Bangor University

DOCTOR OF PHILOSOPHY

Drivers and consequences of individual movement patterns in northern fulmars (Fulmarus glacialis)

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Summary

The study of animal movement has remained of central importance to the study of animal behaviour, as a critical component of how animals survive and reproduce. Through an ever-increasing wealth of telemetry studies, the role of individual decision-making, in response to internal and external cues, has been recognised as important in shaping movement patterns. However, further work is required to better understand the mechanistic drivers and demographic consequences of these decisions, which underpin the long-term stability of populations. As the influence of anthropogenic stressors rapidly increases it becomes critically important to understand the capacity of different species to respond to possible threats.

Here, I study a widespread and generalist seabird, the northern fulmar (*Fulmarus glacialis*), which has undergone a large population expansion in recent centuries but is currently in decline. Focussing on adult birds breeding at the colony of Eynhallow (Orkney Islands, UK) I build on recent tracking studies and past observational studies of this species, to better understand their individual movement patterns, possible drivers of these and links with breeding success. Fulmars from this colony use a range of movement strategies throughout the annual cycle, visiting the North Sea, the Norwegian Sea, the Mid-Atlantic Ocean and the Barents Sea, resulting in large variation in how far they travel from the colony (< 500 km to > 2000 km).

In Chapter 3, I quantify individual consistency of movement patterns throughout their annual cycle. To separate behaviourally discrete periods throughout the year, I used a combination of daily summaries of location, light level and salt-water immersion, enabling me to quantify inter-annual variation in spatial distributions at individually relevant timescales. I find individual consistency throughout the non-breeding period, including in late winter, despite high levels of population-level consistency at this time and some instances of individual flexibility.

In Chapter 4, I focus in more detail on late winter and pre-breeding, which in fulmars represent an extended period of central place foraging, where they associate with the breeding colony but still spend significant time at sea. There was large variation in trip-taking behaviour in both sexes. Males were more likely to remain resident, but large numbers of both sexes took multiple long foraging trips away from the colony, likely travelling thousands of kilometres more each year than their resident counterparts. I also find that females take longer trips than males and are more likely to revisit familiar areas on pre-laying exodus than males, suggesting biological differences in how fulmars trade off time spent foraging against time at the breeding colony. However, I find no evidence of variation between years, or of carry-over effects linking these behaviours with breeding success.

In Chapter 5, I use high-resolution accelerometry data to describe almost instantaneous flight mechanics and provide insight into how fulmars achieve these highly transitory movements. I find surprising reliance on predominantly flapping flight for a Procellariiform seabird, and evidence that like other seabird species, fulmars moderate their energetic expenditure at different wind speeds, but no clear mechanistic link. Together, these findings suggest that in fulmars the importance of energy gain from dynamic wind features has possibly been over-estimated.

This thesis expands our understanding of the movements of fulmars throughout their annual cycle, at broad and fine spatial and temporal scales. Making use of long-term data, I demonstrate how additional insight can be gained by using individually specific pattern recognition techniques, to augment the interpretation of low-resolution data. Additionally, I demonstrate the value of state-of-the-art high resolution data loggers, to mechanistically understand how broad-scale movements are achieved.

Declaration

I hereby declare that this thesis is the results of my own investigations, except where otherwise stated. All other sources are acknowledged by bibliographic references. This work has not previously been accepted in substance for any degree and is not being concurrently submitted in candidature for any degree unless, as agreed by the University, for approved dual awards.

Sarah Bond

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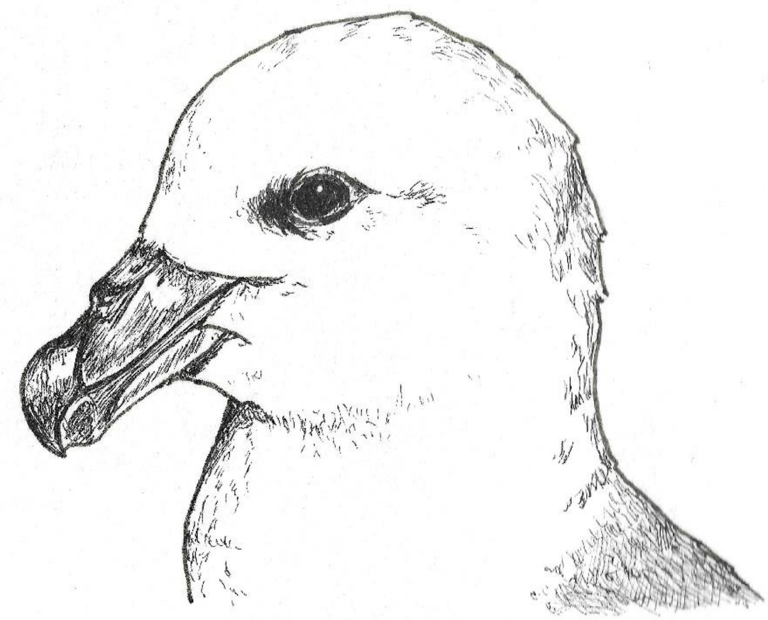
Chapter 1 General Introduction



1.1 Foraging as a driver of animal movement patterns

Movement is a process that is fundamental to life, across the kingdom of Animalia, and driven by animals' ultimate need to survive and reproduce (Breed & Moore, 2011). Movement is achieved through energy expenditure, which must be offset by energy gained through foraging. Animals employ different strategies to achieve this, based on their internal state, their physical and navigational capabilities and external factors such as weather or geography; which in turn shape both the distribution of food in the environment and the costs of movement (Nathan *et al.*, 2008).

As resource availability varies in space and time (Weimerskirch, 2007), different species will employ contrasting strategies to optimise their encounter likelihood with suitable resources (Schoener, 1971; Zollner & Lima, 1999). They do this by balancing their energetic expenditure, which is achieved in sedentary species by reducing their expenditure while waiting for infrequent encounters (Huey & Pianka, 1981). However, resources are finite, so competition will drive animals to find additional ways to balance these needs. More mobile species can reduce competition by expending energy to maximise encounter opportunities (Matthysen, 2005). This also allows access to multiple resources, use of different resources by different individuals, and the use of resources that are distant from other needs, such as a breeding colony.

In order to successfully locate resources across larger spatial scales, animals must become efficient at commuting and searching. Many species have evolved complex cognitive and physiological adaptations that facilitate this (Mueller & Fagan, 2008), allowing them to reallocate time and energy to reproduction. From a cognitive perspective, learning and memory facilitate navigation and reduced search times through the ability to relocate previously productive resources (Bracis *et al.*, 2015). From a physiological perspective, this might be in investment in structures that aid efficient conversion of body reserves into energy, or the development of movement styles that can make use of energy in the environment (Richardson, 2011).

The focus of this thesis is a species that is highly adapted to solve these evolutionary problems, the northern fulmar (*Fulmarus glacialis*). This is a generalist, colony-nesting species, that is highly mobile and exploits favourable wind conditions to access prey patches that are distant from the breeding colony.

1.2 The importance of individuals

Individual variation has been the focus of increasing numbers of studies, building on knowledge of "typical" movement patterns (Shaw, 2020), particularly since a review by Bolnick et al. (2003) highlighted its importance within community ecology. The authors argued that within individual variation had been previously neglected in ecological models (Bolnick *et al.*, 2003) and was likely to significantly affect ecosystem dynamics (Bolnick *et al.*, 2011). Individuals within a generalist population are considered to be specialised when the behavioural variation between individuals exceeds variation within individuals over time and in different contexts (Dall *et al.*, 2012). Within a population, individuals are hypothesised to become more specialist as a result of intra-specific competition, where high competition for common resources leads individuals to diversify and exploit different lower-value resources, widening the population niche (Van Valen, 1965; Bolnick *et al.*, 2003; Svanbäck & Bolnick, 2007).

In a generalist population of specialists, often much of the variation between individuals can be accounted for by differences between groups such as sex (Miller *et al.*, 2017; Paiva *et al.*, 2018), age (Clay *et al.*, 2018), morphology (Camphuysen *et al.*, 2015), breeding status (Clay *et al.*, 2016; Votier *et al.*, 2017) or colony (Ceia *et al.*, 2015; Sánchez *et al.*, 2018; Bolton *et al.*, 2019). The remaining variation between individuals represents the within-individual component of behaviour or individual specialisation, resulting in heterogeneous populations (Bolnick *et al.*, 2003). Understanding how individual variation affects population dynamics and is maintained by ecological interactions is important as it underlies the stability, abundance and extinction risk of a population (Araújo *et al.*, 2011) and consequently can influence evolutionary processes (Bolnick *et al.*, 2011).

Most commonly individual variation and specialisation is found in foraging behaviour, for example in location (Wakefield *et al.*, 2015), time of day (Miller *et al.*, 2017), dive depth or shape (Cleasby *et al.*, 2015), prey type (Woo *et al.*, 2008; Patrick *et al.*, 2015) and foraging habitat (Patrick & Weimerskirch, 2017). However, individuals may also show consistency in migratory phenology, behaviour (Desprez *et al.*, 2018), over-wintering location (Krietsch *et al.*, 2017), migratory routes (Guilford *et al.*, 2011; Baylis *et al.*, 2015) and stop-overs. A review by Ceia and Ramos (2015) found that 12% of extant seabird species have some degree of individual specialisation (Ceia & Ramos, 2015), but the relative success of different strategies varies between populations and species. For example, successful black-browed albatross

(Thalassarche melanophrys) individuals had a narrower niche than failed individuals (Patrick & Weimerskirch, 2014) and pigeon guillemots *(Cepphus coumba)* with more specialised diets had higher fledgling success than generalists (Golet *et al.*, 2000), but there was no difference in reproductive success between specialist and generalist Brünnich's guillemots *(Uria lomvia)* (Woo *et al.*, 2008).

1.3 Environmental factors and their interaction with energetic expenditure

Environmental variability can drive seabird foraging distributions, with basin-wide conditions influencing meso- and fine-scale oceanographic features, which result in predictable aggregations of prey (McDuie *et al.*, 2018). Environmental conditions also interact with individual movement patterns, as individuals may vary in the extent to which they to respond to fluctuating cues. In stable conditions, such as in the tropics where resources are sparsely distributed and unpredictable, individuals are unlikely to specialise, as investing in better search mechanisms is more likely to be successful (Oppel *et al.*, 2017). However, under variable conditions the ability to respond to environmental cues and change strategy will be beneficial (Camprasse *et al.*, 2017; Gilmour *et al.*, 2018). Consequently, either individuals will retain some flexibility, or environmental variability will result in the maintenance of both specialist and generalist strategies within a population (Woo *et al.*, 2008; Abrahms *et al.*, 2018).

The interaction between individual and environmental conditions might also affect breeding success. For example, the most successful strategies in northern elephant seals (*Mirounga angustirostris*) are observed in years where environmental conditions are close to average (Abrahms *et al.*, 2018) and consistent foraging strategies are more successful in African penguins *(Spheniscus demersus)* when conditions are poor (Traisnel & Pichegru, 2019). Alternatively, behavioural mechanisms might work to limit the impact of poor conditions, such as in Cory's shearwaters *(Calonectris borealis)*, where there is higher segregation in years of low prey availability (Paiva *et al.*, 2017).

In species that are dependent on flight for locomotion, wind conditions are likely to affect both commuting and foraging efficiency, which may affect breeding success. In wandering albatross (*Diomedea exulans*), optimal wind speeds for efficient flight vary depending on wind direction (Richardson *et al.*, 2018), with changes in the prevalent winds in the Southern Ocean correlating with reduced trip lengths and increased body condition and breeding success (Weimerskirch, 2018). Individuals may also be able to compensate for unfavourable wind conditions, such as in Antarctic petrels (*Thalassoica antarctica*), which alter their flight altitude to exploit the most favourable wind speeds when crossing large expanses of ice to reach their breeding colony (Tarroux *et al.*, 2016). In species that employ soaring flight, foraging may be more energetically costly than commuting, as landing and take-off require flapping flight (Shaffer *et al.*, 2001).

In addition to energy expenditure during locomotion, individuals expend energy as part of physiological processes such as thermoregulation. When experiencing colder temperatures individuals are expected to expend more energy, with field metabolic rate increasing with breeding latitude (Dunn *et al.*, 2018). Migratory individuals may encounter different conditions at-sea compared to when they are at their breeding grounds. For example, in a comparative study of Atlantic puffins *(Fratercula arctica)* in the North Atlantic, foraging effort and energy expenditure increased with wintering latitude (Fayet *et al.*, 2017). Maximum energy expenditure is limited by an energy ceiling (Elliott *et al.*, 2014b), meaning individuals must respond to unfavourable environmental conditions either through moderating their own body condition (Elliott *et al.*, 2014a), which may affect long-term survival, or through reduced investment in their young, affecting reproductive success (Horswill *et al.*, 2017). In this way energetic expenditure may link changes in environmental conditions to long-term demographic effects.

1.4 Study species and previous work

This thesis focusses solely on understanding the movement patterns, and their environmental drivers and demographic consequences, of northern fulmars *(Fulmarus glacialis*). I studied birds breeding on Eynhallow, a small island located close to the mainland of Orkney, Scotland. Fulmars are a medium-sized (600 – 1000 g) procellariiforme seabird, which breed throughout the North Atlantic and North Pacific Oceans during the boreal summer. Over the last 200 years their range has expanded southwards from their Arctic distribution, extending as far as Brittany, France (Kerbiriou *et al.*, 2012). The drivers of this expansion remain unresolved (Phillips *et al.*, 1999; Burg *et al.*, 2003) although breeding numbers at many colonies are now declining (Parsons *et al.*, 2008). This reduction may be due to declining survival (Cordes *et al.*, 2015), or low reproductive success and subsequent recruitment (Lewis *et al.*, 2009).

Fulmars belong to the Procellariidae family of seabirds and share many life history traits that are typical of species in this family. They are long-lived, recruit late, are socially monogamous, lay a single egg per season and have shared parental care (Dunnet, 1991). These traits contribute to their life-time fitness, meaning that they are expected to have relatively high investment in each breeding attempt, but not at the cost of their own survival. In contrast to many burrow- or cave-nesting shearwater species, fulmars are cliff- and ground-nesters. This means that they may be more vulnerable to localised disturbance (for example by predators) and extreme weather conditions. They are also unconstrained by predators to only attend the colony at night, and are able to arrive and depart throughout the 24-hour period (Mallory *et al.*, 2009a), although during the day is more common (Dott, 1975).

Eynhallow and its population of fulmars have been the focus of a long-running demographic study since the 1950s (Dunnet, 1991), when birds began to be individually marked using metal and coloured-plastic leg rings, with breeding attempts and success being recorded annually. This study has formed the basis of ongoing fulmar research, into factors affecting breeding success (Lewis *et al.*, 2009), egg size (Michel *et al.*, 2003), diet (Owen *et al.*, 2013) and life history traits (Orzack *et al.*, 2011). More recently the development and continued refinement of bird-borne tracking technology has given great insight into both their breeding and non-breeding movements (Edwards *et al.*, 2013, 2016; Quinn, 2014; Quinn *et al.*, 2016).

The fulmars nesting on Eynhallow undertake an annual dispersive migration, departing the breeding colony in August before moulting at-sea (Quinn, 2014; Grissot *et al.*, 2019). They remain largely at sea but begin to return to the breeding colony in January, engaging in long foraging trips and bouts of colony attendance which increase in regularity before breeding commences in May (MacDonald, 1980). Their at-sea distribution is wide, ranging between the North Sea, the Barents Sea and the Mid-Atlantic Ocean, with significant aggregations along the Norwegian Shelf (Quinn, 2014), and individuals spending time in both shelf and oceanic waters. In order to move over these large spatial scales, fulmars are expected to be energetically efficient in flight, and have been classified as using a mixture of flapping and gliding (Spear & Ainley, 1997). Wind is likely to be an important factor for efficient flight, with an early study finding that field metabolic rate reduced with increasing wind speed (Furness & Bryant, 1996). Consequently, fulmars are also expected to be sensitive to environmental variation, with changes in flight costs proposed as a driver of demographic rates.

Weather conditions in the North Atlantic Ocean are driven largely by the North Atlantic Oscillation (NAO), a broad-scale climatic index that influences wind, rainfall and temperatures (Jones *et al.*, 1997). Previous studies of Eynhallow fulmars have linked winter NAO with declines in female survival (Grosbois & Thompson, 2005) and have shown a negative relationship between actual and lagged winter NAO and reproductive success (Thompson & Ollason, 2001), although this relationship may be driven by unsuccessful birds (Lewis *et al.*, 2009). In contrast, extreme local weather events may be also responsible for reproductive failure (Mallory *et al.*, 2009b).

1.5 Thesis aims and scope

A recent review paper which followed a session at the Second World Seabird Conference highlighted the wealth of studies addressing individual variation and specialisation, across a broad range of seabird species (Phillips *et al.*, 2017). This thesis aims to contribute to three of the areas highlighted by this paper for further study: “the level of plasticity in response to the environment, the energetic and other physiological consequences, and effects (immediate and carry-over) on survival and reproduction”.

Using an existent dataset of geolocation data collected between 2007 and 2018, I first aim to describe inter-annual individual consistency in movement patterns throughout the annual cycle, identifying the extent to which consistency is maintained over multiple years, and whether this varies within the annual cycle. Second, I aim to uncover environmental drivers and demographic effects of movement decisions. I consider movement patterns within years, and whether movement decisions in one period influence movement in subsequent periods. Using year as a proxy for environmental conditions, I look for sex and year differences in these patterns, to understand whether birds respond flexibly to conditions between years. Finally, I aim to successfully track fulmars with high-resolution combined GPS and tri-axial accelerometers, in order to describe flight patterns at the scale of the flap-glide cycle, and the effect of wind speeds on flight energetics.

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Chapter 2 General Methods

2.1 Study colony description and background

This study was conducted on the island colony of Eynhallow, which is part of the Orkney archipelago located north of mainland Scotland (longitude = -3.1186, latitude = 59.1434, **Figure 2-1**). The northern fulmars (*Fulmarus glacialis*) that breed here have been the focus of a long-term demographic study, which was initiated in 1950 by George Dunnet (Dunnet, 1991) and has continued until present day, with some interruptions. The island is small (75 hectares) and has been uninhabited since 1851. It consists mainly of unimproved grassland and is regularly grazed by sheep.

Nesting sites consist of small cliffs, rocky areas, ruined stone buildings (**Figure 2-2 A**) and grassy banks, making many of them easily accessible. In addition, birds nest on the larger cliffs in the north-west of the island, but as they are not easily accessed they are not included in the current study. The majority of birds nest around the perimeter, with ~5 pairs nesting in the centre of the island. The population size peaked between 1980 and 2000 at ~200 breeding pairs (Thompson & Ollason, 2001). A large crash in 2004 reduced the number of breeding pairs by approximately half, which has fluctuated between 60 and 100 breeding pairs since then (Cordes *et al.*, 2015).

2.2 Data collection

Demographic data

As part of the ongoing demographic study, adult fulmars were caught at the nest, either by hand or using a landing net or noose on a pole, or in flight using a fleigh net. Birds were captured during the breeding period, either during incubation (late May or early June), chick-guard or chick-rearing (early or late July). Breeding adults were individually marked using a single metal leg-ring and a unique combination of up to three coloured plastic leg-rings (**Figure 2-2 B**). The coloured leg-rings were used to identify individuals visually without requiring them to be recaptured, allowing resightings data to be collected while minimising the disturbance to the birds. Resightings were then used to follow the breeding success of individual nests and birds over multiple years, and to calculate individual survival.

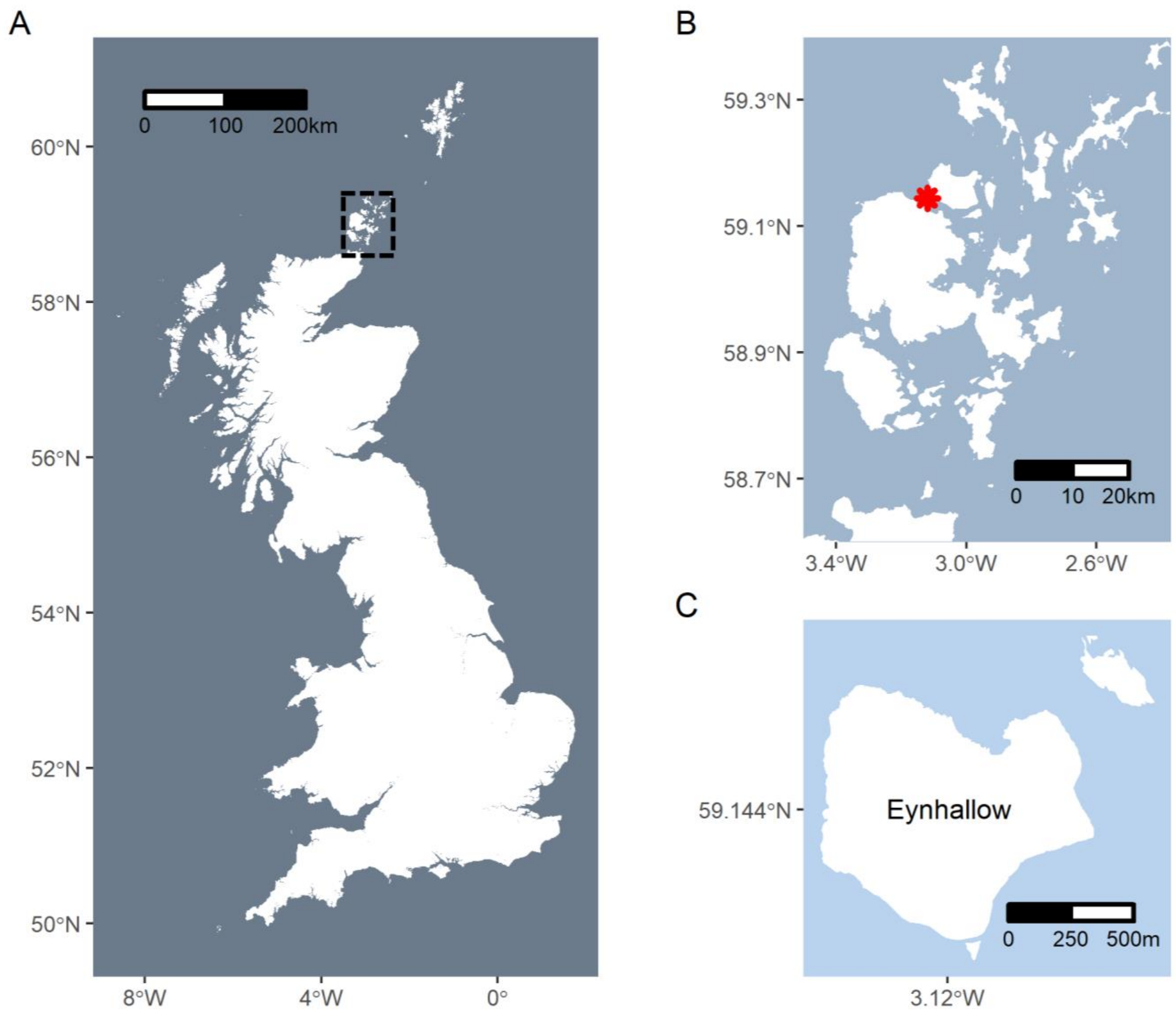

Figure 2-1: Maps showing the location of (C) the study colony Eynhallow within (A) Great Britain and (B) the Orkney Islands. Black dashed lines show the extent of (B) and a red star shows the position of Eynhallow between mainland Orkney and Rousay. Shapefiles from Ordnance Survey (Office for National Statistics, 2019).

Each year, two or three field trips were conducted to record individual breeding success at the colony. In late May, the whole island was surveyed for active nest sites, which were occupied and contained an egg, or had evidence of containing an egg such as a broken shell. Nest sites were compared to previous years and throughout the subsequent visits both partners were identified where possible. In early July, occupied nests were revisited and checked for a chick, indicating hatching success. In mid-August, nests were revisited a final time to record the presence of a large, feathered chick, at which point they are expected to fledge successfully (Lewis *et al.*, 2009). Occasionally, capture or handling of an adult resulted in the nest failing, either due to predation of or accidental damage to the egg, the details of which were also recorded.

Sex data was collected during initial ringing, or on further handling after the retrieval of data loggers. Sex was determined using three methods, in order of certainty: genetic determination from contour feathers (Quinn *et al.*, 2016), discriminant function using measurements of bill length and depth (Dunnet & Anderson, 1961), or inferred from the sex of the partner, if known.

Tracking: short-term combined accelerometry and GPS data

In 2019, short-term tracking was conducted in early July, with thirteen data loggers deployed on breeding adult fulmars either just before hatching or during the chick-guarding stage after hatching. Birds were caught on the nest as above and a data logger was attached dorsally to the feathers using marine fabric tape (tesa, 4651) and reinforced with super glue (Guilford *et al.*, 2008) (**Figure 2-2 D**). Care was taken during attachment to make sure that loggers were attached centrally and orientated in a consistent way, so that the X-, Y- and Z-axes corresponded to the surge, sway and heave movements of the bird, respectively. Data loggers were combined archival GPS and accelerometers (AxyTrek, TechnosmArt, weight = 14 g) which recorded a burst of 15 locations at 1 Hz every 10 minutes and recorded tri-axial acceleration at a rate of 100 Hz continuously. Additionally, an immersion logger (C65 or F100, Migrate Technology, weight = 1 g) was attached to a plastic leg ring using a single cable tie, which recorded the time of transitions between wet and dry bouts that lasted longer than 6 seconds, although the data collected were not analysed in this project. Birds were marked on the head and chest with plumage dye to distinguish them from their partner (**Figure 2-2 E)** and released out to sea. Handling lasted on average 14 minutes (maximum = 16 minutes). After release, an observer remained close to the nest until the adult returned, to ensure the safety of the egg or chick from predation.

Nests were checked daily following logger deployment to record which parent was present. Loggers were removed and downloaded after one or two stints at sea by the instrumented bird by carefully peeling the attachment tape off the feathers. After retrieval, birds were weighed using a 1 kg spring balance scale (+/- 5 g) and photographed with one wing spread open over a 5 cm gridded board (**Figure 2-2 F**). These measurements were subsequently used to calculate wing-loading. Wing area was estimated using ImageJ (Schneider *et al.*, 2012) by using the 5 cm grid to set the scale and then drawing around the wing starting from the mid-line of the bird, using the polygon area-selection tool. Wing loading was calculated as the body mass divided by twice the measured wing area (to account for both wings).

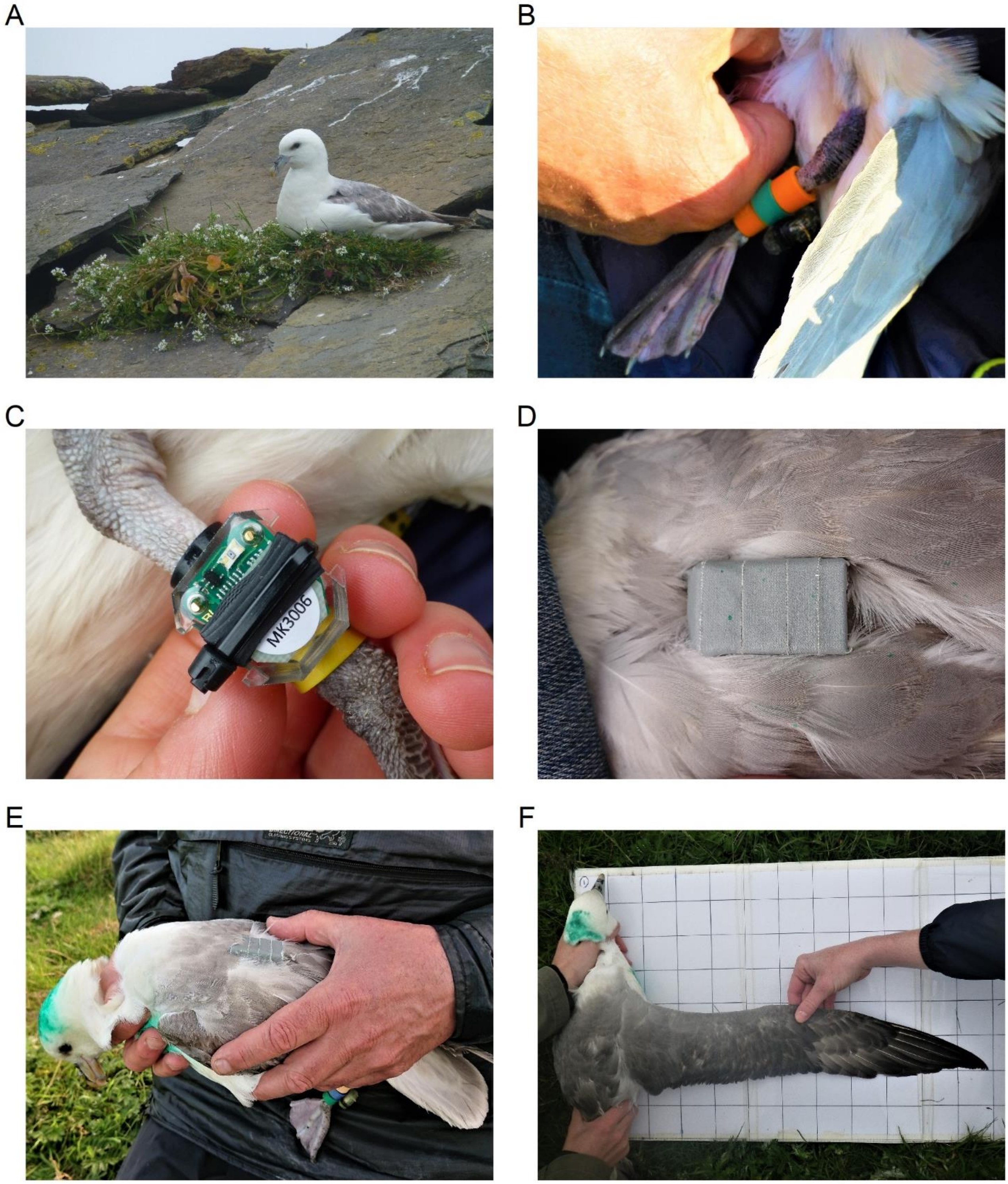

Figure 2-2: *(A) A typical nesting site on Eynhallow, among vegetation on a derelict building. (B) Birds are individually marked with unique combinations of up to three colour rings. (C) A long-term geolocator deployment (MK3006, BioTrack), attached to the middle colour ring through drilled holes with a cable tie. (D) A short-term combined GPS and accelerometer deployment (AxyTrek, TechnosmArt), attached with marine fabric tape to the dorsal feathers. (E) A study bird following recapture, with AxyTrek still attached, head and chest marking and long-term geolocator attached to plastic colour ring. (F) A study bird following logger retrieval, photographed with an open wing above a 5 cm grid to estimate wing area.*

Tracking: long-term geolocation data

Miniaturised archival light loggers ("geolocators") were deployed at the colony from 2006, during the May or July field trips while adult fulmars were attending their nest. Geolocators were attached to one of the plastic leg-rings using a single cable tie, threaded through holes drilled in the outside layer of the colour ring and padded with self-amalgamating tape (**Figure 2-2 C**). They were carried for a full year before retrieval during the subsequent breeding season, when the data were downloaded and the geolocator was replaced. Geolocators that were not recovered after the first year were removed when the birds were next caught. Tracking was conducted as part of previous doctoral projects (Quinn, 2014; Edwards, 2015) and subsequently in collaboration with SEATRACK, a Norwegian multi-species, multi-colony tracking project (www.seapop.no/en/seatrack). In total, 367 loggers were deployed on Eynhallow between 2006 and 2017, although the project is ongoing. Geolocators with attachments weighed 3.6 g or less, manufacturers and models are shown in **Table 2-1**.

Geolocators record light and immersion data, from which both location and behaviour of the bird can be inferred. Maximum light levels in each interval of time are recorded, as well as the number of times that there is conductivity between the two pins in each interval, and temperature when the logger remains immersed for a prolonged period. Differences in logging schedules are detailed in **Table 2-1**. Data used here were collected between 2007 and 2018, with no data collected in the season 2013-2014.

Ethics statement

All work was conducted with ethical approval from Bangor University and the University of Aberdeen. Handling and ringing of fulmars were conducted under permit, and tracking using attachment of data loggers was conducted under special methods license, which were both issued by the British Trust for Ornithology. Feathers were collected as part of other projects, with approval from the Home Office. Fieldwork on Eynhallow was conducted with permission from the Orkney Islands Council.

Table 2-1: Models and logging schedules for geolocators supplied by the British Antarctic Survey (BAS), BioTrack and Migrate Technology. Constant logging schedule means that the time of each transition between wet and dry is recorded. All other schedules result in binned data, corresponding to the number of "wet" events within that interval. Except for C250 loggers, temperature was recorded only when the logger remained wet for at least 20 minutes.

