeds of birds soaring into 5 and 10 m s^{-1} headwinds would have to be 1.1 and 1.6 m s^{-1} before the COT for soaring was equal to the COT for flapping. Therefore, even in this scenario where the energetic efficiency is the same, flapping flight is > 3 times faster.

One further surprising result was the poor relationship between airspeed in flapping flight and wind support. This goes against almost all previous research on the topic showing a clear negative relationship between airspeed and wind support (Hedenström *et al.*, 2002; Liechti, 2006; Spear & Ainley, 1997), however this is most likely due to the confounding influence of prey loading and underestimation of the distance travelled between GPS points (Ryan *et al.*, 2004). Most of our study birds returned to the colony with tailwind, when aeronautical theory predicts they should reduce their airspeed. However, birds will be heavier on the return trip than on the way out (Sato *et al.*, 2008), resulting in higher airspeeds than if speed were driven by tailwind component alone.

Overall, we demonstrate that both the environmental conditions and the biological currency (here time limitation) affect the use of soaring flight in a medium sized bird. It is well established that the stereotypical form of thermal soaring flight, with birds gaining altitude in thermals and glide between them, results in a lower overall cross-country speed compared to powered flight. However, our results highlight that the importance – or cost – associated with slow flight will vary over the annual cycle as well as between species according to their body size (Hedenstrom & Alerstam, 1995). Indeed, we predict that the use of soaring flight may increase outside the breeding season when time constraints are relaxed, and birds are free to select their flight direction in relation to prey availability and the wind, rather than being constrained by the need to return to a central place (Weimerskirch *et al.*, 2016). Indeed, the difference in the sea surface and air temperatures suggests that sea thermals should be available year-round in regions such as the Indian ocean (Chapter 4, see also Weimerskirch *et al.*, 2016). An interesting implication of this is that we may have drastically underestimated how widespread thermal soaring flight is in the tropics, particularly among seabirds, which are typically tagged in the breeding season due to the relative ease with which biotelemetry units can be recovered in this stage of the annual cycle. Even for frigatebirds, which are the group where the morphology is most adapted to thermal soaring flight, soaring represented 82 % of trips during migration (Weimerskirch *et al.*, 2016) and 27 % of foraging trips (Corbeau *et al.*, 2020). A further implication is that models of flight costs, which tend to be based on the exclusive use of flapping flight for most species, may over-estimate the actual flight costs by a substantial margin for periods outside the breeding season. The collection of further high-frequency movement data will provide insight into how flight costs vary throughout the annual cycle, and in relation to both extrinsic and intrinsic factors.

References

Barton, K., & Barton, M. K. (2015). Package 'MuMIn.' *Version*, *1*, 18.

Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R. H. B., Singmann, H., … Green, P. (2018). Package 'lme4.' *Version*, *1*, 17.

Baudinette, R. V, & Schmidt-Nielsen, K. (1974). Energy cost of gliding flight in herring gulls. *Nature*, *248*(5443), 83–84.

Becciu, P., Rotics, S., Horvitz, N., Kaatz, M., Fiedler, W., Zurell, D., … Nathan, R. (2020). Causes and consequences of facultative sea crossing in a soaring migrant. *Functional Ecology*, *34*(4), 840–852.

Berg, A. M., & Biewener, A. A. (2008). Kinematics and power requirements of ascending and descending flight in the pigeon (*Columba livia*). *Journal of Experimental Biology*, *211*(7), 1120–1130. doi: 10.1242/jeb.010413

Bohrer, G., Brandes, D., Mandel, J. T., Bildstein, K. L., Miller, T. A., Lanzone, M., … Tremblay, J. A. (2012). Estimating updraft velocity components over large spatial scales: Contrasting migration strategies of golden eagles and turkey vultures. *Ecology Letters*, *15*(2), 96–103. doi: 10.1111/j.1461-0248.2011.01713.x

Bradbury, T. (1989). *Meteorology and flight: a pilot's guide to weather*. A&C Black.

Corbeau, A., Prudor, A., Kato, A., & Weimerskirch, H. (2020). Development of flight and foraging behaviour in a juvenile seabird with extreme soaring capacities. *Journal of Animal Ecology*, *89*(1), 20–28. doi: 10.1111/1365-2656.13121

de Margerie, E., Pichot, C., & Benhamou, S. (2018). Volume-concentrated searching by an aerial insectivore, the common swift, *Apus apus*. *Animal Behaviour*, *136*, 159–172.

Delignette-Muller, M. L., Dutang, C., Pouillot, R., Denis, J.-B., & Delignette-Muller, M. M. L. (2015). *Package 'fitdistrplus.'* R Foundation for Statistical Computing, Vienna, Austria. URL http://www. R ….

Duriez, O., Kato, A., Tromp, C., Dell'Omo, G., Vyssotski, A. L., Sarrazin, F., & Ropert-Coudert, Y. (2014). How cheap is soaring flight in raptors? A preliminary investigation in freely-flying vultures. *PLoS ONE*, *9*(1). doi: 10.1371/journal.pone.0084887

Duriez, O., Peron, G., Gremillet, D., Sforzi, A., & Monti, F. (2018). Migrating ospreys use thermal uplift over the open sea. *Biology Letters*, *14*(12), 20180687. doi: 10.1098/rsbl.2018.0687

Gardner, A., Duck, C., & Greig, S. (1985). Breeding of the Trindade Petrel *Pterodroma arminjoniana* on Round Island, Mauritius. *IBIS*, *127*(4), 517–522.

Harel, R., Duriez, O., Spiegel, O., Fluhr, J., Horvitz, N., Getz, W. M., … Nathan, R. (2016). Decision-making by a soaring bird: Time, energy and risk considerations at different spatio-temporal scales. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*(1704). doi: 10.1098/rstb.2015.0397

Harel, R., Horvitz, N., & Nathan, R. (2016). Adult vultures outperform juveniles in challenging thermal soaring conditions. *Scientific Reports*, *6*(1), 1–8.

Hartig, F., & Hartig, M. F. (2017). *Package 'DHARMa.'*

Hedenström, A. (1993). Migration by soaring or flapping flight in birds: the relative importance of energy cost and speed. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *342*(1302), 353–361. doi: 10.1098/rstb.1993.0164

Hedenstrom, A., & Alerstam, T. (1995). Optimal flight speed of birds. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *348*(1326), 471–487. doi: 10.1098/rstb.1995.0082

Hedenström, A., Alerstam, T., Green, M., & Gudmundsson, G. A. (2002). Adaptive variation of airspeed in relation to wind, altitude and climb rate by migrating birds in the Arctic. *Behavioral Ecology and Sociobiology*, *52*(4), 308–317. doi: 10.1007/s00265-002-0504-0

Kerlinger, P. (1989). *Flight strategies of migrating hawks*. University of Chicago Press.

Klein Heerenbrink, M., Johansson, L. C., & Hedenström, A. (2015). Power of the wingbeat: Modelling the effects of flapping wings in vertebrate flight. *Proceedings of the Royal Society A: Mathematical, Physical and Engineering Sciences*, *471*(2177). doi: 10.1098/rspa.2014.0952

Liechti, F. (2006). Birds: Blowin' by the wind? *Journal of Ornithology*, *147*(2), 202–211. doi: 10.1007/s10336-006-0061-9

Newton, I. (2010). *The migration ecology of birds*. Elsevier.

Norberg, R. A. (1981). Optimal Flight Speed in Birds when Feeding Young. *The Journal of Animal Ecology*, *50*(2), 473. doi: 10.2307/4068

Pennycuick, C. J. (1975). Mechanics of flight. Avian biology, vol. 5. *Farner DS, King JR & Parkes KC*, *5*, 1–75.

Pennycuick, C. J. (1968). Power requirements for horizontal flight in the pigeon Columba livia. *Journal of Experimental Biology*, *49*(3), 527–555.

Pennycuick, C. J. (1983). Thermal soaring compared in three dissimilar tropical bird species, *Fregata magnificens*, *Pelecanus occidentals* and *Coragyps atratus*. *Journal of Experimental Biology*, *102*(1), 307–325.

Pennycuick, C. J. (2008). *Modelling the flying bird*. Elsevier.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., Heisterkamp, S., Van Willigen, B., & Maintainer, R. (2017). Package 'nlme.' *Linear and Nonlinear Mixed Effects Models, Version*, *3*(1).

R Core Team. (2020). *R: A language and environment for statistical computing*. Retrieved from https://www.r-project.org/

Ripley, B., Venables, B., Bates, D. M., Hornik, K., Gebhardt, A., Firth, D., & Ripley, M. B. (2013). Package 'mass.' *Cran R*, *538*, 113–120.

Ryan, P. G., Petersen, S. L., Peters, G., & Grémillet, D. (2004). GPS tracking a marine predator: The effects of precision, resolution and sampling rate on foraging tracks of African Penguins. *Marine Biology*, *145*(2), 215–223. doi: 10.1007/s00227-004-1328-4

Safi, K., Kranstauber, B., Weinzierl, R., Griffin, L., Rees, E. C., Cabot, D., … Bohrer, G. (2013). Flying with the wind: Scale dependency of speed and direction measurements in modelling wind support in avian flight. *Movement Ecology*, *1*(1), 1–13. doi: 10.1186/2051-3933-1-4

Sapir, N., Wikelski, M., Mccue, M. D., Pinshow, B., & Nathan, R. (2010). Flight modes in migrating European bee-eaters: Heart rate may indicate low metabolic rate during soaring and gliding. *PLoS ONE*, *5*(11), 1–13. doi: 10.1371/journal.pone.0013956

Sato, K., Daunt, F., Watanuki, Y., Takahashi, A., & Wanless, S. (2008). A new method to quantify prey acquisition in diving seabirds using wing stroke frequency. *Journal of Experimental Biology*, *211*(1), 58–65. doi: 10.1242/jeb.009811

Scacco, M., Flack, A., Duriez, O., Wikelski, M., & Safi, K. (2019). Static landscape features predict uplift locations for soaring birds across Europe. *Royal Society Open Science*, *6*(1). doi: 10.1098/rsos.181440

Schmaljohann, H., & Liechti, F. (2009). Adjustments of wingbeat frequency and air speed to air density in free-flying migratory birds. *Journal of Experimental Biology*, *212*(22), 3633–3642. doi: 10.1242/jeb.031435

Schmidt-Nielsen, K. (1972). Locomotion: Energy cost of swimming, flying, and running. *Science*, *177*(4045), 222–228. doi: 10.1126/science.177.4045.222

Shamoun-Baranes, J., Bouten, W., Van Loon, E. E., Meijer, C., & Camphuysen, C. J. (2016). Flap or soar? How a flight generalist responds to its aerial environment. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*(1704). doi: 10.1098/rstb.2015.0395

Shamoun-Baranes, J., van Loon, E., van Gasteren, H., van Belle, J., Bouten, W., & Buurma, L. (2006). A comparative analysis of the influence of weather on the flight altitudes of birds. *Bulletin of the American Meteorological Society*, *87*(1), 47–61. doi: 10.1175/BAMS-87-1-47

Solomon, S., Manning, M., Marquis, M., & Qin, D. (2007). *Climate change 2007-the physical science basis: Working group I contribution to the fourth assessment report of the IPCC* (Vol. 4). Cambridge university press.

Sommerfeld, J., & Hennicke, J. C. (2010). Comparison of trip duration, activity pattern and diving behaviour by Red-tailed Tropicbirds (*Phaethon rubricauda*) during incubation and chick-rearing. *Emu*, *110*(1), 78–86. doi: 10.1071/MU09053

Spear, L. B., & Ainley, D. G. (1997). Flight behaviour of seabirds in relation to wind direction and wing morphology. *Ibis*, *139*(2), 221–233. doi: 10.1111/j.1474-919x.1997.tb04620.x

Vansteelant, W. M. G., Shamoun-Baranes, J., van Manen, W., van Diermen, J., & Bouten, W.

(2017). Seasonal detours by soaring migrants shaped by wind regimes along the East Atlantic Flyway. *Journal of Animal Ecology*, *86*(2), 179–191.

Weimerskirch, H., Bishop, C., Jeanniard-du-Dot, T., Prudor, A., & Sachs, G. (2016). Frigate birds track atmospheric conditions over months-long transoceanic flights. *Science*, *353*(6294), 74–78. doi: 10.1126/science.aaf4374

Weinzierl, R., Bohrer, G., Kranstauber, B., Fiedler, W., Wikelski, M., & Flack, A. (2016). Wind estimation based on thermal soaring of birds. *Ecology and Evolution*, *6*(24), 8706–8718. doi: 10.1002/ece3.2585

Williams, H. J., Holton, M. D., Shepard, E. L. C., Largey, N., Norman, B., Ryan, P. G., … Wilson, R. P. (2017). Identification of animal movement patterns using tri-axial magnetometry. *Movement Ecology*, *5*(1), 1–14. doi: 10.1186/s40462-017-0097-x

Williams, H. J., Shepard, E. L. C., Holton, M. D., Alarcón, P. A. E., Wilson, R. P., & Lambertucci, S. A. (2020). Physical limits of flight performance in the heaviest soaring bird. *Proceedings of the National Academy of Sciences*, *117*(30), 17884–17890. doi: 10.1073/pnas.1907360117

Wilson, R. P., Börger, L., Holton, M. D., Scantlebury, D. M., Gómez-Laich, A., Quintana, F., … Shepard, E. L. C. (2020). Estimates for energy expenditure in free-living animals using acceleration proxies: A reappraisal. *Journal of Animal Ecology*, *89*(1), 161–172. doi: 10.1111/1365-2656.13040

Wilson, R. P., Holton, M. D., Virgilio, A., Williams, H., Shepard, E. L. C., Lambertucci, S., … Duarte, C. M. (2018). Give the machine a hand: A Boolean time-based decision-tree template for rapidly finding animal behaviours in multisensor data. *Methods in Ecology and Evolution*, *9*(11), 2206–2215. doi: 10.1111/2041-210X.13069

Woodcock, A. H. (1975). Thermals over the sea and gull flight behavior. *Boundary-Layer Meteorology*, *9*(1), 63–68. doi: 10.1007/BF00232254

Young, I. R., Zieger, S., & Babanin, A. V. (2011). Global Trends in Wind Speed and Wave Height. *Science*, *332*(6028), 451–455. doi: 10.1126/science.1197219

Chapter 4 – High costs in low flying birds: Changing air density matters at sea level

Abstract

There is a need for greater mechanistic understanding of how environmental conditions affect the movements, energetics and foraging efficiency of seabirds, in order to predict their responses to global change. This is particularly pertinent for tropical seabirds, which are less studied than their temperate and polar counterparts. We quantify the effects of wind, uplift availability, and air density on flight costs using red-tailed tropicbirds (*Phaethon rubricauda*) breeding year-round on Round Island, Mauritius, as a model system. High-frequency data from multi-sensor loggers revealed extended periods of thermal soaring, demonstrating that this behaviour is not confined to specialist soaring fliers. However, there was no seasonal variation in uplift intensity or the use of passive flight. Neither was there a strong effect of wind on the costs of powered flight. Variation in air density, equivalent to a difference in flight height of 250 m, was the most important factor driving changing flight costs at seasonal scales, outstripping the effect of increasing mass during foraging. The effects of air density have largely been considered for birds undertaking dramatic altitudinal changes. Here we demonstrate how changing air density can modulate flight effort even for species that operate close to sea level. We suggest that air density may be more important than wind in modulating the flight costs of tropical species in general, which typically experience low wind speeds but marked seasonal changes in temperature. Converting average air densities to equivalent altitudes at a global scale demonstrates that birds flying at sea level can experience effective altitudes ≤ 1 km greater in the tropics than in high latitudes. This highlights a previously underappreciated route by which tropical birds in particular may be impacted by global change.

Introduction

In temperate regions, the majority of marine and terrestrial birds tend to time their reproduction to exploit well-defined seasonal increases in productivity (Lack, 1968), leading to a single breeding season (Allen & Wolfe, 2013; Borstad *et al.*, 2011; Hetmański, 2004). In contrast, many tropical marine systems are oligotrophic year-round. This is associated with much more variable breeding phenologies, with peak breeding season varying between and within tropical seabirds, presumably timed to coincide with changes in productivity, which are regionally variable and relatively small (Balance *et al.*, 1999; Behrenfeld *et al.*, 2005) compared to the seasonal variation in weather (cyclones season, monsoon) (Nicoll *et al.*, 2017; Veldhuis *et al.*, 1997). This raises the question as to whether seasonal changes in foraging costs are more influential than food availability in driving variation in foraging efficiency in these systems.

Seasonal changes in resource availability are not straightforward to assess in oligotrophic waters, as remotely sensed data such as chlorophyll a concentrations often show little variation over the scales that seabirds operate (Behrenfeld *et al.* , 2005). Information on horizontal movement paths from animal-attached GPS and satellite trackers can be used to infer and map foraging activity (Browning *et al.*, 2018; Weimerskirch *et al.*, 2016), however it can be difficult to extrapolate this to prey encounter rates and foraging success. Other biologging sensors have been used to provide important insight here, as prey encounter rates can be inferred from changes in hydrostatic pressure for diving animals (Sala *et al.*, 2012) or barometric pressure in surface feeders (Weimerskirch *et al.*, 2005; Yoda *et al.*, 2007), as well as fine-scale changes in orientation e.g. using magnetometers (Simeone & Wilson, 2003). However, in all cases, additional sensors (or previous validations, Wilson *et al.*, 2002) are required to provide further information on likely success (Machovsky-Capuska *et al.*, 2016), because the number of dives is not always proportional to success rate (Shealer, 1996).

Animal-attached accelerometers have proved valuable in this regard as they can be used to characterise prey pursuits and even capture, if their placement allows (Chimienti *et al.*, 2017; Hernandez-Pliego *et al.*, 2017). Acceleration metrics also allow the estimation of effort in flapping flight, e.g. through changes in wingbeat frequency and dynamic body acceleration (Halsey *et al.*, 2009; Wilson *et al.*, 2006). Previous studies have shown acceleration metrics vary with both foraging success and a headwind component, reflecting changes in bird mass and speed respectively (Sato *et al.*, 2008). This raises the prospect of combining information on foraging success and prey encounter rates to assess overall foraging efficiency and how this varies with environmental conditions.

Seasonal changes in temperature may impact foraging efficiency by affecting prey abundance or accessibility (Peck *et al.*, 2004; Ramos *et al.*, 2002). Temperature can also affect flight costs and capacities, both directly (Daunt *et al.*, 2006), and through associated weather parameters such as wind (Lewis, Phillips *et al.*, 2015), air density (Schmaljohann & Liechti, 2009), and even the development of cyclones. The effect of wind on flight costs varies depending on the flight trajectory with respect to the wind, with flight costs decreasing in tailwinds and increasing in headwinds for flapping fliers (Hedenström, 2003). Overall, flight costs are likely to increase with wind speed when birds are foraging from a central place (*cf*. Furness & Bryant, 1996 for dynamic soaring birds), as the time spent flying into a headwind is likely to result in costs that outweigh the gains from the shorter phase when birds can exploit tailwinds (though see Collins *et al.*, 2020). Where wind-related costs are substantial, birds may adapt their foraging strategy to maintain a similar flight effort (Elliott *et al.*, 2014), and consequently changes in flight effort need to be considered in relation to trip duration. Temperature may also be related to flight effort through the development of sea-thermals (Woodcock, 1940), which birds can use to gain altitude and cover ground at low cost (Duriez *et al.*, 2018; Weimerskirch *et al.*, 2016).

In this study, we use high frequency data on the movements of red-tailed tropicbirds (*Phaethon rubricauda*) to assess how foraging efficiency varies across a full range of seasonal conditions. While these birds breed seasonally in some location, they breed year-round on Round Island, Mauritius, making this a model system in which to examine the effects of the changing biotic and abiotic environment. Specifically, we quantify how changing environmental conditions affect (1) flight effort, assessing the specific responses to changing wind speed and air density, and (2) the behavioural responses to these changing costs, in terms of trip duration and direction. We then consider (3) the implications of changing movement costs for overall foraging efficiency, quantifying rates of prey encounter and using wingbeat frequency as a proxy for foraging success. Overall, this should provide insight into the relative importance of different environmental parameters in affecting foraging efficiency and provide mechanistic insight into how tropical seabird populations may be affected by global change (see Lewis *et al.*, 2016; Weimerskirch *et al.*, 2012, Clay *et al.*, 2020).

Methods

Our study focused on red-tailed tropicbirds nesting on Round Island, Mauritius (19.8486° S, 57.7885° E) (Gardner *et al.*, 1985). Breeding activity peaks between August and October when > 25% of nest sites are occupied. The lowest breeding activity occurs between January and April when < 5% of nests are occupied (Ruhomaun, 2017, unpublished results; Tatayah, 2010).

Breeding adults were tagged during chick rearing in the low season (February 1st - March 17th, 2018) and high season (September 14th - October 17th, 2018). Birds were weighed and photographed to quantify wing loading following Pennycuick (2008). They were then equipped with a Daily Diary (Wildbyte Technologies, Swansea University, UK) and a GPS logger (GiPSy 5, Technosmart Europe, Guidonia-Montecelio, Italy). The Daily Diary recorded acceleration and magnetic field strength in 3 axes at 40 and 13 Hz respectively, and pressure and temperature at 4 Hz. The GPS was set to log one location per minute. Both loggers were placed in a zip-lock bag and fixed to the back feathers using Tesa tape (Wilson & Wilson, 1989). The loggers, housing and tape weighed 27.7 g, representing < 3% of the average body mass (mean body mass for tagged birds was 826 g), and 4.3% of the lowest body mass recorded during this study (650 g). Ethical permissions for the deployment of loggers on tropicbirds were granted by Swansea University AWERB, permit 040118/39.

Wind speed, direction, atmospheric pressure, relative humidity and temperature were recorded every 5 minutes by a portable weather station (Kestrel 5500L, Kestrel instruments, USA) mounted on a 5 m pole and stationed at the highest point of Round island (265 m ASL). Wind records were interrupted due to battery failure between 09/02 and 20/02, during which 7 flights were recorded. They were replaced by hourly wind records from Sir Seewoosagur Ramgoolam International Airport in Mauritius, approximately 65 km from Round Island (http://www.wunderground.com). Temperature, pressure, wind speed, wind direction and relative humidity were synchronised with the GPS data and linearly interpolated to 1 minute.

Flight metrics

Flight was evident as periods with variable altitude and this was categorised as flapping or non-flapping flight using a simple acceleration threshold. Specifically, the Vectorial sum of the Dynamic Body Acceleration (VeDBA) was calculated according to Wilson (2020), using smoothed raw acceleration values over two seconds to derive the static component. VeDBA values were also smoothed over two seconds (sVeDBA) in order to produce a metric that varied between high and low levels of activity. A threshold of $\geq 0.3\ g$ was used to identify flapping flight, which distinguished between flight types across individuals and seasons. The identification of flapping and gliding was undertaken in R Studio version 4.0.0 (R Core Team, 2020).

Wingbeat frequency was used as a proxy for flight effort rather than DBA (Wilson *et al.*, 2020), as we identified a difference in the stability of the accelerometers between the two seasons, which lead to consistent differences in the amplitude of the acceleration signal (Chapter 5). Wingbeat frequency was robust to such changes in logger attachment and has been used to estimate work rate in a range of studies (Taylor *et al.*, 2019). Individual wingbeats were identified from peaks in the dynamic heave acceleration, smoothed over 3 events (0.075 s). Each segment from peak to peak was counted as a wingbeat cycle, and the duration was used to calculate wingbeat frequency (see Figure 1). Frequencies of < 4 Hz were considered as erroneous for birds of this body mass and therefore removed (Pennycuick 2008).

Flight altitude above sea level was calculated using the barometric pressure recorded by the Daily Diary, and the mean sea-level pressure from Earth (https://earth.nullschool.net/) with a resolution of 3 hours and 0.5 x 0.5 degrees. Raw pressure values were smoothed over 2 s and the rate of change of altitude (V_z) was calculated over 1 second intervals. The air density at flight altitude was estimated using the ideal gas law, using pressure measured by the Daily Diary, as well as the temperature and relative humidity recorded by the weather station at 265 m altitude (Schmaljohann & Liechti, 2009).

Red-tailed tropicbirds are surface feeders known to target flying fish (Le Corre *et al.*, 2003). Prey pursuits were evident as abrupt, rapid reductions in altitude combined with a cessation of flapping flight and characteristic low-frequency changes in the acceleration data that indicate manoeuvring. Due to the variability in rate of change of altitude associated with prey pursuits, these events were identified manually using the custom-written animal movement analysis software DDMT (Wildbyte Technologies, http://wildbytetechnologies.com/software.html). Prey encounter rate was estimated as the number of pursuits recorded during a foraging trip divided by the total distance of the trip, and foraging efficiency as the number of pursuits divided by the total number of wingbeats (Ropert-Coudert *et al.*, 2006).

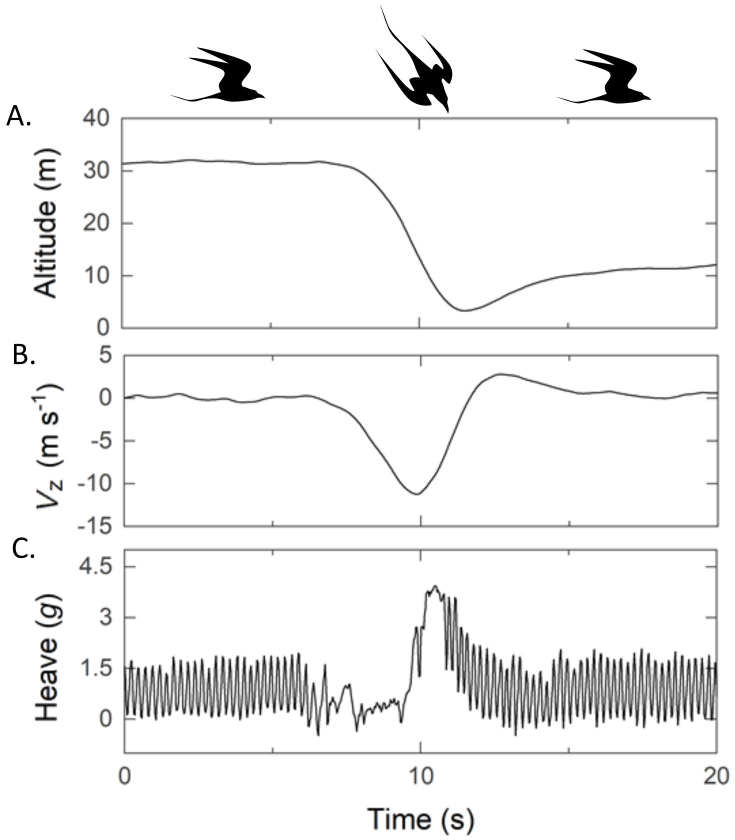

Figure 1. Identification of aerial pursuits*. Pursuits are typified by (A) loss of altitude, (B) rapid vertical velocity (V_z), with negative values indicating descending flight, and (C) a switch from flapping to passive flight, as evident in the heave (dorso-ventral) acceleration values.*

The bird's groundspeed (V_g) was taken as the haversine distance between GPS fixes divided by the time. The airspeed was estimated in order to assess how this varied in relation to both wind and air density. Airspeed (V_a) was calculated as the magnitude of the resulting vector of wind speed and groundspeed:

$$(1)\ V_a = \sqrt{V_g^2 + V_w^2 + 2V_gV_w\cos\left(\frac{\theta \times \pi}{180}\right)}$$

where V_g is the groundspeed, V_w the wind speed and θ the angle between the bird heading and the wind direction (ranging between 0 and 180 degrees, where wind direction is the direction it was blowing). The headwind and crosswind components were then calculated as the two components of the wind acting on airspeed. The headwind component (HWC) is the projection of the wind vector on the airspeed vector. A positive HWC indicates a headwind and a negative HWC corresponds to a tailwind. The crosswind component (CWC) is the projection of the wind vector on a line perpendicular to the airspeed vector. HWC and CWC were calculated using formulae (2) and (3) respectively:

$$(2)\ HWC = \cos\left(\varphi \times \frac{\pi}{180}\right) \times V_w$$

$$(3)\ CWC = \sin\left(\varphi \times \frac{\pi}{180}\right) \times V_w$$

where V_w is the wind speed and φ is the angle in degrees between the airspeed vector (i.e. the true heading of the bird before the drift caused by the wind) and the wind vector (ranging from 0 - 180 °).

Statistical analysis

Wilcoxon tests were used to test for seasonal differences in the body mass and wing area of tagged tropicbirds, as well as wind speed and temperature. Student's t-tests were used to compare seasonal changes in air density and the age of the chicks. Environmental variables were averaged over all flights per day to avoid pseudo-replication. Simple LMM models were used to test whether total distance covered, wingbeat frequency, prey encounter rate and foraging efficiency varied between the two seasons, with individual as a random factor, as several flights were recorded for some birds.

We then looked at the consequences of seasonal changes in both biotic and abiotic factors for flight costs, using wingbeat frequency as a proxy for power use. Airspeed is one of the key determinants of power use, and it is well established that birds vary their airspeed in relation to the wind (increasing airspeed in headwinds and reducing it in tailwinds). We therefore opted to include airspeed, but not wind, in the model of wingbeat frequency. We also ran a model of airspeed to see how much variation was explained by the wind, where airspeed was that during level flapping flight (taken as periods where $-0.2 < V_z < 0.2$ and sVeDBA was > 0.3 *g*) in order to control for changes in airspeed that occur in relation to climbing and descending flight (Chapter 2). Birds were also expected to increase their airspeed with decreasing air density (due to increasing altitude or temperature) (Hedenström, 2003; Pennycuick, 2008). An LMM model was used to test this hypothesis, using the birds' individual ID as random intercept nested within foraging trip to account for unmeasured differences between days and individuals. Air density was included in the model as a fixed factor. Flight altitude was also included to account for potential changes in currency (and associated speed selection) between relatively high and low altitude flight. The model included the fixed effects of headwind and crosswind components, as well as wind strength in order to test whether the estimated head and crosswind components captured all the variation due to changing wind conditions. We tested for collinearity by calculating the Variance Inflation Factors (VIF) of every fixed effect using the package "performance" (Lüdecke *et al.*, 2021). An autocorrelation structure of order 1 was also integrated to the model to account for the high level of autocorrelation in the GPS data (lag = 40). We examined the distribution of residuals against fitted values using the function "plot.lme" from the R package "nlme" (Pinheiro et al., 2017, version 3.1-151) to verify that there was no pattern in the distribution of residuals, which would suggest a non-linear relationship. In addition, the function "simulateResiduals" from the R package DHARMa (Hartig & Hartig, 2017, version 0.4.5) was used to obtain QQ plots of the model and identify whether assumptions made to create the model were correct.

In the final LMM model of wingbeat frequency we averaged values of airspeed, air density and flight altitude between successive prey pursuits in order to distinguish the effects of foraging success i.e. increasing body mass, from those of the physical environment. Only foraging trips with 5- 15 pursuits and between-pursuit intervals of > 1 minute were included (resulting in 345 segments recorded over 48 trips from 41 birds). One outlier segment with a mean altitude > 250 m was excluded, as all other segments had a mean altitude < 150 m. The number of pursuits was included as a fixed-effect in interaction with season, to identify any seasonal differences in capture rate. The presence of airspeed in the model accounted for the expected effects of the wind on the power output. Air density and altitude were both included in the model to enable us to distinguish between the effects of changing flight altitude and seasonally changing weather systems. "Individual" was used as random intercept nested within "foraging trip". Diagnostic plots were produced to assess the quality of the model, using the same method as previously explained. Statistical analyses were carried out using R

Studio, using the packages nlme (Pinheiro *et al.*, 2017, version 3.1-151) and MuMIn (Barton & Barton, 2015, version 1.43.17).

Results

A total of 55 red-tailed tropicbirds were equipped with GPS-DD loggers and tracked over 76 foraging trips; 31 during low season in the austral summer (February-March) and 45 during high season (September-October). There was no evidence for seasonal variation in body mass (Student's t-test: t = 0.282, p-value = 0.779) or wing area (Student's t-test: t = -0.773, p-value = 0.446) suggesting that birds did not vary in their stage of moult. However, the chicks of tropicbirds tagged in September-October were on average 2.7 days younger than those tagged in February-March (Wilcoxon test: W = 629, $p < 0.001$).

Foraging trips covered an average of 100.1 km in 5.4 hours, and distance remained consistent between the two seasons (LMM: std. error = 2.085, t-value = 1.343, p = 0.185). Birds foraged in diverse directions from the island although most flights were directed to the south of Round Island (Figure 3), away from the main study colony (Table 1). The average heading taken by birds when leaving their nest did not vary between season (Watson-Williams test of homogeneity of means: W = 0.254, p = 0.881). However, flight altitudes were on average 13.5 m higher during the low season (LMM: estimate = -13.542, std. error = 5.050, t-value = -2.681, p = 0.010). The average air temperature during the low season was 4.1 °C higher than during the high season (Wilcoxon test: W = 378, $p < 0.001$) and air density was 0.03 kg m^{-3} lower (Student's t-test: estimate = -0.032 kg m^{-3}, t = -19.632, $p < 0.001$), however the difference in temperature between sea and air remained stable across seasons (Wilcoxon test: W = 237, p = 0.183).

Table 1: Comparison of weather conditions and flight performance between low (February-March) and high (September-October) season. Values are the means ± s.d.

Variable	**Low Season**	**High Season**	**Significance**
Air Density (kg m^{-3})	1.16 ± 0.01	1.19 ± 0.01	**
Wind Direction (degrees)	81.9 ± 0.9	89.2 ± 0.2	**
Wind Speed ($m.s^{-1}$)	5.0 ± 3.5	6.3 ± 2.2	NS
ΔT (°C)	3.7 ± 1.4	3.6 ± 0.6	NS

Trip Distance (km)	83.5 ± 58.1	111.5 ± 105.4	NS
Trip Duration (hours)	5.1 ± 7.8	5.6 ± 8.2	NS
Outward Heading (degrees)	158.6 ± 1.0	154.5 ± 1.1	NS
Airspeed (m s^{-1})	9.1 ± 2.4	9.8 ± 2.2	NS
Mean Flight Altitude (m)	69.8 ± 23.3	55.5 ± 16.5	**
Passive Flight (% of time)	12.0 ± 8.7	13.4 ± 6.9	NS
Wingbeat Frequency (Hz)	4.0 ± 0.1	3.9 ± 0.1	**
Number of Pursuits	8.5 ± 6.4	8.0 ± 6.6	NS
Pursuit distance from colony (km)	21.8 ± 16.6	27.2 ± 26.8	NS
Foraging efficiency (Pursuits for 10,000 Wingbeats)	2.8 ± 1.7	2.2 ± 1.4	NS

Foraging efficiency

On average, pursuits occurred at a distance of 25.02 ± 23.29 km (mean ± s.d.) from the colony, which did not vary between seasons (LMM: t-value = 0.992, p = 0.326; see Figure 2 and Table 1). Prey encounter rate (number of pursuits per km travelled) did not vary significantly between seasons (Wilcoxon test: W = 857, p-value = 0.093), with one pursuit being recorded every 8.0 km during the low season, and one every 10.8 km in the high season. In addition, foraging efficiency (the number of pursuits divided by the total number of wingbeats per flight) also remained constant across seasons (LMM: t-value = -1.342, p = 0.185, see Table 1). Finally, there was no evidence for seasonal variation in foraging success, as the slope of the relationship between number of pursuits and wingbeat frequency did not vary (Table S3).

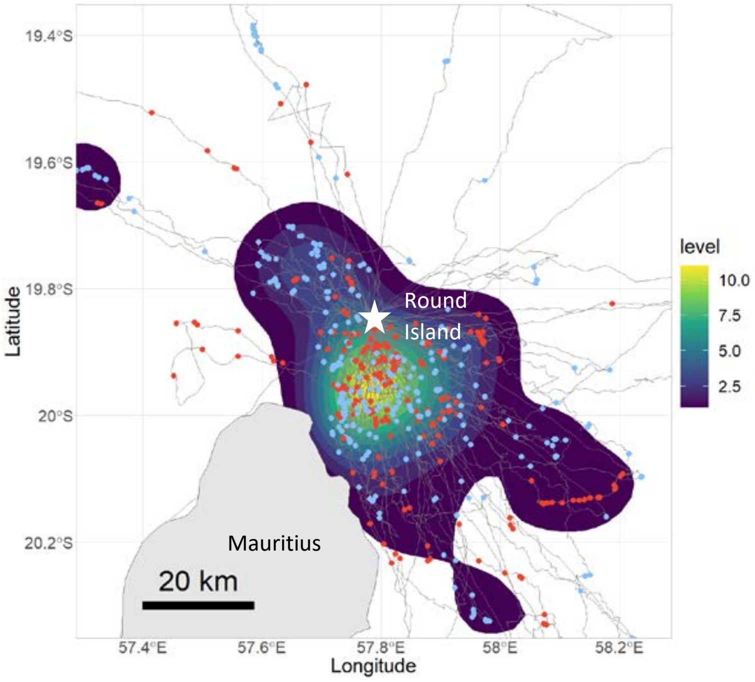

Figure 2. ***Density and distribution of prey pursuits around Round Island****. Foraging tropicbird tracks are represented by the grey lines and prey pursuits by red (low season) and blue (high season) dots. Pursuit density in both seasons is represented by a coloured gradient, with higher density areas in yellow and lower density areas in dark blue. Map created using ggmap (Kahle & Wickham, 2013).*

Flight effort

The magnetometer data revealed that tropicbirds used thermal soaring flight, climbing at a mean rate of 0.56 m s^{-1} in thermals, to a maximum altitude of 481 m. Birds used passive flight for periods of 0.2-204 minutes per trip (Figure 3), which represented a mean of 13% (maximum 34%) of their flight time per foraging trip. There was no difference in the proportion of time spent in passive flight between seasons (Wilcoxon test: W = 546, p-value = 0.1108).

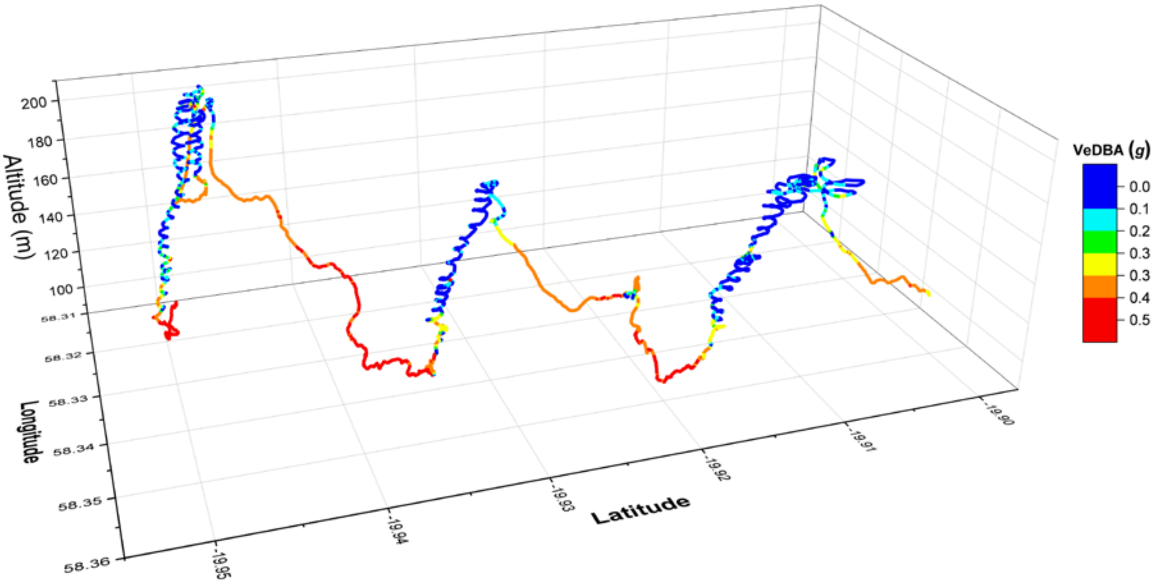

Figure 3. A 45-minute section of a tropicbird flight with periods of thermal soaring, reconstructed using dead-reckoning (Gunner et al. in submission). The dead-reckoned track is coloured according to VeDBA, where blue sections indicate periods without flapping.

Airspeeds remained stable between the two seasons (LMM: std. error = 0.373, t-value = -1.329, p = 0.188, see Table 1), consistent with the lack of a seasonal difference in mean wind speed but slightly at odds with the seasonal difference in air density (Table 1). Wind and density were both significant predictors in our model of airspeed, although the overall R^2 was relatively low (Estimate = 0.38, R^2_m = 0.18, R^2_c = 0.25, see Table S2). No collinearity was found between wind speed, headwind and crosswind component, but headwind component and wind speed had an effect of similar magnitude (scaled estimates: 0.82 for headwind and 1.03 for wind speed). Airspeed was not affected by the crosswind component. In line with theoretical predictions, birds increased their airspeed in conditions of lower air density and higher altitudes (Table S2). No collinearity was found between altitude and density.