			Immersion			
Manufacturer	Model	Light	Frequency	Interval	Max count	Temperature
BAS	MK 4	10 min	3 sec	Constant	NA	20 min (wet)
BAS	MK 13	10 min	3 sec	10 min	200	NA
BAS	MK 14	10 min	3 sec	10 min	200	NA
BAS	MK 15	10 min	3 sec	10 min	200	20 min (wet)
BAS	MK 19	10 min	3 sec	Constant	NA	20 min (wet)
BioTrack	MK 3006	10 min	3 sec	10 min	200	20 min (wet)
Migrate Technology	C250 mode 6	5 min	30 sec	10 min	20	8 hr 20 min (wet)
Migrate Technology	C250 mode 7	5 min	6 sec	5 min	50	8 hr 20 min (wet)

2.3 General data processing

Deriving locations from light data

The manual processing of light data to infer locations was conducted by SEATRACK. This initial processing was conducted in the program TransEdit, for BAS/BioTrack loggers, or IntiProc, for Migrate Technology loggers. Data were visualised using the software, which automatically places sunrise and sunset according to when recorded light levels cross a predetermined threshold (“transitions”, 9 for BAS/BioTrack, 11 for Migrate Technology), to check each transition for quality. Transitions that occurred in the middle of the day, transitions that had a jump in time over one hour from the previous day and transitions where there was interference resulting in a noisy light curve were all removed. Transitions which were incorrectly placed but the correct position could be identified with high confidence were adjusted manually. Raw location was then calculated using the same programs by comparing the day length and time at midday recorded by the loggers, with calculated day length and time at midday derived from astronomical equations (Hill & Braun, 2001). Raw latitude and longitude, corresponding to day length and time at midday respectively, were supplied to me by SEATRACK, as well as processing information such as sunrise and sunset times.

Light-level geolocation is a valuable tracking method as the low power requirements result in small loggers which can be carried for prolonged periods of time, with minimal impact to the tracked animal (Gillies *et al.*, 2020). However, there is a high level of error associated with each calculated location (Lisovski *et al.*, 2012). This error results from multiple processes and so is difficult to quantify, as it varies throughout the year and with location, as well as according to weather conditions and individual behaviour. Accuracy is particularly low close to the equinoxes and at equatorial locations, as day length becomes homogenous. Geolocation is also difficult in the polar regions, especially close to the solstices, when there is 24-hour daylight and darkness. Even when a sunrise and sunset occur, it is difficult to accurately identify the exact timing of transitions during prolonged twilight periods. Additionally, the logger can be subject to localised shading events. These can be caused by bird behaviour, such as leg-tucking (Burke *et al.*, 2015; Fayet *et al.*, 2016) or colony visitation; or caused externally, by habitats such as vegetation (Lisovski *et al.*, 2012), or weather such as clouding, reducing the light levels recorded by the logger (Lisovski *et al.*, 2018). When these events occur during the twilight periods light-level geolocation is not possible.

All subsequent data processing and analyses were conducted in the statistical programming environment R 4.2.0 (R Core Team, 2015). I used the package *probGLS* (Merkel *et al.*, 2016) to calculate improved location estimates from the sunrise and sunset times provided by SEATRACK. The package uses an algorithm to compute likely locations using a range of sun elevation angles to create a cloud of particles, which are then weighted according to behaviour (speed compared to immersion) and environmental factors (logger temperature compared to remotely sensed sea-surface temperature) resulting in probable movement paths. The output path is then the median of all probable movement paths. The values for all input parameters are shown in **Table 2-2**, with wet and dry speeds estimated from birds that were tracked using GPS loggers as part of another project (Wakefield *et al.*, 2021).

Table 2-2: Input parameters to calculate location from light, immersion and temperature data using probGLS algorithm (Merkel *et al.*, 2016; Wakefield *et al.*, 2021).

Parameter description	Value
particle.number	2000
iteration.number	100
sunrise.sd & sunset.sd	2.49/0.94/0
range.solar	-7.0, -1.0
boundary.box	-87, 80, 20, 85
days.around.spring.equinox	10
days.around.fall.equinox	10
speed.wet (mean, sd, max)	0.48, 0.36, 2.50
speed.dry (mean, sd, max)	7.91, 3.05, 23.70
sst.sd	0.5
max.sst.diff	6
east.west.comp	TRUE

Daily individual summaries

For each day I calculated summary metrics from the processed locations and the raw light and immersion data, with each 24-hour period starting at midnight. Geolocation by light levels results in two locations per day, one associated with midday and one with midnight. Using the function “midPoint” from the package *geosphere* (Hijmans, 2021) I calculated the point halfway between the two locations as a mean location, to the reduce the influence of single erroneous transitions. I used these mean daily locations to calculate the distance of each point from Eynhallow and the distance travelled per day between subsequent locations using the function “distVincentyEllipsoid”.

Both light and immersion data can be used to infer individual behaviour. In fulmars, prolonged periods with low light levels reaching the logger during the day are likely to be caused by colony visitation, as birds often obstruct the logger when they are at the nest. To compare mean light levels during the day I first replaced missing times for sunrise and sunset by linear interpolation using the function “na_interpolation” from the package *imputeTS* (Moritz & Bartz-Beielstein, 2017). As different light scales were used depending on logger manufacturer, I created an adjusted scale where values of 0-64 for BAS and BioTrack loggers corresponded to 1-100 for Migrate Technology (James Fox 2020, personal communication, 16th December) and data collected by Migrate Technology loggers were clipped so that 100 was the maximum possible value. I then calculated the mean adjusted light, between the times of sunrise and sunset. I also calculated the total adjusted light for the whole 24-hour day, divided by the maximum possible light per day (if it was light all the time). Both these variables were subsequently used to identify probable visits to the colony, which was signalled by a drop in light levels. Mean adjusted light accounted for changes in day length, but was vulnerable to artefacts due to interpolation, whereas total adjusted light was robust to these artefacts, but varied throughout the year.

Geolocators also record whether there is conductivity between the two pins on the logger, indicating that it is immersed in saltwater. In seabirds, intervals where only wet events are recorded mean the bird is likely to be sat on the sea-surface, whereas intervals without wet events recorded are expected to be associated either with flight or time spent on land. I calculated multiple summary metrics from these data as I used different metrics depending on the behaviour of interest. Total wet count and the minimum number of transitions between wet and dry were standardised as a proportion of the maximum possible value, to attempt to account for differences in logging schedules and different sensitivities between logger models. Time dry and time wet were calculated as the number of minutes where the interval contained no wet counts and only wet counts respectively. Longest dry was calculated as the longest time in minutes that the logger was continuously dry. It was not possible to standardise between logging schedules completely, but summary metrics were selected to reduce the potential bias this could cause. Daily summaries were used to identify the signals for different behaviours within individual tracks, rather than compare between birds, to limit the impact of this.

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Chapter 3 Consistent non-breeding movement patterns

3.1 Abstract

Animal movements, from individual foraging decisions to species-wide distributions, are driven by the interactions between an individual's changing internal state and spatio-temporal variation in both the biotic and abiotic environment. Species' distributions have historically been determined through survey methods that are often unable to identify individuals. Consequently, species ranges may fail to capture key aspects of the distribution such as restricted use of habitats or areas by individuals, or the degree of connectivity between different areas. Technological developments have meant that individual animals can be followed remotely over long periods of time, and repeated tracking over multiple years has resulted in a better understanding of how individual movements contribute to population and species-level distributions.

In this study, successive year-round deployments (n = 220) of miniature archival light loggers (geolocators) were used to analyse how consistency in space-use at the individual and population level shape the at-sea distribution of a generalist seabird with variable non-breeding movements, the Northern fulmar, (*Fulmarus glacialis*). Specifically, I analysed the amount of time birds spent in four different regions of the North Atlantic, corresponding to the North Atlantic Ocean, the Norwegian Sea, the Barents Sea and the North Sea, and compared this between four distinct periods of the annual cycle. At the individual level, I found a high degree of consistency throughout the annual cycle, which in some periods was driven by individuals repeatedly using a subsection of the population's range. However, in other periods, consistency was apparent at the population-level, with the whole population residing in a relatively restricted range. I discuss the mechanistic processes that might give rise to individual and population levels of consistency and relate this to how the structuring of population distributions could impact on important conservation decisions, such as the designation of marine protected areas.

3.2 Introduction

Animal movement patterns emerge as animals are driven by their internal state to seek resources that exist heterogeneously, but often predictably, in space and time (Nathan *et al.*, 2008). Factors impacting animal movement to generate these patterns are complex and varied, but include physical and navigational constraint, trade-offs in allocation of time and energy and external interactions such as inter- and intra-specific competition. Distributions are often considered at the population level, but may consist of individuals that vary their behaviours in consistent and predictable ways, driving both demographic and ecological processes (Bolnick *et al.*, 2003; Dall *et al.*, 2012). Understanding inter- and intra-individual variation is key when trying to assess the abilities of populations or species to respond to direct or indirect anthropogenic stressors such as prey depletion, bycatch and climate change. For example, tracking may highlight the specific dependence of a population on a single resource, such as Manx shearwaters (*Puffinus puffinus*) on the Irish seafront (Dean *et al.*, 2015), or sex-specific exposure to bycatch, as recorded in northern (*Macronectes halli*) and southern giant petrels (*Macronectes giganteus*) (González-Solís *et al.*, 2008; Gianuca *et al.*, 2019).

Quantifying variation in animal movement and understanding it in the context of individuals, populations and species, is therefore going to be increasingly crucial to understanding the potential effects of anthropogenic stressors on individual fitness and the subsequent stability of populations, leading ultimately to effective conservation strategies.

Individual specialisation, where individual variance in a trait or behaviour is less than the population variance, indicates that individuals are utilising a subset of the population niche (Bolnick *et al.*, 2003), and has been well-characterised in multiple seabird species (12% of the extant species reviewed by Ceia and Ramos 2015). However, gaps remain in linking short-term and long-term strategies and how they translate into overall fitness. Over short timescales many seabirds exhibit foraging site fidelity, a form of specialisation where individuals return to the same foraging area over multiple foraging trips (Wakefield *et al.*, 2015). Site fidelity may result from local peaks in resource availability, particularly when it occurs within a single season (Carroll *et al.*, 2018). Where predictable resources occur as a result of oceanographic features (Weimerskirch, 2007), this site fidelity may persist and lead to longer-term consistency. The potential benefits of this specialisation are in reduced search times, increased foraging efficiency and reduced competition. However, specialisation will not always be the optimal strategy. While specialist strategies are expected to be favoured when there is high intra-specific competition, generalist or flexible strategies will be favoured when intra-specific competition is low or when inter-specific competition is high (Araújo *et al.*, 2011). Additionally, if variable environmental conditions make foraging patches less predictable, generalist individuals may be more able to respond, making them more successful (Abrahms *et al.*, 2018).

Over longer timescales, individual consistency in migratory timings (Kürten *et al.*, 2022), routes (Van Bemmelen *et al.*, 2017) and wintering areas (Ramírez *et al.*, 2016; Kürten *et al.*, 2022) have been shown to persist over multiple non-breeding seasons. This consistency may result from responding to seasonal and environmental cues in the same way over multiple years, or from using memory of past conditions to actively follow previously successful strategies. How young birds develop and maintain migratory routes remains an area of active research (Yoda *et al.*, 2017; Wynn *et al.*, 2021), but in long-lived species there is a lag of several years between attaining physical maturity and starting to breed. Evidence of exploratory behaviour during this time (Campioni *et al.*, 2019), which becomes more refined with age (the exploration-refinement hypothesis (Guilford *et al.*, 2011)), suggests that the role of learning may be critical. In adult birds, past experience will reflect a range of environmental conditions associated with different locations, which may influence their current decision-making. The consistency of environmental conditions during early life might then predict the extent to which a movement strategy becomes dominant and an individual's capacity for flexibility later in life.

Northern fulmars (*Fulmarus glacialis*) are a particularly suitable species in which to study individual consistency because as a wide-ranging, generalist species they make use of a variety of different areas throughout their annual cycle. They migrate soon after completing breeding, spending on average three months in a single area while conducting moult (Quinn *et al.*, 2016; Grissot *et al.*, 2019). They then return to the breeding grounds in January and attend the breeding colony with increasing regularity throughout the rest of the winter period (MacDonald, 1980), leading up to a pre-laying exodus that occurs directly before the start of incubation (Hunter, 1999). A previous study at the breeding colony of Eynhallow (Orkney Islands, UK) found that mean locations for the whole non-breeding period were more similar within than between individuals (Quinn, 2014). However, examining individual consistency at a behaviourally defined timescale would be beneficial, as drivers of movement are likely to be different throughout the annual cycle. Individuals from this colony make use of areas that have a wide spatial extent, (North Sea = less than 500 km from the breeding colony, compared to Mid-Atlantic Ocean and Barents Sea = more than 2000 km (Quinn, 2014)), which combined with their transitory behaviour in late winter means that individuals cover vastly different distances throughout the year. Fulmars are long-lived (~ 34 years (Dunnet, 1991)), and so if these spatial differences persist over many years, they may result in differences in energetic expenditure, reproductive output and survival, which would suggest that individuals follow different life-history strategies (Jenouvrier *et al.*, 2018).

In this study I use salt-water immersion and light data that was collected over ten years using geolocators. This data is used to describe the inter-annual broadscale movement patterns of fulmars, based on four discrete time periods within the annual cycle, which are identified in individual yearly tracks using an algorithm that I developed to recognise patterns in daily immersion values. This allowed the comparison of spatial patterns between individuals, across behaviourally equivalent time periods. I compare space-use between years, in each time period, to quantify inter-annual seasonal consistency and explore this at both the individual and the population level.

3.3 Methods

Data collection and preparation

Breeding adult fulmars from Eynhallow, a small uninhabited island located north of mainland Scotland in the Orkney archipelago, were tracked throughout their annual cycle using geolocators. Data were collected between 2007 and 2018 and were processed to obtain daily individual summaries. These daily summaries were derived from light and salt-water immersion data and consisted of an estimate of location in latitude and longitude, distance in kilometres from Eynhallow, time in minutes that the logger was continuously dry and total daily light levels. Details of the study site, tracking methods and initial data processing to produce daily summaries are described in Chapter 2: General Methods.

Segmentation of the annual cycle

All data processing and analyses were conducted in the statistical programming environment R 3.6.1 (R Core Team, 2015). Several general packages were also used: for spatial analyses – *sf* (Pebesma, 2018) and *raster* (Hijmans, 2019); for plotting – *ggplot2* (Wickham, 2016), *ggspatial* (Dunnington, 2018), *patchwork* (Pedersen, 2019), *rnaturalearth* (South, 2017) and *rnaturalearthhires* (South, 2020); and for data manipulation – *zoo* (Zeileis & Grothendieck, 2005) and *dplyr* (Wickham *et al.*, 2019). Tracks were assigned to a "bird" year, to ensure that the non-breeding season was considered in an uninterrupted time period. Bird year commenced on 1st July and continued until 31st July of the following year. Bird years are subsequently referred to as year, corresponding to the year that the track ends in (for example, bird year 2008-2009 is referred to as 2009). The chick-rearing period of the breeding season is not considered in this study, as regular attendance to the breeding colony causes shading of the geolocator which results in too many unreliable locations. Locations in July were therefore included to assist with track segmentation, but not included in further analysis.

To explore variation in consistency throughout the annual cycle the bird year was split into four separate periods. These were informed by the general behaviour of the birds but were defined for each track to account for differences in individual phenology. The amount of time that the logger was dry each day was used to infer the behaviour of the bird. The over-wintering period was split into "early" and "late", where early winter was associated with reduced time dry, commencing when birds left the colony after the completion of breeding and extending until they had completed moult and started to re-attend the breeding colony.

While the term “early winter” is used here to describe this period, in most birds the actual season is autumn, or late summer in failed breeders. Late winter was associated with more time spent in flight, both at sea and at the breeding colony, resulting in large variation in the amount of time that immersion loggers were dry each day. The third period was associated with pre-laying exodus, a single long (~3 weeks) foraging trip that occurs just before egg-laying, as recorded in many Procellariiform species. The final period corresponded to foraging trips undertaken during incubation, where fulmars alternate with their partners between stints of egg incubation and foraging.

Incomplete tracks were excluded, which lasted 150 days or less, or had days missing within the first 100 days. If there were gaps at beginning of the track, due to the logger being replaced during the chick-rearing period, the bird year started after the gap. I used the function “lavielle” from the package *adehabitatLT* (Calenge, 2006) to identify changes in the time dry per day that were associated with changes in behaviour in the different periods. The method of Lavielle identifies the best segmentation of a time series, depending on a given number of segments, between which the mean or variance varies (Lavielle, 1999), although mean was used here. The number of segments were specified, rather than identifying the optimum number of breaks based on the decrease in the contrast function, as I had *a priori* expectations of pre-defined periods.

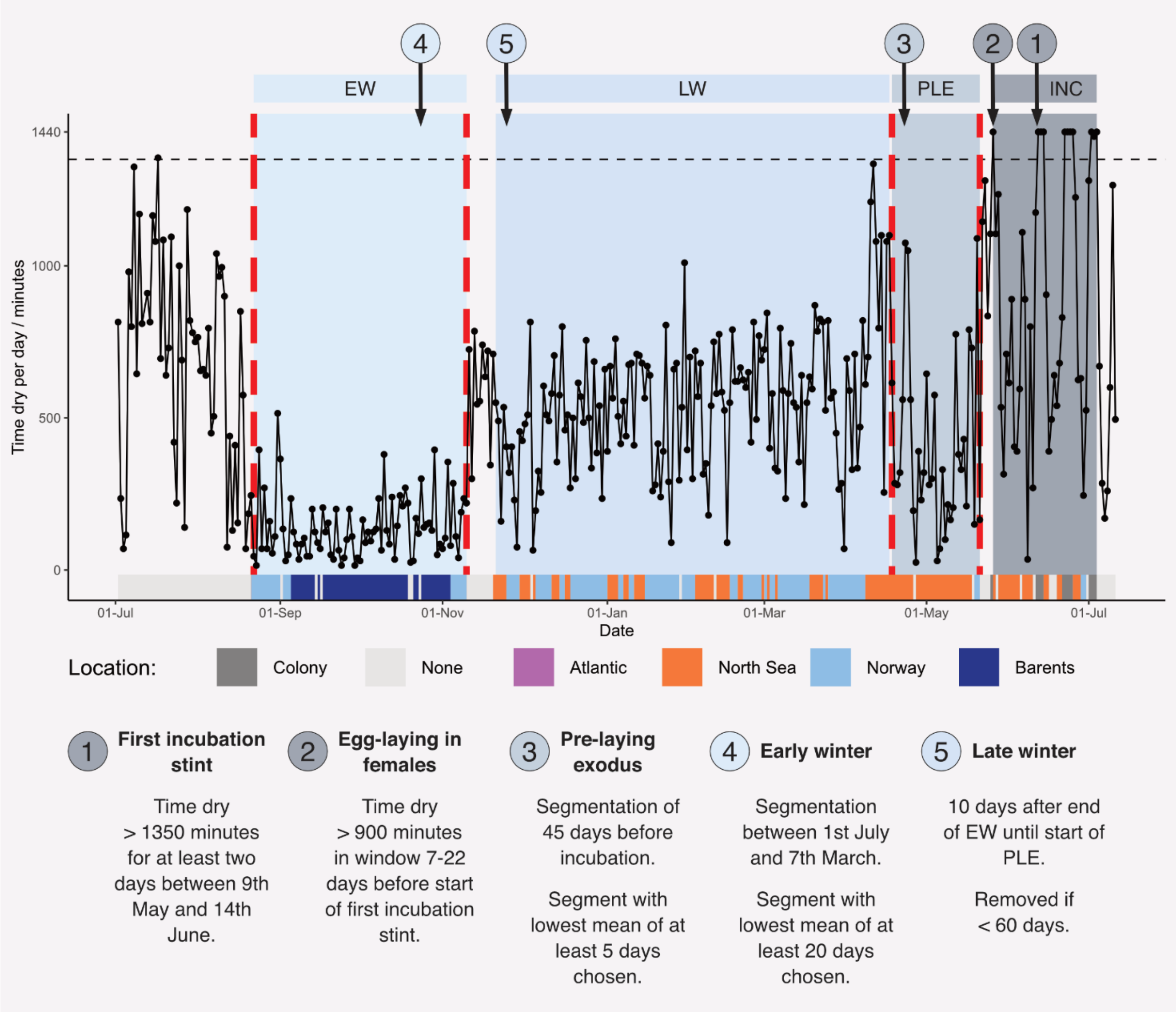
Segmentation was conducted individually for each track, an example of which is shown in **Figure 3-1**. Within the script, incubation (INC) was identified first as it is associated with the strongest signal in the data. The period between 9th May and 14th June was searched for the start of incubation. Days where the logger was dry for at least 1350 minutes (22.5 hours) were assumed to be spent at the colony. In males the first day where the individual spent at least two consecutive days at the colony was identified. Females often return to the colony only to lay their egg, departing straight away for a relatively long foraging trip while their partner takes the first incubation stint (Mallory, 2009). To account for this, in females the first clear incubation stint was identified as for males, then the most recent peak in time dry was assigned as egg-laying. This peak was conservatively only included if time dry was higher than 900 minutes (15 hours) and it occurred 7 to 22 days before the first clear incubation stint, reflecting expected initial foraging trip duration. If consistent incubation stints were not maintained and the time dry per day became erratic with no clear patterns of prolonged dry periods it was assumed that the nest had failed. Positions after this were not included in the incubation period. The last day of incubation was identified as the latest day where the time dry was at least 1410 minutes (23.5 days), or the stint at the colony was at least 3 days long.

Pre-laying exodus (PLE) was then identified in the 45 days preceding the start of incubation. The method of Lavielle was used to break this period into 3 segments of at least 4 days long, according to the mean time dry, as clear changes were expected in behaviour associated with before, during and after the pre-laying exodus. The mean time dry and length of each segment was calculated, and the segment with the lowest mean time dry that ended within 20 days of incubation commencing was selected. Where the mean time dry was at least 900 minutes pre-laying exodus was not assigned, as high values of time dry are unlikely to be associated with foraging trips away from the colony.

Early winter (EW) was identified between 1st July and 7th March in the following year, or the date of geolocator failure if this was before 7th March. The method of Lavielle was used to identify 4 segments according to daily time dry, with a minimum segment length of 10 days. I imposed 4 segments on each track, as four clear changes in behaviour were expected: chick-rearing and wintering before, during and after moult. As before, the mean time dry and length of each segment was calculated and the segment with the lowest mean that was at least 20 days long was selected as the early winter period.

Late winter (LW) was then identified as commencing the day after early winter ended and running until the start of the pre-laying exodus. If no incubation or pre-laying exodus could be identified, late winter was ended the day before the mean start day of pre-laying exodus for all birds. As I expected late winter to be the longest period, I removed periods that lasted less than 60 days as these were unlikely to have been identified correctly (n = 1).

To check whether periods had been well-identified, distance from Eynhallow was then plotted against day of the year, with each of the periods identified. Where individuals performed large movements, I checked whether these occurred at the same time as changes in period, and that late winter was associated with more time spent closer to the breeding colony. The late winter period often began with some days of residency, before a large commuting movement back closer to the colony. This is likely to be a limitation of the segmentation method, so the first 10 days were removed from further analysis for the late winter period.



① **First incubation stint**

Time dry > 1350 minutes for at least two days between 9th May and 14th June.

② **Egg-laying in females**

Time dry > 900 minutes in window 7-22 days before start of first incubation stint.

③ **Pre-laying exodus**

Segmentation of 45 days before incubation.

Segment with lowest mean of at least 5 days chosen.

④ **Early winter**

Segmentation between 1st July and 7th March.

Segment with lowest mean of at least 20 days chosen.

⑤ **Late winter**

10 days after end of EW until start of PLE.

Removed if < 60 days.

Figure 3-1: Example of track segmentation to identify four key periods in the annual cycle, highlighting the main parameters used for this process. Daily raw values of minutes dry per day are shown for a single bird over one year. Horizontal black dashed line shows the threshold above which the bird is assumed to be at the breeding colony. Vertical red dashed lines show the start and finish of early winter and pre-laying exodus, which were identified using the method of Lavielle (Lavielle, 1999)*. Shaded boxes show the extent of each of the periods. Coloured ribbon along the bottom corresponds to the spatial area that each day was assigned to, as shown in Figure 3-2. Days that were outside of the four periods were not assigned to an area. Abbreviations: EW = early winter, LW = late winter, PLE = pre-laying exodus, INC = incubation.*

Assigning spatial area

In order to compare movement patterns in each period the population range was split into four areas, based on the observed clustering of locations for all birds. These corresponded broadly with the North Atlantic Ocean, the Norwegian Sea, the Barents Sea and the North Sea (referred to here as Atlantic/ATL, Norway/NOR, Barents/BAR and North Sea/NSE). To set boundaries between these areas I extracted the 700m depth contour from The General Bathymetric Chart of the Oceans (GEBCO Group 2020) and used this to separate the four main areas, as it closely mapped onto the broad areas identified in previous studies (Quinn, 2014) . This resulted in two areas associated with mainly deep oceanic areas (Atlantic and Norway) and two areas corresponding to shallow shelf areas (Barents and North Sea), with the North Sea area extending to the edge of the continental shelf around the UK and including locations around the colony (**Figure 3-2**).

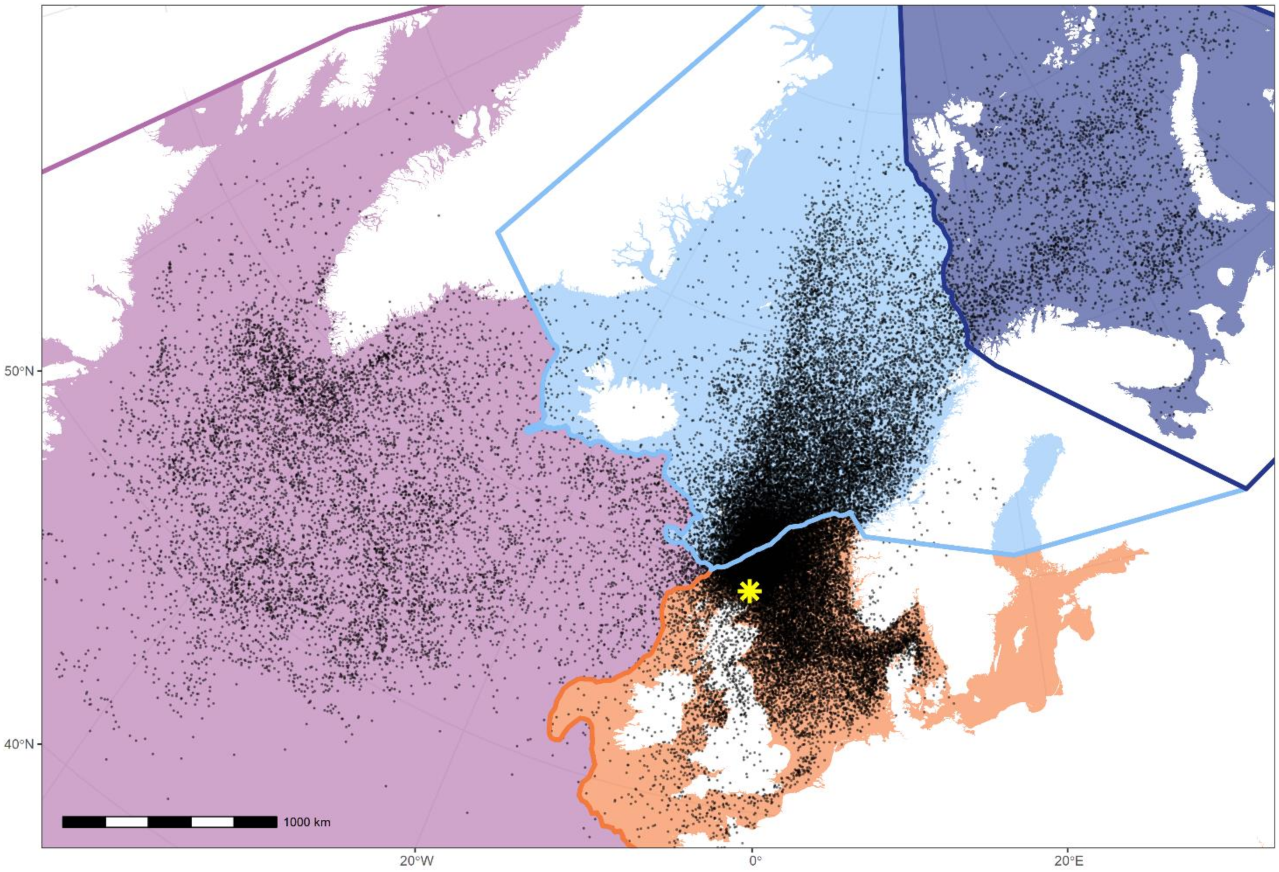


Figure 3-2: Map showing the daily locations for all individuals and all years with the boundaries between different areas. Pink = North Atlantic, orange = North Sea, light blue = Norwegian Sea, dark blue = Barents Sea. All locations of birds shown in black. Yellow star marks colony location. Lambert azimuthal equal-area projection.

Points that had been identified as at the breeding colony were removed. A spatial overlay was then performed to assign each daily location to the area that it fell within. One of the limitations of tracking using geolocators is that when day length becomes too short in winter, or too long in summer, it is not possible to accurately identify the times of sunrise and sunset, and so location cannot easily be calculated (Lisovski, 2018; Lisovski *et al.*, 2020). In fulmars this occurs during large northwards movements, with some individuals experiencing both 24-hour darkness and daylight. This meant that some tracks had large gaps with no locations assigned. I examined total daily light levels using thresholds to identify days where lack of location was likely to be due to northwards movements (EW ≤ 0.05 or ≥ 0.95, LW ≤ 0.05, PLE ≥ 0.85, INC ≥ 0.95). High total light levels (as opposed to low) in early winter were due to failed birds departing the colony early. I retrospectively assigned these days to Barents in early winter or Norway in all other periods, when the progression of day length meant that Barents and Norway could not be distinguished. In late winter, pre-laying exodus and incubation I also grouped Barents and Norway in the same way, even when location could be resolved, meaning that the Barents area was only used in early winter. Periods were also removed from the analysis if at least 60% of the days could not be assigned to an area, or if they consisted of 4 or fewer days that could be assigned to an area.

Quantifying consistency

To quantify how consistent individuals were in the areas that they used, I calculated the proportion of time they spent in each area for each period and compared this distribution between pairs of years. I used an adjusted version of Bhattacharyya's Affinity (BA), which quantifies the similarity of distributions (Fieberg & Kochanny, 2005), in this case similarity between the proportion of days spent in each of the four areas. This resulted in a number between 0 and 1, where 0 represented no overlap in distribution at all, and 1 represented an identical distribution (**Figure 3-3**). BA was used in this way, rather than how it is used more conventionally to compare utilisation distributions (Wakefield *et al.*, 2015), because this allowed the different spatial scales of movement between birds and the lack of accuracy of individual locations associated with light-level geolocation to be accounted for. For every extra year that each individual was tracked there was an increasing number of pairwise values for BA. To reduce the influence of individual birds that had a high number of repeat tracks, the individual median BA for each bird was calculated.

High values of Bhattacharyya's Affinity could result from either individual-level consistency or population-level consistency. To understand whether individuals were consistent when compared to other birds within the population, a null expectation was generated by re-sampling the data. For each period BA was calculated for every possible bird and year combination. I then randomly selected *n* values of BA with replacement, where *n* was the number of within-individual comparisons. This re-sampling was performed in a semi-structured way so that in years where at least 10 individuals were tracked the pool of possible values was restricted to pairs of birds that were tracked in the same combination of years. This allowed year effects to be accounted for except in years when sample size was small. Medians were then calculated to reflect the structure of the individual medians in the original data. I repeated this process 10 000 times and calculated the median BA for each repeat. I used a one-tailed test to estimate the *p*-value, as the number of repeats where the median was equal or higher than the observed within-individual median, divided by the total number of repeats (10 000). One was added to both the numerator and the denominator to reflect the inclusion of the observed data in the sample distribution (Ruxton & Neuhäuser, 2013). This analysis was conducted separately for males and females to account for sex differences in spatial distributions (Quinn, 2014).