A comparison of wingbeat frequency in level flapping flight showed that flight was on average more costly in the low season, with an increase of 0.10 Hz in wingbeat frequency (corresponding to 94% of the standard deviation of wingbeat frequency in the high season) (LMM: Estimate = -0.096, std. error = 0.030, t-value = -3.194, p = 0.002). Air density was the strongest driver of wingbeat frequency (Scaled estimate = -0.084), with lower flight effort at higher air densities, which occurred in the high season (LMM: Raw estimate = -5.392, p =

0.004, see Table S3). Surprisingly, we did not find any effect of airspeed on wingbeat frequency (p = 0.226), however, airspeed had a positive effect on the slope of the relationship between air density and wingbeat frequency (Raw estimate = 0.266, p = 0.014), showing that the effect of air density on wingbeat frequency was reduced at high speed.

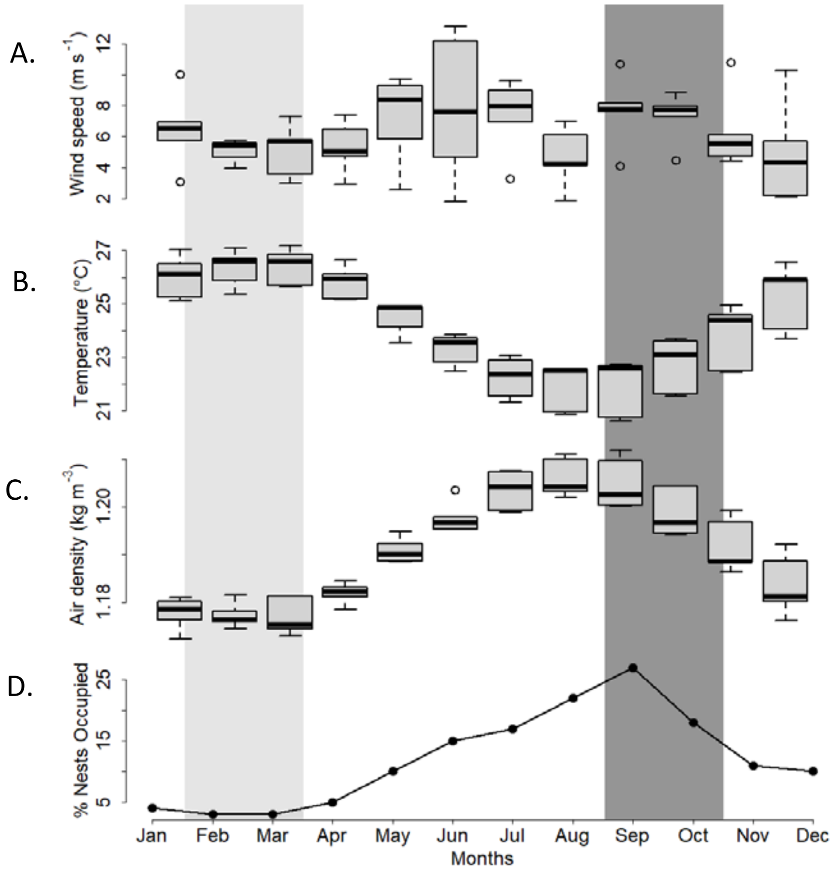

Figure 4. Seasonal variation of the average monthly wind speed (A), temperature (B) and air density (C) in Mauritius between 2015 and 2019, compared to the monthly variation in the proportion of nest sites occupied by tropicbirds on Round Island in 2017 (Ruhomaun, 2017, unpublished results). *On the boxplots, thick black lines represent the median value for a given month, extremes of the box show the first and third quartile and whiskers show extreme values, excluding outliers. Colour rectangles correspond to the low (light grey) and high (dark grey) seasons.*

Discussion

Foraging efficiency

Energy gain and energy use are typically considered separately, despite the importance of the net rate of energy gain in individual foraging decisions (Pyke, 1984; Weimerskirch *et al.*, 2003) as well as ultimately, factors such as when to breed (*cf.* Nathan *et al.*, 2012). Integrating movement costs into assessments of life-history traits, such as breeding phenology, is particularly important for animals that spend a lot of time in flight, given the scale of the movement costs (Butler, 2016) and their dependence on wind speed (Elliott *et al.*, 2014; Furness & Bryant, 1996b; Liechti, 2006), the availability of updrafts (Duriez *et al.*, 2014) and, as is apparent in this study, air density. Indeed, given that power-use is proportional to the cube of the wingbeat frequency, our results indicate a notable increment in movement costs in the low breeding season that appears to be due solely to the decreased air density. Against this, there is no seasonal effect of winds or thermals, although the latter presumably reduce foraging costs appreciably (see Duriez *et al.*, 2014).

Our finding that the number of prey capture attempts or foraging success did not vary between seasons is surprising, as while prey availability is a pre-requisite to successful breeding, we predicted that the 5-fold increase in breeding activity would be accompanied by a change in prey availability. Nonetheless, our metric of foraging success was based on an increase in body mass (cf. Sato *et al.*, 2008), which ignores changes in energy density. It may be that peak season could be associated with an increase in more profitable prey. For instance, in the Mozambique channel, tropicbirds mainly feed on dolphinfish (*Coryphaena hippurus*) during the austral summer, which are more profitable than prey caught in other seasons such as squid (Le Corre *et al.* 2003). Nonetheless, little is known about prey types targeted by or available to tropicbirds breeding on Round Island (Le Corre *et al.* 2003; Le Corre, 2001; Williams & Newell, 1957). It is also possible that we sampled tropicbird behaviour in an atypical year with increased prey availability during the austral summer. Further data collection on prey type and foraging effort is therefore required to establish the full role of prey availability in the breeding phenology of this population, which shows a markedly different patterns to other populations in the region (Le Corre 2001, 2003).

While our measure of foraging efficiency did not vary between seasons, we did reveal notable changes in flight costs between breeding seasons. Against our expectations, the seasonal difference in effort was not driven by wind speed, as while wind was an important driver of airspeed at the trip level, there were no seasonal differences in wind speed or airspeed, and no differences in the use of thermal soaring (see later). Tropicbirds adapted their airspeed as expected, by flying faster into headwinds, at higher altitude, and in conditions of low air density, but wingbeat frequency was not affected by airspeed. This may be influenced by limitations in our airspeed estimates due to (i) differences in wind speed between the anemometer and bird locations and (ii) the underestimation of distance flown between successive GPS fixes. The fact that wind speed had a stronger effect on airspeed than the headwind component confirms the latter did not capture all the effects of wind, as there is no biological reason for birds to increase their airspeed in high wind conditions irrespective of the headwind.

Instead, seasonal differences in wingbeat frequency were predicted by changes in air density, driven by changes in air temperature, which are consistently higher in February-March (low season). Birds flew on average 13.5 m higher in the low season, but the corresponding difference in air density (0.002 kg m^{-3}) is minor compared to the difference in density between seasons (0.03 kg m^{-3}). Indeed, the seasonal difference is equivalent to birds flying ~250 m higher in the low season (assuming standard atmospheric conditions) (Figure 5). The effect of air density on flight effort is well known (Bishop *et al.*, 2015; Pennycuick, 2008; Schmaljohann & Liechti, 2009), with lift decreasing with increasing altitude/ decreasing density (Pennycuick, 2008; Rayner, 1988), whereas weight remains essentially unchanged. Birds flying at lower air densities must therefore increase their wingbeat frequency and associated lift production for the same airspeed. However, ecologists have only considered this as a factor affecting flight effort when birds make substantial changes in flight height, such as the extreme changes in elevation recorded in birds migrating over the Himalayas (>8000 m, Bishop *et al.*, 2015) or the Sahara (Sjöberg *et al.*, 2021). Here we demonstrate that changes in density can be the main driver of seasonal changes in flight effort, and that this can occur independently of flight altitude.

Indeed, density may be the main factor affecting seasonal changes in flight effort for tropical seabirds in general, given the relatively low difference in mean wind speeds. In Mauritius, air density reaches an annual low in February and March with median values around 1.18 kg m^3 (Figure 4 and 5). Birds are clearly able to compensate for these costs, as populations in other areas show a peak in breeding activity during the austral summer. Indeed, in the Mozambique Channel, there is a marked summer peak in productivity (Tew-Kai & Marsac, 2009), which can compensate for more costly flight conditions. Nonetheless, it is worth noting that air densities will decrease further with global increases in temperature, for instance an increase in mean temperature from 27 °C to 28 °C (at a sea level pressure of 1000 hPA), would increase the density altitude by 40 m. This is likely to be particularly pertinent for birds in the tropics, which experience low air densities year-round due to the high temperatures. Indeed, examining patterns in density altitude at a global scale demonstrates that birds flying at sea level in the tropics routinely experience air densities equivalent to 500 – 800 m above those operating at high latitudes (Figure 5). This leads to the broader question of whether geographical trends in air density could affect the distribution of flying animals according to their morphology and flight style.

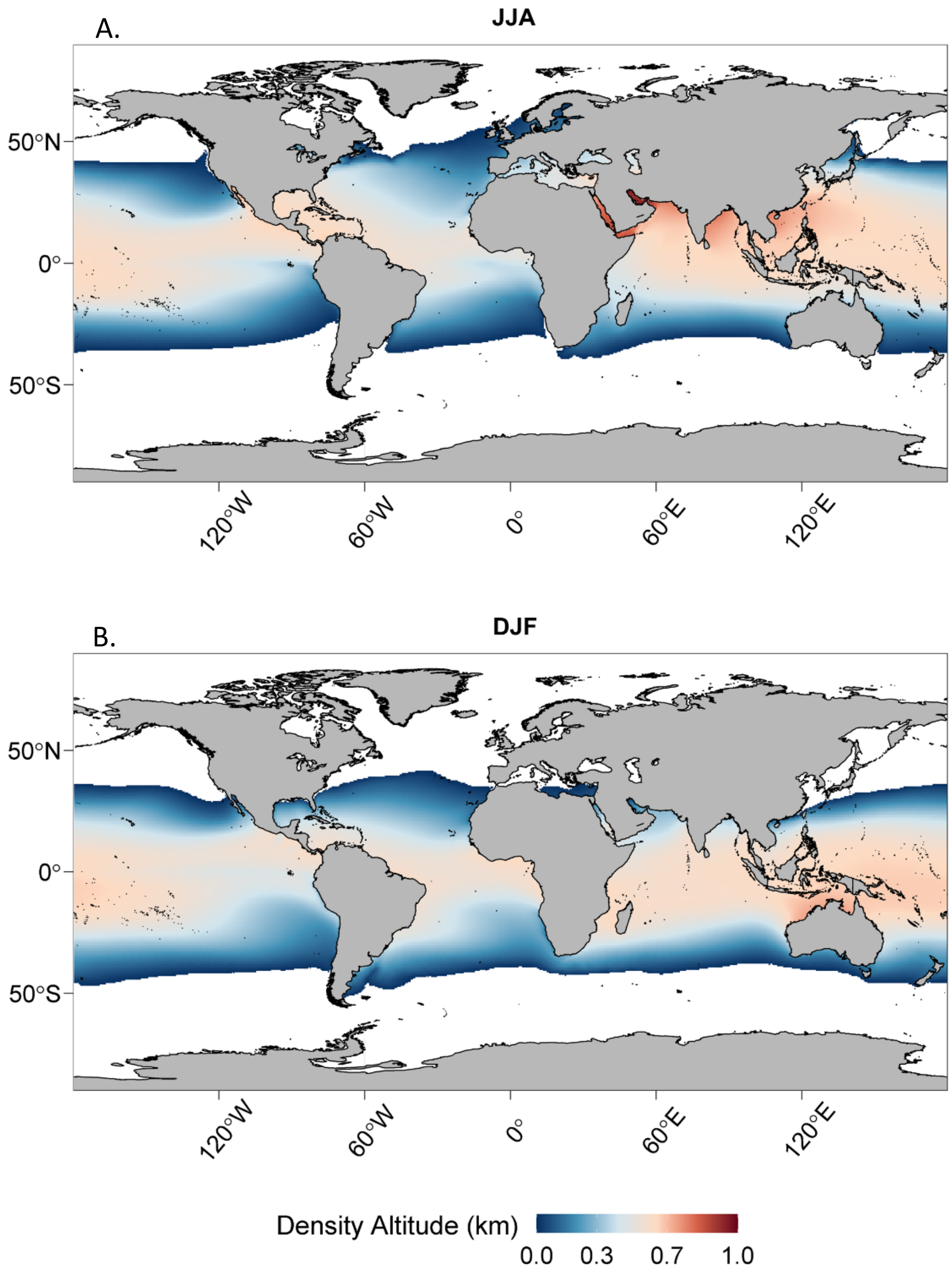

Figure 5: Density altitude experienced by birds flying at sea level in A. June-July-August (JJA) and B. December-January-February (DJF). Density altitude is calculated as the altitude corresponding to a given air density compared to the reference air density at sea level (1.255 kg m^{-3}) according to the international standard atmosphere (ISA). The density altitudes scale is truncated to zero metres ASL but we note that birds at higher latitudes will experience altitudes less than standard sea level values. Air density was acquired from ERA5 monthly means at: https://cds.climate.copernicus.eu/cdsapp#!/dataset/reanalysis-era5-single-levels-monthly-means?tab=overview

Energy saving strategies

Our data revealed a further unexpected result, which was that tropicbirds engaged in extended periods of thermal soaring, with passive flight representing on average 13%, and up to 34% of the flight time in a foraging trip. In comparison, frigatebirds spend 82% of their time in passive flight during long-distance flights (Henri Weimerskirch *et al.*, 2016) and 27% in foraging bouts (Corbeau *et al.*, 2020). Frigatebirds show clear adaptations for exploiting sea thermals, with extremely low wing loading; a trait that is associated with low sink rates, flight speeds and turn radii, all of which help them turn and climb within sea thermals, which are both narrower and weaker than terrestrial thermals (Duriez *et al.*, 2010). The wing loading of red-tailed tropicbirds is some 1.5 greater than the magnificent frigatebird (Brewer & Hertel, 2007), being closer to brown boobies (*Sula leucogaster*), which are almost twice their mass. The fact that they are still able to exploit sea thermals demonstrates that this behaviour is not confined to specialist soaring fliers and suggests it may well be widespread among seabirds, given that terns have even lower wing loading than frigatebirds (Hertel & Ballance, 1999). Nonetheless, the time spent in passive flight styles (i.e. soaring and gliding) did not vary between seasons, because the summer increase in air temperature was mirrored by an increase in water temperature, such that the difference between the two remained constant year round.

Overall, our results demonstrate the value of high-frequency information in estimating both the rate of prey encounter and flight effort. We demonstrate that variation in air density, driven by seasonal temperature changes, is sufficient to make flight costlier. The costs of flying in lower air densities are underestimated in our modelling approach, as we only examine the effects for level flapping flight, whereas tropicbirds repeatedly climb tens to hundreds of metres to search for and pursue prey, which represents a substantial cost when achieved by powered flight. This highlights an additional way in which high temperature increases could impact breeding adults in the low season, and raises the possibility that while it is currently profitable for red-tailed tropicbirds to breed in the austral summer, further increases in costs could affect the energetic balance.

References

Allen, S. E., & Wolfe, M. A. (2013). Hindcast of the timing of the spring phytoplankton bloom in the Strait of Georgia, 1968–2010. *Progress in Oceanography*, *115*, 6–13.

Ballance, L. T., Pitman, R. L., Adams, N. J., & Slotow, R. H. (1999). Foraging ecology of tropical seabirds. *22 Int. Ornithol. Congr.*

Barton, K., & Barton, M. K. (2015). Package 'MuMIn.' *Version*, *1*, 18.

Behrenfeld, M. J., Boss, E., Siegel, D. A., & Shea, D. M. (2005). Carbon-based ocean productivity and phytoplankton physiology from space. *Global Biogeochemical Cycles*, *19*(1), 1–14. doi: 10.1029/2004GB002299

Bishop, C. M., Spivey, R. J., Hawkes, L. A., Batbayar, N., Chua, B., Frappell, P. B., … Butler, P. J. (2015). The roller coaster flight strategy of bar-headed geese conserves energy during Himalayan migrations. *Science*, *347*(6219), 250–254. doi: 10.1126/science.1258732

Borstad, G., Crawford, W., Hipfner, J. M., Thomson, R., & Hyatt, K. (2011). Environmental control of the breeding success of rhinoceros auklets at Triangle Island, British Columbia. *Marine Ecology Progress Series*, *424*, 285–302. doi: 10.3354/meps08950

Brewer, M. L., & Hertel, F. (2007). Wing Morphology and Flight Behavior of Pelecaniform Seabirds. *Journal of Morphology*, *877*(October), 1042–1154. doi: 10.1002/jmor

Browning, E., Bolton, M., Owen, E., Shoji, A., Guilford, T., & Freeman, R. (2018). Predicting animal behaviour using deep learning: GPS data alone accurately predict diving in seabirds. *Methods in Ecology and Evolution*, *9*(3), 681–692. doi: 10.1111/2041-210X.12926

Butler, P. J. (2016). The physiological basis of bird flight. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*(1704), 20150384. doi: 10.1098/rstb.2015.0384

Chimienti, M., Cornulier, T., Owen, E., Bolton, M., Davies, I. M., Travis, J. M. J., & Scott, B. E. (2017). Taking movement data to new depths: Inferring prey availability and patch profitability from seabird foraging behavior. *Ecology and Evolution*, *7*(23), 10252–10265. doi: 10.1002/ece3.3551

Clay, T. A., Joo, R., Weimerskirch, H., Phillips, R. A., den Ouden, O., Basille, M., … Patrick, S.

C. (2020). Sex-specific effects of wind on the flight decisions of a sexually dimorphic soaring bird. *Journal of Animal Ecology*, *89*(8), 1811–1823. doi: 10.1111/1365-2656.13267

Collins, P. M., Green, J. A., Elliott, K. H., Shaw, P. J. A., Chivers, L., Hatch, S. A., & Halsey, L. G. (2020). Coping with the commute: behavioural responses to wind conditions in a foraging seabird. *Journal of Avian Biology*, *51*(4). doi: 10.1111/jav.02057

Corbeau, A., Prudor, A., Kato, A., & Weimerskirch, H. (2020). Development of flight and foraging behaviour in a juvenile seabird with extreme soaring capacities. *Journal of Animal Ecology*, *89*(1), 20–28. doi: 10.1111/1365-2656.13121

Daunt, F., Afanasyev, V., Silk, J. R. D., & Wanless, S. (2006). Extrinsic and intrinsic determinants of winter foraging and breeding phenology in a temperate seabird. *Behavioral Ecology and Sociobiology*, *59*(3), 381–388.

Duriez, O., Kato, A., Tromp, C., Dell'Omo, G., Vyssotski, A. L., Sarrazin, F., & Ropert-Coudert, Y. (2014). How cheap is soaring flight in raptors? A preliminary investigation in freely-flying vultures. *PLoS ONE*, *9*(1). doi: 10.1371/journal.pone.0084887

Duriez, O., Peron, G., Gremillet, D., Sforzi, A., & Monti, F. (2018). Migrating ospreys use thermal uplift over the open sea. *Biology Letters*, *14*(12), 20180687. doi: 10.1098/rsbl.2018.0687

Elliott, K. H., Chivers, L. S., Bessey, L., Gaston, A. J., Hatch, S. A., Kato, A., … Hare, J. F. (2014). Windscapes shape seabird instantaneous energy costs but adult behavior buffers impact on offspring. *Movement Ecology*, *2*(1), 1–15.

Furness, R. W., & Bryant, D. M. (1996a). Effect of Wind on Field Metabolic Rates of Breeding Northern Fulmars. *Ecology*, *77*(4), 1181–1188. doi: 10.2307/2265587

Furness, R. W., & Bryant, D. M. (1996b). Effect of Wind on Field Metabolic Rates of Breeding Northern Fulmars. *Ecology*, *77*(4), 1181–1188. doi: 10.2307/2265587

Gardner, A., Duck, C., & Greig, S. (1985). Breeding of the Trindade Petrel *Pterodroma arminjoniana* on Round Island, Mauritius. *IBIS*, *127*(4), 517–522.

Halsey, L. G., Portugal, S. J., Smith, J. A., Murn, C. P., & Wilson, R. P. (2009). Recording raptor behavior on the wing via accelerometry. *Journal of Field Ornithology*, *80*(2), 171–177. doi: 10.1111/j.1557-9263.2009.00219.x

Hedenström, A. (2003). Twenty-Three Testable Predictions About Bird Flight. In *Avian Migration* (pp. 563–582). Berlin, Heidelberg: Springer Berlin Heidelberg. doi: 10.1007/978-3-662-05957-9_38

Hernandez-Pliego, J., Rodriguez, C., Dell'Omo, G., & Bustamante, J. (2017). Combined use of tri-axial accelerometers and GPS reveals the flexible foraging strategy of a bird in relation to weather conditions. *PloS One*, *12*(6), e0177892.

Hertel, F., & Ballance, L. T. (1999). Wing ecomorphology of seabirds from Johnston Atoll. *The Condor*, *101*(3), 549–556.

Hetmański, T. (2004). Timing of breeding in the Feral Pigeon *Columba livia f. domestica* in Słupsk (NW Poland). *Acta Ornithologica*, *39*(2), 105–110.

Lack, D. L. (1968). *Ecological adaptations for breeding in birds*.

Le Corre, M. (2001). Breeding seasons of seabirds at Europa Island (southern Mozambique Channel) in relation to seasonal changes in the marine environment. Journal of Zoology, 254(2), 239–249. doi: 10.1017/S0952836901000759

Le Corre, M., Cherel, Y., Lagarde, F., Lormée, H., & Jouventin, P. (2003). Seasonal and inter-annual variation in the feeding ecology of a tropical oceanic seabird, the red-tailed tropicbird Phaethon rubricauda. *Marine Ecology Progress Series*, *255*, 289–301. doi: 10.3354/meps255289

Lewis, S., Phillips, R. A., Burthe, S. J., Wanless, S., & Daunt, F. (2015). Contrasting responses of male and female foraging effort to year-round wind conditions. *Journal of Animal Ecology*, *84*(6), 1490–1496.

Liechti, F. (2006). Birds: Blowin' by the wind? *Journal of Ornithology*, *147*(2), 202–211. doi: 10.1007/s10336-006-0061-9

Lüdecke, D., Ben-Shachar, M., Patil, I., Waggoner, P., & Makowski, D. (2021). performance: An R Package for Assessment, Comparison and Testing of Statistical Models. *Journal of Open Source Software*, *6*(60), 3139. doi: 10.21105/joss.03139

Machovsky-Capuska, G. E., Priddel, D., Leong, P. H. W., Jones, P., Carlile, N., Shannon, L., … Raubenheimer, D. (2016). Coupling bio-logging with nutritional geometry to reveal novel insights into the foraging behaviour of a plunge-diving marine predator. *New Zealand Journal of Marine and Freshwater Research*, *50*(3), 418–432. doi: 10.1080/00288330.2016.1152981

Nathan, R., Spiegel, O., Fortmann-Roe, S., Harel, R., Wikelski, M., & Getz, W. M. (2012). Using tri-axial acceleration data to identify behavioral modes of free-ranging animals: General concepts and tools illustrated for griffon vultures. *Journal of Experimental Biology*, *215*(6), 986–996. doi: 10.1242/jeb.058602

Newton, I. (2010). *The migration ecology of birds*. Elsevier.

Nicoll, M. A. C., Nevoux, M., Jones, C. G., Ratcliffe, N., Ruhomaun, K., Tatayah, V., & Norris, K. (2017). Contrasting effects of tropical cyclones on the annual survival of a pelagic seabird in the Indian Ocean. *Global Change Biology*, *23*(2), 550–565. doi: 10.1111/gcb.13324

Peck, D. R., Smithers, B. V, Krockenberger, A. K., & Congdon, B. C. (2004). Sea surface temperature constrains wedge-tailed shearwater foraging success within breeding seasons. *Marine Ecology Progress Series*, *281*, 259–266.

Pennycuick, C. J. (2008). *Modelling the flying bird*. Elsevier.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., Heisterkamp, S., Van Willigen, B., & Maintainer, R. (2017). Package ‘nlme.’ *Linear and Nonlinear Mixed Effects Models, Version*, *3*(1).

Pyke, G. H. (1984). Optimal foraging theory: a critical review. *Annual Review of Ecology and Systematics*, *15*(1), 523–575.

R Core Team. (2020). *R: A language and environment for statistical computing*. Retrieved from https://www.r-project.org/

Ramos, J., Maul, A., Ayrton, V., Bullock, I., Hunter, J., Bowler, J., … Pacheco, C. (2002). Influence of local and large-scale weather events and timing of breeding on tropical roseate tern reproductive parameters. *Marine Ecology Progress Series*, *243*, 271–279. doi: 10.3354/meps243271

Rayner, J. M. V. (1988). Form and function in avian flight. In *Current ornithology* (pp. 1–66). Springer.

Ropert-Coudert, Y., Kato, A., Wilson, R. P., & Cannell, B. (2006). Foraging strategies and prey encounter rate of free-ranging Little Penguins. *Marine Biology*, *149*(2), 139–148.

Ruhomaun, K. (2017). *Determining nest fidelity , return rates and apparent adult and chick survival rates for Red-tailed Tropicbird , Phaethon rubricauda on Round Island , a Volcanic Island found off the North-East Coast of Mauritius in view of optimising our seabird transloc*. University of Edinburgh.

Sala, J. E., Wilson, R. P., & Quintana, F. (2012). How Much Is Too Much? Assessment of Prey Consumption by Magellanic Penguins in Patagonian Colonies. *PLoS ONE*, *7*(12), 21–25. doi: 10.1371/journal.pone.0051487

Sato, K., Daunt, F., Watanuki, Y., Takahashi, A., & Wanless, S. (2008). A new method to quantify prey acquisition in diving seabirds using wing stroke frequency. *Journal of Experimental Biology*, *211*(1), 58–65. doi: 10.1242/jeb.009811

Schmaljohann, H., & Liechti, F. (2009). Adjustments of wingbeat frequency and air speed to air density in free-flying migratory birds. *Journal of Experimental Biology*, *212*(22), 3633–3642. doi: 10.1242/jeb.031435

Shealer, D. A. (1996). *Foraging habitat use and profitability in tropical roseate terns and sandwich terns*. *113*(1), 209–217.

Simeone, A., & Wilson, R. P. (2003). In-depth studies of Magellanic penguin (*Spheniscus magellanicus*) foraging: can we estimate prey consumption by perturbations in the dive profile? *Marine Biology*, *143*(4), 825–831.

Sjöberg, S., Malmiga, G., Nord, A., Andersson, A., Bäckman, J., Tarka, M., … Hasselquist, D. (2021). Extreme altitudes during diurnal flights in a nocturnal songbird migrant. *Science*, *372*(6542), 646–648. doi: 10.1126/science.abe7291

Tatayah, R. V. V. (2010). The breeding biology of the Round Island Petrel (*Pterodroma arminjoniana*) and factors determining breeding success. *Unpublished PhD Thesis, University of Mauritius, Moka, Mauritius*.

Taylor, L. A., Taylor, G. K., Lambert, B., Walker, J. A., Biro, D., & Portugal, S. J. (2019). Birds invest wingbeats to keep a steady head and reap the ultimate benefits of flying together. *PLOS Biology*, *17*(6), e3000299. doi: 10.1371/journal.pbio.3000299

Tew-Kai, E., & Marsac, F. (2009). Patterns of variability of sea surface chlorophyll in the Mozambique Channel: A quantitative approach. *Journal of Marine Systems*, *77*(1–2), 77–88. doi: 10.1016/j.jmarsys.2008.11.007

Veldhuis, M. J. W., Kraay, G. W., Van Bleijswijk, J. D. L., & Baars, M. A. (1997). Seasonal and spatial variability in phytoplankton biomass, productivity and growth in the northwestern Indian Ocean: the southwest and northeast monsoon, 1992–1993. *Deep Sea Research Part I: Oceanographic Research Papers*, *44*(3), 425–449.

Weimerskirch, H., Le Corre, M., Ropert-Coudert, Y., Kato, A., & Marsac, F. (2005). The three-dimensional flight of red-footed boobies: Adaptations to foraging in a tropical environment? *Proceedings of the Royal Society B: Biological Sciences*, *272*(1558), 53–61. doi: 10.1098/rspb.2004.2918

Weimerskirch, Henri, Ancel, A., Caloin, M., Zahariev, A., Spagiari, J., Kersten, M., & Chastel, O. (2003). Foraging efficiency and adjustment of energy expenditure in a pelagic seabird provisioning its chick. *Journal of Animal Ecology*, *72*(3), 500–508. doi: 10.1046/j.1365-2656.2002.00720.x

Weimerskirch, Henri, Bishop, C., Jeanniard-du-Dot, T., Prudor, A., & Sachs, G. (2016). Frigate birds track atmospheric conditions over months-long transoceanic flights. *Science*, *353*(6294), 74–78. doi: 10.1126/science.aaf4374

Wilson, R. P., Börger, L., Holton, M. D., Scantlebury, D. M., Gómez-Laich, A., Quintana, F., … Shepard, E. L. C. (2020). Estimates for energy expenditure in free-living animals using acceleration proxies: A reappraisal. *Journal of Animal Ecology*, *89*(1), 161–172. doi: 10.1111/1365-2656.13040

Wilson, R. P., White, C. R., Quintana, F., Halsey, L. G., Liebsch, N., Martin, G. R., & Butler, P. J. (2006). Moving towards acceleration for estimates of activity-specific metabolic rate in free-living animals: The case of the cormorant. *Journal of Animal Ecology*, *75*(5), 1081–1090. doi: 10.1111/j.1365-2656.2006.01127.x

Wilson, R., Steinfurth, A., Ropert-Coudert, Y., Kato, A., & Kurita, M. (2002). Lip-reading in remote subjects: an attempt to quantify and separate ingestion, breathing and vocalisation in free-living animals using penguins as a model. *Marine Biology*, *140*(1), 17–27. doi: 10.1007/s002270100659

Woodcock, A. H. (1940). Convection and soaring over the open sea. *Journal of Marine Research*, (203), 248–253.

Yoda, K., Kohno, H., & Naito, Y. (2007). Ontogeny of plunge diving behaviour in brown boobies: Application of a data logging technique to hand-raised seabirds. *Deep-Sea Research Part II: Topical Studies in Oceanography*, *54*(3–4), 321–329. doi: 10.1016/j.dsr2.2006.11.004

Chapter 5 – Ecological inference using data from accelerometers needs careful protocols

Disclaimer

This work has been sent to review to Methods for Ecology and Evolution as:

Garde B., Wilson R. P., Fell A., Cole N., Tatayah V., Holton M. D., Rose K. A. R., Metcalfe R. S., Robotka H., Wikelski M., Tremblay F., Whelan S., Elliott K. H., Shepard E. L. C. Ecological inference using data from accelerometers needs careful protocols

Abstract

Accelerometers in animal-attached tags have proven to be powerful tools in behavioural ecology, being used to determine behaviour and provide proxies for movement-based energy expenditure. Researchers are collecting and archiving data across systems, seasons and device types. However, in order to use data repositories to draw ecological inference, we need to establish the error introduced according to sensor type and position on the study animal and establish protocols for error assessment and minimization. Using laboratory trials, we examine the absolute accuracy of tri-axial accelerometers and determine how inaccuracies impact measurements of dynamic body acceleration (DBA), as the main acceleration-based proxy for energy expenditure. We then examine how tag type and placement affect the acceleration signal in birds using (i) pigeons *Columba livia* flying in a wind tunnel, with tags mounted simultaneously in two positions, (ii) back- and tail-mounted tags deployed on wild kittiwakes *Rissa tridactyla.* Finally, we (iii) present a case study where two generations of tag were deployed using different attachment procedures on red-tailed tropicbirds *Phaethon rubricauda* foraging in different seasons. Bench tests showed that individual acceleration axes required a two-level correction (representing up to 4.3% of the total value) to eliminate measurement error. This resulted in DBA differences of up to 5% between calibrated and uncalibrated tags for humans walking at different speeds. Device position was associated with greater variation in DBA, with upper- and lower back-mounted tags in pigeons varying by 9%, and tail- and back-mounted tags varying by 13% in kittiwakes. Finally, DBA varied by 25% in tropicbirds between seasons, which may be attributable to tag attachment procedures. Accelerometer accuracy, tag placement, and attachment details critically affect the signal amplitude and thereby the ability of the system to detect biologically meaningful phenomena. We propose a simple method to calibrate accelerometers that should be used prior to deployments and archived with resulting data, suggest a way that researchers can assess accuracy in previously collected data, and caution that variable tag placement and attachment can increase sensor noise and even generate trends that have no biological meaning.

Introduction

Animal-attached tags have revolutionized our understanding of wild animal ecology (Bograd *et al.*, 2010; Sequeira *et al.*, 2021; Yoda, 2019). Of the sensors often used, accelerometers (Yoda *et al.*, 1999) are regarded as particularly powerful tool for studying wild animal behavioural ecology, with studies using them to look at the occurrence and intensity of behaviour (Chakravarty *et al.*, 2019; Fehlmann *et al.*, 2017), assess movement characteristics (Shepard *et al.*, 2008) and as a proxy for energy expenditure (Wilson *et al.*, 2020). The latter has developed rapidly since the demonstration that dynamic body acceleration (DBA) is related to energy expenditure across a range of vertebrates and invertebrates (Halsey *et al.*, 2009; Wilson *et al.*, 2019, 2006). Such measurements have great potential for understanding animal strategies, in particular studying how animals respond to change in food availability (Kokubun *et al.*, 2011), climate (Gudka *et al.*, 2019) and anthropogenic threats or activity (Nickel *et al.*, 2021; Payne *et al.*, 2015; Yorzinski *et al.*, 2015).

In mammals, accelerometers tend to be attached using collars, and while collars have their own complications in terms of the need to obtain a good fit and account for collar rotation in data interpretation (Wilson *et al.*, 2020), the position of attachment is largely standardised. In contrast, researchers use different attachment positions on birds. For instance, tags are deployed on the lower back, the tail or the belly of seabirds depending on the species and the tag position associated with least detriment (Elliott, 2016; Ropert-Coudert *et al.*, 2003; Vandenabeele *et al.*, 2014). While some species appear to show less of a response to tags mounted on the back, there are lower weight limits for what can be attached to the tail, and both positions impact flight forces. Researchers working with raptors may deploy tags using backpack or leg-loop harnesses (e.g. Harel *et al.*, 2017; Williams *et al.*, 2015, respectively), which results in differences in tag position. The widespread availability and use of accelerometers means that large datasets, collected over years, are now available, providing valuable information about behaviour including flight effort across temporal and spatial scales (Kranstauber *et al.*, 2011). Unsurprisingly, these data have been collected using different methods of attachment and by deploying a variety of different tags without critical analysis of the compatibility of different datasets (Sequeira *et al.*, 2021).

Tag position on the body is likely to affect acceleration values, as pointed out by Wilson *et al.* (2020), who noted that DBA (Qasem *et al.*, 2012) varied with tag position in humans wearing back and waist-mounted tags running on a treadmill (with DBA values varying by ~ 0.25 g at intermediate speeds). This is easy to understand since humans have a flexible spine. Birds, on the other hand, have an essentially immoveable box-like thorax (Baumel, 1993). Differences in acceleration between tags placed on the back and the neck (Kölzsch *et al.*, 2016) or the tail (Elliott, 2016) are easy to associate with independent movement of the head or tail, but the thorax itself can experience pitch changes over the wing beat cycles (Su *et al.*, 2012; Tobalske & Dial, 1996), which may affect the acceleration recorded by loggers depending on their position. As part of that, we note that the precise position of the accelerometer chips on the circuit boards may also affect the acceleration measured by the sensors, particularly in cases where the circuit board is long relatively to the bird's back and where the chip could be positioned close to either end.

At a more fundamental level, the fabrication of loggers with accelerometers involves extensive heating as the sensors are soldered to the circuit boards. This is known to change their sensory performance (output *versus* acceleration) (Ruzza *et al.*, 2018), even if they are carefully calibrated prior to this process (see https://www.mouser.fr/datasheet/2/389/lsm303dlhc-955106.pdf). Specifically, while the vector sum of the 3 acceleration channels should be 1 when a unit is at rest, this can vary after heating, resulting in error in the estimation of the Earth's gravitational component. This can in turn introduce error into the estimation of the "dynamic" acceleration, or acceleration due to movement, which is the basis for acceleration-based proxies for the energy expenditure (Wilson *et al.*, 2020).

In this chapter, we assess the error associated with the sensors themselves and how the position and fixing of the accelerometer on the study animal affects acceleration metrics before proposing solutions to minimize these issues. Specifically, we first examine how variability in VeDBA relates to improperly calibrated tri-axial accelerometers, using a case with humans walking defined courses at fixed speeds. We then examine how tag position affects VeDBA and signal amplitude using pigeons (*Columba livia*) flying in a wind tunnel with two tags placed on different locations of their back. Finally, we examine two examples of variation in the acceleration signal based on retrospective analysis of field studies involving; (1) red-tailed tropicbirds (*Phaethon rubricauda*) equipped with two different types of loggers attached using marginally different protocols in two separate seasons, and (2) black-legged kittiwakes (*Rissa tridactyla*) equipped with a tag on the back and one on the tail, as two positions favoured by seabird researchers for tag placement.

Materials and Methods

Measurement of acceleration accuracy of tri-axial sensors

We first calibrated tri-axial accelerometers within 5 Daily Diary tags (inch board) (Wildbyte Technologies, Swansea University, UK) (Wilson *et al.*, 2008), by setting them motionless on a table in a series of defined orientations (each for *ca*. 10 seconds). Six orientations (hereafter the '6-O method') were chosen so that the tags always had one of their three acceleration axes perpendicular to gravity and these were rotated according to the 6 axes of a die so that each of the 3 accelerometer axes nominally reads -1 *g* and 1 *g*.

The outputs of these motionless calibrations were then used to derive the six respective maxima of the acceleration vectorial sum given by;

$$\|a\| = (x^2+y^2+z^2)^{0.5}$$

where x, y and z are the raw acceleration values, for the periods when they were held still. Note that there are 6 maxima because each axis has two values: a minimum and a maximum, which become positive in the vectorial sum. In a device with perfect acceleration sensors, all maxima should be 1.0 *g* (although the acceleration on earth varies with latitude by up to a maximum of 0.0053 *g* due to the earth's shape and the centrifugal force generated by the planet spinning as well as other processes (Novák, 2010). However, values were always either marginally higher or lower than 1.0 *g* (see Results). Furthermore, the two maxima for each axis differed. This therefore requires 2 steps to be corrected, where (1) a correction factor is applied to the lower value to ensure both "maxima" are the same and then (2) the same offset is applied to both readings to convert readings to exactly 1.0 *g*.

Subsequently, tags were deployed on 12 people, attached to the lower back using elastic. All participants were healthy adults and gave informed consent (protocol approved under code: PG201416A). Each person walked back and forth on a 25 m straight-line course at four different speeds (0.69, 0.97, 1.25 and 1.53 m s^{-1}; randomly ordered), each for 3 minutes.

Speeds were held constant using a metronome. The mean VeDBA (defined as VeDBA = $(x_D^2+y_D^2+z_D^2)^{0.5}$ where x_D, y_D and z_D are the dynamic body acceleration recorded by each of the three channels of acceleration - for details see Wilson *et al.* (2020), was calculated across each 3-minute trial with, and without, the calibration corrections.

Effect of tag position on acceleration

The effect of tag position was first tested on three pigeons (*Columba livia*) flying under controlled conditions in a wind tunnel at speeds ranging from 10 to 22 $m.s^{-1}$. Birds were equipped simultaneously with two tags recording acceleration at 150 Hz ("Thumb" Daily Diary (DD) units, hereafter type 1 tag). One tag was placed on the upper back, the other on the lower back, both in the dorsal mid-line. Units measured 22 by 15 by 9 mm and the distance between them was *ca.* 4 cm. The tagging of pigeons and the procedure of flight in a wind tunnel was approved by the government of Upper Bavaria, "Sachgebiet 54 – Verbraucherschutz, Veterinärwesen, 80538 München" with the record number: Gz.: 55.2-1-54-2532-86-2015.