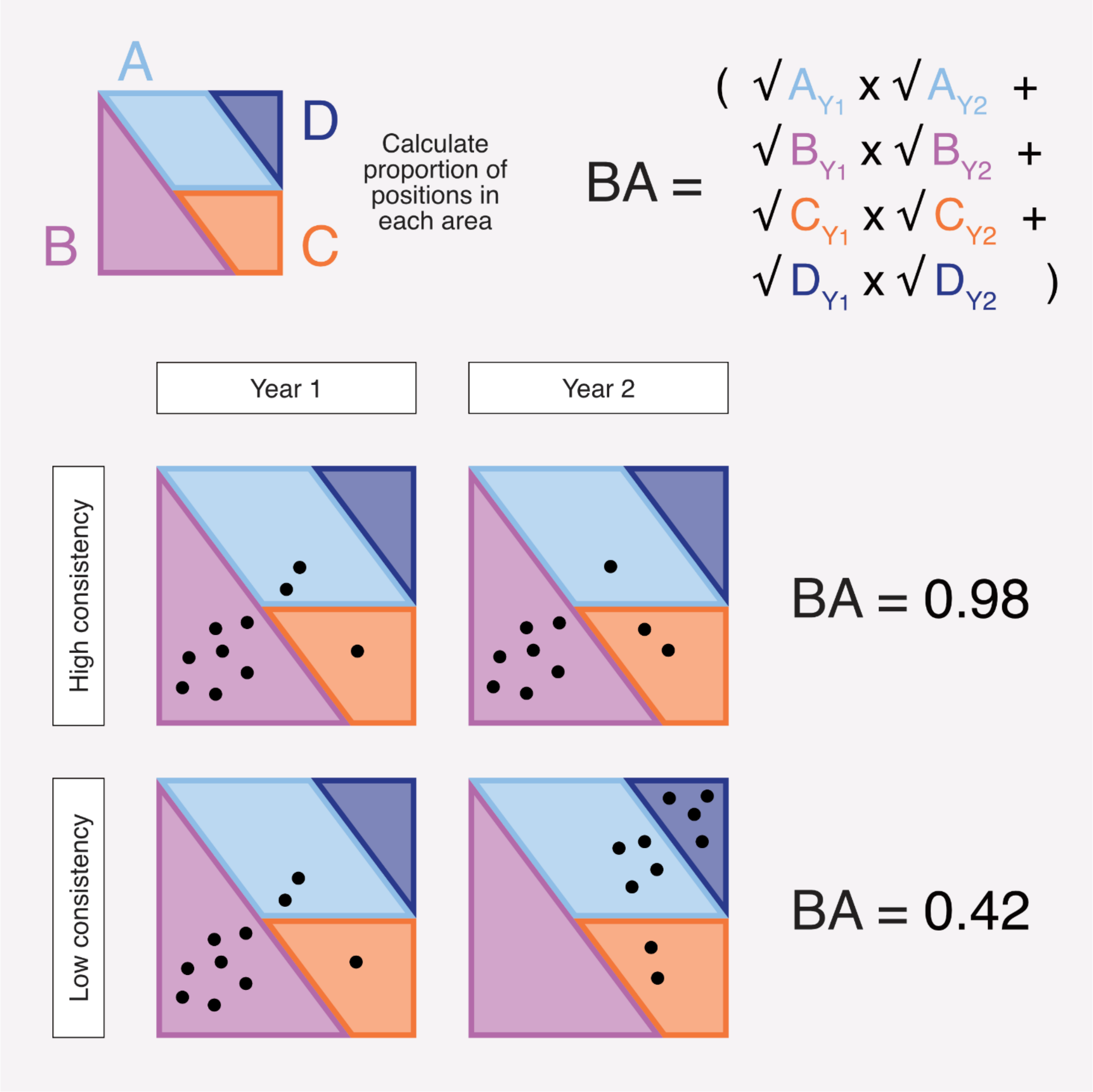


Figure 3-3: Calculation of Bhattacharyya's Affinity (BA) to quantify similarity in space-use between years, based on the proportion of time spent in each of the four areas. Stylised examples for high and low consistency shown. The proportion of time spent in each area is compared between two years, resulting in a value of one for identical distributions and zero for distributions with no overlap.

3.4 Results

220 over-winter tracks were recorded from 113 individuals (50 females and 63 males) that had sufficient data to include in this analysis. 60 individuals were tracked more than once, resulting in 167 repeat tracks (2 years = 36, 3 years = 11, 4 years = 7, 5 years = 2, 6 years = 4). Sample sizes varied between years, as different numbers of loggers were deployed between years, some loggers were lost or failed to record data, and some loggers were not retrieved. In early winter, sample sizes were: 2008 = 9, 2009 = 15, 2010 = 22, 2011 = 37, 2012 = 13, 2013 = 3, 2015 = 31, 2016 = 29, 2017 = 27, 2018 = 34. There were no tracks that ended in 2014. Sample sizes were similar in early and late winter but were reduced for pre-laying exodus and incubation as loggers failed early, were removed at the beginning of incubation, the individual did not breed, or pre-laying exodus could not be reliably identified.

I compared the proportion of days that all birds spent in each of the four areas, between periods and between sexes (**Figure 3-4**). In late winter and incubation males and females were similar in their distributions, with the North Sea being the main area used during incubation and Norway being used slightly more than the North Sea in late winter. In early winter the main area used by females was the Atlantic (48% days), followed by Barents (22% days). In males the main area used in early winter was the North Sea (56% days) followed by the Atlantic, Norway and Barents (14%, 13% and 10% days respectively). In pre-laying exodus males were more likely to use the North Sea area (63% days), whereas females were split between North Sea and Norway (36% and 42% days). Across all the periods, females spent slightly more time than males in the Atlantic area. The proportion of days with no location or at the colony was similar in males and females in all periods except incubation, when males spent a higher proportion of days at the colony than females.

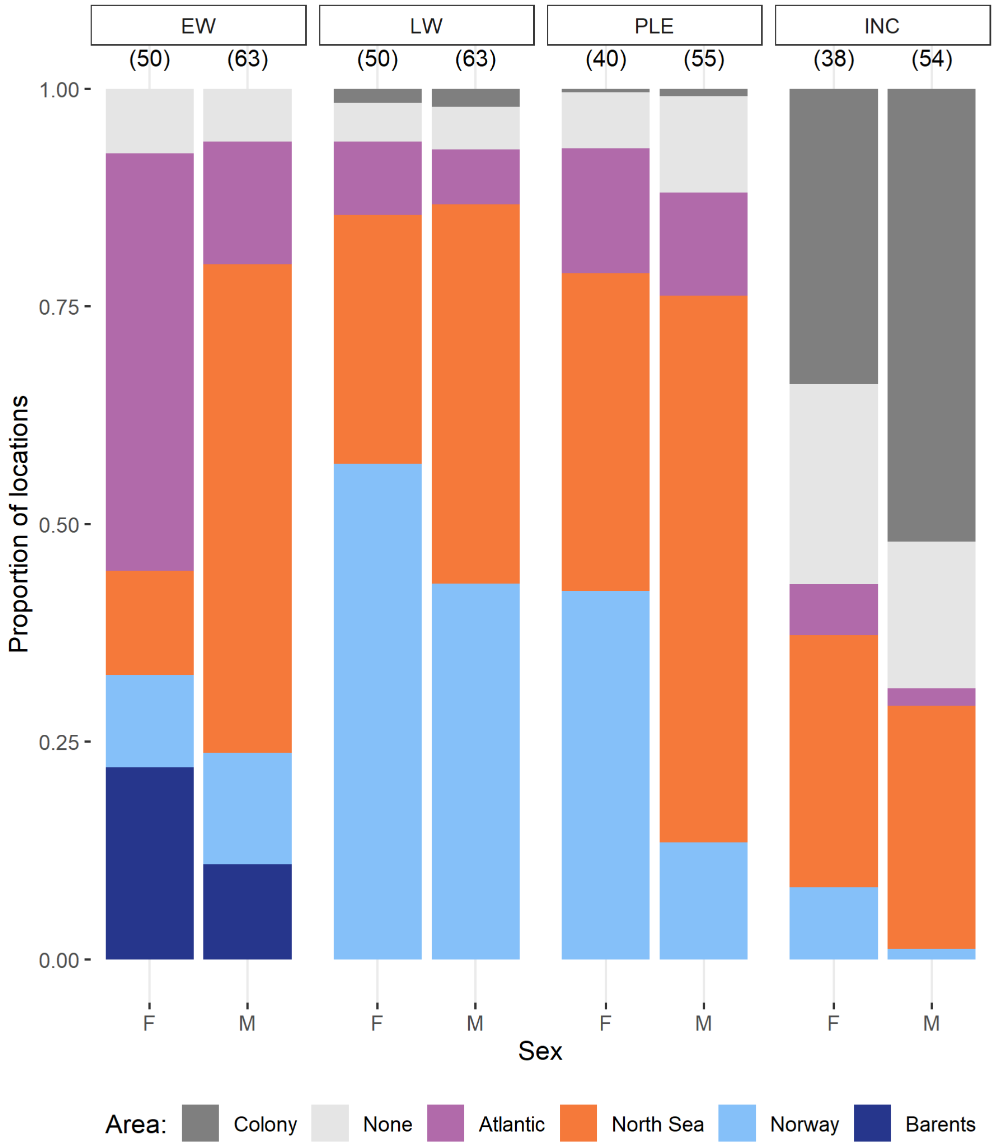


Figure 3-4: Proportion of days spent in each area by all birds, over the entire tracking period. Bars are coloured by area and split by sex, for the four periods. Days marked as "colony" were identified using immersion data, where the logger was dry for most of the day. Days marked as "none" occur where location could not be resolved, either due to shading of the logger at sunrise and sunset (often caused by colony attendance) or due to day length becoming indistinct (associated with high latitude movements). Barents and Norway areas combined for LW, PLE and INC. Abbreviations: EW = early winter, LW = late winter, PLE = pre-laying exodus, INC = incubation.

In general, within-individual Bhattacharyya's Affinity was high in all periods. The distribution of BA was highly skewed towards one, meaning that between years, most individuals spend very similar amounts of time in each area (Error! Reference source not found.). This was particularly extreme in late winter when the lowest value of BA was 0.58. During both early winter and pre-laying exodus, there were more values of BA that were intermediate, meaning that individuals spent more variable amounts of time in each area. There was also a small but notable second peak of very low values, clustering close to zero, meaning that in these two periods some individuals spend all their time in completely different areas between years. Examples of individual variation in the proportion of days spent in each area are shown in **Figure 3-5**. In early winter in 2016 both bird 1153 and 1881 changed the area that they spent most of their time, resulting in a BA of close to zero for comparisons of that year, but BA close to one for comparisons between the other years. In contrast, bird 1614 changed distribution each year, resulting in intermediate values of BA. Similarly, in late winter, bird 1153 would have high BA when calculated between consecutive years, but low BA when comparing between 2009 and 2017, and intermediate BA when comparing between all other years.

In order to understand how within-individual BA related to consistent space-use by the whole population, median within-individual BA was compared to the null distribution, composed of median BA of 10 000 populations of randomly repaired birds (**Figure 3-6**). In early winter and late winter, median BA was significantly higher than expected under the null distribution (*p*-values, randomisation: females EW < 0.001, LW = 0.022, males EW < 0.001, LW = 0.006), meaning that individual consistency is higher than population consistency. In both pre-laying exodus and incubation, median BA fell within the null distribution meaning individuals were not significantly more consistent than randomly paired birds (*p*-values, randomisation: females PLE = 0.083, INC = 0.061, males PLE = 0.108, INC = 0.706). Within-individual median BA was similar between all periods and for both sexes, ranging between 0.88 and 0.96. Slight differences between periods were reflected in both sexes, except in incubation, when median BA was higher in males (0.96) than females (0.88). Variation in the significance of within-individual median BA was therefore driven by changes in the null distribution, rather than changes in individual consistency.

The null distributions for each period and sex represent levels of consistency within the population, as they were constructed by resampling randomly paired birds, and so can be used to infer differences in population-level consistency. Across all the periods population-level BA was lowest in females in early winter, with the highest variation in resampled values. In late winter, population-level consistency was high in both males and females, with a very narrow distribution. Males in incubation had a similarly high and narrow distribution of population-level BA, while the female distribution was wider and reflecting lower population-level BA.

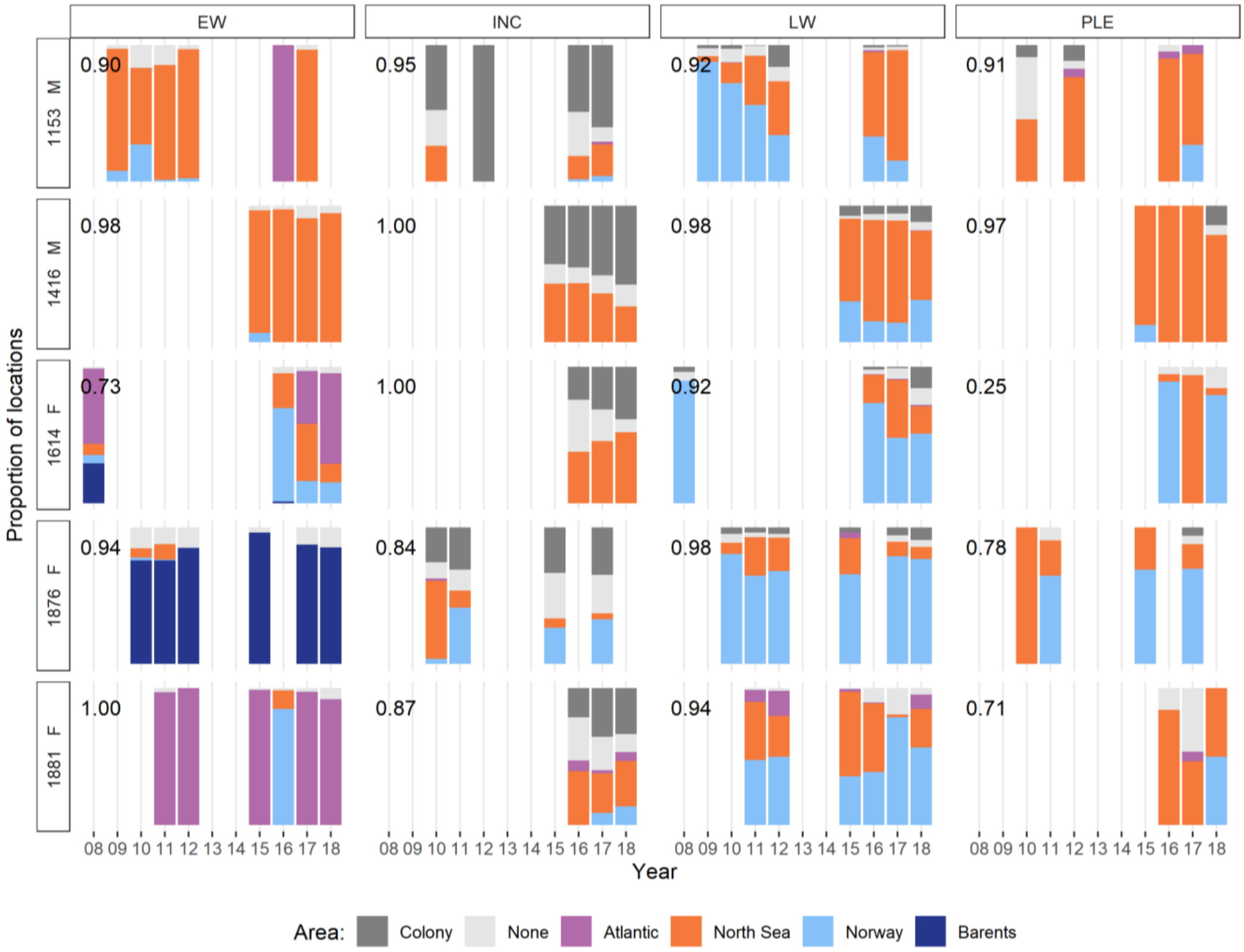


Figure 3-5: Examples showing the proportion of days spent in each area by different individuals, compared between years and periods. Median BA for each bird in each period is shown in the top left of each panel. Days marked as "colony" and "none" as for ***Figure 3-4****, but not included in the calculation of BA. Birds 1153 and 1416 are male, birds 1614, 1876 and 1881 are female. In EW, birds 1416 and 1876 consistently used the North Sea and Barents areas respectively, birds 1153 and 1881 were generally consistent, but both used a different area in 2016, while bird 1614 used a mix of areas in different proportions across all years. In LW all birds used a fairly consistent mix of the North Sea and Norway areas, with bird 1153 gradually switching from Norway to North Sea over time. In PLE birds 1614, 1876 and 1881 showed changes in their main area used, the pattern of which was also repeated in INC for bird 1876. Abbreviations: EW = early winter, LW = late winter, PLE = pre-laying exodus, INC = incubation; M = male, F = female.*

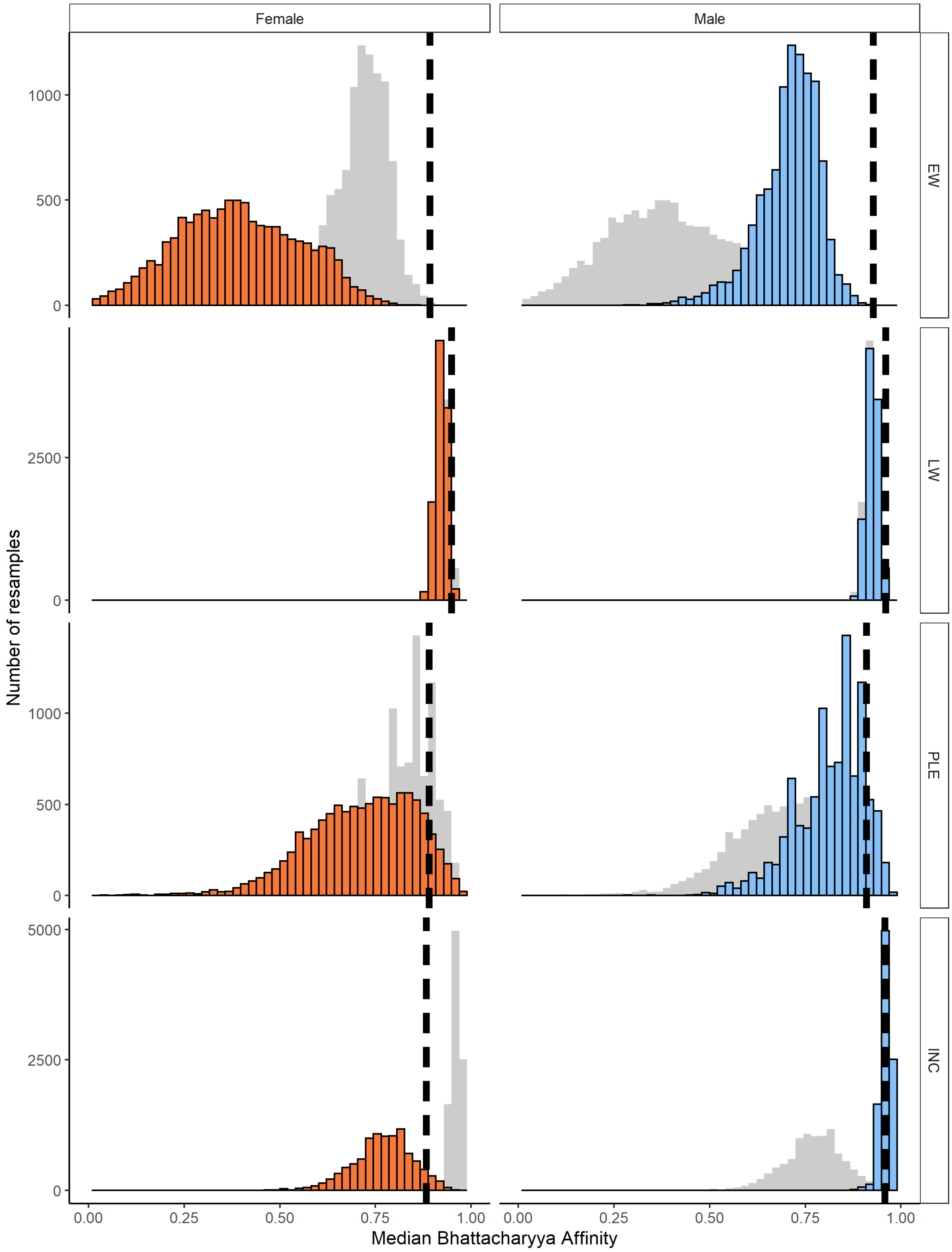


Figure 3-6: *Null distributions and observed median Bhattacharyya's Affinity, split by period and sex. Frequency histograms show the distributions of median BA for randomly repaired birds, reflecting population-level consistency (10,000 resamples). Vertical black dashed line shows the observed median BA, representing consistency within individuals. Distributions are coloured by sex (female = orange, male = light blue). Grey shadow distribution shows the equivalent null distribution of the opposite sex. Abbreviations: EW = early winter, LW = late winter, PLE = pre-laying exodus, INC = incubation.*

3.5 Discussion

I examined individual interannual seasonal consistency in a generalist and wide-ranging seabird, using biologging data collected over ten years. Northern fulmars are considered a generalist species, with a dispersed distribution, but this study finds strong evidence of individual consistency in the areas used throughout the non-breeding period, suggesting that at the individual level, fulmars are not as generalist as previously thought. Most individuals were highly consistent in the areas that they used, across all periods of the annual cycle, but the drivers of this consistency varied depending on the seasonal time period. During pre-laying exodus and incubation, consistency reflected restricted population-level movements, with most of the population occupying the same area. However, in early winter and late winter, individual consistency was significantly higher than population-level consistency, meaning that consistency reflected individuals repeatedly using different subsets of the population range. Additionally, in early winter and incubation there was lower population-level consistency in females than males, reflecting their more varied spatial distributions. These differences in space-use might have consequences both in terms of energetic expenditure, given the large distances travelled by some birds, and in exposure to different environmental conditions, such temperature and daylight, for example between the Barents and North Seas.

Individual consistency was most different from population consistency during the early winter period, which is also when there was most variation in the areas used. This period is the most similar to a classical migration, with many birds leaving the colony locality and remaining in a single area for roughly three months. During this time birds undergo wing moult (Quinn *et al.*, 2016) resulting in less time spent in flight and more time spent resting on the water (Grissot *et al.*, 2019). While the ability to fly is retained during this period, the loss of primary feathers means that flight will be energetically costly and large relocations may result in a loss of body condition. In Cory's shearwaters (*Calonectris borealis*), reduced stress levels in failed breeders in the post-breeding period suggests that this time might be important for recovering the costs of breeding (Ramos *et al.*, 2018), supported by birds with higher breeding investment spending more time at wintering areas (Gatt *et al.*, 2021b). Assuming this is true in fulmars, individuals may favour consistency in order to maximise the benefits of site familiarity and reduce the risk of having to relocate. They may also be less likely to relocate in the event of choosing an unproductive area, as the cost of relocation during moult might outweigh the cost of staying.

In late winter, individual consistency was also higher than population-level consistency, despite high values for both. In late winter fulmars are already attending the breeding colony and spending time locally, while continuing to undertake long foraging trips. This reliance on the areas close to the colony by all birds results in population consistency, while individual consistency results from between-individual variation in the areas visited on longer trips. A similar pattern of shared space-use by birds in late winter was recorded in brown skuas (*Stercorarius antarcticus*) (Krietsch *et al.*, 2017), although that population-level aggregation occurred before returning to the colony locality. Conversely in long-tailed skuas (*Stercorarius longicaudus*) the nearest-neighbour distance between tracks increased late in the wintering period before the return migration (Van Bemmelen *et al.*, 2017).

During pre-laying exodus and incubation individual consistency was no higher than population consistency, as most birds remained close to the colony. A similar pattern of non-breeding colony attendance in late winter (Dunn *et al.*, 2020) and consequent lack of individual specialisation due to the population using broadly the same area is seen in common (*Uria aalge*) and Brünnich's guillemots (*Uria lomvia*) in spring (Merkel *et al.*, 2020). However, both species of guillemot generally showed little evidence of specialisation during autumn, in contrast to fulmars' high fidelity to their apparent moulting locations. This may be due the flightless period that occurs in guillemots but not fulmars, which would constrain their movements to certain areas. Movement over the smaller spatial scales seen in pre-laying exodus and incubation meant that in these periods the low resolution of locations intrinsic to geolocator data was more limiting. As GPS loggers become smaller, future tracking may find individual consistency in these periods, particularly in females, where more variation in areas used means that population-level consistency was lower.

While I did not find any sex differences in within-individual consistency, I did find clear differences between the underlying population distributions of males and females in both early winter and incubation, representing variation between sexes in how many areas are used. These reflected sex differences in spatial distributions, with males more likely to remain closer to the colony in the North Sea area, and females more likely to use the other three areas. Similar sex-linked patterns of space-use have been recorded in Cory's shearwater (Pérez *et al.*, 2014) and Monteiro's storm petrel (*Hydrobates monteiroi*) (Paiva *et* *al.*, 2018), while the opposite patterns are seen in Campbell albatross (*Thalassarche impavida*) (Sztukowski *et al.*, 2018), where females remain closer to the colony and have higher within-individual specialisation by males. Spatial partitioning by sex in some species arises where predictable wind patterns allow birds of different body sizes to select wind conditions that optimise their flight efficiency (Jiménez *et al.*, 2017), although may not explain differences in consistency. In species where there is overlap in sexual dimorphism, more work to disentangle the effect of sex from body size on spatial distributions and how this interacts with environmental conditions might help elucidate whether these sex differences are driven by differing nutritional needs, competitive ability or locomotive costs.

An important consequence of partial sex segregation relates to the environmental and anthropogenic conditions that different individuals are exposed to. The large differences in distances involved (~ 2,000 km) mean that individuals are likely to experience very different environmental conditions, affecting prey availability and energetic costs of foraging. The smaller range and predominant use of the North Sea area by males may mean that they are more at risk of bycatch, as they are known to interact with fisheries in this area (Pirotta *et al.*, 2018; Darby *et al.*, 2021) and sex differences in bycatch have been found in the Pacific subspecies (Beck *et al.*, 2021), although females are also exposed to high fishing intensity in the Barents Sea (Dupuis *et al.*, 2021). Tracking studies are invaluable for identifying which at-sea areas are of importance to seabirds (Lascelles *et al.*, 2016). Recently, the Mid-Atlantic ridge has been recognised as supporting large numbers of multiple species (Davies *et al.*, 2021; Wakefield *et al.*, 2021), and subsequently was designated as the NACES Marine Protected Area. Birds from Eynhallow were recorded using the Atlantic area in all periods, but particularly females in early winter. It is important to understand how these sex differences in spatial distribution may link to either increased exposure to threat, or enhanced protection, and result in sex-specific variation in survival or productivity, which would have consequences for population stability.

In addition to high levels of individual consistency, some individuals were observed that used a varying mix of the four areas, as well as otherwise consistent individuals that changed area for a single year. This suggests that in terms of movement patterns this population is composed of both specialists and generalists, and that at least some specialist individuals are capable of behavioural plasticity in areas used. A similar pattern of some flexibility in over-wintering areas is also described in long-tailed skuas (Van Bemmelen *et al.*, 2017) and Cory's shearwaters (Zango *et al.*, 2019). Understanding the potential environmental drivers of such changes in behaviour and their consequences for both breeding success and survival would elucidate whether flexibility confers an adaptive advantage and help predict population resilience to climate change (Merkle *et al.*, 2022). There is good evidence at the population-level that animals do adjust their movement patterns in response to environmental conditions, for example, stronger sexual segregation in Cory's shearwaters when the North Atlantic Oscillation is negative (Paiva *et al.*, 2017) and Laysan (*Phoebastria immutabilis*) and black-footed albatrosses (*Phoebastria nigripes*) travelling further and being less successful under La Niña conditions (Thorne *et al.*, 2015). However, evidence of individuals directly altering their behaviour in response to environmental conditions is more scarce, which is of particular importance in long-lived species.

Flexibility could also reflect the past experience of individuals, as they might be more likely to change area if they were already familiar with other areas and so had prior knowledge of the likelihood of the new area providing successful foraging. Fulmars are long-lived and like many other seabird species have a delay of several (~ 10) years between physical maturity and the onset of breeding (Dunnet, 1991). In other species this period of immaturity has been linked with their reliance on ephemeral and spatially disparate resources, requiring exploratory behaviour early in life (Dias *et al.*, 2011; Votier *et al.*, 2017; Campioni *et al.*, 2019). This becomes more refined with age, with experience enhancing the ability of individuals to locate and exploit resources efficiently (the exploration-refinement hypothesis (Guilford *et al.*, 2011)). Beyond this dataset there is no information about the previous experience of individuals, so it is not possible to know whether individuals are also familiar with the strategies that they are not observed using. However, it seems likely that a similar process would occur in fulmars, whereby areas where they were successful in finding prey early in life would be favoured and become their primary strategy as adults.

Consistency may also be linked to other factors, such as individual personality. Specifically, boldness has been linked to exploratory behaviour during foraging (wandering albatross (*Diomedea exulans*) (Patrick *et al.*, 2017)) and site fidelity during foraging (black-legged kittiwake (*Rissa tridactyla*) (Harris *et al.*, 2020)), and low reactivity towards extraction from the nest has been linked to winter residency (Cory's shearwater (Gatt *et al.*, 2021a)). Tracking with geolocators is a relatively un-invasive method (Gillies *et al.*, 2020), requiring a single handling event each year, which is similar to the amount of annual disturbance experienced by the other birds on this colony as part of a long-term study conducted since 1950 (Dunnet, 1991). However, if nest philopatry or recapture probability covaried with these individual characteristics or at-sea behaviour, then future studies should consider whether remote-download devices might overcome any inherent bias from datasets being built primarily of birds that are resilient to disturbance and return to breed at the same nests year on year.

This study demonstrates the value of automating species-specific data processing approaches to isolate behaviours of interest from large bio-logging datasets. With the wealth of geolocator data that is now available, immersion data remains under-utilised in providing behavioural inferences to supplement spatial data and allow more nuanced interpretation of movement patterns. Here, I built on previous work, improving the spatial and temporal scales at which individual consistency is identified, finding that sex differences in space-use underpin individual-level, relative to population-level, consistency. Additionally, the different patterns in consistency and spatial distribution that were observed between early and late winter support that these are behaviourally distinct periods, that merit separation when studying fulmar over-wintering behaviour. Further work that incorporates environmental drivers, to determine the degree to which fulmars can flexibly respond to broad-scale fluctuations would be valuable. Adult survival in fulmars has been linked to variation in the winter North Atlantic Oscillation (Thompson & Ollason, 2001), which influences weather conditions and ocean productivity throughout the range of fulmars breeding at this study colony. Linking movement patterns, environmental drivers and demography would help to elucidate the likely impacts of future climate change on population stability.