To ensure that only steady sustained level flight was included in the analysis, we selected sections of consistent flapping flight lasting for at least 2 s (corresponding to *ca*. 10 wingbeat cycles), with no gliding or wingbeat interruptions. The stability of the flight was controlled by selecting sections where VeDBA values smoothed over 1 s were between 0.75 and 3 *g* and varied by less than 1.0 *g*, with no apparent trend (increasing or decreasing) over time. We also discarded the first second of any flight.

We first assessed whether the VeDBA values differed with tag position. VeDBA was calculated using a 2 s smoothing window to derive the "static" component (Shepard *et al.*, 2008) and then subtracting static values from the raw acceleration data in each axis, before summing the differences vectorially (Qasem *et al.*, 2012). We then assessed whether the peak amplitude per wingbeat differed according to tag location, with the peak amplitude calculated as the difference between the maximum and the minimum value of heave acceleration. For this, peaks were detected in the heave axis (Bishop *et al.*, 2015) to synchronise every wingbeat to a defined start point. Finally, to understand which parts of the wingbeat signal were affected by the difference in tag position, we analysed the acceleration signals across average wingbeats in the three acceleration axes. Each acceleration datapoint was attributed to a percentage progression across the wingbeat cycle. Then, for every whole percentage value, the heave, surge and sway accelerations were averaged across 10 wingbeats from the same logger. The average values for the heave, surge and sway accelerations of the upper back-mounted tag were expressed against the values of the lower back-mounted tag in a linear model, the slope of which was used to determine the difference in signal amplitude between the two tags for each acceleration axis.

To examine putative changes in heave signal amplitude (see above) and VeDBA associated with tag placement, we compared them between upper- and lower-back tags using a paired Student's t-test for VeDBA and a Wilcoxon signed-rank test for amplitude (due to non-homogeneous variances between the two groups (Levene's Test: F-value = 4.159, p = 0.049)). Wingbeat frequency also contributes to the variation of VeDBA (Van Walsum *et al.*, 2020). Wingbeat frequency was also compared between the two tags using a paired Student's t-test. The statistical analysis was performed in RStudio, using R version 4.0.3 (R Core Team, 2020).

Acceleration error in field studies

As a *post hoc* example of how different deployment protocols may affect accelerometer-based results, we compared the amplitude of the heave acceleration signal and VeDBA during the flight of black-legged kittiwakes for two different setups. Twelve kittiwakes were captured and tagged during their breeding season on Middleton Island, Alaska (59.43 N, 146.33 W) and equipped with an accelerometer (type 1 DD) placed under their tail, sealed inside heat shrink tubing for waterproofing: This method is popular as it prevents the bird from trying to preen off the package. We equipped 4 other birds with the same tags placed on their back and wrapped in two zip-lock bags to protect them from splash damage, while allowing pressure sensors to function: This other method is particularly favoured in studies aiming to measure altitude, as it does not require a full waterproofing, which alters pressure recordings. Tail-mounted tags were also tied to a GPS, while the back-mounted units were in an independent package so that the back-mounted logger package was 1 g heavier (total masses; tail = 21 g, back = 22 g). Two 1-min sections of level flapping flight were identified for each tag and deployment. The selection was made based on the altitude data from the loggers' pressure sensors (< 5 m difference between the highest and lowest altitude measurements), after verifying that there was no interruption in the wingbeat pattern found in heave, ascertaining that the bird flapped regularly for the whole period.

In a similar manner, we examined red-tailed tropicbird data from two different nesting seasons using tags placed in a standard position on their lower back while using different tags. For this, red-tailed tropicbirds at Round Island (19.85 S, 57.79 E) were captured on their nests and equipped with two different units by the same person using 4 strips of Tesa tape placed under the feathers and around the tags (Wilson & Wilson, 1989). Ethical permissions for the use of biologgers on wild red-tailed tropicbirds and black-legged kittiwakes were granted by Swansea University AWERB, permit 040118/39 and 110619/1590 (IP-1819-18), respectively.

Nineteen birds were tagged between February and March 2018 (using type 2 DDs, Figure 1) while 36 birds were tagged during the second season (September and October 2018, type 2 DDs, Figure 1). Importantly, during the second season though, the tags were attached using only 3 strips of tape. At the time, this was considered adequate and helped reduce the weight of the unit. Both units were set to the same sampling frequency (40 Hz). They were however built with different accelerometers (type 1: LSM9DS1, type 2: LSM303DLHC, STMicroelectronics, Geneva, Switzerland), with a substantial difference in sensitivity (type 1: 0.061 m*g*, type 2: 1.0 m*g* sensitivity at +/- 2 *g* range). In addition, the accelerometer is placed at the front of the type 1 unit, and at the back of the type 2 unit, leading to an estimated distance of up to 1 cm between them once placed on the bird's back. The type 1 tags used in the second season were slightly lighter (masses; type 1 unit = 25.0 g, type 2 unit = 27.7 g). As with the kittiwakes, level flapping flight was selected to discard the effect of gliding, thermal soaring or climbing on acceleration metrics (Williams *et al.*, 2015). We considered level flapping flight to be any section where VeDBA > 0.3 *g* and where the rate of change of altitude (measured by the pressure sensor of the Daily Diary at 4 Hz) was between -0.5 and 0.5 ms^{-1}.

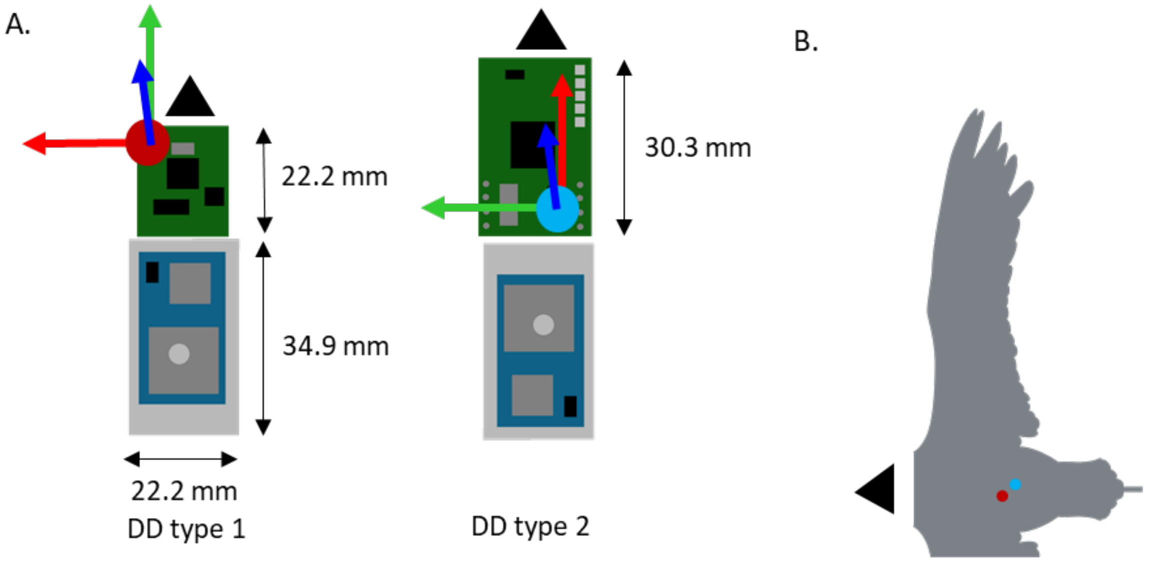

Figure 1: (A) Location of the accelerometer [interception point of the 3 arrows depicting tri-axial acceleration] on the circuit boards of two different DD tags [the battery is in grey, the GPS in blue and the DD in green] and (B) location of the accelerometers within the tags on the back of a red-tailed tropicbird for the type 1- (red dot) and type 2- (blue dot) tags.

VeDBA, wingbeat frequency and the amplitude of heave in level flapping flight were derived from accelerometer data for both tropicbirds and kittiwakes following the same process as pigeons. Data were not paired, since birds carried one tag at a time, so non-paired Student's t-tests and Wilcoxon tests were used to compare the three parameters between loggers.

Since both the tropicbird and kittiwake data were collected from uncalibrated accelerometers (see above), a situation that we believe represents most of the accelerometer deployments made by the community to date, we attempted to assess the potential for accelerometer error *post hoc.* We did this by measuring the variability in the vectorial sum at times when the tags were motionless (though not on the study animals) and in different tag orientations, finding up to 5 different orientations per logger (for example when units were placed inside bags and the bag placed on the floor/ground). The mean vectorial sum of the three axes of acceleration was calculated for each orientation, and compared between loggers and between tag versions using two ANOVAs.

Results

Measurement of acceleration accuracy of tri-axial sensors

Static calibrations of the 15 separate accelerometers within the 5 tags showed that axis offsets needed corrections up to between -0.043 and 0.025 *g* and had multiplicative factors ranging between 0.97 and 1.023. Mean multipliers (across all three axes) for any one tag ranged between 0.9933 and 1.0147.

In the walking speed trials with people, the minimum and maximum differences in VeDBA between calibrated and uncalibrated tags for any one participant ranged between 0.37% and 5.04%. Mean VeDBAs per participant across speeds showed that the difference between calibrated and uncalibrated tags could amount to 2.5% of the calibrated reading. Inspection of the measures undertaken to calibrate each tag (see above) showed that the percentage difference between the uncalibrated and calibrated was primarily due to the acceleration multiplicator (see above) (Figure 2).

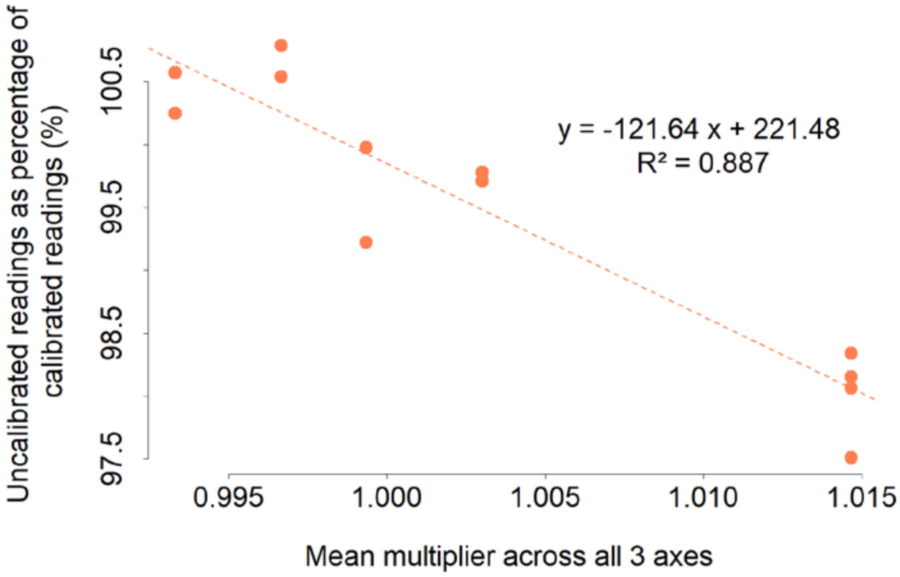

Figure 2 – Percentage difference between VeDBA values derived during controlled speed trials with walking humans using uncalibrated against calibrated (corrected) values. The mean multiplier is one applied across all three axes and does not represent the range of values between axes, which can be considerably higher (see text).

Effect of tag position on raw acceleration in pigeons

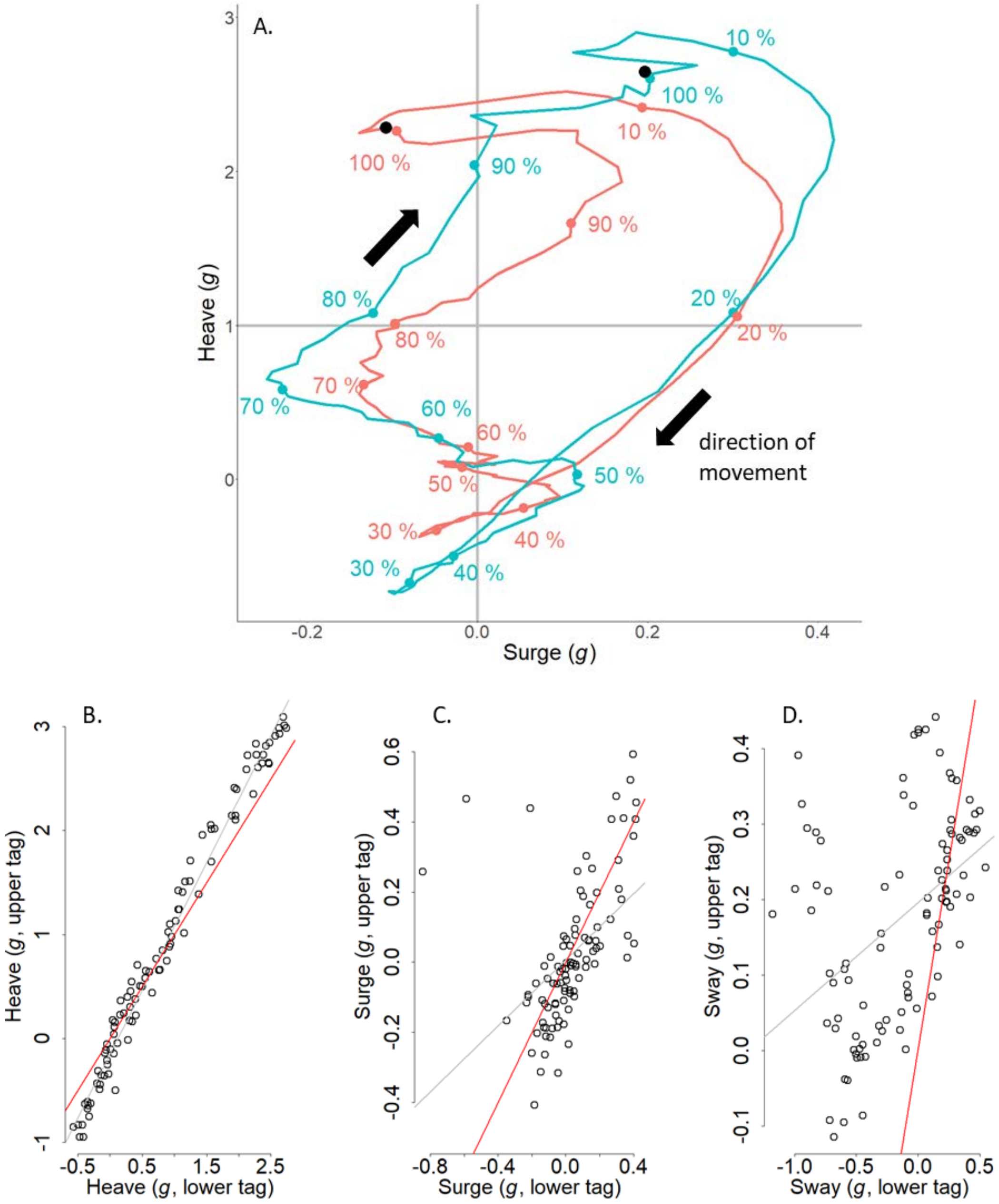

Figure 3: (A) Plot of mean heave versus surge acceleration through time for a pigeon during an average wingbeat cycle derived from a lower back (red) and an upper back-mounted tag (blue), both recording at 150 Hz. Each point corresponds to a mean value of acceleration calculated across all flights for a given percentage through the wingbeat, starting from the peak of acceleration of the downstroke (black point). The value of each point was smoothed over a window of 10 points (10%) to reduce noise. Regressions of the upper against lower tag acceleration for defined points throughout the wingbeat cycle show; (B) heave, (C) surge and (D) sway accelerations (note the changing axis scales). The regression between the two tags is represented in grey, and the y = x line is shown in red.

In our controlled study with pigeons, plots of surge *versus* heave acceleration showed how wingbeats under identical conditions returned markedly different profiles of acceleration depending on the tag position (Figure 3. A). We also found corresponding differences in values of the heave and surge according to tag position (Figure 3. B, C and D): the upper tag recorded a lower magnitude of surge (LM: Estimate = 0.76, $p < 0.001$, $R^2 = 0.41$, with a slope < 1, Figure 3. C), but a higher magnitude of heave than the lower tag (LM: Estimate = 1.2, $p < 0.001$, $R^2 = 0.97$) (Figure 3. D). The sway model however, showed a weak fit (LM: Estimate = 0.18, $p < 0.001$, $R^2 = 0.18$) and the slope of their relationship was < 1 (Figure 3. B).

Effect of tag position on acceleration metrics

Differences in raw acceleration values also resulted in some variation in acceleration-derived metrics in both the controlled studies on pigeons and in the *post hoc* studies on wild birds: Upper back-mounted tags recorded a slightly higher VeDBA than lower back-mounted tags in pigeons (paired Student's test: difference = -0.167, t = -2.184, p = 0.043), which was largely due to higher heave values (Wilcoxon signed-rank test: difference = 0.82 *g*, W = 94, p = 0.007) (Figure 4. A, D).

In red-tailed tropicbirds, the type 1 tags, used during the second deployment, recorded both a higher VeDBA (by 25%) (Wilcoxon test: difference = 0.14 *g*, W = 19, p < 0.001) and heave amplitude (by 29%) (Student's t-test: difference = 0.40 *g*, t = -11.78, df = 47.718, p < 0.001) than the type 2 tags (Figure 4. B, E). In kittiwakes, the tail tags recorded both a higher VeDBA (by 18%) (Wilcoxon test: difference = 0.14 *g*, W = 14, p = 0.001), and a higher heave amplitude (by 27%) (Student's t-test: difference = -0.60 *g*, t = -4.4304, df = 9.0178, p-value = 0.002) than the back-mounted tags (Figure 4. C, F).

There were no differences in estimated wingbeat frequency according to where tags were mounted in either pigeons (paired Student's t-test: t = 1.954, p = 0.067) or kittiwakes (Wilcoxon test: W = 100, p = 0.227). In tropicbirds, there was a seasonal difference in wingbeat frequency, with type 2 tags recording a higher wingbeat frequency (by 3%) than the type 1 DDs (Student's t-test: difference = -0.14 Hz, t = 3.72, df = 35.19, p < 0.001).

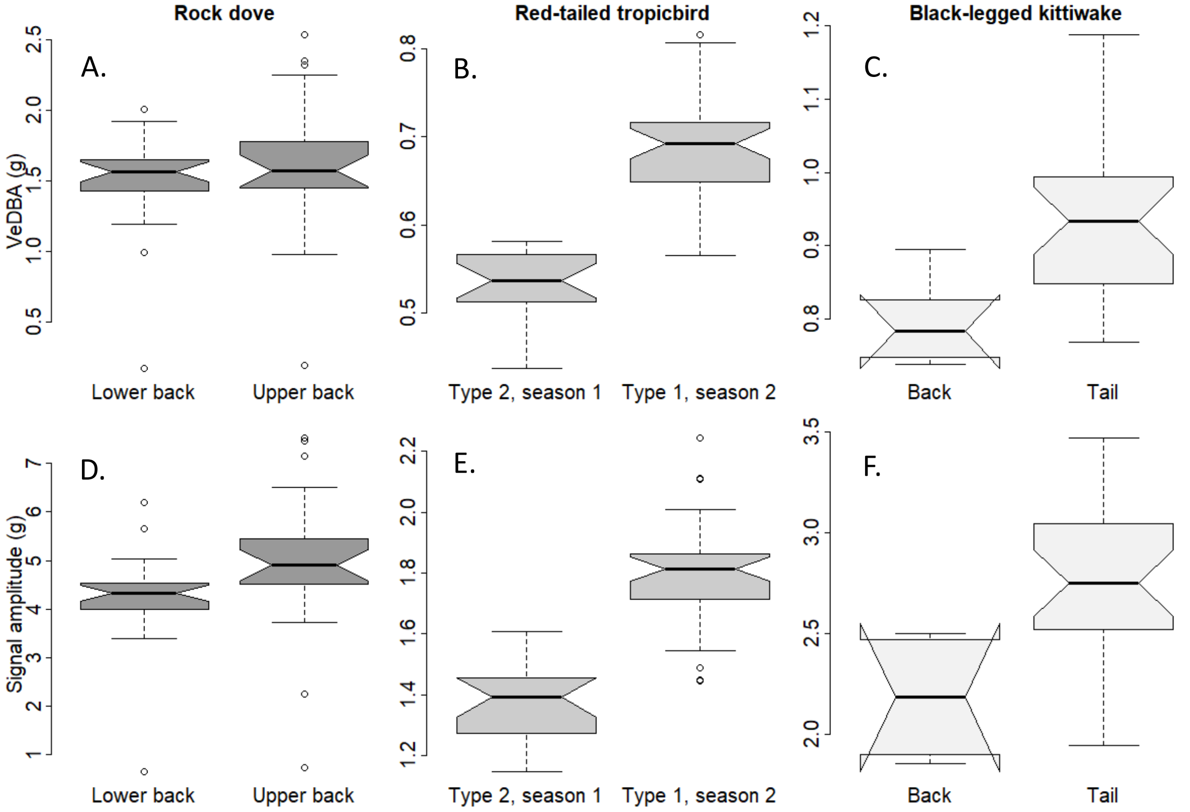

Figure 4: Comparison of VeDBA (A, B, C) and heave signal amplitude (D, E, F) between tags in pigeons (A, D), red-tailed tropicbirds (B, E) and black-legged kittiwakes (C, F). Bold horizontal lines indicate the median vectorial sum for each tag, extremes of the box the upper and lower quartiles, and whiskers the extreme values (excluding outliers, represented by open circles). Notches represent 1.58 IQR/√n (n being the number of observations) on either side of the median and suggest a significant difference when they do not overlap.