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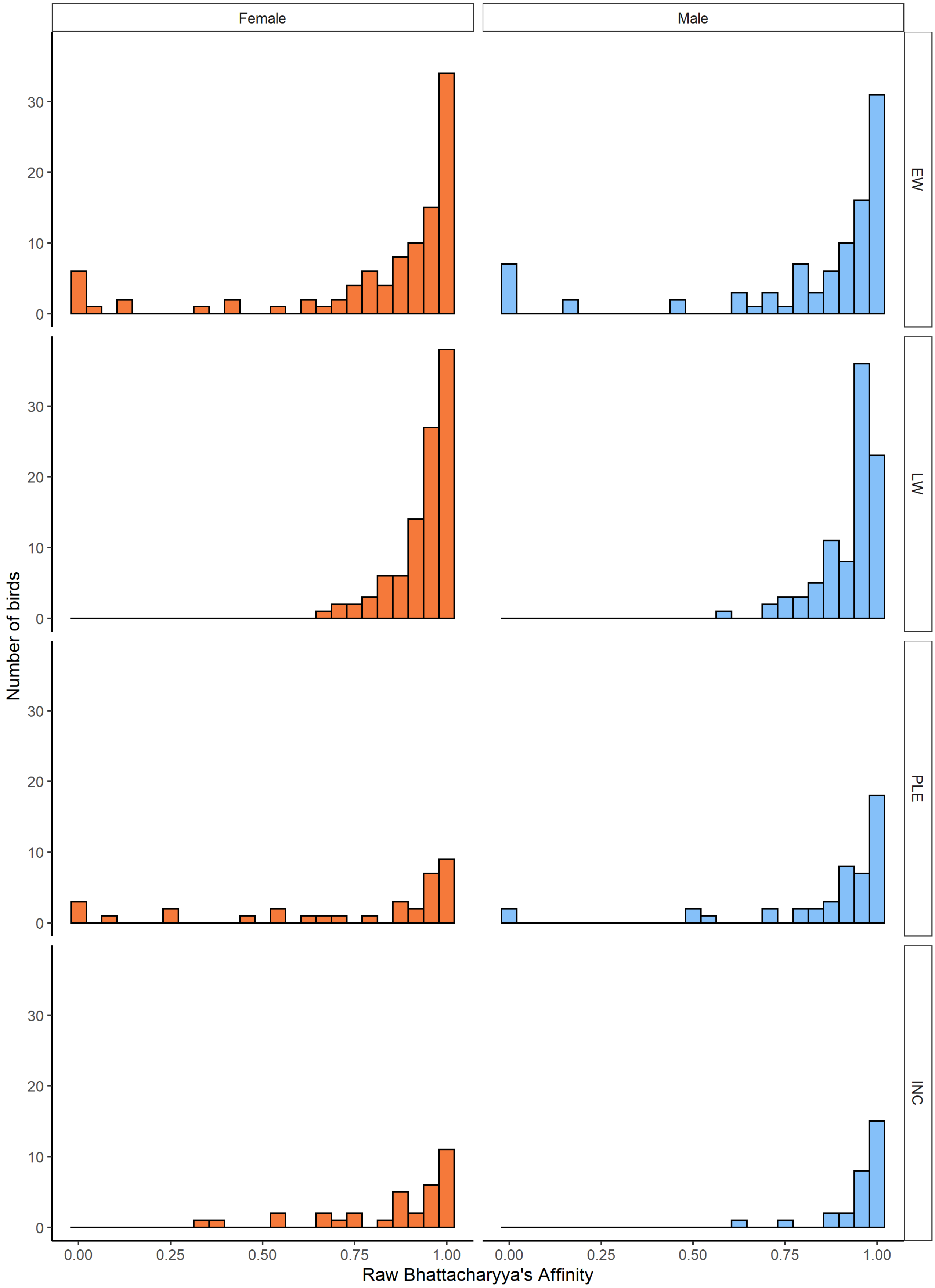
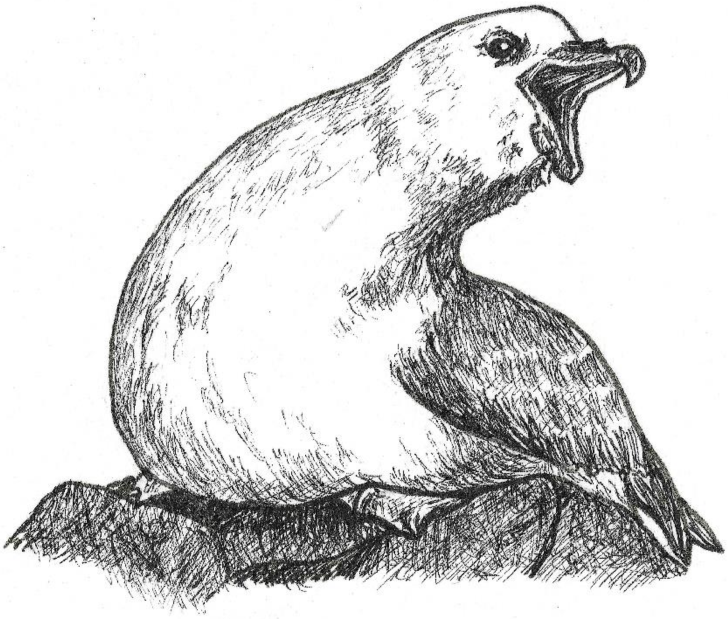


Supplementary 3-1: Frequency distributions showing observed values of within-individual Bhattacharyya's Affinity, split by period and sex. Abbreviations: EW = early winter, LW = late winter, PLE = pre-laying exodus, INC = incubation.

Chapter 4 Sex differences in late winter trip-taking behaviour



4.1 Abstract

Animals make movement decisions throughout their lives to optimise the trade-off between reproduction and survival and thus maximise fitness. In temperate regions, these movements are shaped by the annual cycle, where seasonally variable environmental conditions drive food availability and influence the timing of breeding and migration. During the non-breeding season, survival and recovery from the previous breeding effort are intrinsic to subsequent breeding success, but movements during this period are often less well understood than in the breeding season. Among seabirds, northern fulmars (*Fulmarus glacialis*) are known to return to the area around the breeding colony early, long before the start of the breeding season, but it is unknown what drives this return and how returning interacts with their need to forage to maintain body condition.

Fulmars were tracked with miniaturised archival light-loggers throughout the non-breeding period to study trip-taking behaviour during this extended pre-breeding colony attendance period. Using immersion to infer behaviour and geolocation to estimate daily locations in the late winter and pre-laying periods, trips that involved movements further than 500 km from the colony that lasted for at least three days were identified. I quantified number of late winter trips, trip duration, changes in area visited and whether birds revisited the same areas between late winter and pre-laying exodus. I compared these variables between years (as a proxy for environmental conditions) and between sexes. I then tested whether these behaviours predicted fledging success, to understand whether late winter behaviour influences breeding success.

I found sex differences in trip-taking behaviour, with females more likely to take long trips in late winter, and more likely to visit the same areas during pre-laying exodus that they had previously visited in late winter. Despite variation in both environmental conditions and colony-level breeding success between years, I found no strong effects of year on late winter behaviour except for females taking longer trips than males in both 2016 and 2017. None of these differences predicted fledging success, suggesting that late winter trip-taking behaviour is not a strong driver of breeding success, despite the increased energetic costs that are likely to be incurred when commuting. My results demonstrate that fulmars are highly variable in their late winter behaviour, with males and females differing in how they allocate their time and resources between foraging and colony attendance.

4.2 Introduction

In temperate and polar regions, animal movement patterns normally follow the annual cycle, where breeding coincides with high resource availability (Perrins, 1969). Many species then seasonally relocate, often performing long distance migrations, which allow them to escape reduced food availability and unfavourable weather conditions in their breeding area (Dingle & Drake, 2007). However, there is a wide diversity of migratory strategies, ranging between the classical relocation of whole populations to a distant area (Egevang *et al.*, 2010), to partial (Pérez *et al.*, 2014) and dispersive movements (Fayet *et al.*, 2016a) of varying length, and more complex strategies such as multi-generational migrations (Reppert & de Roode, 2018). Animals that live in the marine environment may exploit wind and ocean currents to move large distances with relatively low energetic costs, resulting in highly transitory life history strategies where individuals cover thousands of kilometres over their lives, linking environments over large spatial and temporal scales (Weimerskirch *et al.*, 2014). While events during the breeding season are clearly an intrinsic part of reproductive rates, behaviour during the non-breeding period may affect both survival to the next breeding attempt and subsequent breeding success. How movement patterns vary during the non-breeding season is therefore an important factor in understanding individual life history strategies.

Body condition at the beginning of the breeding season has been shown to influence breeding success (Chastel *et al.*, 1995; Salton *et al.*, 2015; Abrahms *et al.*, 2018). In many seabird species this is particularly important, as they must withstand extreme weight fluctuations caused by fasting during incubation (Gillies *et al.*, 2022). The impacts of environmental fluctuations and individual behaviour in one season or year are often linked to behaviour or breeding success in the following season (Shoji *et al.*, 2015; Fayet *et al.*, 2016b; Whelan *et al.*, 2020; Gatt *et al.*, 2021). Hence, extreme years with very good or very poor resource availability might impact breeding success beyond that year, with the presence of carry-over effects also varying annually (Catry *et al.*, 2013; Bogdanova *et al.*, 2017; Ramos *et al.*, 2018). It seems likely that prey availability, driven by inter-annual variation in environmental conditions, affects whether individuals manage to regain good body condition by late winter. This in turn would influence the importance of late winter and pre-breeding behaviour on their subsequent breeding success but requires datasets that span multiple years to understand fully.

Northern fulmars (*Fulmarus glacialis*) are an interesting species to study in this context, as the latter part of the non-breeding period (late winter) is spent attending the colony (MacDonald, 1980). This means that fulmars spend a prolonged period of time where they appear to engage in behaviours that are similar to those observed in other seabird species during pre-breeding (Arizmendi-Mejía *et al.*, 2013; Quillfeldt *et al.*, 2019). Tracking work using miniaturised archival light loggers "geolocators" has provided important insight into their non-breeding movements (Quinn *et al.*, 2016; Grissot *et al.*, 2019; Dupuis *et al.*, 2021). Fulmars conduct a relatively short, dispersive migration after finishing breeding, where they generally remain in a single area while they moult their flight feathers (Grissot *et al.*, 2019; Chapter 3). Once complete, they return to the area around the breeding colony. Fulmars have been recorded at their breeding colonies throughout the non-breeding period (Dott, 1973; MacDonald, 1980), although in Autumn these birds are assumed to be immatures or failed breeders that moulted early. From January, breeding adults return and spend the subsequent five months mixing time at sea, often hundreds of kilometres from the colony, with increasingly regular colony attendance (MacDonald, 1980). Like many Procellariiformes, fulmars perform a pre-laying exodus, where all females and most males conduct a foraging trip which lasts up to three weeks (MacDonald, 1977; Hunter, 1999), before the female lays a single egg from the end of May and the incubation period commences. Mean incubation stints then between 1.5 and 9.9 days, depending on location (Mallory *et al.*, 2008).

One consequence of attending the breeding colony outside of the breeding season is the need to travel to find prey, as like during breeding, colony visits might constrain their ability to access distant resources. By interacting with the breeding colony outside of the breeding season, fulmars effectively forage under the constraints of central-place foraging for a larger proportion of the annual cycle than breeding necessitates. Unlike some other Procellariiformes such as Manx shearwaters (*Puffinus puffinus*) (Guilford *et al.*, 2009) or sooty shearwaters (*Puffinus griseus*) (Hedd *et al.*, 2012), there is large inter-individual variation in wintering locations, with some birds remaining close (< 500 km) to the colony throughout the annual cycle, and some visiting locations more than 2000 km away (Quinn *et al.*, 2016). Individual variation in the extent to which fulmars remain resident and the frequency of long foraging trips might result in varying energetic expenditure due to the cumulative time spent commuting to relocate between areas. Attendance at the breeding colony may also be condition-dependent, if birds in poor condition are less able to attend, or might result in a relatively higher cost of attendance. Combined with varying environmental conditions experienced throughout the non-breeding range, these differences may influence body condition and subsequent breeding success.

Colony attendance outside of the breeding season is poorly understood but is assumed to be functionally important due to the energetic cost of time lost from foraging activities and the additional constraint of central place foraging. Understanding how individuals optimise the resultant trade-off between colony attendance and time foraging would allow insight into the relative importance of both behaviours. Previous studies suggest that time spent at the breeding colony might be important for pair behaviours (Guilford *et al.*, 2012), defence of nest sites (Harris *et al.*, 2006; Bennett *et al.*, 2022) or mate guarding (Hunter, 1999). A consequence of colony attendance and the semi-resident behaviour seen in late winter is that birds will be accessing the same areas that are used during the breeding season. This may allow more explorative behaviour early in the year, allowing individuals to become familiar with environmental conditions and locate resources that may be predictable later in the year. This substantial spatial and behavioural similarity between the latter part of the non-breeding period and breeding could potentially provide the opportunity for learning and refinement via experience, providing the mechanism for a knowledge-, rather than condition-, mediated carry-over effect. Establishing site familiarity early in the year could be beneficial during the breeding attempt, when unsuccessful foraging trips are likely to be more costly, due to abandonment of the nest by the partner (Gillies *et al.*, 2022), or insufficient provisioning of the chick.

In this study, I use geolocators to: (i) describe the variation in movement patterns of adult fulmars during the late winter period; (ii) understand whether the same areas are visited between late winter and pre-laying exodus and; (iii) test whether either (i) or (ii) predict subsequent breeding success. I explore both sex and year as predictors of variation in behaviour. I use year as a proxy for environmental conditions, studying these questions over four years when the breeding success of the colony varied between very low, very high, and mixed.

4.3 Methods

Data collection

Adult fulmars were studied at the breeding colony of Eynhallow, a small island located off mainland Orkney, northern Scotland. To quantify non-breeding movements in late winter, geolocators were deployed on plastic leg rings between 2014 and 2018, resulting in the 118 individual tracks analysed here. During annual visits to the colony, breeding attempts and outcomes were recorded for the year following logger retrieval. Details of logger deployment, colony observations and initial data processing to produce daily summaries are provided in Chapter 2: General Methods. All individuals in this study are uniquely marked using colour rings, allowing the identification of both parents attending each nest. Where both partners from a nest were tracked and the response variable was breeding success, I removed one partner quasi-randomly, to avoid pseudo-replication. The partner with the most complete logger data was retained, then in all other cases randomly selected males and females to minimise the difference in sample size between sexes in each year.

Routine for assigning breeding success

Where possible, breeding success for each bird was assigned using observations during the tri-annual visits to the colony during the breeding season, described in Chapter 2: General Methods. Due to the restricted nature of the observation periods, in some cases loggers were retrieved from birds that were no longer associated with an egg but may have suffered an early breeding failure. Additionally, some birds were not observed at the colony in a season, but their geolocator was recovered in subsequent years. In both these cases I assigned breeding success from a combination of partner behaviour and success (where available, n = 5) and attendance patterns inferred from daily time dry and shading of the geolocator (n = 19). I examined the attendance patterns of birds with known breeding outcomes to inform my interpretation of breeding status for birds that were not seen. If the breeding status of the previous or subsequent partner of a tracked bird was known, this information was used in combination with the attendance patterns of the tracked bird.

I assigned breeding status to three categories: “nonbreed”, “egg” and “fledge”. Egg-laying was assigned when time dry and shading indicated attendance of the colony at the end of May or beginning of June. In females this could be a single day whereas in males an incubation stint of two days was required. If no signal for egg-laying or incubation was found, I assigned “nonbreed”. I assigned “fledge” where regular incubations stints continued for roughly 50 days, followed by a period of highly variable daily time dry which continued until early September, indicating regular colony attendance throughout the chick-rearing period. Throughout the incubation period, I looked for breaks in the individual patterns of attendance, with multiple days of low time dry indicating that the bird was at-sea. This was assumed to occur after breeding failure, so "egg" was assigned. I did not distinguish between egg-failure and chick-failure, as attendance patterns at the end of incubation varied between individuals, meaning that it was difficult to separate extended incubation with an egg not hatching, from the chick dying soon after hatching. Additionally, towards the end of chick-rearing, adults attend the colony for less time, meaning that failure of a large chick could still be assigned to "fledge". This was considered to be comparable to the breeding success assigned from colony visits, where "fledge" was assigned to large, well-feathered chicks that were expected to fledge successfully, rather than actual confirmation of fledging. Breeding failure late in the chick-stage is unusual, so this is unlikely to influence my results. In some cases, where research activity at the breeding colony was known to affect breeding outcome, "egg" was assigned, but nests were excluded from analysis of fledging success (n = 3).

Manual identification of pre-laying exodus

The late winter and pre-laying exodus periods were identified by individual track, following the same procedure as in Chapter 3. This algorithm identifies patterns in the daily immersion data associated with behavioural changes between the two periods. Due to the data storage limitations of the geolocators, in several cases activity data stopped before the end of the track, but light data continued throughout (n = 12). One bird was removed completely as light data ended in late winter. Additionally, where egg-laying occurred (confirmed during a colony visit), but the nest failed early, the signal for incubation was not identified by the algorithm (n = 12). In both these instances I manually identified pre-laying exodus from daily light levels rather than time dry, in order to maximise the sample size. For each bird I plotted four variables against day of year: "time dry" – the number of minutes where the logger did not register any wet counts; "mean light" – mean light levels between sunrise and sunset; "total light" – normalised total light levels for the whole 24-hour period and "distance from Eynhallow" – the great circle distance between the mean daily logger location and the breeding colony. Details of how daily summary variables were calculated are found in Chapter 2: General Methods. An example of how patterns across these variables compare is shown in **Figure 4-1**.

Where data were complete and egg-laying and pre-laying exodus had been previously identified, I compared patterns in time dry with the two light variables to compare the signals of colony attendance around the pre-laying period. Long dry periods were normally associated with sharp decreases in mean daily light levels and total light levels, as light to the logger is often blocked when birds attend the colony. I looked for these sharp decreases in total light at the end of May and beginning of June, indicating egg-laying and incubation, then counted back to the last previous drop in light levels. In general, total light levels provided a cleaner signal than mean light, as the timing of sunrise and sunset was occasionally interpolated, resulting in some artefacts in the mean light variable. However, large northwards relocations disrupted the daily incremental change in total light due to changing day length throughout the year, so both variables were retained. I then examined distance from Eynhallow in this period to check that large movements corresponded with the newly identified pre-laying exodus.

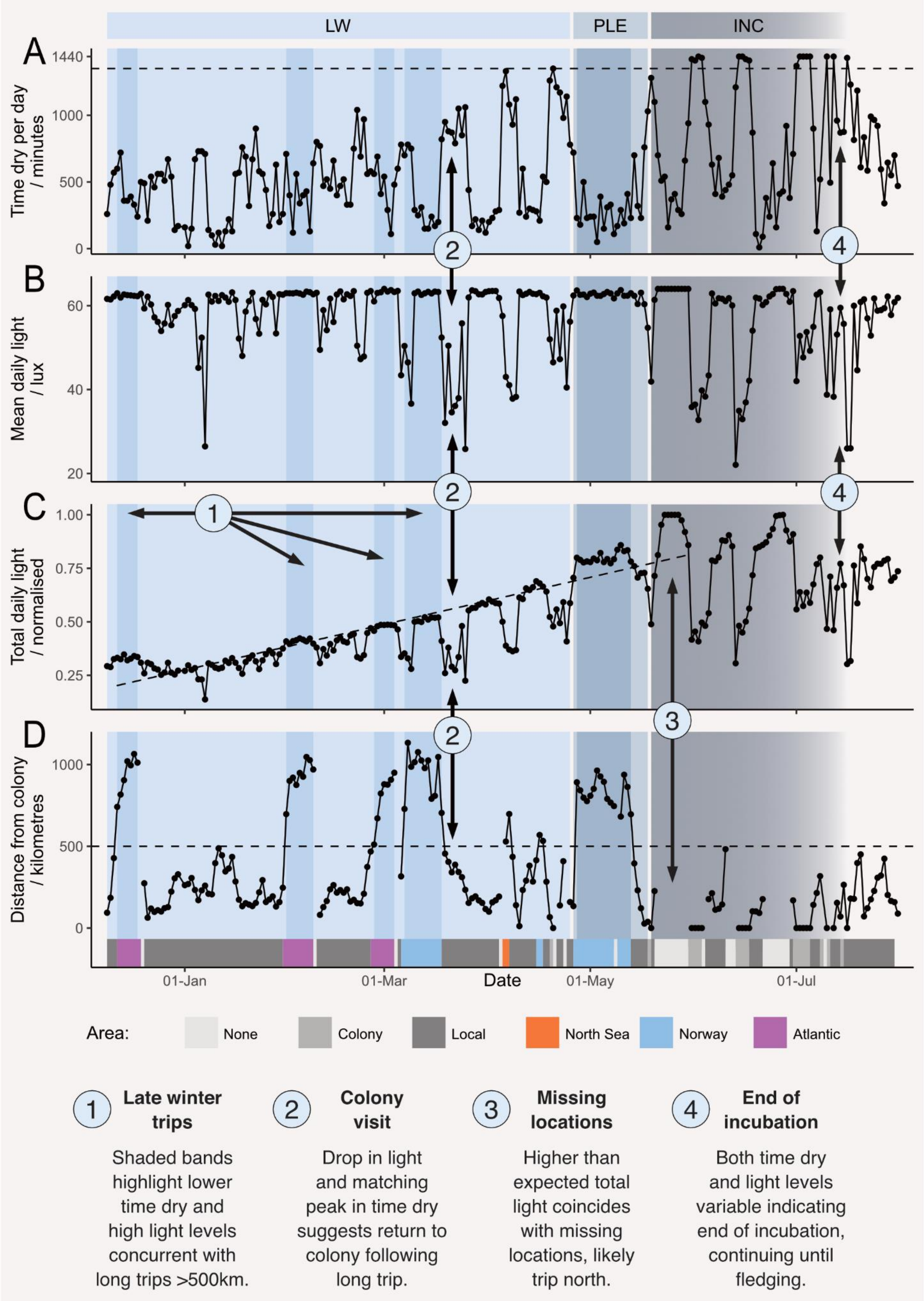


Figure 4-1: Example plots of daily summaries used to compare (A) Daily time dry, (B) Mean daily light during daylight hours, (C) Total normalised daily light and (D) Distance from colony. ***(Continued on next)****.*

*(**Continued from previous**). These variables were used to identify pre-laying exodus and egg-laying in birds with incomplete data. Black dashed line in (A) shows threshold of 1350 minutes dry, above which birds were assumed to be visiting the colony. Black dashed line in (D) shows threshold of 500 km, beyond which was assigned as a long foraging trip. Coloured ribbon at the bottom of (D) shows the area that the bird was assigned to, where none means that a location could not be resolved. In this example, in late winter the bird spent most of its time in the Local area, taking three long trips to the North Atlantic area and one trip to the Norway area. Although the bird appeared to also visit the North Sea area, this was not assigned as a trip because it lasted less than three days. During the pre-laying exodus period, the bird revisited the Norway area on a long trip. Incubation trips were not included in this study as there was a high proportion of missing locations in this period, but daily summaries were used to infer breeding success where necessary, as variable time dry continuing through July indicated continuing regular colony attendance that is not seen in failed breeders. Abbreviations: LW = late winter, PLE = pre-laying exodus, INC = incubation.*

Spatial processing and classifying trips

Following the same method as in Chapter 3, every location was assigned to the area that it fell within, either “Atlantic”, “Norway” or “North Sea”. As in Chapter 3, days where location could not be resolved but total daily light levels were ≤ 0.05 in late winter or ≥ 0.85 in pre-laying exodus were assigned to Norway, as days are shorter and longer respectively at higher latitudes during these time periods. These birds were assigned the mean distance from Eynhallow for all birds in the same period for the purposes of identifying trips. Birds where the logger was dry for at least 1350 minutes (22.5 hours) were assumed to be at the colony, so their distance from Eynhallow was corrected to be 0 km. As the breeding colony is located close to the border between the North Sea and Norway areas, I assigned all locations within 500 km of the colony to a fourth area, named “Local”. I removed periods that were incomplete where the logger had failed and periods where location could be determined for less than 40% of days, or less than four days during pre-laying exodus. I also trimmed the beginning of the late winter period, so that for each bird it began on their first return to the local area within 500 km of the colony.

Trips were assigned to all movements away from the local area that lasted for at least three days. I calculated trip duration in days and assigned each trip to either late winter or pre-laying exodus. In some cases, the pre-laying exodus trip did not match up completely with pre-laying exodus period. Days that fell outside of the pre-laying exodus period, but were part of the pre-laying exodus trip, were reassigned to pre-laying exodus. If more than one trip occurred in the pre-laying exodus period and the trips were separated by more than one day, it was assumed that the bird had returned to the colony and so the trip closest to egg-laying was retained for pre-laying exodus. If the trips were separated by one day only, it was assumed that the bird had not returned and so the two trips were combined. One bird was removed from all analyses as it did not properly return to the local area, remaining in the Norway area until breeding commenced.

Description of key variables and modelling approach

Models were constructed to: (i) describe variation in movement patterns during the late winter period; (ii) test for a link between late winter and pre-laying exodus movements and; (iii) test whether trip-taking behaviour in late winter and pre-laying exodus predicts subsequent breeding success. For each global model structure, a set of candidate models were constructed for comparison using AICc. The global model structures are numbered and referred to as a "Model set", which are detailed in **Table 4-1**.

Table 4-1: Details of model types and global model structures for all analyses. For each Model set number, a set of candidate models including every combination of fixed explanatory parameters and interactions were fitted and compared to the null model using AIC.

Model type	Model set number	Parameters	
		Response ~ Fixed	Random
(i) Movement patterns during the late winter period			
Zero-infl. Poisson hurdle GLMM	1	number of LW trips ~ year + sex	individual
Negative binomial GLMM	2	trip duration ~ year + sex	individual
Binomial GLMM	3	changes in area ~ year + sex	individual
(ii) Link between behaviour in late winter and pre-laying exodus			
Binomial GLMM	4	previous visits in LW ~ year + sex	individual
(iii) Breeding success			
Binomial GLM	5	fledge ~ number of LW trips + year	none
Binomial GLM	6	fledge ~ median trip duration + year	none
Binomial GLM	7	fledge ~ previous visits in LW + year	none

To understand how late winter behaviour varied between years and between sexes, I calculated the number of trips taken by each individual ("number of late winter trips", Model set 1) and the number of days each trip lasted ("trip duration", Model set 2). To understand whether birds visited the same areas on different trips, I calculated Bhattacharyya's Affinity (BA) between consecutive trips, following the methodology used in

Chapter 3. BA compares the proportion of days spent in each area between two distributions, resulting in a value between 0 (no overlap between distributions) and 1 (identical distributions). A change in area was defined as BA of less than 0.7, as this corresponded to less than 50% of time spent in the same area. This was assigned a binary response variable for whether birds changed area or not ("changes in area", Model set 3).

To understand whether birds that took a trip during pre-laying exodus visited an area that they had already visited in late winter, I used BA as before to calculate how similar the distribution of the pre-laying exodus trip was to all previous late winter trips. I assigned a binary response variable ("previous visits in late winter", Model set 4) as zero when all values of BA were less than 0.7, indicating that the pre-laying exodus trip was to a different area compared to late winter trips. If at least one value of BA was more than 0.7, I assigned one, indicating that the bird took at least one trip during late winter to the same area as the pre-laying exodus trip.

For parts (i) and (ii) I used the package *glmmTMB* (Brooks *et al.*, 2017) to run generalised linear mixed effects models (GLMMs) including individual as a random effect to account for tracking the same individual over multiple years. For each global model set of interest, I constructed a set of five candidate models with different combinations of fixed effects: year and sex with interaction, year and sex without interaction, year only, sex only and null (random intercept). I compared AICc values and weights between models using the package *MuMIn* (Barton, 2022) and retained the model with lowest AIC. Where multiple models were within 2 AIC values of each other, I retained the simplest model. I used the package *DHARMa* (Hartig, 2022) to plot and check for patterns in the simulated residuals indicating incorrect model specification, overdispersion and homogeneity of variance. In the case of Model set 1, I fitted a zero-inflated Poisson hurdle model, as the function "testZeroInflation" indicated that the count data contained more zeros than would be expected under the Poisson distribution. Zero-inflated hurdle models fit the probability of observing a zero as arising from a separate distribution to the rest of the data, resulting in a two-part model structure where a zero can occur in the zero-inflation model but not the conditional model (Blasco-Moreno *et al.*, 2019). For Model set 2, I applied an initial transformation to the data of subtracting three from all values, as the minimum possible trip length was three days, which otherwise resulted in a truncated distribution and poor model fit. I then fitted a negative binomial model (quadratic parameterisation) as the data were overdispersed. In all other instances a binomial model was fitted as the response variable was binary.

To explore the effect of late winter behaviour on breeding success (part (iii)) I tested whether fledging was predicted by number of late winter trips (Model set 5), median trip duration (Model set 6) and whether birds had previously visited their pre-laying area in late winter (Model set 7). I ran each of these models with and without interactions between the main effect and year, then compared each pair of models to a null model containing year only, using AIC values as above. I retained year in the null model, as breeding success at this colony is highly variable between years. It was not possible to compare between Model sets 5-7, as slightly different subsets of data were included each time, depending on individual trip-taking behaviour. I only included nests that had laid an egg and where both partners were tracked, one bird from each pair was removed as described above in “Data collection” to prevent pseudo-replication of breeding success. I did not include sex in these models as it should not be biologically possible for breeding success to differ between sexes, so any differences would be due to sampling effects. While breeding success is likely to result from a combination of the behaviour of both male and female birds, here the sample of nests where both partners were tracked was too small to test this. It was also not possible to run separate models for males and females, as splitting the data resulted in some groups with very few data points. I did not include individual as a random effect, as there were not enough repeat observations to allow model convergence.

I used the package *sjPlot* (Lüdecke, 2021) to extract coefficients from the highest ranked models for plotting and the package *emmeans* (Lenth, 2022) to extract post-hoc estimates of p-values for all pairwise contrasts, with Tukey adjustment for pairwise comparisons of eight estimates. Model estimates are reported as means on the response scale, directly followed by 95% confidence intervals in square brackets. For binomial models, probabilities are reported, after back-transformation from log-odds using *emmeans*.

4.4 Results

(i) Movement patterns during the late winter period

During the late winter period the “Local” area was used most frequently, with 82 [74, 88]% (97/118, binomial confidence intervals) of birds remaining within 500 km of the colony for more than half of the period. I found that it was common for both males and females to take multiple foraging trips of three or more days away from this local area, in all years of the study. Using a zero-inflated Poisson hurdle GLMM, there was strongest support for sex predicting the number of late winter trips (**Table 4-2**: Model set 1), although in this two-part model this sex difference was driven by the zero-inflated, rather than conditional, component. This means that the probability of observing a zero (no trips taken) in females was 0.02 [0.00, 0.12], whereas the probability of males not taking any trips was 0.21 [0.13, 0.33]. Of the birds that took at least one trip (the conditional component of the model), there was no difference between females and males in the number of trips taken (modelled means: females = 4.79 [4.04, 5.67] trips, males = 4.26 [3.55, 5.12] trips). There was no support for a difference between years in the number of trips taken. Raw data and output of the conditional model are presented in **Figure 4-2**.

The median trip duration for all observations was six days (IQR = 4-10 days). The best supported model included both year, sex and their interaction as predictors of trip duration (**Table 4-2**: Model set 2). Post-hoc comparisons indicated that within sexes, trip durations were similar between years, but that there were sex differences in trip duration in both 2016 and 2017. In both years females went on longer trips than males (modelled means: **2016** female = 12.30 [9.52, 16.26] days, male = 6.05 [5.21, 7.22] days; **2017** female = 8.87 [7.31, 11.00] days, male = 5.38 [4.49, 6.80] days). A visualisation of trips durations between years and sexes is shown in **Figure 4-3**, indicating that the general pattern across all years was that females went on longer trips and were also more varied in their trip durations.

Birds varied in whether they visited different areas while on trips, with birds changing area between 0 and 5 times. However, there was not strong evidence that the likelihood of changing area was predicted by sex or year, as the null model was the best supported (**Table 4-2**: Model set 3). The probability of changing area at least once was 0.45 [0.33, 0.57] (null model mean). The second-ranked model retained sex with a model weight of 0.25, but probability estimates between males and females only varied by 0.06 (with males more likely than females to change area), suggesting that any possible effect is marginal.

Table 4-2: *Model comparison tables for Model sets 1-3, describing late winter trip-taking behaviour. All models were fitted with individual as a random effect. The model shown in bold was retained, either as it had the lowest AICc value, or there was a model with a simpler structure where ΔAIC was less than 2. Number of observations (n) is reported for each Model set with number of individuals in brackets.*

Response	Explanatory variables	df	logLik	AICc	ΔAIC	Weight
Model set 1: n = 118 (71)						
number of LW trips	**sex**	**5**	**-266.86**	**544.25**	**0**	**0.85**
	year + sex	11	-261.96	548.40	4.15	0.11
	year x sex	17	-255.46	551.04	6.78	0.03
	1 (null)	3	-273.42	553.05	8.80	0.01
	year	9	-268.63	556.92	12.67	0
Model set 2: n = 494 (65)						
trip duration	**year x sex**	**10**	**-1365.24**	**2750.93**	**0**	**0.75**
	sex	4	-1373.18	2754.44	3.51	0.13
	year + sex	7	-1370.16	2754.55	3.62	0.12
	1 (null)	3	-1380.50	2767.05	16.11	0
	year	6	-1378.32	2768.82	17.89	0
Model set 3: n = 104 (65)						
changes in area	**1 (null)**	**2**	**-70.89**	**145.91**	**0**	**0.66**
	sex	3	-70.78	147.80	1.90	0.26
	year	5	-70.00	150.62	4.71	0.06
	year + sex	6	-69.89	152.66	6.75	0.02
	year x sex	9	-69.67	159.26	13.35	0

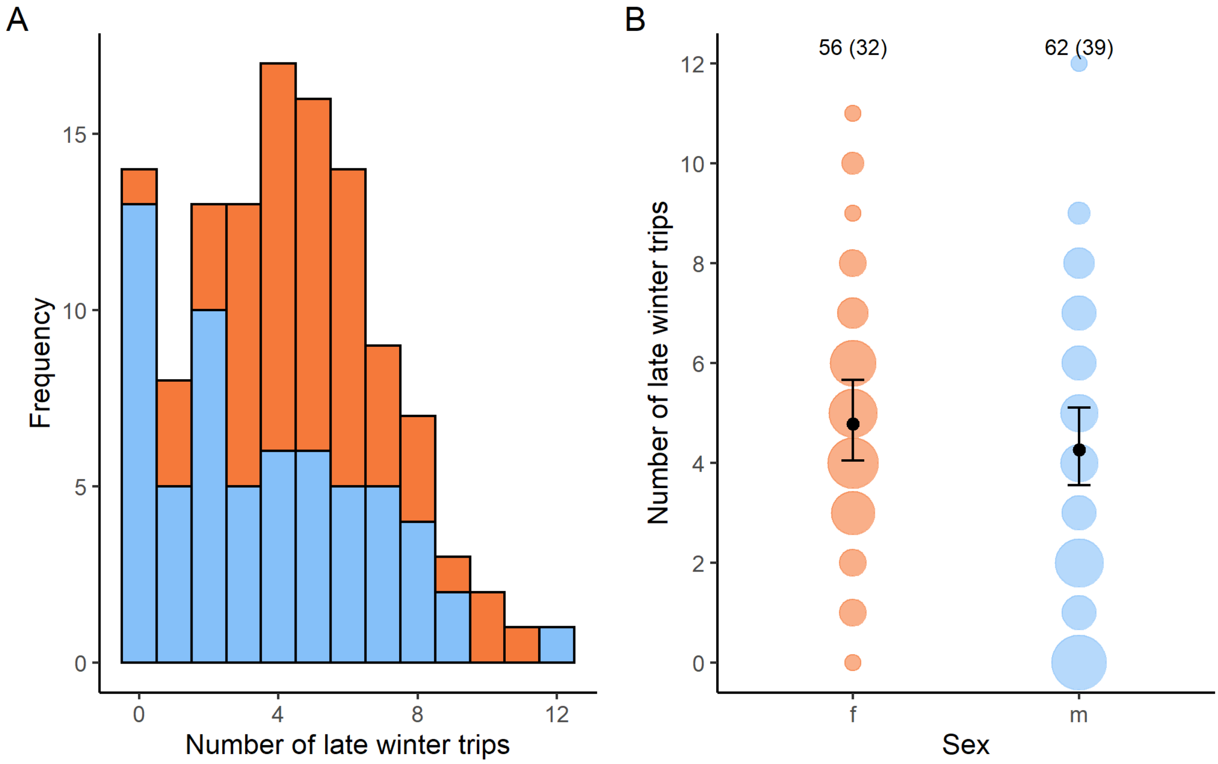


Figure 4-2: Number of trips taken in late winter, split by sex (orange = females, blue = males). Trips were assigned when a bird remained further than 500km from the colony for at least three days. (A) Frequency histogram highlighting the large number of males that took zero trips. (B) Bubble plot showing the raw number of late winter trips, where area of circle corresponds to the number of birds with each value (smallest = 1, largest = 13). Black points show estimates of conditional model intercept, with error bars showing 95% confidence intervals. Zero-inflation model not shown, males were more likely than females to not take any trips (estimates in main text). Number of observations by sex is shown at top, followed by number of individuals in brackets.

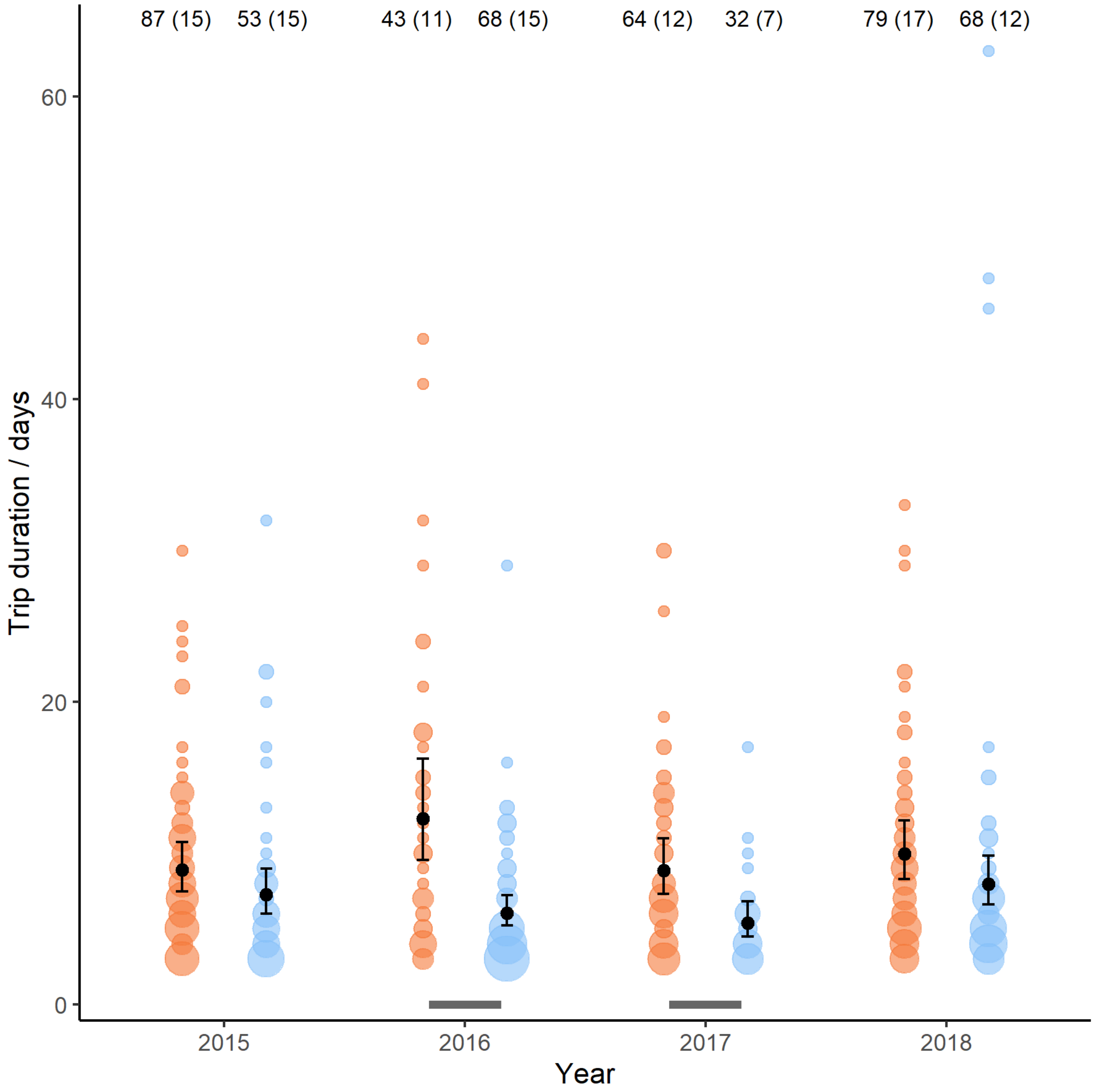


Figure 4-3: Bubble plot showing raw individual trip durations by year, split by sex (orange = females, blue = males) with circle area corresponding to the number of observations with this value (smallest = 1, largest = 20). Black points show estimates of conditional model intercept, with error bars showing 95% confidence intervals. Number of observations are shown at top, followed by number of individuals in brackets. Bars at bottom show contrasts where adjusted p values were < 0.05 in post-hoc comparisons.

(ii) Link between behaviour in late winter and pre-laying exodus

Of birds that took long trips during pre-laying exodus, individuals were highly variable in how many times they had previously visited the same area in late winter, with some using a completely new area during pre-laying exodus and some visiting an area that they had previously visited up to ten times (**Figure 4-4 A**). I modelled this as a binary response variable (**Figure 4-4 B**), representing whether birds revisited an area that they had already visited at least once and so could potentially have built site familiarity. The best supported model retained sex but not year as predictors (**Table 4-3**: Model set 4), with females more likely than males to visit an area that they had visited previously. The probability of females conducting their pre-laying exodus trip to an area where they had made at least one trip to in late winter was 0.78 [0.62, 0.89], whereas the probability of males revisiting the same area as in pre-laying exodus as late winter was 0.51 [0.36, 0.67].

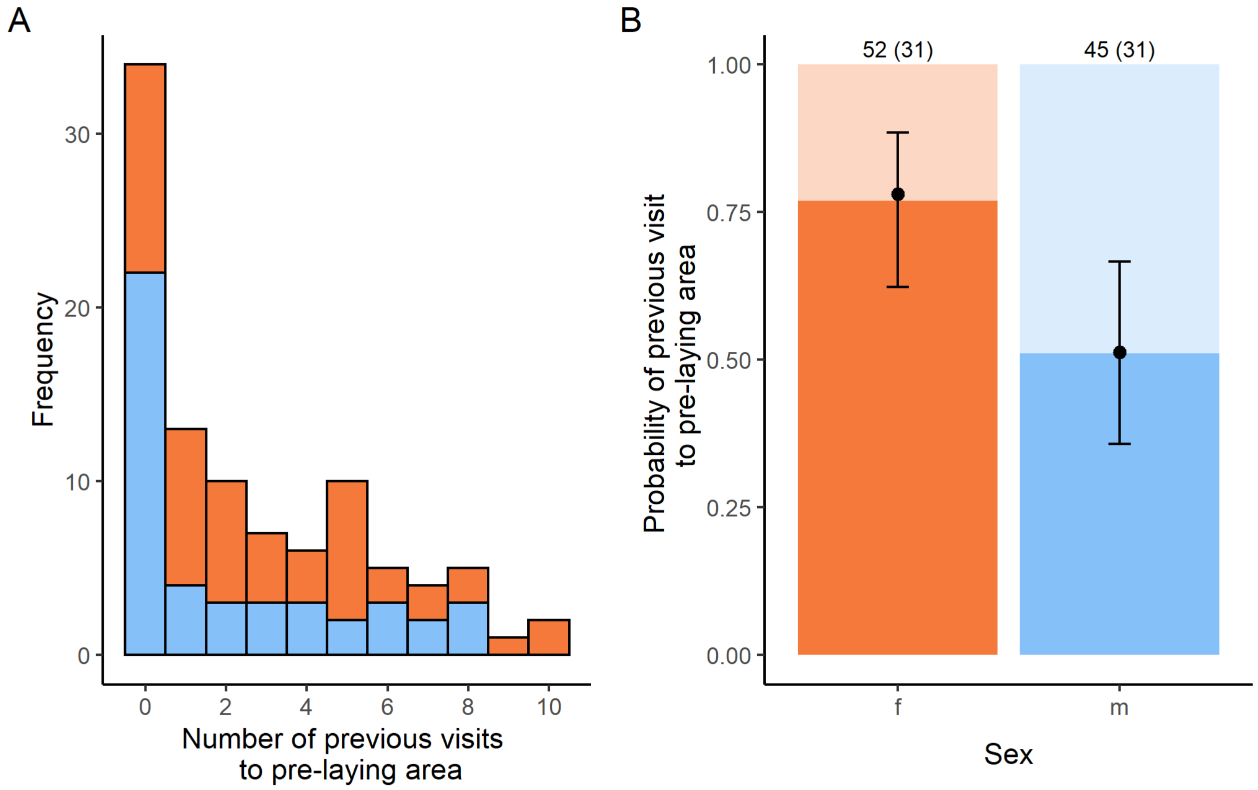


Figure 4-4: Previous visits made in late winter, to the same area that was visited during pre-laying exodus on long trips, split by sex (orange = females, blue = males). (A) Frequency histogram of raw number of previous visits to pre-laying area. (B) Bar chart showing the raw proportion of birds in pre-laying exodus that used an area which they had previously visited in late winter (dark = proportion of birds with previous visit, light = proportion of birds without previous visit). Black points show modelled probabilities, with error bars showing 95% confidence intervals. Number of observations by sex shown at top, followed by number of individuals in brackets.

Table 4-3: Model comparison table for Model set 4, which described whether birds visited areas in pre-laying exodus which they had already visited in late winter. Individual was included as a random effect. The model shown in bold was retained, either as it had the lowest AICc value, or there was a model with a simpler structure where ΔAIC was less than 2. Number of observations (n) is reported with number of individuals in brackets.

Response	Explanatory variables	df	logLik	AICc	ΔAIC	Weight
Model set 4: n = 97 (62)						
previous visits in LW	**sex**	**3**	**-59.17**	**124.61**	**0**	**0.70**
	year + sex	6	-57.32	127.57	2.97	0.16
	1 (null)	2	-62.42	128.97	4.37	0.08
	year x sex	9	-54.84	129.75	5.14	0.05
	year	5	-61.23	133.13	8.52	0.01

(iii) Breeding success

I did not find strong evidence that fledging success was predicted by late winter or pre-laying trip-taking behaviour. The null model, retaining year only, was best supported as a predictor of fledging success (**Table 4-4**), when compared to models that also contained number of late winter trips (Model set 5), median trip duration (Model set 6) and previous visits in late winter to pre-laying area (Model set 7). The model weighting for the null model was 0.71 and 0.75, for number of late winter trips and previous visits in late winter, suggesting little support for the inclusion of these variables as predictors. However, for median trip duration (Model set 6) the interpretation was more ambiguous, as the model weights were split between the three candidate models and the two models that contained median trip duration were also within two AICc values of the null model. This suggests that median trip duration may contribute to predicting breeding success, but with the data presented here is difficult to interpret further.

Table 4-4: Model comparison table for Model sets 5-7, which described whether fledging success was predicted by behaviours in late winter and pre-laying exodus. No random effects were fitted. Models were tested against a null model that retained year, as fledging success is known to be highly variable between years. The model shown in bold was retained, either as it had the lowest AICc value, or there was a model with a simpler structure where ΔAIC was less than 2. Number of observations (n) is reported for each Model set with number of individuals in brackets.

Response	Explanatory variables	df	logLik	AICc	ΔAIC	Weight
Model set 5: n = 93 (63)						
fledge	**year (null)**	**4**	**-52.97**	**114.39**	**0**	**0.71**
	number of LW trips + year	5	-52.81	116.30	1.92	0.27
	number of LW trips x year	8	-52.49	122.69	8.30	0.01
Model set 6: n = 85 (56)						
fledge	**year (null)**	**4**	**-47.51**	**103.51**	**0**	**0.42**
	median trip duration x year	8	-42.94	103.77	0.25	0.37
	median trip duration + year	5	-47.07	104.90	1.39	0.21
Model set 7: n = 63 (45)						
fledge	**year (null)**	**4**	**-38.44**	**85.56**	**0**	**0.75**
	previous visits in LW + year	5	-38.43	87.92	2.36	0.23
	previous visits in LW x year	8	-37.28	93.23	7.67	0.02

4.5 Discussion

Here I investigated the unusual late winter and pre-breeding behaviour of the northern fulmar, finding sex but not year differences in trip-taking behaviour. In late winter, females were more likely to take trips, and on average female trips were longer than male trips. In pre-laying exodus, females were more likely than males to take trips to areas that they had already visited at least once in late winter. Despite comparing between four years of highly contrasting breeding success, defined as the probability of fledging a chick having laid an egg, there was little effect of year on trip-taking behaviour, suggesting that this is probably not driven by year-to-year changes in prey availability. While there was a great deal of variation in the trip-taking behaviour exhibited by fulmars, within the sexes neither individual stereotypy nor year explained this variation, with intra-individual variation across years and inter-individual variation within years. For example, many birds were highly transitory in the late winter period, performing multiple long trips away from the area local to the colony. This contrasted with others that remained resident within 500 km of the colony throughout the entire period, demonstrating that there are resources available locally to support at least some of the population throughout the annual cycle. Birds that completed multiple long foraging trips are likely to incur higher energetic costs and spend more time commuting, but these costs could be offset by higher prey encounter rate and reduced search times, if accessing more predictable or abundant prey patches. The lack of effect of late winter and pre-laying behaviour on fledging success suggests that birds are maintaining sufficient condition to not strongly incur carry-over effects. However, the breadth and depth of the dataset precluded the analysis of the effect on rarer events such as skipping breeding, which would only represent behaviour and environmental conditions before the start of the breeding season.

Sex differences in late winter behaviour

The patterns of sex differences observed in this study support those found in previous studies at this colony (Quinn, 2014), with males more likely to remain close to the colony. Similar patterns are found in the migratory destinations of Cory's shearwaters (*Calonectris borealis*), where males are more likely to remain resident over winter rather than migrating (Pérez *et al.*, 2014), although in fulmars the proportion of males remaining resident is higher. Arguably the movement patterns that were observed in late winter are similar to their movements during the breeding season, with the colony or area around the colony acting as a central place from which foraging trips are conducted. Similar sex differences in distribution during the breeding season have been recorded in giant petrel species (*Macronectes giganteus* and *Macronectes halli*), where larger males are more likely to feed at seal carcasses whereas females and smaller males are more likely to feed pelagically (González-Solís *et al.*, 2008; Krüger *et al.*, 2018; Reisinger *et al.*, 2020). Additionally, in mollymawk albatrosses (*Thalassarche melanophrys* and *Thalassarche chrysostoma*), sex differences in wing loading are linked to visiting areas with higher or lower average wind speeds (Phillips *et al.*, 2004). Fulmars also exhibit sexual dimorphism, but with significant overlap (Dunnet & Anderson, 1961). One hypothesis that could be tested in future would be whether the tendency to go on long trips is associated with smaller biometrics, perhaps accounting for the behavioural sex differences reported here, as observed in southern giant petrels (Krüger *et al.*, 2018). The role of competition in determining these sex differences is also unknown but might occur if male fulmars are able to defend foraging resources aggressively using their larger body size. However, there is little direct evidence of competition between seabirds at sea, although aggressive behaviour between individuals has been recorded in feeding aggregations of Scopoli's shearwaters (*Calonectris diomedea*) (Michel *et al.*, 2022).

I explored whether individuals visit areas during pre-laying exodus that they have already visited in late winter, as this might suggest that they were able to benefit from site familiarity gained during late winter. I found that of the birds that took long trips during pre-laying exodus, females were more likely to use areas that they had previously visited, and that this did not vary by year. Females are known to go on longer pre-laying exodus trips (Edwards, 2015), so are maybe able to better access more distant areas that they had visited in late winter. The energetic cost of laying an egg is large (Bond & Diamond, 2010), with females also often taking a long foraging trip during the first full incubation stint, presumably to recover body condition (Mallory, 2009). This might make them more risk averse to visiting new areas and less likely to engage in exploratory behaviour at this time. Additionally, it is likely that they have different nutritional needs to males while the egg is developing. In this study, foraging areas were broadly assigned, but more accurate locations would allow the identification of specific areas that are important to females during pre-laying exodus, as well as better understanding of how close they are to their previous foraging locations. It is possible that revisitations of late winter areas continue into incubation, as birds from this colony are known to conduct long incubation trips (Edwards *et al.*, 2013; Wakefield *et al.*, 2021), but with the occurrence of longer days during this time it becomes difficult to resolve locations from geolocator data.

Colony attendance as a driver of late winter behaviour

Other potential drivers of sex differences in trip-taking relate to the function of colony attendance outside of the breeding season, which in remains poorly understood. While some Procellariiform species such as Chatham's petrels (*Pterodroma axillaris*), only return directly before copulation (Rayner *et al.*, 2012), fulmars are known to attend the breeding colony throughout the non-breeding season. They increase their attendance from January until the run-up to departing on pre-laying exodus trips in May, with males more likely to attend their nest site than females, in a type of passive mate guarding behaviour (Hunter, 1999). Fulmars have sperm storage glands (Hatch, 1983), but the peak in copulation rates occurs around 30 days before egg-laying (Hunter, 1998). Given that regular colony attendance occurs for up to five months before laying, it seems likely that there are further drivers of colony attendance in late winter.

In Balearic shearwaters (*Puffinus mauretanicus*) partners are synchronised in their winter colony attendance, suggesting a pair function in attending the colony (Guilford *et al.*, 2012). Weather conditions have also been linked with non-breeding colony attendance, with attendance negatively correlated with wind speeds in fulmars (MacDonald, 1980; Mudge *et al.*, 1987), Cape gannets (*Morus capensis*) (Pistorius *et al.*, 2015), common guillemots (Birkhead, 1978), but the possible mechanistic link with wind remains unclear. Field metabolic rates are also negatively correlated with wind speed in fulmars (Furness & Bryant, 1996), so it is possible that they reduce the time cost of colony attendance by attending during windows of poor wind conditions for foraging and commuting.

In common guillemots, non-breeding colony attendance is thought to be driven by defence of high-quality nest sites, with early return negatively correlated with population size (Harris *et al.*, 2006) and higher quality sites more likely to be occupied (Bennett *et al.*, 2022). At this study colony, the current population is more than 50% lower than the recent peak breeding population (Cordes *et al.*, 2015), suggesting that competition for nest sites is unlikely to drive attendance, although it cannot be entirely ruled out if potential nest sites differ considerably in quality. While broadly socially monogamous, fulmars occasionally switch partner (5% per annum, Ollason & Dunnet, 1978). Early attendance at the breeding colony might allow birds to re-encounter their partner, giving them more time to assess their condition and decide to switch partner, or find a new mate if their partner has died. The lack of a distinct signature of colony attendance in the geolocator immersion profiles meant that it was not possible to include colony attendance in this study. In the future, equipping nests with RFID readers or using VHF transmitters might allow the study of how the frequency of colony attendance varies among individuals and years, shedding further light on its function and aiding the interpretation of fulmar distributions in late winter, especially where both partners were tracked.

Lack of year effects on late winter behaviour and links to breeding success

Using year as a proxy for environmental conditions, I was surprised not to find evidence of inter-annual variation in trip-taking behaviour, across individuals. While year was used as a proxy for environmental conditions, the precise effect of broad scale drivers such as the Winter North Atlantic Oscillation (WNAO) on the timing of seasonal increases in chlorophyll-α and subsequent trophic cascades that increase prey availability remain unclear. Throughout the study period WNAO remained positive, fluctuating between 0.91 and 2.33 (Updated from Jones *et al.*, 1997, Climate Research Unit, University of East Anglia). Positive WNAO has been linked to lower breeding success, lower proportion of colour ringed birds recorded (Thompson & Ollason, 2001) and lower adult survival (Grosbois & Thompson, 2005) at this colony, but the mechanisms by which these effects arise are unknown. Behavioural changes possibly only occur under extreme conditions that result in complete prey scarcity or abundance.

Birds were expected to go on more frequent and longer foraging trips in years where environmental conditions led to low prey availability close to the colony, tipping the trade-off between time spent searching for prey or commuting to good foraging locations and the benefits of colony attendance. I also expected that birds would change area more often, as exploratory behaviour is often associated with less predictable resources (Paiva *et al.*, 2010, 2013). The lack of variation in these metrics between years, at a part of the annual cycle when local productivity is expected to be low (Henson *et al.*, 2009), suggests that birds either cannot or do not respond to environmental conditions in this way. The split in strategies seen here may occur if individuals vary in how they optimise finding prey, with birds that remain close to the colony allocating more energy to searching, and birds that conduct long foraging trips allocating time and energy to commuting to less ephemeral resources.

Despite large inter-annual variation in fledging success, I did not find that late winter behaviour predicted breeding success. In order to maintain variation in foraging strategies within a population the success of different strategies is expected to vary under different environmental conditions, as found in northern elephant seals (*Mirounga angustirostris*) (Abrahms *et al.*, 2018). Late winter and pre-laying exodus are likely to be important periods for species with protracted breeding seasons such as fulmars, as birds that reach the beginning of the breeding season in poor body condition are unlikely to breed successfully (Chastel *et al.*, 1995; Salton *et al.*, 2015). While the sample size in this study was small, the patterns observed in fledging success were similar to those observed across the Eynhallow population (Paul Thompson 2021, personal communication, 14th April). However, the binary response variable of fledgling success bluntly reflects the integration of movement decisions of both partners over a long time period, as well as external factors such as local weather conditions and predation. This means that without partner information, only large effects of late winter behaviour would likely have been detected statistically. Nonetheless, my finding that late winter behaviour bore out no relationship with breeding success is interesting since I expected a priori that this could be a major source of variation. I was also limited in my interpretation by the near complete breeding failure and near complete success observed in 2015 and 2016, as this meant that some categories of my analyses were composed of very few individuals. This made it impossible to split meaningful variation from stochastic effects, but the lack of variation between these years in late winter behaviour points to a more proximate cause of breeding success. Better measures of breeding success, such as timing of breeding failure would be helpful for exploring these.

Drivers of movement patterns in late winter

Movement decisions throughout the annual cycle have the potential to shape individual reproductive success, survival and resultant fitness, but understanding how they are made, and their consequences, remains a challenge in the field of movement ecology. In this study I examined the late winter and pre-laying periods of the annual cycle in fulmars, finding sex differences but not year differences in trip-taking behaviour, as well as significant variation between individuals and (anecdotally) within individuals. I propose that the decreased likelihood of taking foraging trips and shorter trip durations in males is driven by differences in how males and females resolve the trade-off between colony visitation and time spent foraging. The tendency toward foraging in females might relate to the higher energetic costs that they incur early in the breeding season.

I also hypothesised that engaging in central place foraging during the non-breeding season might allow individuals to benefit from annually specific site familiarity in the breeding season, mechanistically linking the two seasons. As there was no evidence of carry-over effects between late winter and subsequent breeding this mechanism seems unlikely, although further exploration with high-resolution spatial data continuing into incubation would be valuable to confirm this. I found that while some individuals were consistent in returning to a single area multiple times, others visited multiple areas, suggesting that in general birds are familiar with a variety of different foraging locations. Little is known about the behaviour of immature fulmars before recruitment, but the exploration-refinement hypothesis proposes that this is when individuals develop their life-long strategy, by repeatedly revisiting areas where they are initially successful at finding food (Guilford *et al.*, 2011). In fulmars the modal age of recruitment is ten in males and twelve in females (range = 5-20 years, Dunnet, 1991), meaning that they are likely to experience a wide range of broad scale environmental conditions and may have developed site familiarity with multiple areas. This could explain the highly consistent area use, but occasional flexibility observed in mature fulmars here (Chapter 3), where individuals may have preferred movement strategies but retain prior information that reduces the potential cost of switching area under certain conditions.

The majority of birds that were studied spent more than 50% of their time within 500 km of the breeding colony, suggesting that this area forms their core range, from which they undertake longer foraging trips. However, for some individuals the inverse was observed, with birds spending as little as ~20% of their time spent in the local area, so that trips could be described as occurring in the opposite direction, visiting the colony area from their wintering ground. It would be interesting to target birds belonging to this group, to see if this behaviour is sustained over multiple years, reflecting a discrete strategy within the population, or is a temporary strategy employed under specific circumstances.

In this study I provide insight into the often-neglected late winter period in the annual cycle of northern fulmars. The combination of remaining resident to the area around the breeding colony and conducting long foraging trips from this central place, highlight the variation between individuals in allocation of time and energy. As fulmars are expected exploit favourable wind conditions to minimise the energetic costs of commuting, this highly transitory strategy might mean they are vulnerable to changes in wind regimes or local prey availability under future climate scenarios.

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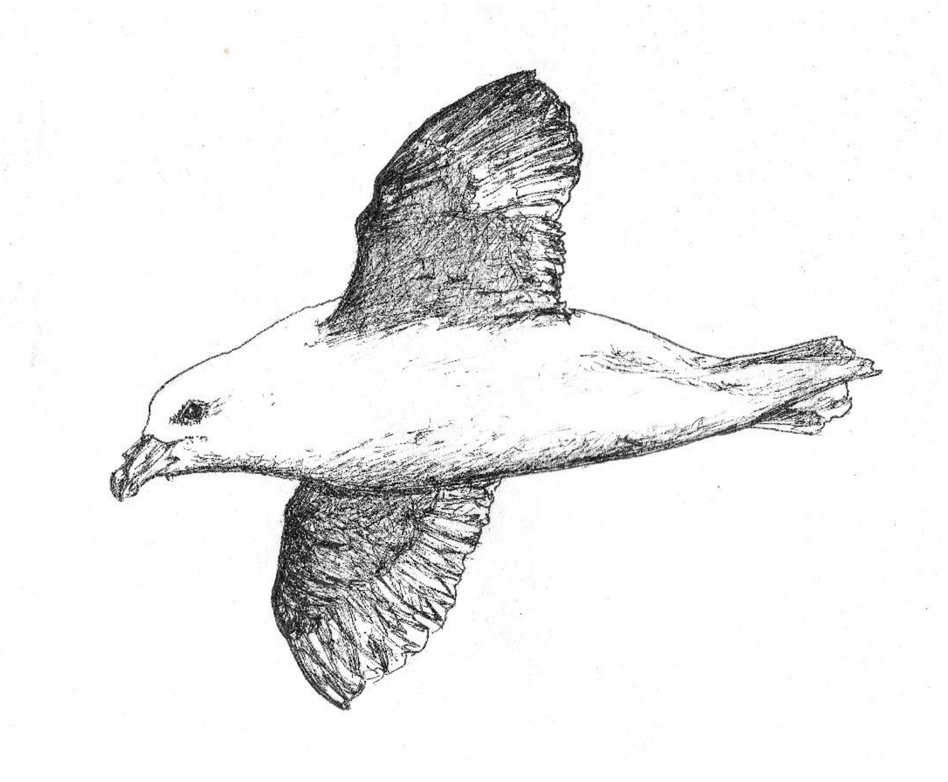
Chapter 5 Effect of wind conditions on flight dynamics



5.1 Abstract

Animal movement patterns, behaviour, reproductive success and survival are regularly linked to changes in environmental and weather conditions. Seabirds are particularly vulnerable to changes in wind patterns as they are constrained to breed on land and so must commute over large distances to access prey at sea. Consequently, Procellariiform seabirds have supreme adaptations to reduce the cost of flying, exploiting energy from wind to maximise flight efficiency. Understanding how flight dynamics and energetic expenditure are linked to wind speeds is necessary to predict the effect of future climate scenarios on population resilience.

Previous research has frequently focussed on the extremes of the different flight modes used by seabirds, including dynamic soaring, thermal soaring and continuous flapping. In this study I focus on a medium-sized Procellariiform, the northern fulmar (*Fulmarus glacialis*), which, like many other species in the family Procellaridae, uses a mix of flapping and gliding flight, the ratio of which can be adjusted in different wind conditions. This may allow them to flexibly exploit wind effects in variable wind regimes, reducing the energetic cost of flight in favourable conditions, while still permitting flight in unfavourable conditions.

I combine location data with high-resolution tri-axial accelerometry and remotely sensed wind data to describe the flight patterns of fulmars, during foraging trips from their breeding colony in the North-East Atlantic Ocean. Fulmars flew with a clear flap-glide cycle, which lasted ~3 seconds. Kinematic variables were clustered by individual, with wingbeat frequency varying between 4 and 5 Hz and root-mean-squared Z-axis dynamic acceleration varying between 6 and 8 ms^{-2} The birds tracked here used predominantly flapping flight, probably reflecting the relatively low wind speeds during the tracking period. Birds flew with reduced airspeeds in tailwinds and increased airspeeds in headwinds, which was partially but not fully explained by proportion of time spent flapping, suggesting that fulmars also make use of dynamic wind features.

5.2 Introduction

Long-term survival and successful reproduction rely on individuals successfully balancing energetic intake and expenditure (Nathan *et al.*, 2008). For species that must cover large distances to forage and locate prey, the energetics of locomotion are particularly important. As central place foragers, the movements of breeding seabirds largely comprise commutes between their land-based breeding colonies and prey located at sea. Efficient navigation and locomotion between these critical resources is therefore essential. Foraging trips require efficient strategies for searching and commuting, as the patchy distribution of prey at sea can require individuals to undertake journeys that span hundreds of kilometres (Edwards *et al.*, 2013; Dean *et al.*, 2015; Clay *et al.*, 2019; Chapter 4). Balancing speed and energetic expenditure to optimise flight during these foraging trips would reduce time away from the nest while maximising opportunities for energy gain.

The primary factor affecting individual flight efficiency is wind conditions, which at sea can be highly dynamic. If ground speed is maintained, winds in the direction of travel will reduce energetic expenditure through wind assistance, while winds opposing the direction of travel will increase energetic expenditure through increased drag. Many studies have addressed how wind conditions affect flight energetics, initially from field observations (Pennycuick, 1982; Spear & Ainley, 1997); then directly using wind tunnels (Rosén & Hedenström, 2001) and doubly labelled water (Furness & Bryant, 1996); and more recently using biologgers to measure broad- and fine-scale movements and heart rate (for example: Ropert-Coudert et al. 2006; Amélineau et al. 2014; Bishop and Butler 2015; Gibb et al. 2017; Hernández-Pliego et al. 2017).

Different seabird families have evolved a range of complementary morphologies and behavioural strategies which allow them to reduce the energetic costs of commuting or foraging, often with considerable associated trade-offs. For example, auk species such as thick-billed murres (*Uria lomvia*) trade off efficient flapping flight to maximise diving ability (Elliott *et al.*, 2013); frigatebird species (e.g. *Fregata minor*) have extremely low wing loading which allows them to use weak thermals that occur over the sea to soar to more than 1000 m and perform long distance glides, but are unable to dive as they lack waterproofing (Weimerskirch *et al.*, 2016); and albatross species have extremely high aspect-ratio wings, facilitating efficient high-speed gliding but considerably increasing the time and effort required to take-off (Sakamoto *et al.*, 2013). Auks, albatrosses and frigatebirds illustrate the extreme ends of the flap-glide spectrum (*sensu* Spear and Ainley 1997), resulting in an array of potential mechanisms that can be used to modify flight under different wind conditions for maximum efficiency.