We found a positive relationship between wingbeat frequency and heave amplitude during tropicbird level flapping flight (LMM, Season 1: estimate = 0.249, intercept = 0.254, std. error = 0.021, t = 13.339, p < 0.001; Season 2: estimate = 0.746, intercept = -1.084, std. error = 0.024, t = 19.710, p < 0.001; R^2_m = 0.56, R^2_c = 0.72). The slope was however steeper during season 2 (Figure 5), in line with the higher amplitude of heave recordings (see Figure 4).

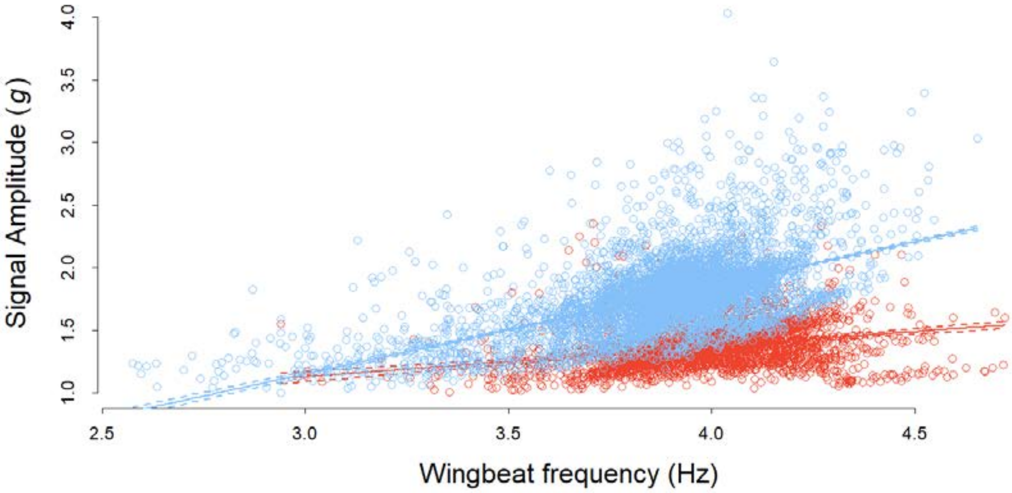

Figure 5: Relationship between the wingbeat frequency and heave amplitude of red-tailed tropicbirds during two field seasons. Birds were equipped with type 2 tags in season 1 (red) and type 1 tags in season 2 (blue), using one less strip of tape, which could reduce tag stability. Full lines represent the linear relationship between wingbeat frequency and amplitude and dashed lines its confidence interval.

***Post-hoc* quantification of accelerometer inaccuracy**

The comparison of stationary data recorded by the two tag types deployed on tropicbirds indicated that the vectorial sum was lower in the type 2 tag (Wilcoxon test: W = 98, p = 0.005, difference = 0.03 *g*) (Figure 6). Standard deviations of the vectorial sum (Type 1: 0.03; Type 2: 0.05) however, indicate that errors are more variable within type 2. We could not determine multipliers for the three acceleration channels to calibrate the data based on this approach, as the heave and surge channels did not cover the whole spectrum of their possible distribution (-1 to 1 *g*) while the tag was motionless.

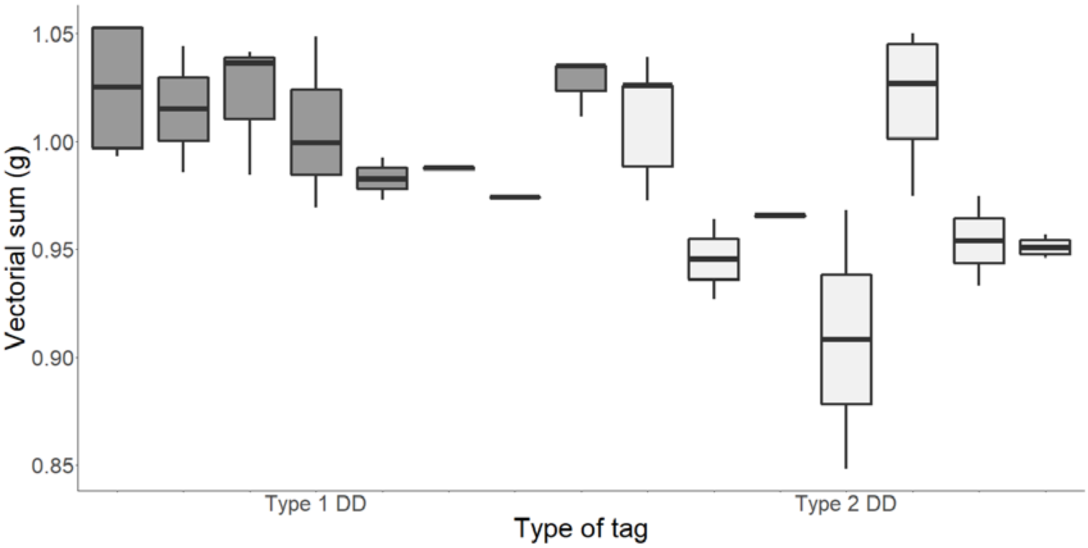

Figure 6: Comparison of the vectorial sum of the raw acceleration recorded by various immobile type 1 (dark boxes) and type 2 tags (light boxes). Each point corresponds to a different unknown orientation. Thick black lines indicate the median vectorial sum for each tag, extremes of the box the upper and lower quartiles, and whiskers the extreme values (excluding outliers).

Discussion

This work highlights that variation in acceleration measured by tags on flying birds (and presumably other animals engaged in any activity) can be due to; (i) differences in sensitivity (Table S4) and calibration between sensors, (ii) variation due to the placement of the tag (or the sensor within the tag) and (iii) variation due to the animal itself. Of these, it is normal to attribute all variation to the activity of the animal itself but the validity of doing this is critically dependent on the other two. Studies that do not consider points (i) and (ii) may, therefore, be misrepresenting animal activity both in terms of intensity and extent. We propose here a calibration method to prevent sensor-induced errors, and provide some recommendations about tag attachment method to avoid interpreting tag position effect as biological.

The variation in acceleration is used to examine animal behaviour within a multitude of research thrusts, some of which use acceleration data in slightly different ways. These range from the precise definition of heave, surge or sway values or derivatives (such as pitch and roll and DBA) used in algorithms to identify behaviours (e.g. Fehlmann *et al.*, 2017; Nathan *et* *al.*, 2012) through the use of acceleration-derived metrics to define energy expenditure (in e.g. doubly labelled water *versus* DBA regressions (Pagano & Williams, 2019)), to measure travelling speed (Bidder *et al.*, 2012; Gunner *et al.*, 2021) and studies looking at animal effort over time and space (Duriez *et al.*, 2018; Halsey *et al.*, 2011). Errors due to sensor inaccuracy and differences in placement are most severe when axes are considered individually (e.g. deriving pitch from the surge axis). However, they are also relevant when all three orthogonal axes are considered, as inaccuracies in one axis can either be mitigated or compounded by inaccuracies in another (see Figure 2). Within vectorial (or absolute) sums of acceleration metrics, the overall error will depend on the relative errors of the different axes and the extent to which they vary during the activity in question. For example, in flapping birds or bats, almost all variation in acceleration measures occur in the heave and surge axes (e.g. Wilson *et al.*, 2008, and see Figures 3 A-E) so errors in the sway are less important. Cognisance of the axis-specific errors will help mitigate those errors that could be interpreted as a biological effect.

Calibrations

The issue of inaccurate sensors can be at least partially mitigated by the 6-O method suggested in this work, although we note that this only effectively calibrates between -1 and 1 *g,* while the gravitational component experienced by some animals e.g. during turning (Wilson *et al.*, 2013), will increase beyond these limits. Although, ideally, the tags should be calibrated with each of the accelerometer axes held perfectly vertically (something that is challenging to do once a circuit board is potted in a housing), in practice, this is not critical, and holding the axes as close to vertical as possible should suffice. This is because the response of an accelerometer to the static acceleration of the earth's gravity follows a sine wave so that an accelerometer that is placed 10° off the vertical (i.e. at 80°), reads a value that is 98.5% of the full-scale value that would be given if the accelerometer axis were held perfectly vertical (so that if there is an error in this axis, 98.5% of it will be covered by this orientation). If it is impossible to reliably estimate the angle of the logger because of the housing, for instance, gently rotating the logger around in every direction would be needed to cover all 6 orientations. Using this calibration will therefore allow researchers to ascribe the most substantive variation in acceleration signal to specific axes.

Our suggestion of dealing with errors *post hoc* by looking at the vectorial sum of the acceleration when tags were stationary could not be used to correct the various axes in our study because all 6 orientations required for the calibrations were not known. However, this process does at least serve to indicate some of the extent of deviation of the sensors from the expected range (see above – Figure 4). In this regard, we note that we have presented results in this work from only one tag manufacturer (type 1 and type 2 tags use two different chips; the type 1 is far superior having a sensitivity of 0.061 m*g* (in a range of +/- 2 *g*), while the type 2 only has a sensitivity of 1 m*g* for this range), but we have measured, in passing, more substantive variation by other manufacturers (see S4).

Why does accelerometer position affect acceleration?

The position of an accelerometer on an animal should affect the acceleration perceived by the sensor during movement according to its location, and indeed that is the basis behind many biomechanical studies (e.g. Giansanti *et al.*, 2003; Hyde *et al.*, 2008). However, there is poor appreciation in the behavioural ecology community that this premise is also valid for trunk-mounted tags. This may seem irrelevant for birds where the thorax can be considered a single immobile unit, in contrast to bead-string models that may indicate what is expected in species with a flexible back (Underhill & Doyle, 2006). Our work has shown, however, that the location of trunk-mounted accelerometers on birds does play a role in modulating acceleration values (Figure 3) and this is presumably because the bird body pitches during the wingbeat cycle (although part of the differences that we observed may also be due to the movement of the scapulae and perhaps the neck during flapping). Depending on the degree of pitch, the centre of pitch rotation and the position of the accelerometer, this will change the extent of movement (d), which can be defined by the length of a section of a circumference around the centre point of rotation according to $D = 2\pi r(360/P)$, where r is the radius or distance between the centre of pitch rotation and the sensor, and P is the maximum pitch angle (in degrees). The duration of the wingbeat cycle will define the vertical speed of the tag at its location, with the recorded acceleration being the change in speed over time. The formula shows how the effect of changed acceleration will be manifest more with increasing distance of a tag from the centre point of rotation and so will have the greatest potential to vary in larger birds, all other things being equal. This may also account for the changed acceleration metrics in tail- versus body-mounted tags (Figure 4 C, F) in our kittiwake study although part of that is presumably due to the relative instability of the tail. In fact, to our knowledge, there is little information on the extent of bird body change in pitch during flight (but see Su *et al.*, 2012; Tobalske & Dial, 1996) although controlled experiments with multiple calibrated accelerometers could change that. In the meantime, we suggest that users attempt to place accelerometers in identical positions on their study animals for comparative purposes, which should also involve knowing the position of the sensors within the tags rather than just considering the tags themselves (Figures 1 and 3).

Fortunately, there is no *a priori* reason why tags placed differently on a bird thorax or inaccurate accelerometers should affect determination of wingbeat frequency since points of inflection will still be represented correctly with respect to time within the wingbeat cycle (Figure 3 A, B). Indeed, this is what we observed in our controlled pigeon flight trials and in the kittiwakes (despite a small difference in tag mass, see Whelan *et al.*, 2021). In contrast, the tropicbird work indicates that there was indeed a change in wingbeat frequency across the two seasons, and this seems to be related to changes in environmental conditions (Garde *et al., in prep*).

***Post-hoc* studies and differences between tags**

The bigger question is the extent to which observed differences between conditions in uncalibrated accelerometers can be attributed to the animals rather than to tag position, attachment techniques or sensor variability. In our tropicbird example, the differences in VeDBA and signal amplitude were not consistent with the differences found in pigeons (higher values in the upper tag), suggesting that they were not related to tag position. Importantly, the difference in amplitude was appreciably larger between the type 1 and type 2 tags on tropicbirds, than between the upper and lower tags used in pigeons, even though the tropicbird tags were placed in a way that minimised the distance between their respective accelerometers. The variability in the vectorial sum of the acceleration between orientations of the same tags (Fig. 4) only amounted to an average difference of 3%, which is close to the difference found between tags used for the <6-O calibration (2%). In contrast, in flapping flight, the difference in VeDBA between tags and seasons reached 25%. This order of magnitude difference, coupled with the observation that the difference between vectorial sum values in 6-O calibrated tags and uncalibrated tags (in general) amounted to a mean maximum of 2.5% (similar to VeDBA differences across human walking trials of 2.5%), would appear to indicate that the differences observed in the tropicbird studies were due to seasonal changes in the birds' interactions with the environment. This is backed up by the changes in wingbeat frequency between the two seasons, which would not be affected by either tag position or sensor inaccuracies. However, Wilson *et al.* (2021) note how accelerometers on loosely fitted collar tags on mammals provide a signal that effectively depends on collar tightness: Under normal conditions, when the tag is tightly associated with the body, the unit replicates the body movement and accelerations faithfully. However, when the attachment is loose, the tag is projected forward and upward during the initial phase of a stride cycle because the tag (and/or collar) abuts the body. This is followed by a short-term dissociation when the tag is not in proper contact with the body, followed again by substantive acceleration as the body catches up with the tag in the proximate interaction. Importantly, this acceleration is higher than that of the body because the animal body is surging forward and upward again while the tag is falling back so that the recorded acceleration spike mirrors the difference between these two processes. Although the attachment of devices to birds using tape (Wilson *et al.*, 1997) provides a much more intimate association between the tag and the bird body, we believe that if this method is not standardized (and it was not in our study), it can lead to major variation in acceleration values, particularly in animals with highly dynamic movement. In birds, this issue may be exacerbated by tag movement due to air flow over the body which can cause the device to vibrate more or less depending on attachment (cf. Wilson *et al.*, 2020). It is also germane to consider that tag attachment stability may change over time in longer-term deployments. These issues have long been recognised in the wearable sensors industry for humans (Jayasinghe *et al.*, 2019). Consequently, we cannot, in good faith, compare VeDBA or wingbeat amplitudes of tropicbirds between seasons although the wingbeat frequency will be unaffected.

Conclusions: The importance of calibrating loggers and standardising protocols

Accelerometer inaccuracies can result in errors in the raw acceleration of up to 5% per axis and, depending on the extent and direction of the errors across all three orthogonal axes, this can affect DBA metrics accordingly. Tag placement can also result in errors in DBA metrics of up to 9.7% in flapping flight for our units, although we note that the scale of the errors varies between device types. Finally, non-standardized tag attachment procedures can result in highly variable dynamic acceleration values. Taken together, these represent a potentially important source of error in both raw acceleration values, which are commonly used to calculate body pitch and roll and/or as parameters to define particular behaviours, and derived metrics such as DBA. Attachment procedures should be adapted to the species tagged, as the effect of different tag placements may vary from one species to the other (e.g. Kölzsch *et al.*, 2016; Vandenabeele *et al.*, 2014), and to the study, as different metrics may be measured more reliably using one particular method (Kölzsch *et al.*, 2016), making the use of a standardised procedure difficult. Animal disturbance and study purposes should be considered before adjusting tag placement for the compatibility of datasets, and therefore, researchers should be aware of the attachment methods used to compare acceleration metrics between studies reliably (Sequeira *et al.*, 2021). Importantly, we highlight that sensor inaccuracy can be mitigated by performing a rapid calibration. There is therefore a need for researchers to undertake such calibrations prior to each deployment and include this in their archived data as well as to standardize their tag attachment procedure as much as possible. The last decade has been hailed as a golden age in bio-logging, due to the availability of powerful sensors in animal-attached technologies. The data repositories that archive these data represent extremely valuable resources for the community (e.g. Davidson *et al.*, 2020), but there is an urgent need for calibrations that allow data to be standardized in order for their full potential to be realized now and in the years to come.

References

Baumel, J. J. (1993). Handbook of avian anatomy: *nomina anatomica avium*. In *Publications of the Nuttall Ornithological Club (USA). no. 23.*

Bidder, O. R., Qasem, L. A., & Wilson, R. P. (2012). On Higher Ground: How Well Can Dynamic Body Acceleration Determine Speed in Variable Terrain? *PLoS ONE*, *7*(11), e50556. doi: 10.1371/journal.pone.0050556

Bishop, C. M., Spivey, R. J., Hawkes, L. A., Batbayar, N., Chua, B., Frappell, P. B., … Butler, P. J. (2015). The roller coaster flight strategy of bar-headed geese conserves energy during Himalayan migrations. *Science*, *347*(6219), 250–254. doi: 10.1126/science.1258732

Bograd, S., Block, B., Costa, D., & Godley, B. (2010). Biologging technologies: new tools for conservation. Introduction. *Endangered Species Research*, *10*, 1–7. doi: 10.3354/esr00269

Chakravarty, P., Cozzi, G., Ozgul, A., & Aminian, K. (2019). A novel biomechanical approach for animal behaviour recognition using accelerometers. *Methods in Ecology and Evolution*, *10*(6), 802–814. doi: 10.1111/2041-210X.13172

Davidson, S. C., Bohrer, G., Gurarie, E., LaPoint, S., Mahoney, P. J., Boelman, N. T., … Hebblewhite, M. (2020). Ecological insights from three decades of animal movement tracking across a changing Arctic. *Science*, *370*(6517), 712–715. doi: 10.1126/science.abb7080

Duriez, O., Peron, G., Gremillet, D., Sforzi, A., & Monti, F. (2018). Migrating ospreys use thermal uplift over the open sea. *Biology Letters*, *14*(12), 20180687. doi: 10.1098/rsbl.2018.0687

Elliott, K. H. (2016). Measurement of flying and diving metabolic rate in wild animals: Review and recommendations. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, *202*, 63–77. doi: 10.1016/j.cbpa.2016.05.025

Fehlmann, G., O'Riain, M. J., Hopkins, P. W., O'Sullivan, J., Holton, M. D., Shepard, E. L. C., & King, A. J. (2017). Identification of behaviours from accelerometer data in a wild social primate. *Animal Biotelemetry*, *5*(1), 6. doi: 10.1186/s40317-017-0121-3

Giansanti, D., Macellari, V., Maccioni, G., & Cappozzo, A. (2003). Is it feasible to reconstruct body segment 3-D position and orientation using accelerometric data? *IEEE Transactions on Biomedical Engineering*, *50*(4), 476–483.

Gudka, M., Santos, C. D., Dolman, P. M., Abad-Gómez, J. M., & Silva, J. P. (2019). Feeling the heat: Elevated temperature affects male display activity of a lekking grassland bird. *PLOS ONE*, *14*(9), e0221999. doi: 10.1371/journal.pone.0221999

Gunner, R. M., Holton, M. D., Scantlebury, M. D., van Schalkwyk, L., English, H. M., Williams, H. J., … Börger, L. (2021). *Dead-Reckoning Animal Movements in R–A Reappraisal Using Gundog. Tracks*.