Birds are expected to commute along the most efficient route, which in a uniform habitat should be the beeline, although in seabirds the avoidance of land causes significant deviations (Padget *et al.*, 2019). From a mechanical perspective, birds must experience a minimum airspeed passing over their aerofoil wings to generate enough lift to remain aloft, which is dependent on their mass and surface area. Airspeed is increased by converting chemical energy in the flight muscles to kinetic energy through flapping (Bishop & Butler, 2015), or by using potential energy by falling from altitude under gravity (Shepard *et al.*, 2011). Commuting time is related to ground speed rather than airspeed, which in turn results from both the movement of the bird (airspeed) and the movement of the airmass over the ground (wind speed). This means that by optimising flight direction with respect to wind direction and speed, birds can reduce flapping and energetic expenditure by exploiting favourable winds (Liechti *et al.*, 1994).

In addition to optimising wind direction and speed, the complex wind features that result from the interaction between the wind and the surface of the sea can be exploited to reduce flight costs substantially (Weimerskirch *et al.*, 2000), particularly by species belonging to the families Procellaridae and Diomedeidae. Shear or dynamic soaring occurs where an S-shaped flight path allows birds to sharply gain altitude and potential energy by turning into the wind and rising through the shear layer, caused by friction reducing wind speeds close the sea surface, followed by a glide phase in the opposite direction (Sachs, 2005). Gust soaring follows a similar mechanism, except rather than rising through the shear layer, birds fly in the protected air behind the crest of a wave, gaining altitude by turning into the faster winds above the wave (Richardson, 2011). Slope soaring can occur where wind hits waves generating orographic lift (updraft) on the windward side (Pennycuick, 1982) or as ocean waves travel through otherwise still air (Stokes & Lucas, 2021). These mechanisms are all enhanced by ground effect, where drag is reduced by disruption of the vortices caused by the movement of air over the wing, which occurs when a bird flies within a wingspan of the ground (or sea-surface) (Rayner, 1991). A combination of these processes means that smaller Procellaridae species can also optimise flight by remaining close to the sea-surface and timing flapping bouts to move between the protective lee of wave sets (Spivey *et al.*, 2014; Kempton *et al.*, 2022).

The northern fulmar (*Fulmarus glacialis*) is a medium-sized seabird, which among Procellariiformes has intermediate wing-loading, allowing comparatively easy take-offs despite high aspect-ratio (Warham, 1977). They are classified as “flap-gliders”, meaning that their dominant mode of flight should be gliding, interspersed with short bursts of flapping (Spear & Ainley, 1997). Flap-gliding gives fulmars three measurable ways by which they might kinematically vary their energetic expenditure to manipulate airspeed. Firstly, they can increase how quickly they flap, their wingbeat frequency. Secondly, they can increase the amplitude of each wingbeat as the amount of effort put into each wingbeat. Finally, they can alter the amount of time that they flap for, compared to the amount of time spent gliding. In addition to biomechanical variation, fulmars are expected to aerodynamically exploit wind features, possibly using a combination of the process described above to reduce energetic expenditure or increase airspeed. As cliff-nesting birds, their ability for slow, controlled flight around the breeding colony has been described in detail (Pennycuick & Webbe, 1959). Controlled, low-speed flight presumably comes at the cost of high-speed gliding performance, though the ability of fulmars to vary their wing shape may mitigate this trade-off to some extent (Pennycuick, 1960).

In this study I analyse the commuting flight of breeding fulmars, using high-frequency accelerometry data to: (i) describe flight patterns in terms of the flap-glide duty cycle; (ii) quantify kinematic variables and their interactions, through which energetic expenditure might be controlled; (iii) test for relationships between wind speeds and ground speeds or airspeeds; and (iv) test whether airspeed is controlled by proportion of time spent flapping. I discuss my results in the context of recent biologging studies of the related Manx shearwater (*Puffinus puffinus*) and seminal observational studies of fulmars.

5.3 Methods

Movement data were collected in 2019 by instrumenting adult fulmars that were breeding at the small colony Eynhallow (Scotland, latitude = 59.1441, longitude = -3.1201), during the chick-guard phase of breeding (9th-17th July). Full details of the fieldwork are found in Chapter 2: General Methods. Thirteen individuals were equipped with combined triaxial accelerometers and GPS loggers (AxyTrek, TechnosmArt, weight = 14 g), for up to 7 days, to collect high-resolution data from fulmars while they were foraging away from the colony. On logger retrieval, birds were weighed, photographed with a wing outstretched above a 10 cm grid and wing loading was calculated (mass / wing area).

Location data processing

All data processing, visualisations and analyses were performed in the program R (R Core Team, 2015) using the packages stated and general packages: *data.table* (Dowle & Srinivasan, 2021), *ggplot2* (Wickham, 2016), *scales* (Wickham & Seidel, 2022), *plotrix* (Lemon, 2006), *patchwork* (Pedersen, 2019), *ggsn* (Santos Baquero, 2019), *raster* (Hijmans, 2019) and *zoo* (Zeileis & Grothendieck, 2005). Combined data loggers recorded a burst of 15 locations at 1 Hz every 10 minutes, and recorded acceleration in three axes continuously at a rate of 100 Hz. GPS data were filtered to remove locations with low certainty (< 3 satellites, horizontal dilution of precision > 10) (Ranacher *et al.*, 2016; Gupte *et al.*, 2022).

To identify individual foraging trips the locations from each individual were overlaid with an outline of Eynhallow (Office for National Statistics, 2019) including a 100 m buffer (package: *sf* (Pebesma, 2018)). Positions occurring over land or within the buffer were removed. Each time a bird left the buffer zone was considered a new trip. Trips shorter than 6 hours were removed as often birds that are disturbed will remain close to the colony, resting on the water before returning to the nest. Trips were visually checked and in one instance manually split into two trips, as a gap of eight hours between fixes occurred near the colony. This was likely to be caused by the logger losing signal while the bird attended the nest.

Each burst of locations were grouped, representing an “observation” window of high-resolution spatial data which was used to infer the behaviour of the bird. Bursts consisting of less than eight fixes or with gaps of more than one second between fixes were removed. Additionally, the first two positions of each burst were removed, as initial visualisations of bursts indicated movements that were more erratic between these points, and on this logging schedule positions later in the burst should have higher accuracy (TechnoSmArt, 2018). To identify bursts that were likely be commuting flight, I ran a Gaussian mixture model on ground speed, which was calculated as the sum of the distance travelled between consecutive locations in each burst (package: *geosphere* (Hijmans, 2021)) divided by time. I $\log_e$-transformed the data to accentuate the peaks in the distribution, after adding one to all values to ensure positive values after transformation (Freeman *et al.*, 2010). The mixture model was run with three components (package: *mixtools* (Benaglia *et al.*, 2009)) to assign each burst the probability of belonging to three possible states, corresponding to the expected behaviours of resting on the water, foraging, and commuting (Fayet *et al.*, 2015). For all subsequent analyses I retained only the high-speed state, corresponding to commuting flight.

Calculation of movement and wind vectors

In order to quantify the movement of the bird with respect to wind conditions during each burst, I compared the ground speed, airspeed and wind speed vectors, where the length of each vector corresponded to speed in metres per second (ms^{-1}). Descriptions and equations for all terms are shown in **Table 5-1**. The ground speed vector (Gv) was composed of speed (as above) and direction of travel, calculated as the bearing between the first and the last location within the burst (package: *geosphere* (Hijmans, 2021)).

The zonal and meridional winds at 10 m altitude for the location of each burst were downloaded from the European Centre for Medium-Range Weather Forecasts ERA5 reanalysis dataset (one hour temporal resolution, 0.25 degree spatial resolution, (Hersbach *et al.*, 2018)). From these the wind speed vector (Wv) was calculated as the wind speed and the direction it was blowing towards. I subtracted the wind direction from the direction of travel to calculate the direction of travel relative to the wind direction (θ), so that 0° indicated a tailwind and 180° indicated a headwind. I then used the law of cosines to estimate the airspeed vector (Av), defined as the speed of the bird relative to the air, and the heading of the bird relative to the wind (γ). The diagram in **Figure 5-1** illustrates these vectors.

Table 5-1: Definitions and equations for wind, movement and accelerometry terms.

Abbreviation	Name	Description	Equation
Gv	Ground speed vector	Bird speed and direction relative to ground	distance / time
Av	Airspeed vector	Bird speed and direction relative to air	$\sqrt{(AWC_{ground}^2 + (Gv - TWC_{ground})^2)}$
θ	Theta	Direction of travel relative to wind direction	wind direction – bird direction
γ	Gamma	Direction of heading relative to wind direction	$\theta \pm \cos^{-1}((Av^2 + Gv^2 - Wv^2) / (2 \times Av \times Gv))$
TWC_{ground}	Tail wind component relative to ground speed vector	Wind speed in same direction as bird travel	$\cos(\theta) \times Wv$
AWC_{ground}	Across wind component relative to ground speed vector	Wind speed perpendicular to bird direction of travel	$\sin(\theta) \times Wv$
TWC_{air}	Tail wind component relative to airspeed vector	Wind speed in same direction as bird heading	$\cos(\gamma) \times Wv$
AWC_{air}	Across wind component relative to airspeed vector	Wind speed perpendicular to bird heading	$\sin(\gamma) \times Wv$
WBF	Wingbeat frequency	Number of wingbeats per second	total wingbeats / time
VeDBA	Vectoral dynamic body acceleration	Measure of dynamic acceleration in three axes	$\sqrt{(X_{dyn}^2 + Y_{dyn}^2 + Z_{dyn}^2)}$
RMSZ	Root-mean-squared Z-axis dynamic acceleration	Measure of dynamic acceleration in Z-axis only	$\sqrt{(\sum Z_{dyn(1)}^2 + Z_{dyn(N)}^2 / N)}$
Power	Power in the body	Proxy for work done over time	$RMSZ^2 / WBF$

Using trigonometry, I decomposed wind speed into wind in the direction of movement (tail wind component, "TWC") and perpendicular to the direction of movement (across wind component, "AWC"), when compared to both the ground speed and airspeed vectors. This allowed me to describe the strength of wind compared to movement of the bird with either the ground or the air as the frame of reference. For the tail wind component, negative values indicated flying into a headwind, whereas positive values indicated flying with a tail wind. For the across wind component, differences in flight dynamics between winds from the left or right of the bird were not expected, and so the absolute value was used, resulting in all positive values.

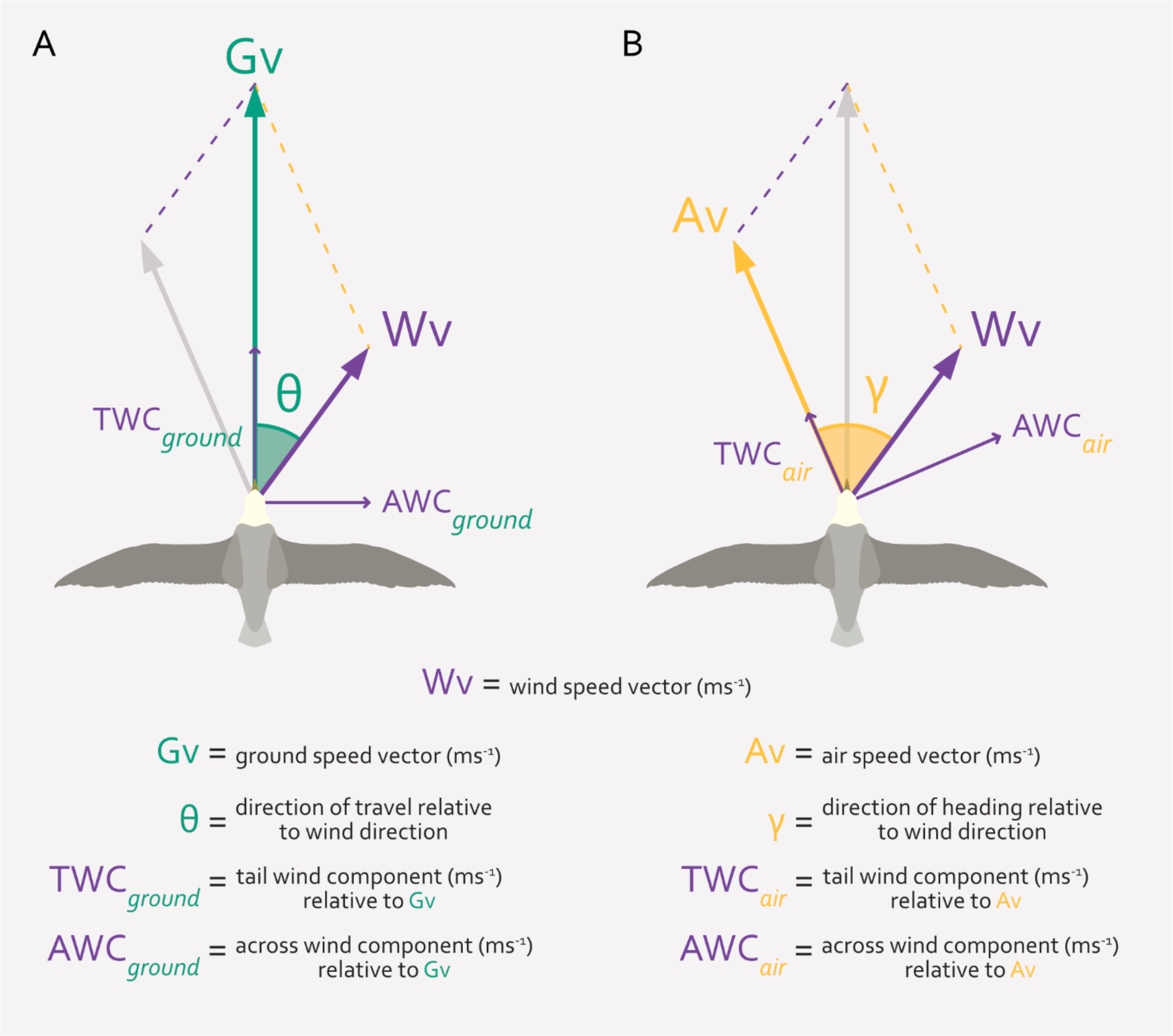


Figure 5-1: Calculation of wind speeds relative to (A) movement of the bird with respect to the ground (ground speed vector) and (B) movement of the bird through air (airspeed vector). Wind speeds are decomposed into the tail wind and across wind components, calculations found in Table 5-1.

Processing of acceleration data

Tri-axial accelerometers measure acceleration in three directions, made up of the surge (X), sway (Y) and heave (Z) axes, which correspond to forwards, sideways and upwards movement, respectively. Acceleration data were used to quantify several flight characteristics, which quantified different ways by which birds might adjust their energetic expenditure in response to different wind conditions. Fulmars utilise a mix of flapping and gliding flight, so "duty cycles" were identified within each burst as a bout of flapping, followed by a glide. The main variables of interest were: wingbeat frequency ("WBF"), representing how quickly birds flapped; root-mean-squared Z-axis dynamic acceleration ("RMSZ"), a proxy for energetic expenditure associated with flapping (Spivey & Bishop, 2013); and proportion of time flapping during the duty cycle, where birds can reduce expenditure by extending the time gliding between bouts of flapping. Definitions and equations are included in **Table 5-1**.

For each bird, each burst of locations that was identified as consisting of commuting behaviour was matched in time to the acceleration data. The 15 seconds before and after the burst were included to allow the duty cycles to start and finish outside of the observation window. This meant that the acceleration data were analysed in sections of approximately 15 seconds, although the length was greatly increased in some cases that contained long periods of gliding. Dynamic acceleration was calculated independently in each axis by subtracting each value from the 1-second running mean and taking the absolute value. This removes an estimation of static acceleration due to gravity and the variable orientation of the logger (Shepard *et al.*, 2008). These values were combined into a single measure of acceleration in any direction, VeDBA, as the square root of the sum of each axis squared.

To calculate wingbeat frequency, I used the zero-crossing algorithm described in Spivey et al 2014, which transforms raw acceleration in the heave (Z) axis to centre around zero, then records each time the transformed signal crosses zero, from negative to positive, indicating a full wingbeat (Spivey *et al.*, 2014). Transformation involved smoothing by half the expected length of a wingbeat (0.2 seconds), then taking the differences between the values and smoothing again, repeating this three times.

In order to separate flapping from gliding flight, I calculated the running mean of the absolute of transformed Z and assigned high values as flapping flight and low values as gliding flight. A threshold of 0.011 was chosen manually after viewing a frequency histogram of all acceleration values, shown in **Supplementary 5-2**. Changes between flapping and gliding with a duration of less than the expected wingbeat length were ignored. To calculate wingbeat frequency the number of zero-crossings that occurred during flapping flight was divided by the time (in seconds) spent in flapping flight. Mean RMSZ was also calculated during flapping flight only. To understand the relationship between WBF and RMSZ I calculated a proxy for power in the body as $RMSZ^2/WBF$ (Spivey & Bishop, 2013) as an estimate of work done per second. Individual duty cycles were then grouped as a burst of flapping, followed by a period of gliding. Duty cycles that started and finished outside of the observation window for each burst were retained to maximise the number of complete duty cycles. This extended window was used to calculate the proportion of time spent flapping so that 0.5 corresponded to equal time flapping and gliding and 1 corresponded to continuous flapping. Examples illustrating the steps of the zero-crossing algorithm and examples of predominantly flapping and predominantly gliding flight are shown in **Figure 5-2**.

Bursts were plotted to visually check that the algorithm had successfully labelled flapping within the duty cycle. Two bursts were excluded from further analysis as they did not contain any flapping bouts. Eighteen bursts were removed because they included either a take-off or a landing, often resulting in an extended bout of flapping, and were likely to have a different relationship with wind direction. Additionally, some duty cycles included wingbeats with very high values of VeDBA, resulting from an intense side-to-side movement in the Y-axis, and thought to be caused by the bird shaking (Guilford *et al.*, 2022; Carlo Catoni 2021, personal communication, 13th December). This elevated acceleration was unlikely to be related to flight dynamics, and so thirty duty cycles which contained wingbeats with more than four records of VeDBA that exceeded 3 g (29.4 ms^{-2}) were removed. The rest of the duty cycles in these bursts were retained.

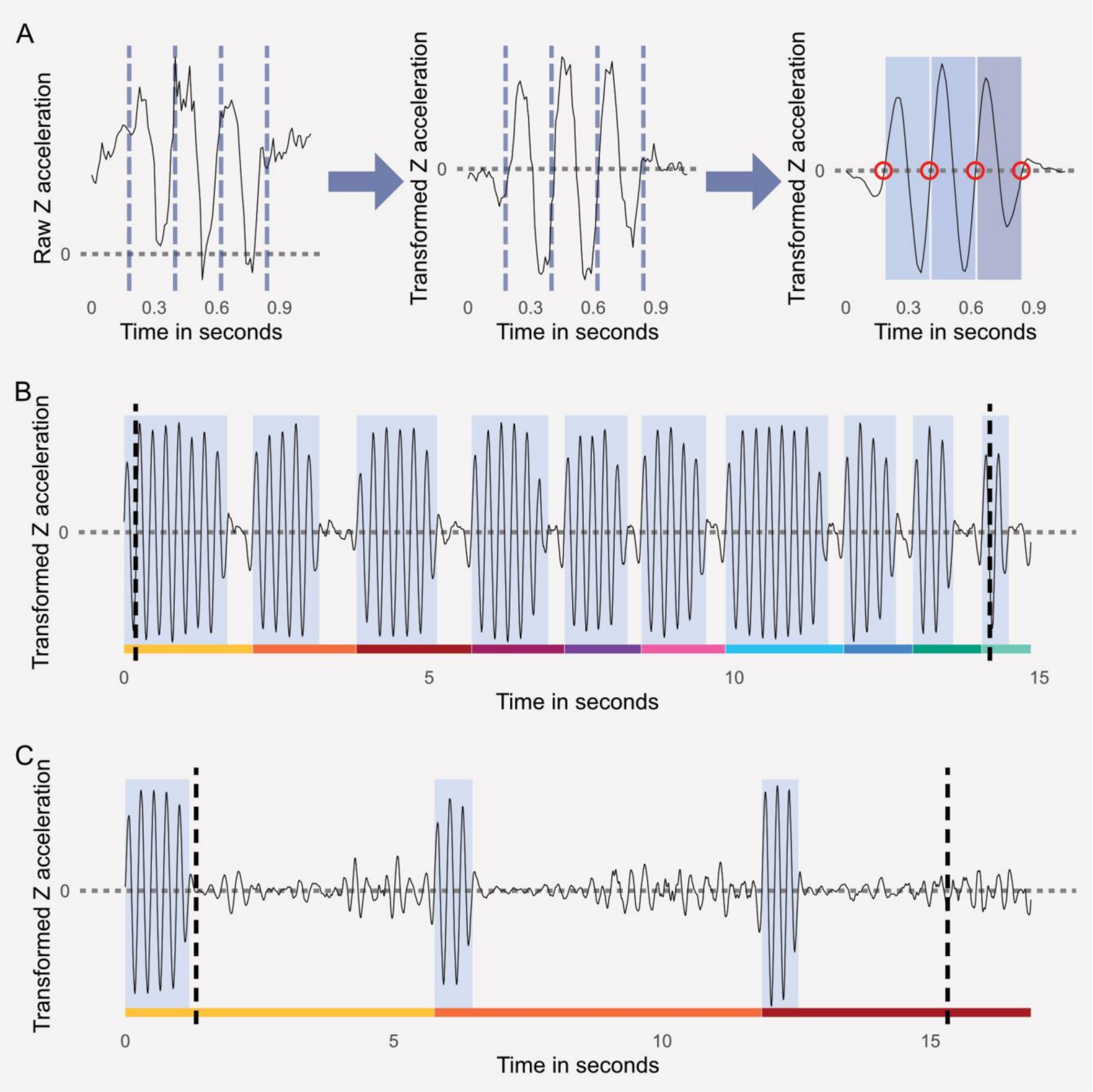


Figure 5-2: Processing of Z-axis acceleration to derive wingbeat frequency and duty cycle. (A) shows three individual wingbeats (upright dashed lines) and how these are isolated from raw Z-axis acceleration (left), after transformation around zero (centre) and after smoothing (right), with individual wingbeats shaded in blue and zero-crossing points circled in red. (B) and (C) show example observation windows and duty cycles with predominantly flapping flight and predominantly gliding flight respectively. Observation windows, coinciding with high-frequency GPS locations are shown with vertical dashed black lines, with individual duty cycles allowed to start and finish outside of this period. Individual duty cycles are indicated by the coloured horizontal ribbon along the bottom of each plot and bouts of flapping are shaded blue.

Data analysis

To describe how flight was structured, summaries of each burst were used to describe the variation in time spent flapping, time spent gliding, duty cycle duration, number of duty cycles and number of wingbeats to construct frequency histograms. To understand the variation in energetic variables between individual I constructed frequency histograms of WBF, RMSZ, power in the body and proportion of time flapping. Of the four flight characteristics, wingbeat frequency, RMSZ and power in the body describe the individual wingbeats, whereas proportion of time spent flapping describes the duty cycle. To explore whether birds change how they flap with how much they flap, I plotted the first three variables against proportion of time spent flapping but as the data were strongly clustered by individual, I did not formally test this.

To understand how ground speed and airspeed were affected by tail and across wind speeds I ran separate linear mixed effects models (LMMs) for each, with bird ID included as a random intercept (package: *lme4* (Bates *et al.*, 2015)). Residual plots were checked to ensure model fit. Likelihood ratio tests were used to compare each model to their respective null intercept-only model, retaining bird ID as a random effect, to obtain p-values. I followed the same process to test whether proportion of time flapping predicted either ground speed or airspeed, as initial exploration suggested that this should be the primary source of variation in energetic input by the bird. When reporting model outputs, 95% confidence intervals are included in square brackets.

Due to differing trip lengths, there was large variation in the number of observations that were analysed for each individual. Additionally, due to stable wind conditions during the study period, observations at higher wind speeds were composed of a single individual. Although mixed-effects models should be fairly robust to such data (Schielzeth *et al.*, 2020), I re-ran all statistical analyses on a subset of data where wind speed was between 2 and 7 ms^{-1}. Results from these models are present in **Supplementary 5-3** for completeness and highlighted in the main text where they differ from the full dataset.

5.4 Results

Summary of foraging trips and wind conditions

Ten loggers were successfully retrieved from thirteen deployments. Of the three birds where the logger was not retrieved, one bird was recaptured after three days but had removed the logger, one nest failed soon after tagging meaning the bird could not be recaptured and one bird continued to attend the nest with its partner but evaded capture. Of the ten successful deployments, four birds had completed two foraging trips, resulting in fourteen trips in total (**Table 5-2**). Trip one by bird 1952 was retained despite remaining much closer to the colony than all other trips, as the bird spent time in all three behaviours.

Table 5-2: Biometric information for the ten tracked birds, ordered by increasing values of wing loading. Details of the fourteen distinct foraging trips taken, including the number of bursts that were analysed after being assigned to commuting behaviour. The temporal overlap of trips between birds is shown in ***Supplementary 5-1****.*

Bird	Sex	Mass / g	Single wing area / cm^2	Wing loading / g cm^{-2}	Trip no.	Duration / hours	Maximum distance colony / km	No. commuting locations
2005	F	590	515	0.57	1	48.08	319.46	123
1881	F	595	507	0.59	1	6.67	30.78	14
1489	M	815	601	0.68	1	11.33	85.13	29
1977	M	860	629	0.68	1	21.67	119.75	47
1888	M	880	619	0.71	1	13.83	53.92	14
					2	12.1	49.32	15
1952	M	865	593	0.73	1	11.67	8.91	5
					2	28.33	199.03	71
1580	M	965	645	0.75	1	13	42.23	16
					2	10.51	44.88	15
1149	M	975	633	0.77	1	18.47	52.5	16
1986	M	830	531	0.78	1	49.5	207.04	96
1924	M	810	515	0.79	1	16.52	63.31	19
					2	16.57	143.31	39

All except one bird travelled north or north-west from the colony to forage (**Figure 5-3**). Bird 2005 travelled to the east and foraged mid-way to Norway (maximum distance from the colony = 319km) before returning along a similar route. Of the other trips, four travelled further than 100km from the colony. Foraging destinations for these longer trips appeared to be associated with two locations along the edge of the continental shelf on the boundary with deeper water.

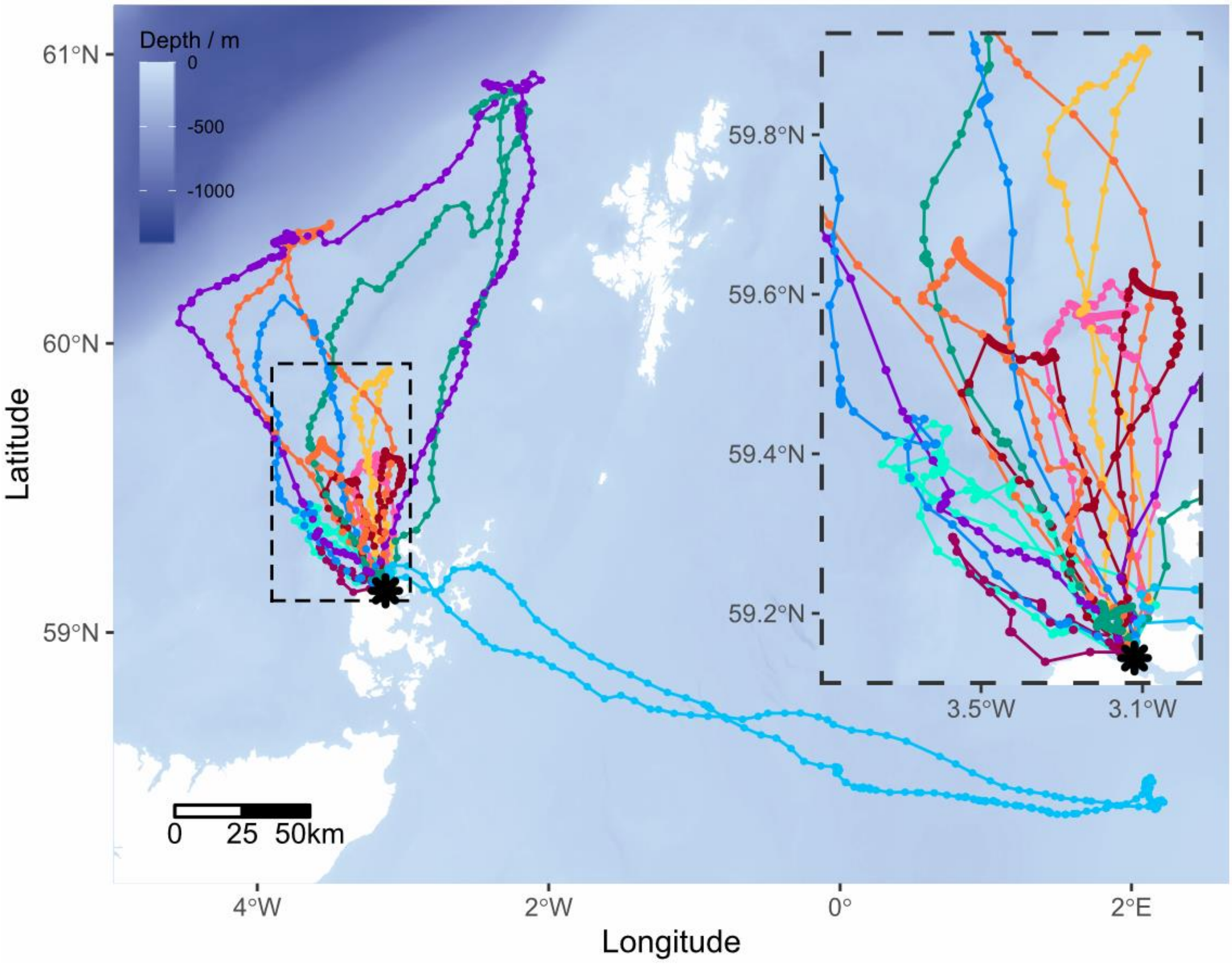


Figure 5-3: Locations from GPS for the ten tracked birds, coloured by individual. Eynhallow is marked by the black star. Shading to show bathymetry (GEBCO Bathymetric Compilation Group, 2020), *with darker blue representing deeper water, to highlight longer northwards trips visiting the shelf edge. Colours for individuals consistent with later plots.*

The fourteen trips resulted in 1623 bursts, which were each assigned using a three-state mixture model to a behaviour, according to ground speed **Figure 5-4**. I expected a tri-modal distribution of speeds, with low, medium and high-speed clusters corresponding to resting on the water, foraging and commuting respectively. Estimates of log-likelihood suggested a two-state model was also supported by this data but made negligible difference to the assignment of the high-speed state, which was of interest here. The estimated mean for the low-speed state was 0.82 ms^{-1} (SD = 0.16 ms^{-1}), for the medium-speed state was 1.62 ms^{-1} (SD = 0.37 ms^{-1}) and for the high-speed state was 11.39 ms^{-1} (SD = 0.21 ms^{-1}). I retained only bursts that were most likely to belong to the high-speed state or commuting flight, resulting in 539 bursts. Following processing of the acceleration data, 519 bursts were retained for all subsequent analysis.