Halsey, L.G., Shepard, E. L. C., Quintana, F., Gomez Laich, A., Green, J. A., & Wilson, R. P. (2009). The relationship between oxygen consumption and body acceleration in a range of species. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, *152*(2), 197–202. doi: 10.1016/j.cbpa.2008.09.021

Halsey, Lewis G., Shepard, E. L. C., & Wilson, R. P. (2011). Assessing the development and application of the accelerometry technique for estimating energy expenditure. *Comparative Biochemistry and Physiology - A Molecular and Integrative Physiology*, *158*(3), 305–314. doi: 10.1016/j.cbpa.2010.09.002

Harel, R., Spiegel, O., Getz, W. M., & Nathan, R. (2017). Social foraging and individual consistency in following behaviour: testing the information centre hypothesis in free-ranging vultures. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1852), 20162654. doi: 10.1098/rspb.2016.2654

Hyde, R. A., Ketteringham, L. P., Neild, S. A., & Jones, R. J. S. (2008). Estimation of Upper-Limb Orientation Based on Accelerometer and Gyroscope Measurements. *IEEE Transactions on Biomedical Engineering*, *55*(2), 746–754. doi: 10.1109/TBME.2007.912647

Jayasinghe, U., Harwin, W. S., & Hwang, F. (2019). Comparing Clothing-Mounted Sensors with Wearable Sensors for Movement Analysis and Activity Classification. *Sensors*, *20*(1), 82. doi: 10.3390/s20010082

Kokubun, N., Kim, J.-H., Shin, H.-C., Naito, Y., & Takahashi, A. (2011). Penguin head movement detected using small accelerometers: a proxy of prey encounter rate. *Journal of Experimental Biology*, *214*(22), 3760–3767. doi: 10.1242/jeb.058263

Kölzsch, A., Neefjes, M., Barkway, J., Müskens, G. J. D. M., van Langevelde, F., de Boer, W. F., … Nolet, B. A. (2016). Neckband or backpack? Differences in tag design and their effects on GPS/accelerometer tracking results in large waterbirds. *Animal Biotelemetry*, *4*(1), 13. doi: 10.1186/s40317-016-0104-9

Kranstauber, B., Cameron, A., Weinzerl, R., Fountain, T., Tilak, S., Wikelski, M., & Kays, R. (2011). The Movebank data model for animal tracking. *Environmental Modelling & Software*, *26*(6), 834–835. doi: 10.1016/j.envsoft.2010.12.005

Nathan, R., Spiegel, O., Fortmann-Roe, S., Harel, R., Wikelski, M., & Getz, W. M. (2012). Using tri-axial acceleration data to identify behavioral modes of free-ranging animals: General concepts and tools illustrated for griffon vultures. *Journal of Experimental Biology*, *215*(6), 986–996. doi: 10.1242/jeb.058602

Nickel, B. A., Suraci, J. P., Nisi, A. C., & Wilmers, C. C. (2021). Energetics and fear of humans constrain the spatial ecology of pumas. *Proceedings of the National Academy of Sciences*, *118*(5), e2004592118. doi: 10.1073/pnas.2004592118

Novák, P. (2010). High Resolution Constituents of the Earth’s Gravitational Field. *Surveys in Geophysics*, *31*(1), 1–21. doi: 10.1007/s10712-009-9077-z

Pagano, A. M., & Williams, T. M. (2019). Estimating the energy expenditure of free-ranging polar bears using tri-axial accelerometers: A validation with doubly labeled water. *Ecology and Evolution*, *9*(7), 4210–4219. doi: 10.1002/ece3.5053

Payne, N. L., van der Meulen, D. E., Suthers, I. M., Gray, C. A., & Taylor, M. D. (2015). Foraging intensity of wild mulloway *Argyrosomus japonicus* decreases with increasing anthropogenic disturbance. *Marine Biology*, *162*(3), 539–546. doi: 10.1007/s00227-014-2603-7

Qasem, L., Cardew, A., Wilson, A., Griffiths, I., Halsey, L. G., Shepard, E. L. C., … Wilson, R. (2012). Tri-axial dynamic acceleration as a proxy for animal energy expenditure; should we be summing values or calculating the vector? *PLoS ONE*, *7*(2). doi: 10.1371/journal.pone.0031187

R Core Team. (2020). *R: A language and environment for statistical computing*. Retrieved from https://www.r-project.org/

Ropert-Coudert, Y., Grémillet, D., Ryan, P., Kato, A., Naito, Y., & Le Maho, Y. (2003). Between air and water: the plunge dive of the Cape Gannet *Morus capensis*. *Ibis*, *146*(2), 281–290. doi: 10.1111/j.1474-919x.2003.00250.x

Ruzza, G., Guerriero, L., Revellino, P., & Guadagno, F. M. (2018). Thermal Compensation of Low-Cost MEMS Accelerometers for Tilt Measurements. *Sensors*, *18*(8), 2536. doi: 10.3390/s18082536

Sequeira, A. M. M., O'Toole, M., Keates, T. R., McDonnell, L. H., Braun, C. D., Hoenner, X., … Weise, M. (2021). A standardisation framework for bio-logging data to advance ecological research and conservation. *Methods in Ecology and Evolution*, *12*(6), 996–1007. doi: 10.1111/2041-210X.13593

Shepard, E., Wilson, R., Quintana, F., Gómez Laich, A., Liebsch, N., Albareda, D., … McDonald, D. (2008). Identification of animal movement patterns using tri-axial accelerometry. *Endangered Species Research*, *10*(1), 47–60. doi: 10.3354/esr00084

Su, J.-Y., Ting, S.-C., Chang, Y.-H., & Yang, J.-T. (2012). A passerine spreads its tail to facilitate a rapid recovery of its body posture during hovering. *Journal of The Royal Society Interface*, *9*(72), 1674–1684. doi: 10.1098/rsif.2011.0737

Tobalske, B. W., & Dial, K. P. (1996). Flight kinematics of black-billed magpies and pigeons over a wide range of speeds. *Journal of Experimental Biology*, *199*(2), 263–280.

Underhill, P. T., & Doyle, P. S. (2006). Alternative spring force law for bead-spring chain models of the worm-like chain. *Journal of Rheology*, *50*(4), 513–529. doi: 10.1122/1.2206713

Van Walsum, T. A., Perna, A., Bishop, C. M., Murn, C. P., Collins, P. M., Wilson, R. P., & Halsey, L. G. (2020). Exploring the relationship between flapping behaviour and accelerometer signal during ascending flight, and a new approach to calibration. *Ibis*, *162*(1), 13–26. doi: 10.1111/ibi.12710

Vandenabeele, S. P., Grundy, E., Friswell, M. I., Grogan, A., Votier, S. C., & Wilson, R. P.

(2014). Excess Baggage for Birds: Inappropriate Placement of Tags on Gannets Changes Flight Patterns. *PLoS ONE*, *9*(3), e92657. doi: 10.1371/journal.pone.0092657

Whelan, S., Hatch, S. A., Benowitz-Fredericks, Z. M., Parenteau, C., Chastel, O., & Elliott, K. H. (2021). The effects of food supply on reproductive hormones and timing of reproduction in an income-breeding seabird. *Hormones and Behavior*, *127*, 104874. doi: 10.1016/j.yhbeh.2020.104874

Williams, H. J., Shepard, E. L. C., Duriez, O., & Lambertucci, S. A. (2015). Can accelerometry be used to distinguish between flight types in soaring birds? *Animal Biotelemetry*, *3*(1), 1–11. doi: 10.1186/s40317-015-0077-0

Wilson, J. W., Mills, M. G. L., Wilson, R. P., Peters, G., Mills, M. E. J., Speakman, J. R., … Scantlebury, M. (2013). Cheetahs, *Acinonyx jubatus*, balance turn capacity with pace when chasing prey. *Biology Letters*, *9*(5), 20130620. doi: 10.1098/rsbl.2013.0620

Wilson, R. P., Börger, L., Holton, M. D., Scantlebury, D. M., Gómez-Laich, A., Quintana, F., … Shepard, E. L. C. (2020). Estimates for energy expenditure in free-living animals using acceleration proxies: A reappraisal. *Journal of Animal Ecology*, *89*(1), 161–172. doi: 10.1111/1365-2656.13040

Wilson, R. P., Holton, M., Wilson, V. L., Gunner, R., Tysse, B., Wilson, G. I., … Scantlebury, D. M. (2019). Towards informed metrics for examining the role of human-induced animal responses in tag studies on wild animals. *Integrative Zoology*, *14*(1), 17–29. doi: 10.1111/1749-4877.12328

Wilson, R. P., Pütz, K., Peters, G., Culik, B., Scolaro, J. A., Charrassin, J.-B., & Ropert-Coudert, Y. (1997). Long-term attachment of transmitting and recording devices to penguins and other seabirds. *Wildlife Society Bulletin*, 101–106.

Wilson, R. P., Rose, K. A., Gunner, R., Holton, M. D., Marks, N. J., Bennett, N. C., … Scantlebury, D. M. (2021). Animal lifestyle changes acceptable mass limits for attached tags. *BioRxiv*, 2021.04.27.441641. doi: 10.1101/2021.04.27.441641

Wilson, R. P., Shepard, E. L. C., & Liebsch, N. (2008). Prying into the intimate details of animal lives: Use of a daily diary on animals. *Endangered Species Research*, *4*(1–2), 123–137. doi: 10.3354/esr00064

Wilson, R. P., White, C. R., Quintana, F., Halsey, L. G., Liebsch, N., Martin, G. R., & Butler, P. J. (2006). Moving towards acceleration for estimates of activity-specific metabolic rate in free-living animals: The case of the cormorant. *Journal of Animal Ecology*, *75*(5), 1081–1090. doi: 10.1111/j.1365-2656.2006.01127.x

Wilson, R. P., & Wilson, M.-P. T. J. (1989). Tape: a package-attachment technique for penguins. *Wildlife Society Bulletin*, 77–79.

Yoda, K. (2019). Advances in bio-logging techniques and their application to study navigation in wild seabirds. *Advanced Robotics*, *33*(3–4), 108–117. doi: 10.1080/01691864.2018.1553686

Yoda, K., Sato, K., Niizuma, Y., Kurita, M., Bost, C., Le Maho, Y., & Naito, Y. (1999). Precise monitoring of porpoising behaviour of Adelie penguins determined using acceleration data loggers. *Journal of Experimental Biology*, *202*(22), 3121–3126. doi: 10.1242/jeb.202.22.3121

Yorzinski, J. L., Chisholm, S., Byerley, S. D., Coy, J. R., Aziz, A., Wolf, J. A., & Gnerlich, A. C. (2015). Artificial light pollution increases nocturnal vigilance in peahens. *PeerJ*, *3*, e1174. doi: 10.7717/peerj.1174

Synopsis

Birds that predominantly use flapping flight prioritise time and safety over energy saving currencies, favouring safety and speed in most conditions. In a broad sense, this outcome was expected, because smaller birds have lower flight costs (relative to their resting costs) and are subject to significant pressure from predators. Compared to large raptors or seabirds therefore, saving energy is far less important to their success.

Nonetheless, some of the strategies that were revealed by high frequency data were surprising and, at times, challenging to interpret. For example, while the fast and costly flight style in solo homing pigeons was consistent with previous studies (Chapter 2), the variable speeds and vertical movements were unexpected. The fact that birds adopt high speeds, with high variability and do so even during climbing flight, is a testament to the power available to these birds (something that may have been selected for through domestication). Nonetheless, it is interesting that this strategy was maintained even though no predators were observed in these trials. This is consistently with the landscape of fear framework, which has shown how animals can be affected by the threat of predation even when predators are not in the immediate vicinity (Laundré et al., 2010), with individuals responding to the perceived predation risk. Similarly, the tropicbirds increased their speed and altitude towards the end of their foraging flights, which could constitute an effective defence against kleptoparasitism, with birds returning high and fast. This pattern was consistent across flights even though frigatebirds no longer occur in their region. If this behaviour is a response to perceived risk, it suggests that the landscape can affect behaviour decades after predators have disappeared from an area (Laundré et al., 2001).

My results also highlight that the selective pressure to minimise time varies through the annual cycle. For example chick-rearing impacts parental priorities as the adults seek to optimise the growth of their chicks by maximising their provisioning rate (Norberg, 1981, but see Houston, 2006). One way to increase provisioning rate is to increase flight speed (Elliott & Gaston, 2005) with all the power implications that this entails (Pennycuick, 2008) or by reducing the amount of resting during foraging trips (Sommerfeld & Hennicke, 2010).

Of course, favouring low risk and/ or time-efficient strategies does not mean that energy is irrelevant for these birds. This is shown by the pigeons gaining altitude gradually to climb over the hill and the use of soaring by tropicbirds; both behaviours demonstrate that these species do not “waste” energy. Thermal soaring allows substantial energy savings (Chapter 3), but this gain has to be pitted against the time invested by circling, which does not necessarily move birds towards their nest, depending on the extent to which the wind is blowing the thermal towards/away from the breeding site. Thus, the use of energy saving mechanisms is not always compatible with other factors that might enhance lifetime reproductive success.

As researchers, we therefore need to be mindful that we usually collect data in a specific season and that bird behaviour and energetics could change substantially outside this period. At certain times of the year and in certain situations, flight costs will be much higher than what could be achieved in optimal conditions. Understanding the interplay of biological currencies and the physical environment on flight decisions and costs is challenging. Nonetheless, there is a real need for such information given that global change is affecting the flight environment, and the implications for avian ecology are unclear (Clay et al., 2020). I hope that this thesis helps to emphasize the insights that can be provided by high-resolution movement data in relation to part of this equation.

Implications in a context of global change

In the current context of global change, a warming of 3.5 °C is expected by 2100 (Tollefson, 2011). This increase in temperatures is predicted to result in 600-900 extinctions of land bird species, 89% of which occur in the tropics (Şekercioğlu et al., 2012). Among seabirds, 96 species are currently threatened by climate change (Dias et al., 2019). The effects of temperature rise on seabirds range from fatal overheating in chicks (Sherley et al., 2012), through match-mismatches between predators and prey (Grémillet et al., 2008) to reduction in productivity at the sea surface (Behrenfeld et al., 2005; Grémillet et al., 2008). But global warming also causes catastrophic changes, manifest, for example, through increases in the occurrence and intensity of storms and flooding. These intense weather events can reduce breeding success and increase mortality, even of adult birds (Hass et al., 2012; Hennicke & Flachsbarth, 2009; Sherley et al., 2012; Weimerskirch & Prudor, 2019).

Weather is also likely to affect some bird populations by modulating both the costs and conditions of travel (Weimerskirch et al., 2012). Results suggest that even non-dramatic changes in overall wind speeds (Solomon et al., 2007) could affect the ecological energetics of soaring species, by changing thermal soaring opportunity and efficiency, in addition to other negative effects that increasing drift may have on species that do not rely on dynamic or orographic soaring (Liechti, 2006). How this interacts with the other main discovery within this thesis, that changes in air density at sea level can affect flight effort in flapping flight, is unclear. Nonetheless, converting worldwide patterns of temperature to density altitude was very striking, as I had not considered that there could be effective invisible global patterns in topography. Indeed, tropical birds effectively fly hundreds of metres higher than birds at low latitudes, also making tropical species more susceptible to further increases in temperature.

Telemetry to predict effects of climate change

Biologging has been described as ‘revolutionary’ in what it can tell us about animal behaviour (Williams et al., 2020; Wilmers et al., 2015). The strength of the approach in the current context is that it provides high frequency (sub-second) assessment of bird position in 3D, as well as metrics that tell us how hard birds have to work in varying conditions. Such high frequency and multi-dimensional data seems well-matched to the challenges of studying movement in an environment as dynamic as air. Biotelemetry can provide very fine-scale data on different aspects of the biology of animals and it is becoming increasingly obvious that this resolution is essential to predict the effects of global change (Grémillet & Boulinier, 2009). Among their notable applications in this domain, biologgers can be used to track space use (Camphuysen et al., 2012), behaviour (Laich et al., 2008), flight style (Williams et al., 2015), foraging success (Chapter 3, Sato et al., 2008) and energy expenditure (Chapter 3, 5, see also Wilson et al., 2020) of birds at sea, all of which may change in our rapidly shifting climate.

Within this, accelerometers have played, and are increasingly playing, a particularly important role (Wilmers et al., 2015). However, in contrast to GPSs, which have been the subject of thorough research over the past 20 years (e.g. Ganskopp & Johnson, 2007; Williams et al., 2004), the limitations of accelerometers seem to have escaped the critical eye of researchers. As evidenced by chapter 4, the effect of accelerometer type, tag type, attachment position and even attachment method makes a difference to the output (e.g. Chapter 4, Kölzsch et al., 2016). Perhaps in the same way that different manufacturers use different methods for deriving and filtering GPS fixes (Xiong et al., 2017), companies do not have a standard protocol for outputting acceleration data. On a personal level, this made data interpretation even more complex (and in many instances, frustrating). From a community perspective, it is as unfortunate as acceleration is a well-defined physical entity and, under identical conditions, should be represented the same way and with the same values. Aside from differences in resolution between tags, which are understandable, users are unlikely to expect additional filtering of the data. Ultimately there needs to be a shift so that the research community itself defines the data standards that manufacturers should supply, rather than having to interrogate and motivate company practice. Certainly, transparency about how tags deal with data is essential to ensure replicability and compatibility of data collected by tags from different manufacturers.

Beyond this, the fact that interpretations of accelerometer data must always be made in the context of precisely how animals were tagged, even if those errors are acknowledged, makes it difficult to disentangle the environmental effects on animal behaviour from the effects of deployment differences. To a give specific example from this thesis, the amplitude of heave acceleration recorded from black-legged kittiwake wingbeats was 0.5 *g* higher for tail tags than back tags (mean = 2.1 *g*), which is larger than the difference we found between kittiwakes and other species, such as tropicbirds or barn owls (a difference of 0.3 *g*). Likewise, we found a 30% difference in heave amplitude between the two seasons where tropicbirds had been equipped with tags in a slightly different manner. Without cognisance of the effects of tag stability, this difference could have been interpreted as biologically significant. Furthermore, these differences meant that I had to use wingbeat frequency as a proxy for flight effort in tropicbirds, despite outlined the benefits of DBA in chapter 1.

The standardisation of methods is, however, often limited by technical and ethical considerations. The position of a GPS tag on the body depends on where a sufficient signal can be found and by what type of data researchers want to record (Kölzsch et al., 2016). Tags are also exposed to different constraints depending on where they are placed. Kittiwakes tagged on the tail are more likely to incur tag submergence, so devices should be contained within a waterproof housing, which prevents most loggers from recording barometric pressure and therefore from assessing flight height accurately. Conversely, while back-mounted tags on kittiwakes can record pressure because they are unlikely to be submerged, they may need a special type of housing to protect them from pecks as they are more accessible to birds. For ethical and scientific reasons, we need to minimize tag-induced abnormal behaviours. Negative effects of biologgers have been noted since the first deployments of tags (Vandenabeele et al., 2011), and are still being found (Wilson 2021, in review), showing the importance of diligence in monitoring the effects of tags on animals, and rapid communication of findings (Bodey et al., 2018).

Overall, one of the main messages I retain from this PhD is that the world of biotelemetry is almost like an ecosystem in itself. Work within it requires an understanding of the study system, the hardware, as well as the physical principles that determine how the sensors work. Each stage from tag programming, calibration, placement, monitoring, and recovery requires thought, and that is before data processing and analysis even begins. The complexity of biologgers has increased dramatically in recent the years, which makes them formidable tools to study the living world, but also fairly formidable techniques to master. I have been extremely lucky to work within and benefit from a group specialising in the acquisition, processing, visualisation and analysis of multi-dimensional data, but not everyone has the same opportunity. I hope that discussions about data standardisation, as dry as they can sometimes be, will therefore help to establish a clearer framework for other students to learn about the details of the use of biologgers, in particular accelerometers, and streamline common practice to ensure the data we collect are more compatible, and therefore more powerful. This is a responsibility beholden to us as a community, as so many of the systems we study are also facing powerful challenges.

References

Behrenfeld, M. J., Boss, E., Siegel, D. A., & Shea, D. M. (2005). Carbon-based ocean productivity and phytoplankton physiology from space. *Global Biogeochemical Cycles*, *19*(1), 1–14. doi: 10.1029/2004GB002299

Bodey, T. W., Cleasby, I. R., Bell, F., Parr, N., Schultz, A., Votier, S. C., & Bearhop, S. (2018). A phylogenetically controlled meta-analysis of biologging device effects on birds: Deleterious effects and a call for more standardized reporting of study data. *Methods in Ecology and Evolution*, *9*(4), 946–955.

Camphuysen, K. C. J., Shamoun-Baranes, J., Bouten, W., & Garthe, S. (2012). Identifying ecologically important marine areas for seabirds using behavioural information in combination with distribution patterns. *Biological Conservation*, *156*, 22–29.