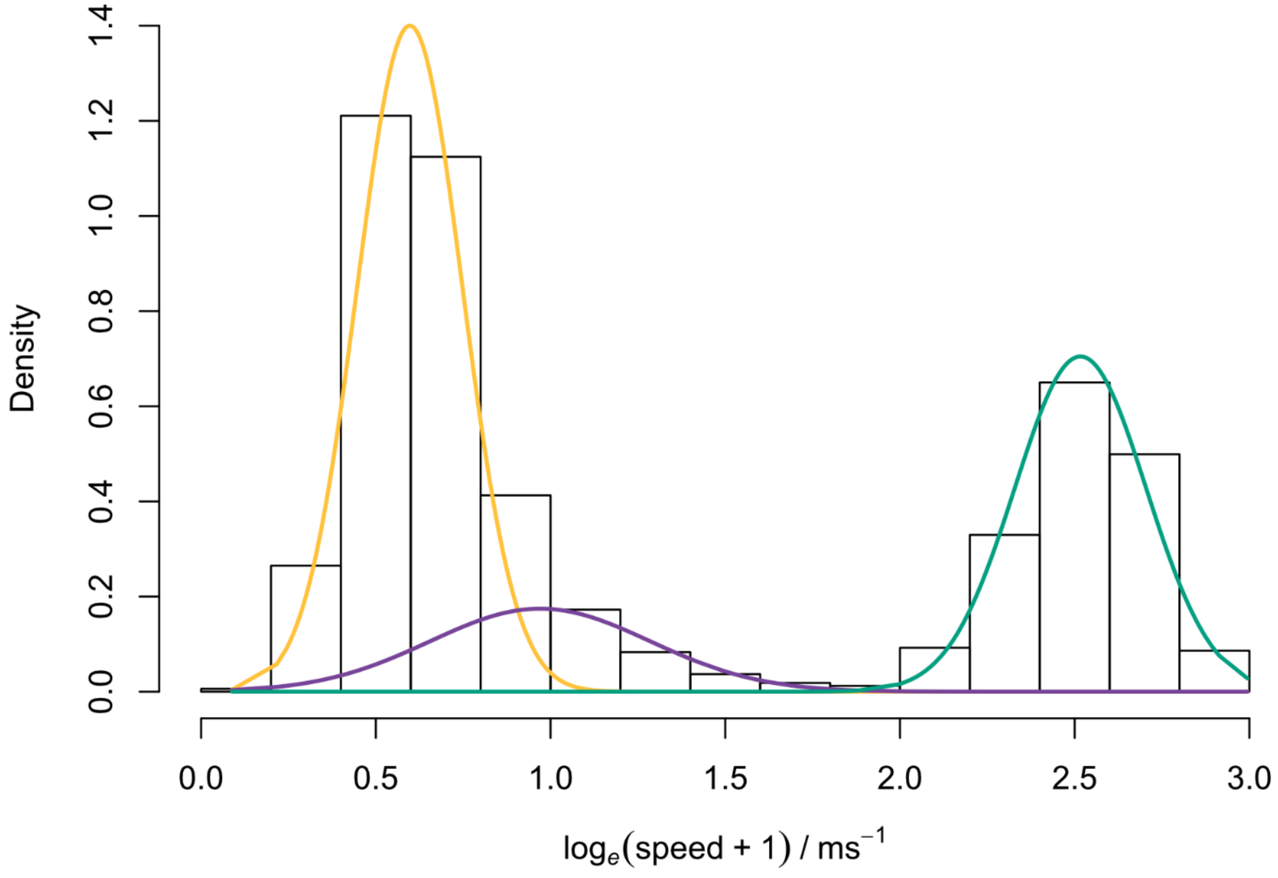


Figure 5-4: Output of the three-state mixture model used to assign bursts to sitting on the water, foraging and commuting behaviours. Histogram shows the distribution of the data, with the yellow, purple and green lines showing the modelled distributions of the three states. High-speed (commuting) state in green retained for subsequent analyses.

Wind conditions experienced by birds during commuting flight were relatively stable. The mean wind speed was 4.9 ms^{-1} (minimum = 0.4 ms^{-1}, maximum = 9.7 ms^{-1}) although the distribution was skewed towards the slower wind speeds. Throughout the tracking period, winds stronger than 8 ms^{-1} were experienced by only one bird (2005). The most prevalent wind direction was from the north-west, which is also the direction of the strongest winds (**Figure 5-5**). Lighter winds also occurred from the west, north-east and south-east. As all except one bird travelled north-west, this meant that most birds experienced a range of wind directions relative to their direction of travel, although the wind strength was more limited. However, there was a lack of absolute tailwinds and headwinds, with most bursts experiencing an aspect of crosswinds.

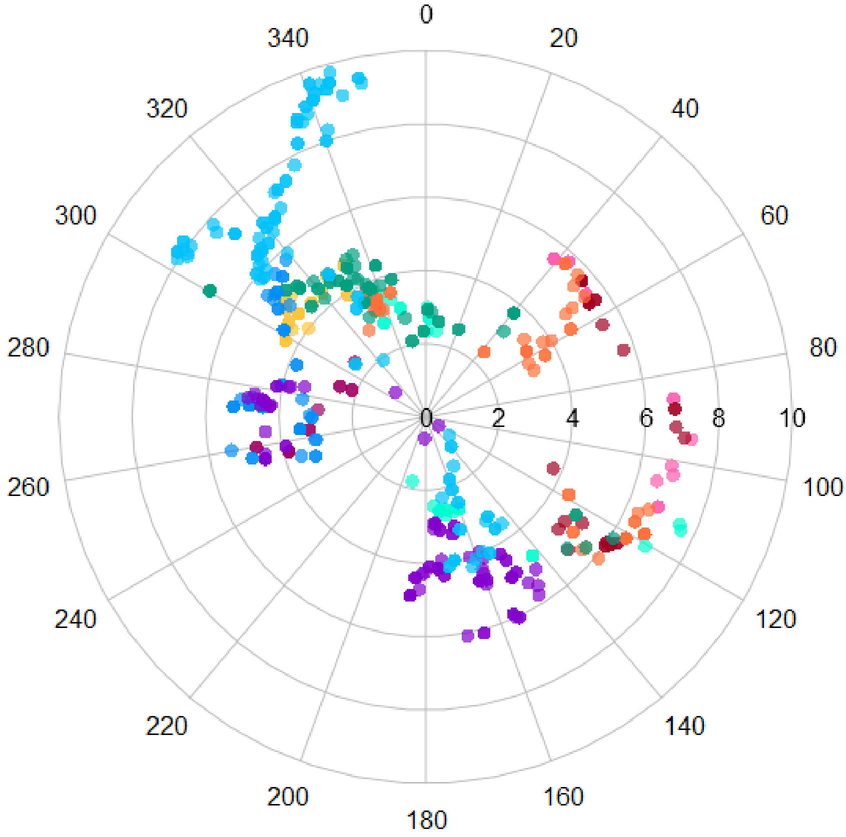


Figure 5-5: Polar plot of wind speed and direction experienced by all bursts assigned to commuting flight. Angle corresponds to the direction that the wind was blowing from in degrees, where zero is north. Speed in metres per second (ms^{-1}) corresponds to distance from centre. Points coloured by individual.

Descriptive flight characteristics

Fulmars flew with a consistent pattern of a bout of flapping, followed by a period of gliding. The only times I found continuous flapping was during take-offs (which were easy to identify visually as variation in Z-axis acceleration was much lower when sitting on the water than when gliding) and were excluded from this analysis. Duty cycles were remarkably consistent in length, with few that were recorded lasting longer than 5 seconds. The mean duty cycle duration was 3.16 seconds, and the mean number of duty cycles was 5.81, as a consequence of the 15-second observation window. As duty cycles longer than 15 seconds were possible, the observation window was extended to include the start and finish of all duty cycles. Mean flapping duration (1.80 seconds) was longer than mean gliding duration (1.36 seconds), although the distribution of gliding duration had a longer tail skewing towards longer durations. The mean number of wingbeats in a duty cycle was 8.15, with higher number of wingbeats per duty cycle associated with almost continuous flapping. Frequency histograms summarising duty cycle metrics are shown in **Figure 5-6**.

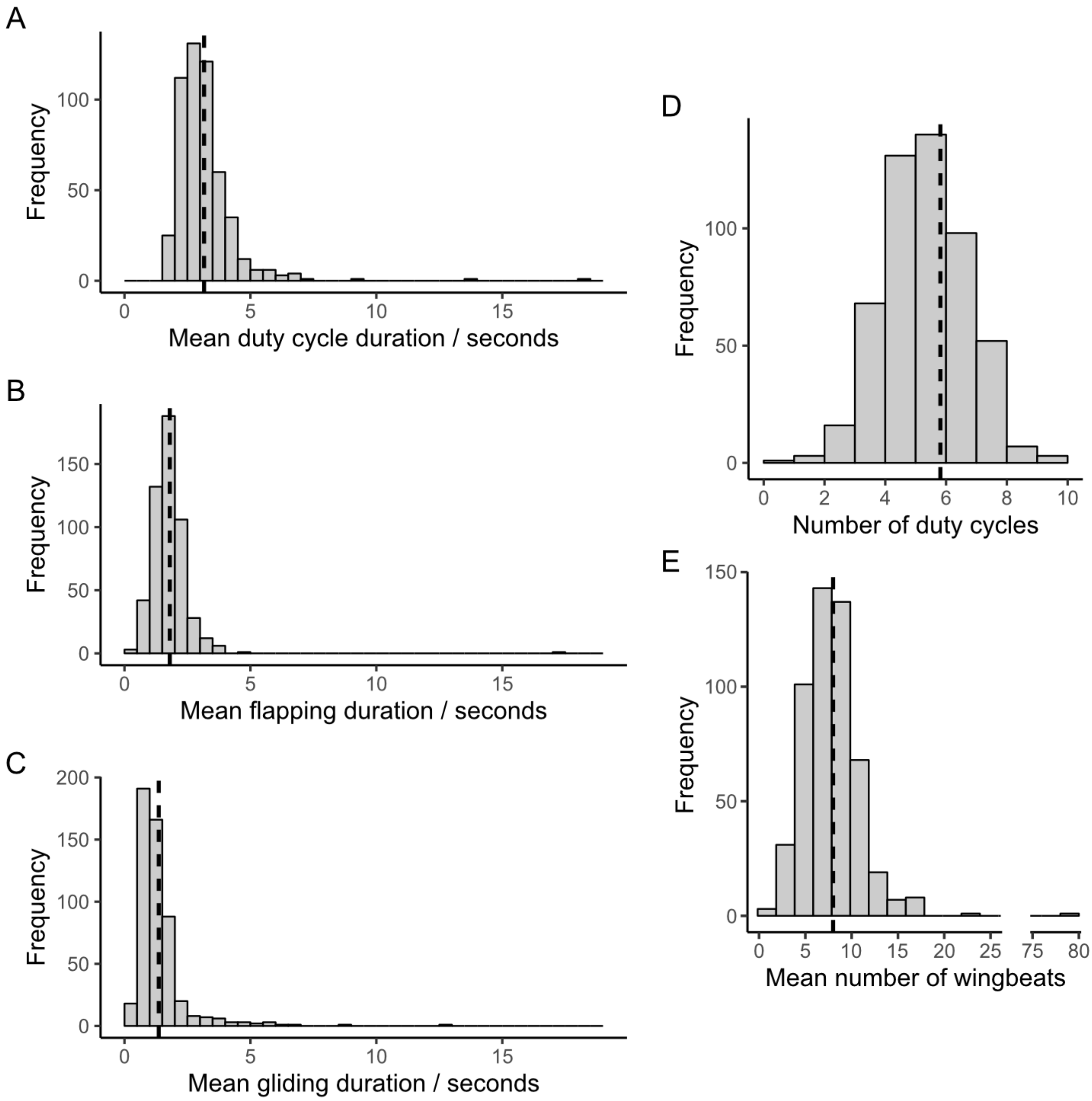


Figure 5-6: Frequency histograms showing the distributions of mean duty cycle metrics in each of 519 observation periods. (A) Mean duty cycle duration, consisting of a bout of flapping followed by a period of gliding. (B) Mean flapping duration per duty cycle. (C) Mean gliding duration per duty cycle. (D) Number of duty cycles in the observation period. (E) Mean number of wingbeats in a duty cycle. Black dashed line shows mean of all observation periods.

I explored the individual distributions of the four energetic flight characteristics through which I hypothesised birds might manipulate their energetic expenditure, shown in **Figure 5-7**. Overall mean wingbeat frequency was 4.52 Hz, with almost all values lying between 4 Hz and 5 Hz. Individuals appeared to occupy a subset of this distribution, with only bird 2005 observed flying at the full range of wingbeat frequencies. Mean RMSZ during flapping was 6.34 ms^{-2} and in general increased with higher wing loading. Power in the body followed a similar pattern to RMSZ, resulting from the wider range of RMSZ. Mean power in the body was 8.98 $m^2 s^{-3}$, although the individual means for all except two birds were below this. Birds 1986 and 1924 had higher power in the body, resulting from higher RMSZ, and for bird 1986, lower wingbeat frequency. Proportion of time spent flapping was also highly variable, with a mean of 0.59 but ranging between 0.05 and 0.92. Distributions were fairly spread, and strongly skewed towards predominantly flapping flight, except for bird 1489, which spent more time in gliding flight than flapping flight (although this was based on relatively few observations). Bird 2005 also spent a large amount of time in predominantly gliding flight and was observed using almost the full range of possible duty cycles.

Figure 5-8 explores whether there is variation in wingbeat frequency, RMSZ and power in the body, depending on the proportion of time spent flapping. As there was clustering by individual, I explored these relationships separately. For bird 2005, which experienced the widest range of wind conditions and flew with the most variation in proportion of time spent flapping, wingbeat frequency increased with the proportion of time spent flapping, while RMSZ while flapping and power in the body while flapping decreased with proportion of time spent flapping. Both RMSZ and power in the body were also more variable when less time was spent flapping. When all individuals were compared, a positive relationship between proportion of time spent flapping and wingbeat frequency was observed in all except one bird (which had the fewest data points), although there were differences between birds in the strength of this relationship and the variation around it. There were no clear relationships that were consistent between most individuals between RMSZ or power in the body while flapping and proportion of time spent flapping. For birds 1986 and 1924, the intercept was higher (as expected from **Figure 5-7 C**) for both RMSZ and power in the body while flapping, although the relationships remained flat.

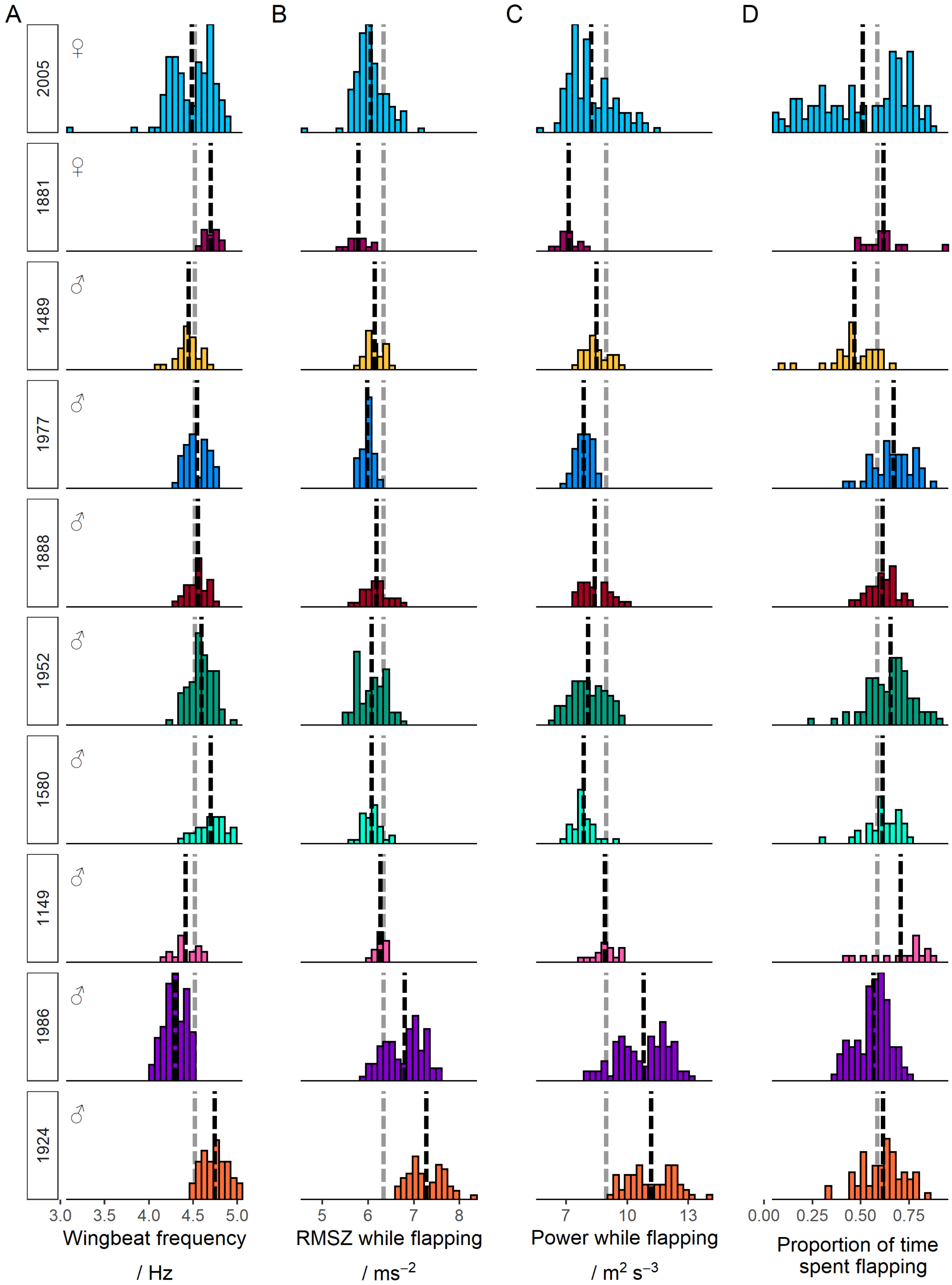


Figure 5-7: Frequency histograms of the flight characteristics of interest, split by individual. (A) Wingbeat frequency. (B) RMSZ while flapping. (C) Power in the body while flapping. (D) Proportion of time spent flapping. Birds are ordered from top to bottom by increasing wing loading. For A-C values are a mean for each burst. Grey dashed line shows the mean for all birds and black dashed line shows individual means.

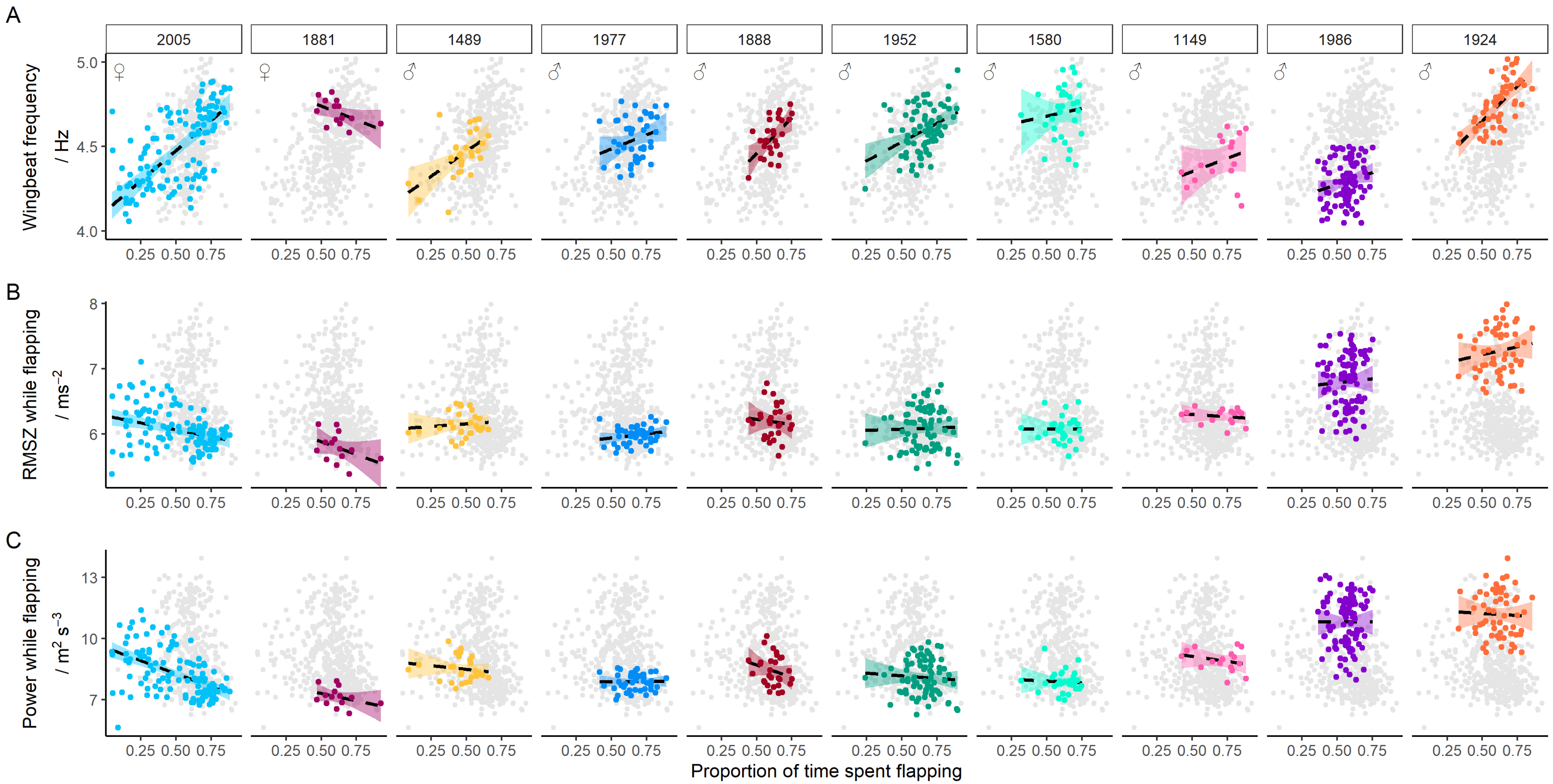


Figure 5-8: *Relationship between proportion of time spent flapping and (A) wingbeat frequency, (B) RMSZ while flapping and (C) power in the body while flapping, split by individual. Birds are ordered left to right by increasing wing loading. For interest, linear relationships are shown with a black dashed line and shaded 95% confidence intervals, although these relationships are not formally tested as data from some individuals showed heteroscedasticity and clustering. Points in light grey show full dataset of all individuals, to highlight clustering within individuals. Three data points were removed from plots to aid visualisation (bird 2005, WBF = 3.10 and 3.85, RMSZ while flapping = 4.65) but retained in analysis.*

Relationship between flight characteristics and wind speeds

All model outputs are reported in **Table 5-3**. I tested whether ground speeds and airspeeds were predicted by the direction and speed of the wind that was experienced by the bird. There was a strong positive relationship between the tailwind component relative to the ground (TWC_{ground}) and the ground speed of the bird (LMM; likelihood ratio test; χ^2 = 497.75, *df* = 1, *p-value* < 0.0001), with strong headwinds associated with low ground speeds and strong tailwinds associated with high ground speeds (**Figure 5-9 A**). When TWC_{ground} was 0 ms^{-1}, ground speed was estimated to be 11.90 [11.54, 12.26] ms^{-1} and increased by 0.52 [0.48, 0.56] ms^{-1} for every metre per second increase in TWC_{ground}. There was a strong negative relationship between the tail wind component relative to the air (TWC_{air}) and the airspeed of the bird (LMM; likelihood ratio test; χ^2 = 391.01, *df* = 1, *p-value* < 0.0001), with the highest airspeeds occurring in headwinds and the lowest airspeeds occurring with tailwinds (**Figure 5-9 D**). When TWC_{air} was 0 ms^{-1}, airspeed was estimated to be 12.01 [11.65, 12.36] ms^{-1} and decreased by 0.43 [0.40, 0.47] ms^{-1} for every metre per second increase in TWC_{air}.

When I considered across wind speeds, the relationships with ground speed and airspeed were less clear. Ground speeds decreased as the across wind component relative to the ground (AWC_{ground}) increased (LMM; likelihood ratio test; χ^2 = 7.09, *df* = 1, *p-value* = 0.0077). Ground speed was estimated to be 12.23 [11.73, 12.73] ms^{-1} when AWC_{ground} was 0 ms^{-1} and decreased by 0.14 [0.04, 0.24] ms^{-1} for every metre per second that AWC_{ground} increased (**Figure 5-9 B**). However, this relationship appeared to be driven by the lower ground speeds observed for bird 2005 when AWC_{ground} was more than 7 ms^{-1}, as when a reduced subset of the data was analysed, this relationship was no longer significant (**Supplementary 5-3 B**). There was also a weak negative relationship between the across wind component relative to the air (AWC_{air}) and airspeed (LMM; likelihood ratio test; χ^2 = 27.18, *df* = 1, *p-value* < 0.0001), which was estimated to be 13.41 [12.95, 13.86] ms^{-1} when AWC_{air} was 0 ms^{-1} and decreased by 0.25 [0.15, 0.34] ms^{-1} for every metre per second that AWC_{air} increased (**Figure 5-9 E**).

As the relationship between energetic variables was clustered by individuals, I tested whether fulmars moderated their ground speed and airspeed through proportion of time spent flapping. Proportion of time spent flapping did not predict ground speed (LMM; likelihood ratio test; χ^2 = 2.28, *df* = 1, *p-value* = 0.1307) (**Figure 5-9 C**). There was a weak positive relationship between proportion of time spent flapping and airspeed (LMM; likelihood ratio test; χ^2 = 5.07, *df* = 1, *p-value* = 0.0244), where airspeed was predicted to be

11.86 [11.08, 12.63] ms^{-1} when birds did not flap at all and increased by 0.13 [0.02, 0.24] ms^{-1} for every increase of 10% of proportion of time spent flapping (**Figure 5-9 F**). When I considered only the subset of data where wind speeds were between 2 and 7 ms^{-1} this relationship became stronger (**Supplementary 5-3 F**), suggesting that the lack of observations where the proportion of time spent flapping was low might be masking a non-linear relationship.

Table 5-3: Model outputs for LMMs shown in ***Figure 5-9****, where figure letters correspond to labels in plot. For all models bird ID was included as a random intercept and p-values were calculated by using likelihood ratio tests to compare each model to a null model with the explanatory variable removed. 95% confidence intervals are shown in square brackets. Model estimates for subset data (wind speeds between 2 and 7* ms^{-1}*) are shown in* ***Table 5-4 (Supplementary material)****.*

Figure	Response	Explanatory	Intercept	Slope	χ^2	*df*	*p-value*
A	ground speed	TWC_{ground}	11.90 [11.54, 12.26]	0.52 [0.48, 0.56]	497.75	1	< 0.0001
B	ground speed	AWC_{ground}	12.23 [11.73, 12.73]	-0.14 [-0.04, -0.24]	7.09	1	0.0077
C	ground speed	proportion of time flapping	11.19 [10.34, 12.04]	0.98 [-0.31, 2.26]	2.28	1	0.1307
D	airspeed	TWC_{air}	12.01 [11.65, 12.36]	-0.43 [-0.40, -0.47]	391.01	1	< 0.0001
E	airspeed	AWC_{air}	13.41 [12.95, 13.86]	-0.25 [-0.15, -0.34	27.18	1	< 0.0001
F	airspeed	proportion of time flapping	11.86 [11.08, 12.63]	1.30 [0.17, 2.44]	5.07	1	0.0244

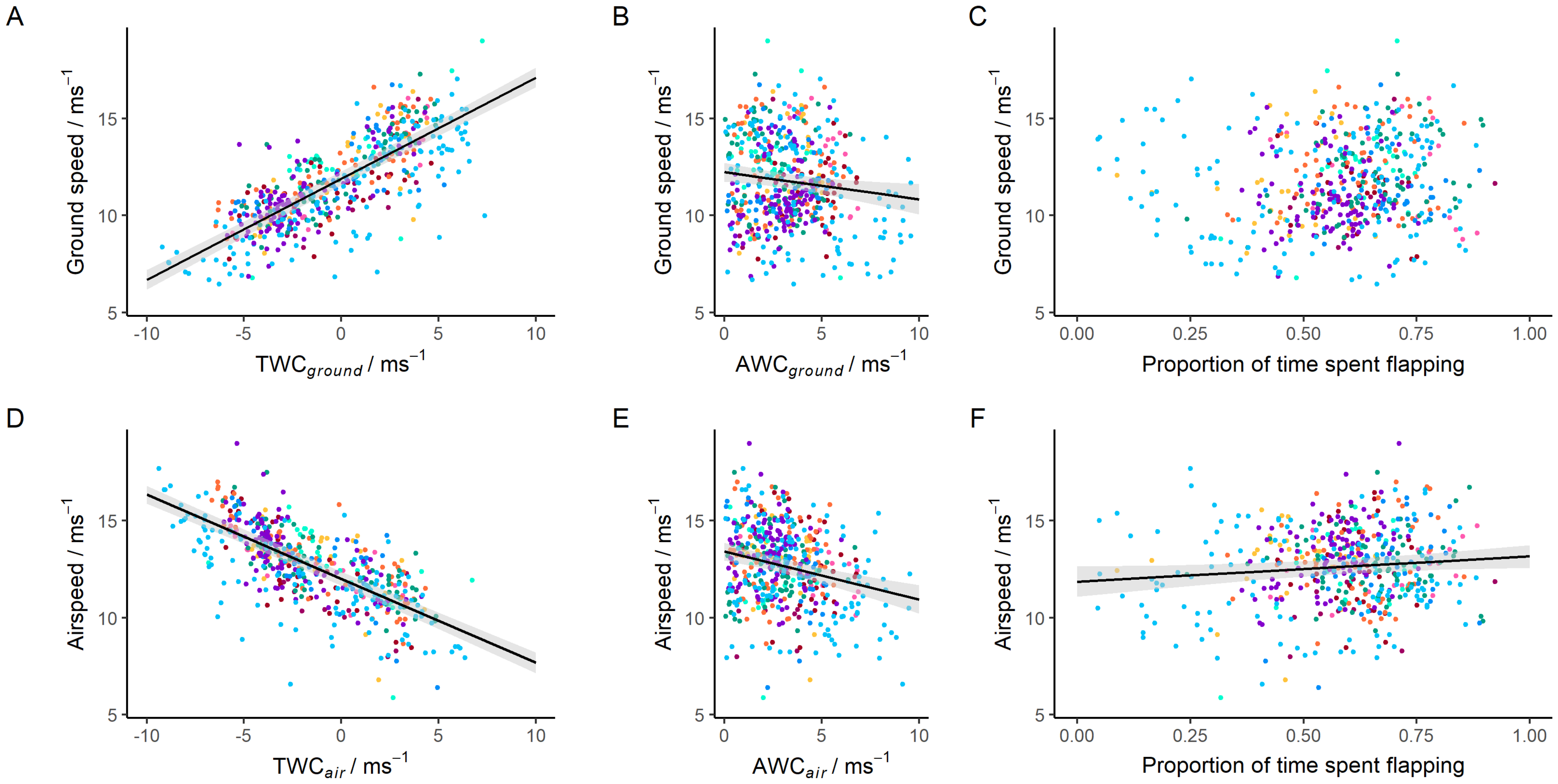


Figure 5-9: Effect of (A and D) tail wind speeds, (B and E) across wind speeds and (C and F) proportion of time flapping on ground speeds (top row) and airspeeds (bottom row). Fitted LMMs are shown in black with shaded grey 95% confidence intervals for significant relationships. Raw datapoints are also shown, coloured by individual. When only wind speeds between 2 and 7 ms^{-1}are included the relationship in (B) becomes non-significant and the relationship in (F) becomes stronger (for figure and details see ***Supplementary** 5-3*).

5.5 Discussion

Breeding fulmars were tracked during chick-rearing foraging trips using combined tri-axial accelerometers and GPS loggers to characterise their flight patterns, quantify energetic expenditure and understand how this interacts with wind conditions. There was a strong cyclic pattern of flapping followed by gliding flight, with relatively short duty cycles and higher than expected proportion of time spent flapping. Both wingbeat frequency and root-mean-squared Z-axis dynamic acceleration ("RMSZ") clustered by individual, resulting in relatively consistent power in the body while flapping. This suggested energetic expenditure was fairly uniform while flapping, leaving proportion of time flapping as the main mechanism by which birds might manipulate their ground and airspeeds. When I considered the effect of wind speeds on both ground speeds and airspeeds, I found that ground speeds increased with tailwind speeds, while airspeeds decreased with tailwind speeds. Two-fold variation in observed airspeeds suggested that fulmars are able to manipulate their airspeeds, as flight in a completely consistent way should result in a flat relationship between wind speed and airspeed. However, the weak positive relationship between proportion of time spent flapping and airspeed suggests that in fulmars, variation in airspeed is also likely to result from other sources, such as exploiting the wind features that result from air flows across the uneven surface of the sea.

Fulmars were expected to use predominantly gliding flight, as they are described as flap-gliders (Spear & Ainley, 1997) and are renowned for their impressive gliding abilities that they exhibit around the breeding colony (Pennycuick & Webbe, 1959). However, fulmars in this study spent a high proportion of time flapping, flying with generally short duty cycles and on average flapping almost two thirds of the time. This is likely to be due partly to the relatively low wind speeds that were recorded during the tracking period, with only one bird encountering wind speeds in excess of 8 ms^{-1}. The same bird was also the only bird to be recorded regularly in predominantly gliding flight and was the only bird to be recorded using almost the full range of duty cycles (from almost constant gliding to almost constant flapping). Notably, across all birds tracked, constant flapping was only observed during take-offs. This behavioural flexibility demonstrates that fulmars are not mechanically constrained to specific duty cycles but might be unable to flap continuously for prolonged periods, given that duty cycles on average lasted ~ 3 seconds (**Figure 5-6 A**).