Clay, T. A., Joo, R., Weimerskirch, H., Phillips, R. A., den Ouden, O., Basille, M., … Patrick, S. C. (2020). Sex-specific effects of wind on the flight decisions of a sexually dimorphic soaring bird. *Journal of Animal Ecology*, *89*(8), 1811–1823. doi: 10.1111/1365-2656.13267

Dias, M. P., Martin, R., Pearmain, E. J., Burfield, I. J., Small, C., Phillips, R. A., … Croxall, J. P. (2019). Threats to seabirds: A global assessment. *Biological Conservation*, *237*, 525–537. doi: 10.1016/j.biocon.2019.06.033

Elliott, K. H., & Gaston, A. J. (2005). Flight speeds of two seabirds: a test of Norberg's hypothesis. *Ibis*, *147*(4), 783–789.

Ganskopp, D. C., & Johnson, D. D. (2007). GPS error in studies addressing animal movements and activities. *Rangeland Ecology & Management*, *60*(4), 350–358.

Grémillet, D., & Boulinier, T. (2009). Spatial ecology and conservation of seabirds facing global climate change: a review. *Marine Ecology Progress Series*, *391*, 121–137.

Grémillet, D., Lewis, S., Drapeau, L., van Der Lingen, C. D., Huggett, J. A., Coetzee, J. C., … Ryan, P. G. (2008). Spatial match–mismatch in the Benguela upwelling zone: should we expect chlorophyll and sea-surface temperature to predict marine predator distributions? *Journal of Applied Ecology*, *45*(2), 610–621.

Hass, T., Hyman, J., & Semmens, B. X. (2012). Climate change, heightened hurricane activity, and extinction risk for an endangered tropical seabird, the black-capped petrel *Pterodroma hasitata*. *Marine Ecology Progress Series*, *454*, 251–261.

Hennicke, J. C., & Flachsbarth, K. (2009). Effects of Cyclone Rosie on breeding Red-tailed Tropicbirds *Phaethon rubricauda* on Christmas Island, Indian Ocean. *Marine Ornithology*, *37*(2), 175–178.

I. Houston, A. (2006). The flight speed of parent birds feeding young. *Journal of Avian Biology*, *37*(6), 545–554.

Kölzsch, A., Neefjes, M., Barkway, J., Müskens, G. J. D. M., van Langevelde, F., de Boer, W. F., … Nolet, B. A. (2016). Neckband or backpack? Differences in tag design and their effects on GPS/accelerometer tracking results in large waterbirds. *Animal Biotelemetry*, *4*(1), 13. doi: 10.1186/s40317-016-0104-9

Laich, A. G., Wilson, R. P., Quintana, F., & Shepard, E. L. C. (2008). Identification of imperial cormorant Phalacrocorax atriceps behaviour using accelerometers. *Endangered Species Research*, *10*, 29–37.

Laundré, J. W., Hernández, L., & Altendorf, K. B. (2001). Wolves, elk, and bison: reestablishing the "landscape of fear" in Yellowstone National Park, USA. *Canadian Journal of Zoology*, *79*(8), 1401–1409.

Laundré, J. W., Hernández, L., & Ripple, W. J. (2010). The landscape of fear: ecological implications of being afraid. *The Open Ecology Journal*, *3*(1).

Liechti, F. (2006). Birds: Blowin' by the wind? *Journal of Ornithology*, *147*(2), 202–211. doi: 10.1007/s10336-006-0061-9

Norberg, R. A. (1981). Optimal Flight Speed in Birds when Feeding Young. *The Journal of Animal Ecology*, *50*(2), 473. doi: 10.2307/4068

Pennycuick, C. J. (2008). *Modelling the flying bird*. Elsevier.

Sato, K., Daunt, F., Watanuki, Y., Takahashi, A., & Wanless, S. (2008). A new method to quantify prey acquisition in diving seabirds using wing stroke frequency. *Journal of Experimental Biology*, *211*(1), 58–65. doi: 10.1242/jeb.009811

Şekercioğlu, Ç. H., Primack, R. B., & Wormworth, J. (2012). The effects of climate change on tropical birds. *Biological Conservation*, *148*(1), 1–18.

Sherley, R. B., Ludynia, K., Underhill, L. G., Jones, R., & Kemper, J. (2012). Storms and heat limit the nest success of Bank Cormorants: implications of future climate change for a surface-nesting seabird in southern Africa. *Journal of Ornithology*, *153*(2), 441–455. doi: 10.1007/s10336-011-0760-8

Solomon, S., Manning, M., Marquis, M., & Qin, D. (2007). *Climate change 2007-the physical science basis: Working group I contribution to the fourth assessment report of the IPCC* (Vol. 4). Cambridge university press.

Sommerfeld, J., & Hennicke, J. C. (2010). Comparison of trip duration, activity pattern and diving behaviour by Red-tailed Tropicbirds (*Phaethon rubricauda*) during incubation and chick-rearing. *Emu*, *110*(1), 78–86. doi: 10.1071/MU09053

Tollefson, J. (2011). Durban maps path to climate treaty. *Nature News*, *480*(7377), 299.

Vandenabeele, S. P., Wilson, R. P., & Grogan, A. (2011). Tags on seabirds: how seriously are instrument-induced behaviours considered? *Animal Welfare-The UFAW Journal*, *20*(4), 559.

Weimerskirch, H., Louzao, M., De Grissac, S., & Delord, K. (2012). Changes in wind pattern alter albatross distribution and life-history traits. *Science*, *335*(6065), 211–214. doi: 10.1126/science.1210270

Weimerskirch, H., & Prudor, A. (2019). Cyclone avoidance behaviour by foraging seabirds. *Scientific Reports*, *9*(1), 1–9. doi: 10.1038/s41598-019-41481-x

Williams, H. J., Shepard, E. L. C., Duriez, O., & Lambertucci, S. A. (2015). Can accelerometry be used to distinguish between flight types in soaring birds? *Animal Biotelemetry*, *3*(1), 1–11. doi: 10.1186/s40317-015-0077-0

Williams, Hannah J., Taylor, L. A., Benhamou, S., Bijleveld, A. I., Clay, T. A., de Grissac, S., … Börger, L. (2020). Optimizing the use of biologgers for movement ecology research. *Journal of Animal Ecology*, *89*(1), 186–206. doi: 10.1111/1365-2656.13094

Williams, S. D. P., Bock, Y., Fang, P., Jamason, P., Nikolaidis, R. M., Prawirodirdjo, L., … Johnson, D. J. (2004). Error analysis of continuous GPS position time series. *Journal of Geophysical Research: Solid Earth*, *109*(B3).

Wilmers, C. C., Nickel, B., Bryce, C. M., Smith, J. A., Wheat, R. E., & Yovovich, V. (2015). The golden age of bio-logging: How animal-borne sensors are advancing the frontiers of ecology. *Ecology*, *96*(7), 1741–1753.

Wilson, R. P., Börger, L., Holton, M. D., Scantlebury, D. M., Gómez-Laich, A., Quintana, F., … Shepard, E. L. C. (2020). Estimates for energy expenditure in free-living animals using acceleration proxies: A reappraisal. *Journal of Animal Ecology*, *89*(1), 161–172. doi: 10.1111/1365-2656.13040

Wilson, R. P., Rose, K. A., Gunner, R., Holton, M. D., Marks, N. J., Bennett, N. C., … Scantlebury, D. M.

(2021). Animal lifestyle changes acceptable mass limits for attached tags. BioRxiv, 2021.04.27.441641. doi: 10.1101/2021.04.27.441641

Xiong, H., Tang, J., Xu, H., Zhang, W., & Du, Z. (2017). A robust single GPS navigation and positioning algorithm based on strong tracking filtering. *IEEE Sensors Journal*, *18*(1), 290–298.

Supplementary Information

Supplementary Information for Chapter 1

Table S1. Complementary information to Table 1.

Species	Location	N	Tag type	WBF selection range	WBF method
Brünnich's guillemot *Uria lomvia*	Coats Island, Nunavut, Canada	13	Daily Diary	3.5 – 13.0 Hz	R
Common guillemot *Uria aalge*	Puffin Island, UK	6	AxyTrek	2.0 – 13.0 Hz	DDMT
Northern fulmar *Fulmarus glacialis*	Saltee Islands, Ireland	3	Daily Diary	3.5 – 8.0 Hz	R
Pigeon *Columba livia*	Radolfzell, Germany	9	Daily Diary	2.0 – 6.0 Hz	R
Red-tailed tropicbird *Phaethon rubricauda*	Round Island, Mauritius	10	Daily Diary	2.0 – 13.0 Hz	DDMT
Great frigatebird *Frigata magnificens*	Europa Island	3	Daily Diary	2.0 – 13.0 Hz	DDMT
Black-legged kittiwake *Rissa tridactyla*	Middleton Island, Alaska, USA	3	Daily Diary	2.0 – 13.0 Hz	DDMT
Imperial cormorant *Phalancrocorax atriceps*	Punta Leon, Argentina	5	Daily Diary	2.0 – 13.0 Hz	DDMT
Barn owl *Tyto alba*	Switzerland	10	AxyTrek	2.0 – 13.0 Hz	DDMT
Grey-headed albatross *Thalassarche chrysostoma*	Marion Island, South Africa	5	Daily Diary	2.0 – 13.0 Hz	DDMT
Wandering albatross *Diomedea exulans*	Marion Island, South Africa	6	Daily Diary	2.0 – 13.0 Hz	DDMT
Streaked shearwater *Calonectris leucomelas*	Awashima Island, Japan	5	Daily Diary	3.5 – 13.0 Hz	R
Dunlin *Calidris alpina*	Sweden	1	Axy XS	8.0 – 18.0 Hz	DDMT

Supplementary Information for Chapter 2

The rate of change of speed and altitude recorded by an ultralight flying a section of the pigeon's flight path shows that the variability in speed and altitude is a specific feature of pigeon flight.

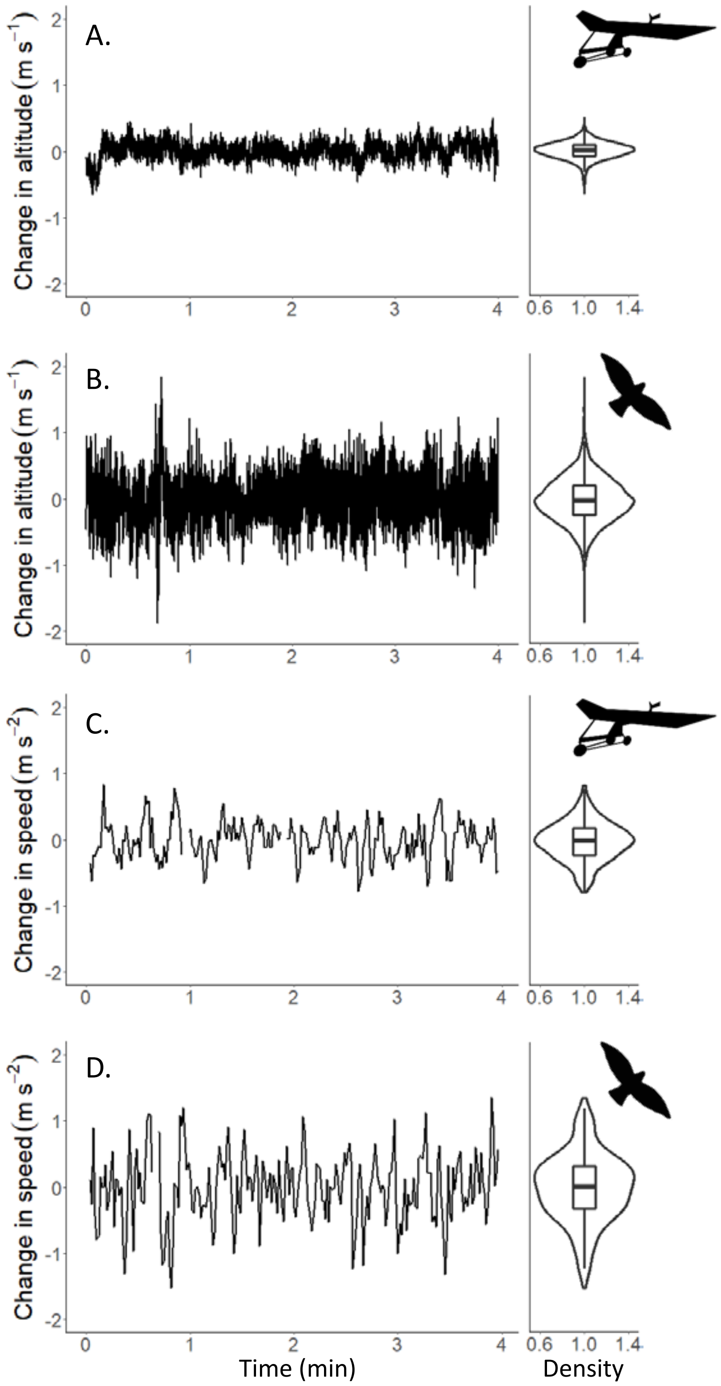

Figure S1: Comparison of the rate of change of altitude and speed of an ultralight (A and C respectively) and a pigeon (B and D), flying at the same time, and with the same loggers. Violin plots show the distribution of the data during the flight; the upper and lower quartiles are represented by the upper and lower extremes of the box and the median by the thick black line.

Supplementary Information for Chapter 3

Histograms

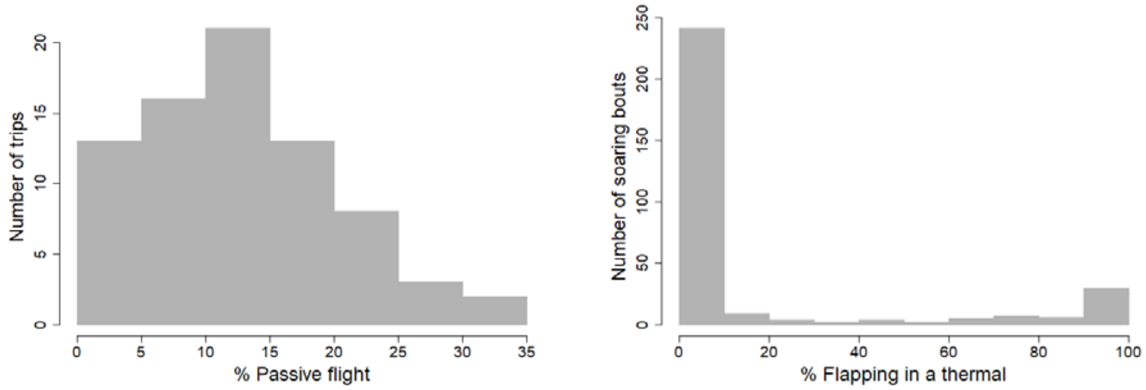

Figure S2. A. Histogram showing the distribution of the proportion of time spent in passive flight (including soring and gliding) across 76 different tropicbird flights. B. Histogram showing the distribution of the proportion of flapping during a soaring bout.

Variation of airspeed and power with wind support

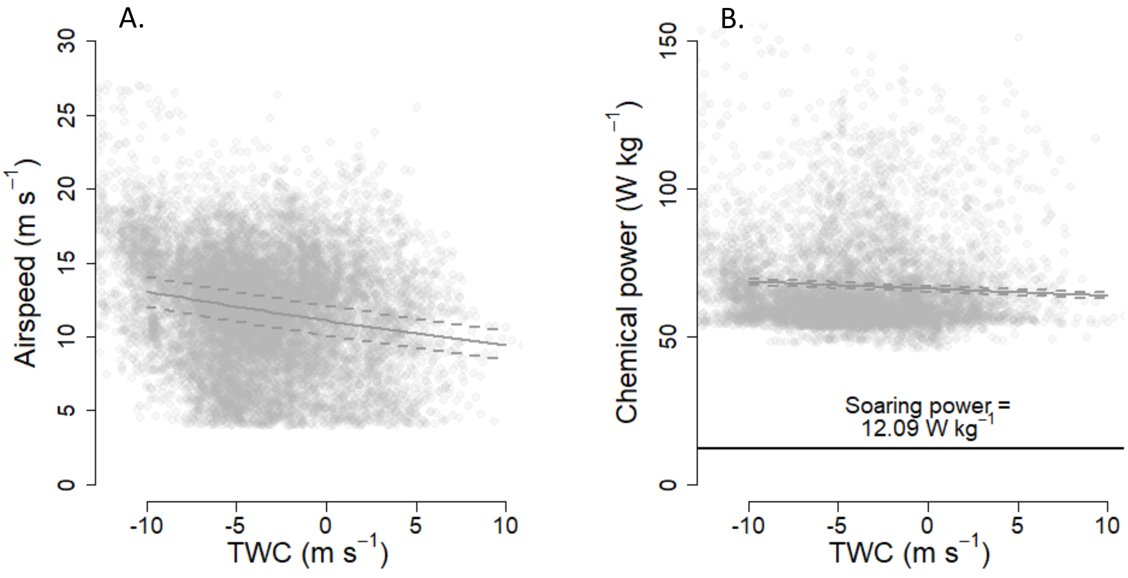

Figure S3. A. Airspeed in relation to the tailwind component (TWC) for level flapping flight; D. Chemical power per kg against TWC for level flapping flight. Dashed lines indicate the standard error. The black line indicates the average power required in soaring-gliding flight for a bird of average body mass.

Effect of the physical environment on airspeed selection

Table S2. Output of the LME model showing the effect of air density, altitude, headwind component (HWC), crosswind component (CWC) and wind speed on airspeed. $R^2_m = 0.18$, $R^2_c = 0.25$.

	Estimate (scaled)	Estimate (raw)	Std. Error	t-value	p	VIF (< 5)
(Intercept)	11.740	49.522	12.669	3.909	< 0.001	NA
Air density (kg m^{-3})	-0.579	-35.305	10.655	-3.313	0.001	2.09
Altitude (m)	0.579	0.019	0.002	8.685	< 0.001	2.08
HWC (m s^{-1})	0.818	0.211	0.017	12.055	< 0.001	1.52
CWC (m s^{-1})	-0.079	-0.036	0.023	-1.604	0.109	1.35
Wind speed (m s^{-1})	1.033	0.376	0.038	9.886	< 0.001	1.41

Wingbeat frequency

Table S3. Output of the LME model showing variation in wingbeat frequency as a function of air density, airspeed, flight altitude and pursuit number in the low and high season, as well as the effect of airspeed on the slope between air density and wingbeat frequency. $R^2_m = 0.13$, $R^2_c = 0.77$.

	Estimate (raw)	Estimate (scaled)	Std. Error	t-value	p
(Intercept)	10.881	4.420	0.029	149.943	< 0.001
Air density (kg m^{-3})	-5.392	-0.084	0.029	-2.913	0.004
Airspeed (True, m s^{-1})	-0.312	0.002	0.002	1.214	0.226
Altitude (m)	-0.003	-0.061	0.008	-7.257	< 0.001
Air density: Airspeed	0.266	0.004	0.002	2.463	0.014
Season:Pursuits (Low)	0.008	0.031	0.007	4.200	< 0.001
Season:Pursuits (High)	0.010	0.039	0.006	6.112	< 0.001

Supplementary Information for Chapter 5

Table S4. Comparison of accelerometer sensitivity between different models. There are a few manufacturers that supply MEMS accelerometers with acceleration ranges of 2, 4, 8, and 16 g, while the sensitivity, the smallest detectable/measurable change, at different ranges can vary greatly. The table below shows a list of sensors possessing comparable acceleration ranges, the first two of which are used on the devices discussed in this paper, with others from well-known manufacturers, in some cases with far less sensitivity than the median. LSM303DLHC is the accelerometer-magnetometer chip built on to type 2 tags, while the LSM9DS1 is the chip built on to type 1 tags. Note that type 1 and type 2 tags have a substantially different sensitivity, far higher in LSM9DS1 accelerometers.

Manufacturer	Sensor	±2 g	±4 g	±8 g	±16 g
ST	**LSM303DLHC**	1	2	4	12
ST	**LSM9DS1**	0.061	0.122	0.244	0.732
ST	**MIS2DH**	0.98	1.95	3.91	11.72
TDK	**ICM-20948**	0.061	0.122	0.244	0.488
TDK	**IAM-20381**	0.061	0.122	0.244	0.488
TDK	**IIM-42652**	0.061	0.122	0.244	0.488
Analog	**ADXL346**	0.015	7.81	15.63	31.25
Kionix	**KX132-1211**	0.061	0.122	0.244	0.488
Bosch Sensortec	**BMA180**	0.244	0.488	0.977	1.953
Bosch Sensortec	**BMA456**	0.061	0.122	0.244	0.488
	Median	0.061	0.122	0.244	0.488 *mg/LSB*