Flight speeds in relations to wind speeds

I found that in fulmars airspeeds were increased in headwinds and decreased in tailwinds (**Figure 5-9 D**). This relationship is predicted by Pennycuick (Pennycuick, 1978) and confirmed in fulmars through field observations (Pennycuick, 1960; Spear & Ainley, 1997). Recent biologging studies recorded similar relationships between tailwind speeds and airspeeds in European shags (*Gulosus aristotelis*) (Kogure *et al.*, 2016) and black-legged kittiwakes (*Rissa tridactyla*) (Collins *et al.*, 2020) both of which use primarily flapping flight and were found to manipulate airspeed by increasing wingbeat strength. Here, proportion of time flapping explained a small amount of the variation in airspeed. I also found a weak effect of crosswind speeds on airspeed, with airspeeds decreasing with increasing crosswind speeds. How to interpret this is less clear as the effect of crosswinds will depend on the relative angle to the wind and the extent to which birds compensate for wind drift (Liechti *et al.*, 1994). Crosswinds allow some species to achieve fast and efficient flight through shear soaring (Weimerskirch *et al.*, 2000; Richardson *et al.*, 2018), trading off ground speed for potential energy by height gain through the wind gradient (Richardson, 2011). As the proportion of time spent flapping in this study is high, it is unlikely that this relationship is influenced by shear soaring.

The intercepts for the relationships between ground speed and wind speed (**Figure 5-9 A** and **B**) and airspeed and wind speed (**Figure 5-9 D** and **E**), all give estimates for ground speeds and airspeeds of fulmars in the absence of all wind, which should be equivalent. These intercepts range between 11.90 and 13.41 ms^{-1}, which is similar to previous estimates of 13.0 ms^{-1} from land-based observations (Pennycuick, 1987). Estimates of airspeeds will be less accurate when birds follow a more tortuous flight path associated with dynamic soaring (Richardson *et al.*, 2018). In general, fulmars in this study had low tortuosity, which was partially accounted for by calculating ground speed throughout the burst of locations rather than between the first and last position. However, when considering the effect of flight patterns on airspeeds, it is important to highlight that estimated airspeed will differ from the instantaneous airspeeds experienced by the bird.

Flight style of fulmars

Compared with diving species of Procellariiformes, fulmars are better adapted for take-offs and landings and exhibit extreme flight control and soaring abilities around the breeding colony. They manipulate their surface area through wing-morphing and use of their tail and feet, allowing fine control in manoeuvring flight while exploiting updrafts around cliffs (Pennycuick & Webbe, 1959), although these features are proposed to represent a trade-off against being able to achieve high groundspeeds in strong winds (Pennycuick, 1960) and perhaps reduce their ability to shear soar. I propose that these abilities might also make fulmars more efficient during predominantly flapping flight in low winds, making use of ground effect and updrafts around waves. A recent study highlighted the importance of slope-soaring in brown pelicans, suggesting that following wave lines could significantly reduce flight costs, even in calm wind conditions (Stokes & Lucas, 2021). It is conceivable that fulmars could use similar behaviours to instead manipulate airspeed whilst maintaining energetic expenditure.

Fulmars are expected to shift towards predominantly gliding flight to reduce energy expenditure when they encounter fast enough wind speeds. This was suggested by Furness and Bryant (1996) who found a negative relationship between wind speeds and both field metabolic rate and overall wingbeat frequency (Furness & Bryant, 1996). In birds with a flap-gliding style, research into understanding the mechanism(s) by which energy is harvested from the wind is ongoing (Richardson, 2011; Spivey *et al.*, 2014; Gibb *et al.*, 2017; Kempton *et al.*, 2022). In Manx shearwaters, this shift towards predominantly gliding flight occurs at wind speeds of 8 ms^{-1} (Gibb *et al.*, 2017). Manx shearwaters have a similar breeding range to the fulmars tracked here, and have comparable wing loading, although lower body weight and lower wing aspect ratio (Warham, 1977). Anecdotally, bird 2005 appears to shift to mainly gliding flight around wind speeds of 7 ms^{-1} although this was not explored further here. During this study, birds experienced a restricted range of wind directions and wind speeds, compared to what they would be expected to encounter throughout the annual cycle. The mean wind speed of 4.9 ms^{-1} observed during tracking was slightly less than the historical mean for July of 5.4 ms^{-1} (Kirkwall Airport 1991-2000 (Met Office, 2020)) and much lower than the historical mean for January (8.2 ms^{-1}), although at-sea wind speeds will be higher and sometimes much more extreme (98th percentile of November to March wind speeds throughout the North Atlantic, ≤ 18 ms^{-1} (Laurila *et al.*, 2021)). Similar Procellariiform species are recorded to maintain flight throughout the range of wind speeds that they might seasonally encounter, suggesting that fulmars are also unlikely to rest on the sea (Nourani *et al.*, 2023). I would therefore expect gliding flight to be important to fulmars in reducing their energetic expenditure outside of the breeding season.

Optimisation of flight speeds

Formal analysis of the relationship between energetic variables was not conducted, as it was difficult to separate clustering caused by individual from the narrow range of winds experienced. RMSZ while flapping appeared to increase with wing loading (**Figure 5-7 B**), meaning that birds with a higher mass to wing area must input more energy into flapping. Wingbeat frequency was clustered by individual, and varied in how it interacted with RMSZ, resulting in a wide range of values for power in the body within individual. The two individuals that had higher mean body power values also had the highest values of wing loading, arising from having a similar wing area to the those with the lowest wing loading, but weighing over 200 g more. This highlights how fluctuation in body weight when returning to feed the chick is also likely to interact with flight kinematics.

Wingbeat frequency appeared to increase with proportion of time spent flapping, which was similar to the relationship observed in Manx shearwaters (Spivey *et al.*, 2014), although this was not tested. In bird 2005, the only bird for which there are observations throughout the range of duty cycles, both RMSZ and body power are higher and more variable when a lower proportion of time is spent flapping. Based on this, I speculate that during predominantly flapping flight, energetic input is relatively uniform, with some moderation of power in the body through wingbeat frequency. Original calculations by Pennycuick (1960) of the available power generated by the pectoralis muscles predicted level flight speeds of 8.8 ms^{-1}, which was lower than expected (Pennycuick, 1960) but suggests that fulmars may have limited extra capacity in their power output in sustained flight. However, if the glide phase permits recovery from brief flapping bouts with high power output, this would allow fulmars to respond to instantaneous and unpredictable wind conditions (such as gusts between waves) with more explosive wingbeats, resulting in the variation seen in bird 2005.

Optimisation of flight speeds is generally discussed in terms of minimum power speed (V_{mp}, the speed that uses the least energy per unit of time) and maximum range speed (V_{mr}, the speed which uses the least energy per distance flown) (Pennycuick, 1978), with most birds flying at speeds somewhere in between (Alerstam *et al.*, 1993; Pennycuick *et al.*, 2013). However, it has been suggested that during central place foraging birds should fly faster than the maximum range speed in order to increase the rate of food transport (Hedenström, 2002; Elliott & Gaston, 2005). Tracking was conducted during the chick-guard phase of breeding, when chicks are vulnerable to predation and have not reached thermal independence, meaning that one adult must always attend the nest and foraging trips are short. Despite this, I found that mean airspeed (12.7 ms^{-1}) was closer to the predicted minimum power speed (10.5 ms^{-1}) than maximum range speed (17.4 ms^{-1}) (Pennycuick, 1987). This was surprising, given the strong relationship between tailwind speeds and airspeed, which is predicted when birds fly at maximum range speed (Alerstam *et al.*, 2019). The observed distribution of airspeeds was very similar to that found by Pennycuick (1987) (**Supplementary 5-4**), with both studies covering the same time-period. Once technology allows, understanding whether this trend towards minimum power speeds is reflected throughout the non-breeding period would enhance our understanding of how fulmars optimise their flight speeds. For example, Eurasian skylarks (*Alauda arvensis*) fly close to minimum power speeds during song flights, but far exceed their maximum range speeds during migration (Hedenström & Alerstam, 1996).

Decisions regarding optimal flight speeds might relate to whether the target is known on departure, or whether birds are searching along the way. Other seabird species with similar morphologies have been found to fly preferentially with crosswinds (Ventura *et al.*, 2020, 2022; Kempton *et al.*, 2022) to increase the opportunity for soaring flight, or time their flights to benefit from predictable tailwinds (Dehnhard *et al.*, 2021). In this study, all except one foraging trip departed in a north to north-westward direction from the colony, although they varied in maximum distance and areas visited. This might be in response to wind conditions on departure (broadly cross- headwinds) or birds might be exploiting predictable resource patches, with some appearing to associate with the shelf break (**Figure 5-3**) (Freeman *et al.*, 2010). A larger sample size with more variable wind conditions would be needed to explore this further.

Considerations for future work

I explored four ways by which birds might be able to kinematically vary their energetic input while flying within the framework of the duty cycle: wingbeat frequency, RMSZ, power in the body (representing a combination of WBF and RMSZ) and proportion of time spent flapping. While there was a small effect of proportion of time flapping on airspeed, it seems likely that fulmars are also able to adjust their airspeeds through use of fine-scale wind features that occur locally around waves, even if wind speeds are too low to allow for shear soaring. Exploring static acceleration and corresponding signals in pitch and roll would be valuable to identify micro-adjustments in the body position throughout the duty cycle.

Additionally, collection of higher resolution GPS data would enable the interrogation of the spacing of GPS fixes throughout the duty cycle and fine scale changes in altitude (Gibb *et al.*, 2017), which both might contain signals of the birds interacting with wind features. For both approaches, the zero-crossing algorithm used here (Spivey *et al.*, 2014) to isolate individual wingbeats would be helpful to allow analysis at this timescale.

This study adds to our growing understanding of how seabirds are affected by and make use of the wind. Much of the current literature focusses either on species that use predominately flapping flight, or on species found in the southern hemisphere where they experience seasonally predictable wind conditions (Wakefield *et al.*, 2009; Raymond *et al.*, 2010; Tarroux *et al.*, 2016; Clay *et al.*, 2020; Dehnhard *et al.*, 2021). Species that use a mix of flapping and gliding flight and occupy ranges with varied and unpredictable wind regimes are likely to utilise a mixture of flight styles, resulting in complex relationships with wind conditions. Quantifying these relationships is important to understand the likely impacts of changing wind regimes through climate change. Additionally, I highlight the value of combined sensors and high frequency accelerometry data for decomposing the components of flight, allowing insight into mechanistic questions of how animals move.

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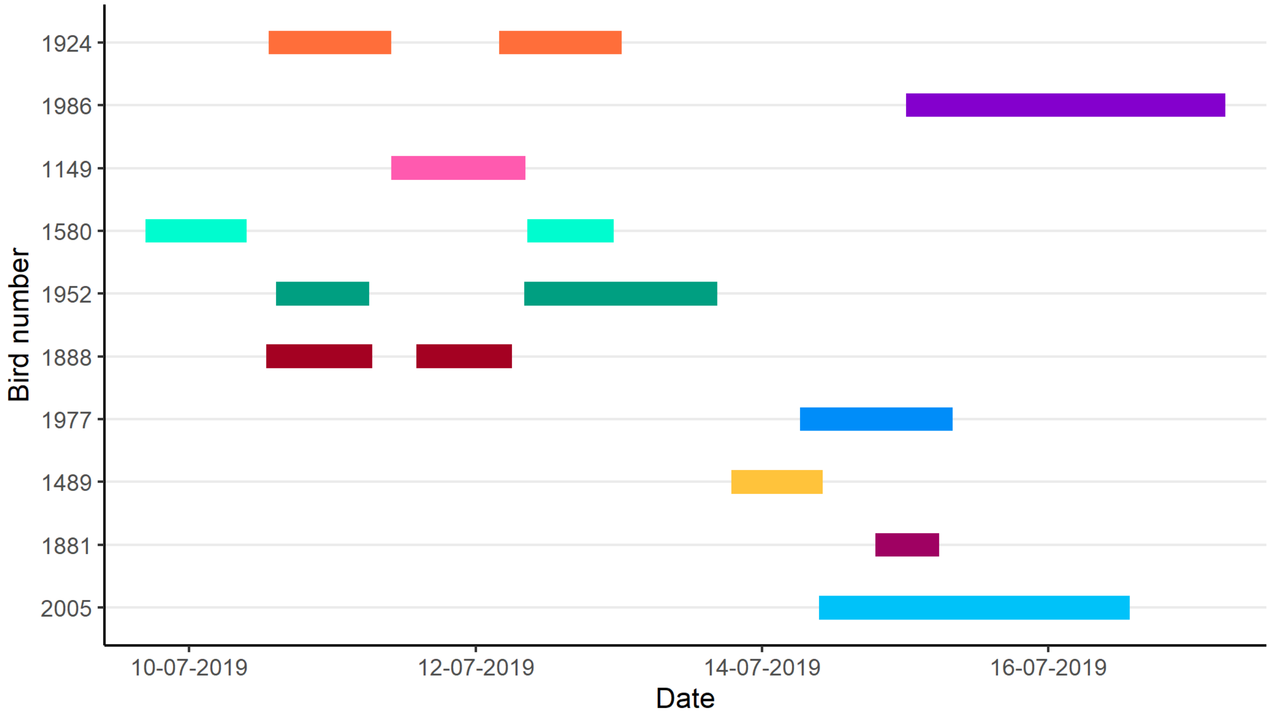
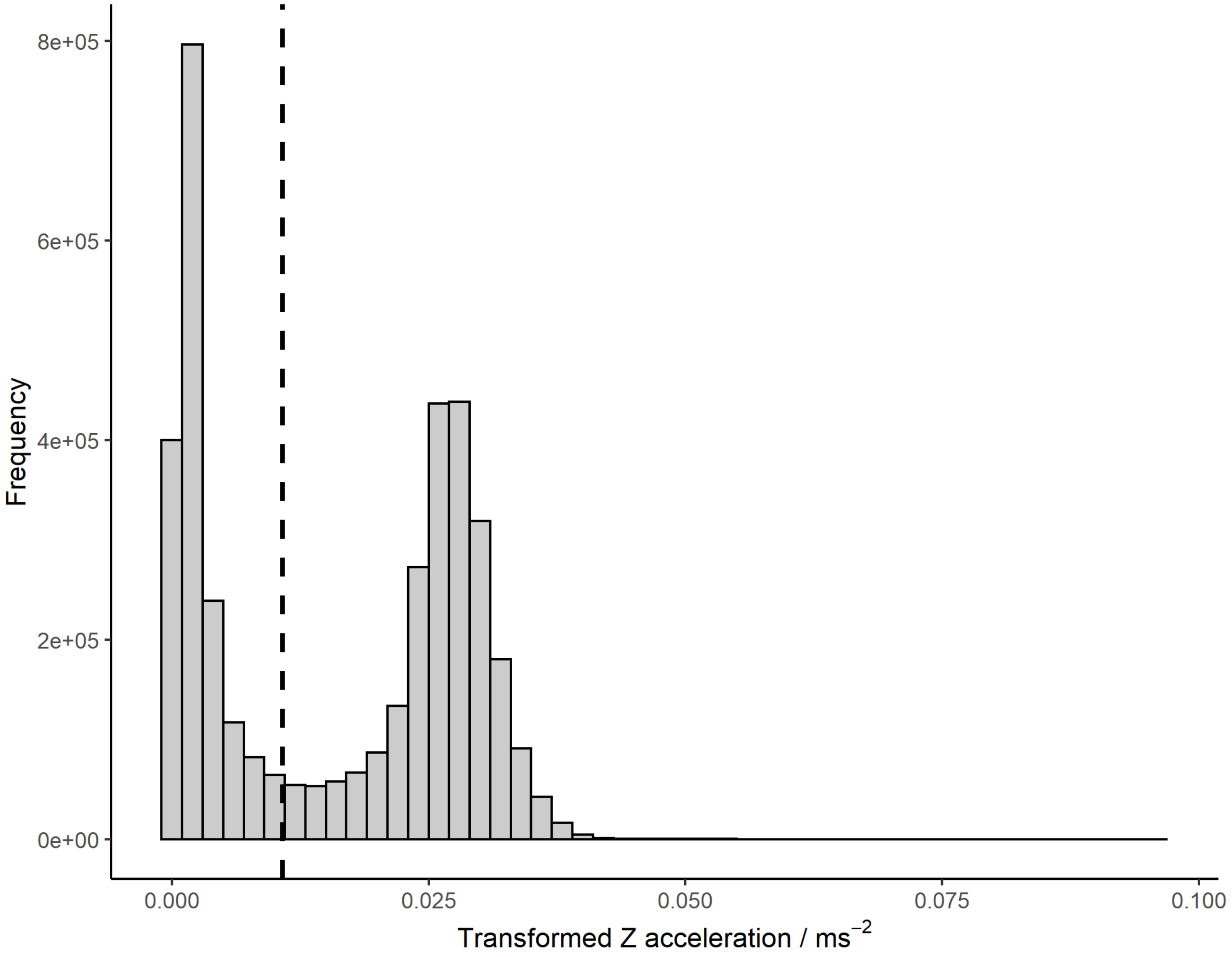
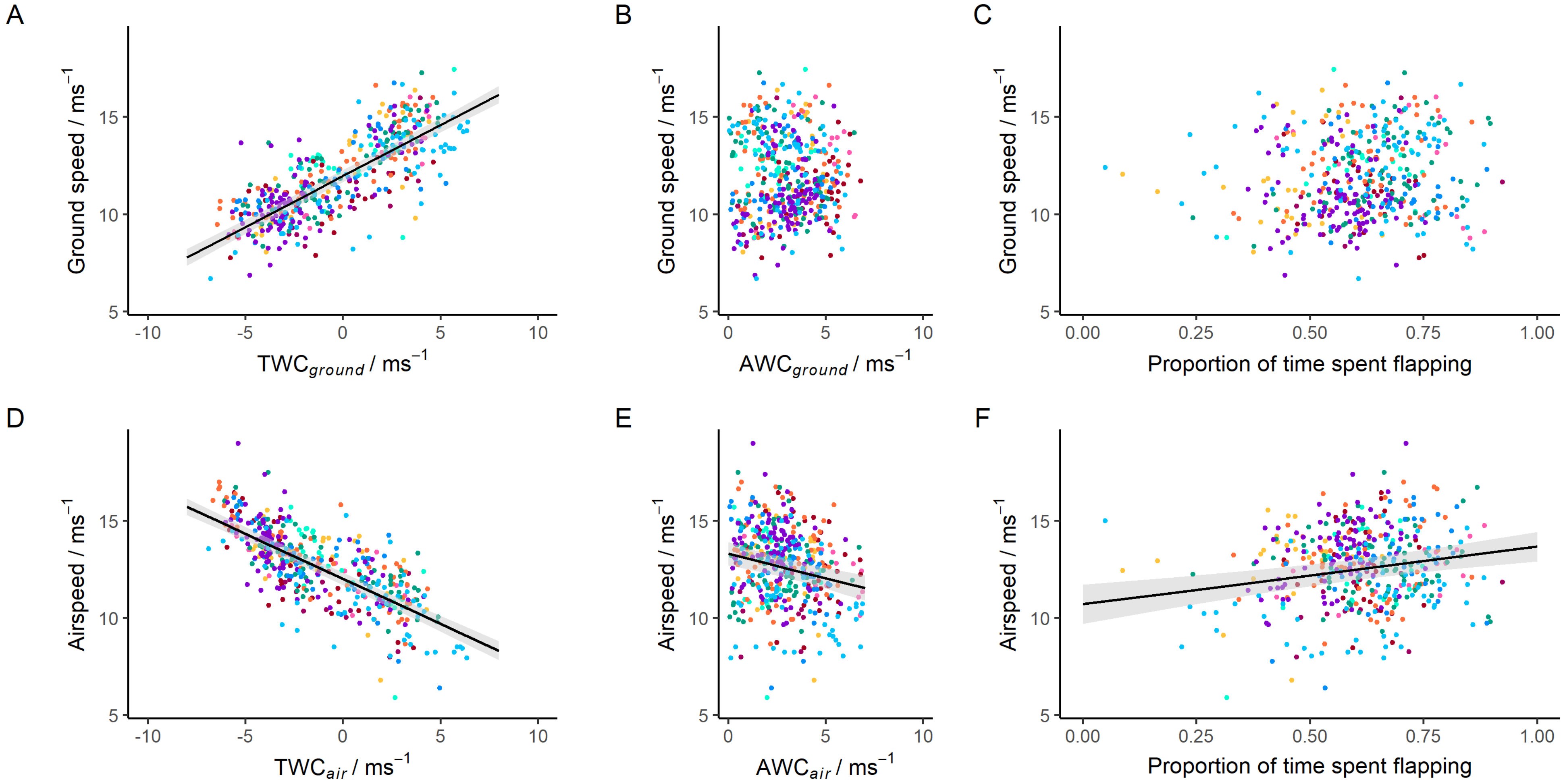
5.6 Supplementary material



Supplementary 5-1: *Timeline showing the degree of temporal overlap between foraging trips, with coloured bars indicating when birds were at sea. Stints away from the colony that lasted less than 6 hours are not shown, as they were not retained in this study.*



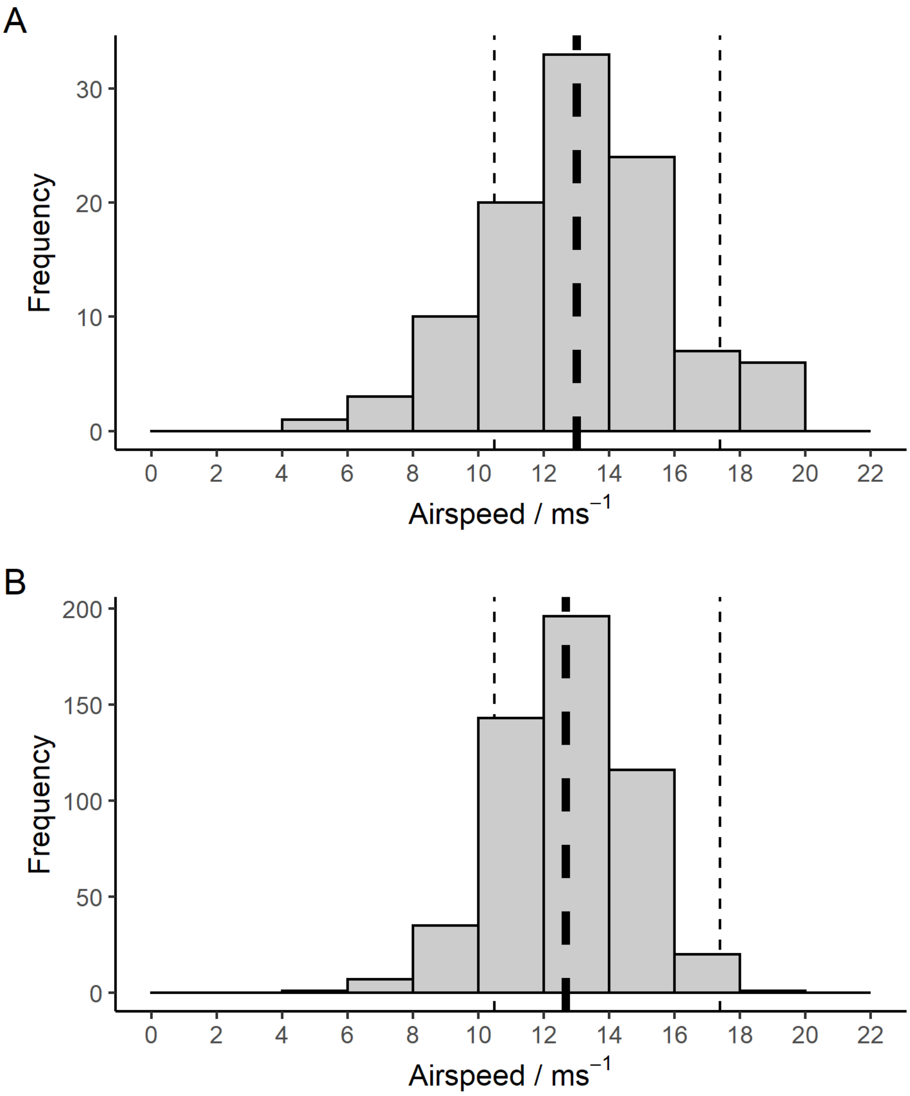
Supplementary 5-2: Frequency histogram showing the threshold (black dashed line) for distinguishing between flapping and gliding bouts. Transformed Z acceleration is Z-axis dynamic acceleration, which has been transformed by applying three rounds of taking the running difference followed by smoothing. The absolute value was then taken and smoothed a final time. Flapping was assigned when this variable remained higher than 0.011 ms^{-1} for longer than the expected length of a single wingbeat. 0.011 ms^{-1} was manually chosen to conservatively retain as many potential wingbeats as possible.



Supplementary 5-3: Repetition of ***Figure 5-9****, retaining only data for wind speeds between 2 and 7 ms*$^{-1}$ *to explore the influence of higher wind speeds experienced by bird 2005. Effect of (A and D) tail wind speeds, (B and E) across wind speeds and (C and F) proportion of time flapping on ground speeds (top row) and airspeeds (bottom row). Fitted LMMs are shown in black with shaded grey 95% confidence intervals for significant relationships. Raw datapoints are also shown (n = 451), coloured by individual. Outputs of LMMs are given in* ***Table 5-4*** *(next page).*

Table 5-4: *Model outputs for LMMs shown in* ***Supplementary 5-3****, run on a subset of data where wind speeds were between 2 and 7 ms*$^{-1}$*, where figure letters correspond to labels in plot. For all models bird ID was included as a random intercept and p-values were calculated by using likelihood ratio tests to compare each model to a null model with the explanatory variable removed. 95% confidence intervals are shown in square brackets.*

Figure	Response	Explanatory	Intercept	Slope	χ^2	*df*	*p-value*
A	ground speed	TWC_{ground}	11.97 [11.66, 12.27]	0.52 [0.48, 0.56]	412.81	1	< 0.0001
B	ground speed	AWC_{ground}	11.86 [11.28, 12.43]	0.02 [-0.11, 0.14]	0.07	1	0.7911
C	ground speed	proportion of time flapping	11.27 [10.24, 12.30]	1.05 [-0.50, 2.59]	1.81	1	0.1784
D	airspeed	TWC_{air}	12.01 [1169, 12.33]	-0.46 [-0.42, -0.50]	332.89	1	< 0.0001
E	airspeed	AWC_{air}	13.29 [12.70, 13.89]	-0.25 [-0.14, -0.36	19.77	1	< 0.0001
F	airspeed	proportion of time flapping	10.71 [9.70, 11.70]	2.96 [1.56, 4.36]	16.70	1	< 0.0001



Supplementary 5-4: Frequency histograms showing the distributions of fulmar airspeeds. (A) Histogram redrawn from Pennycuick 1987 Fig. 1, based on 104 land-based observations of fulmars flying past Foula, Shetland (28th June – 9th July 1986). (B) Equivalent data from present study, based on 519 GPS logger "observations" during commuting flight. In both, the heavy black dashed line shows mean observed airspeed while the light dashed lines show minimum power speed and maximum range speed respectively, as predicted for fulmars by Pennycuick 1987. Data for redrawn figure extracted from original paper using www.plotdigitizer.com.

Chapter 6 General Discussion

In this thesis, I aimed to bring together long-term and short-term datasets, making use of contemporary tracking technology, pattern recognition algorithms and traditional field observations, to understand some of the drivers that underpin movement patterns in wide-ranging seabirds. The focal species of this thesis was the northern fulmar (*Fulmarus glacialis*), a medium-sized boreal Procellariform seabird which, characteristically for the order, has an extremely mobile lifestyle and is at the slow end of the life history continuum. As such, I was able to explore inter- and intra- individual variation in at-sea behaviour, recorded by geolocators and accelerometers throughout the annual cycle, and how this related to environmental and demographic processes. Understanding the link between behavioural mechanisms, that were previously beyond the limit of human observation, environmental drivers such as wind conditions, and demographic rates will be crucial for understanding the impacts of environmental change. This is of particular importance in seabirds, a group that is highly threatened worldwide (Croxall *et al.*, 2012; Dias *et al.*, 2019).

The existing knowledge that this thesis builds on was limited by: (i) the uncertain applicability of knowledge across species; (ii) often short-term, low-resolution datasets; and (iii) the difficulty of analysing small samples of temporally autocorrelated and non-independent observations. As a species, fulmars have been widely studied, forming the basis of many classic observational studies (Fisher, 1952; Pennycuick, 1960; Dunnet, 1991; Hunter, 1999), perhaps partly due to their surface-nesting habits, day-time colony attendance and interesting recent range expansion. They have also been the focus of recent tracking studies which have provided valuable insight into their varied movement patterns (Edwards *et al.*, 2013; Quinn *et al.*, 2016; Darby *et al.*, 2021; Wakefield *et al.*, 2021). However, behavioural studies are more limited, in part due to unique challenges that working with this species pose, limiting sample sizes and scope for experimental studies. This thesis therefore contributes to taxonomically expand our understanding of at-sea seabird behaviour, by focusing on this widespread and generalist, but arguably currently less well-studied, species. This is achieved by taking advantage of a rich 10-year geolocator dataset and combining recent improvements in data processing methods with developing pattern recognition algorithms to tease apart signals for behavioural decision-making. A second general aim of the thesis was therefore to develop the analytical methods needed to analyse data which are difficult to handle using traditional methods. Accelerometers are relatively new, high output devices that are able to provide multi-stream data at 100 Hz. This presents computational challenges, and their interpretation requires a combination of analytical approaches.

6.1 General themes

Animal movement patterns are shaped by a wide range of processes but are fundamentally driven in long-lived species by the need to balance individual survival with maximising reproduction. Within species and populations, there is significant variation in movement patterns and distributions, as individuals make movement decisions in response to a combination of internal and external cues. These movement decisions result in varying energetic intake and expenditure, which are integrated over an animal's life, culminating in its lifetime reproductive success. However, relating these movement decisions to both individual and population-level demographic rates, remains an on-going challenge in movement ecology. This is particularly relevant in long-lived species, where following an individual across its life is not possible.

As environmental conditions vary, the cost of commuting to different resources and the quality of those resources themselves varies, resulting in a dynamic cost-benefit landscape which seabirds such as fulmars must try and maximise energy intake within. Some environmental features remain relatively stable on the scale of weeks to months: For example, the Mid-Atlantic Ridge, provides a consistent source of prey available to seabirds throughout the summer (Wakefield *et al.*, 2021). Wind conditions, on the other hand, vary over much shorter timescales and so the cost-benefit of foraging trips can vary rapidly despite the occurrence of relatively predictable and reliable foraging patches. It is reasonable to assume therefore that seabirds must have evolved sophisticated biophysical mechanisms to reduce the cost of commuting long distances and cognitive mechanisms which integrate memory with current conditions to make sensible decisions about foraging destination, and other aspects of at-sea behaviour.

I found strong evidence of inter-annual consistency in the areas used by fulmars in both early winter and late winter (Chapter 3), demonstrating the importance of individual specialisation in movement strategies, within a generalist population. The revisitation of the same areas over multiple years suggests that individuals do not respond to annually varying broad-scale environmental cues, such as the North Atlantic Oscillation (Iles & Hegerl, 2017), when making movement decisions. However, over the course of the annual cycle, many birds make use of a variety of different areas within this population's range, suggesting that site familiarity and navigational capacity are not limiting movement decisions. Together this suggests some capacity within this population for plasticity in response to changing environmental cues. Although there was little evidence of year effects on late winter behaviour (Chapter 4), variation within the population and lack of link between movement strategy and success, suggest that these are not driving population declines.

As described in previous studies of this species, I found clear sex differences in use of the North Sea and local area around the colony (Chapter 3 and Chapter 4). As a sexually dimorphic species, it is unclear whether these are true sex differences with biological drivers, or size differences with physiological drivers. Competition is unlikely to drive sexual segregation where natural resources are patchily dispersed and so cannot be defended. However, fisheries represent a resource where competition might play a role in foraging success, as they aggregate a finite resource in a semi-predictable way and individual speed and size might ensure successful feeding. Fisheries also represent a potential threat, for sex-specific bycatch (Gianuca *et al.*, 2017; Beck *et al.*, 2021). Other possible sex-specific risks include exposure to extreme and localised weather events. A recent study highlighted that the birds aggregating in the Barents Sea were at high risk of exposure to winter cyclones, where extreme weather can cause mass-mortality through starvation (Clairbaux *et al.*, 2021), which would impact males more than females from this population.

While carry-over effects between winter body condition and breeding success are recorded in little penguins (*Eudyptula minor*) (Salton *et al.*, 2015), how individuals balance the costs of locomotion in this mainly aquatic species is likely to be very different to these decisions in fulmars. Similar to this study (Chapter 4), a study of little auk (*Alle alle*) found no effect on breeding success of a two-fold difference in migratory distance, despite comparatively high flight costs in little auks. This could be either because higher energetic costs are offset by better foraging opportunities, or that flight costs in these species remain fairly insignificant against self-maintenance costs, meaning that the most important impact to fulmars may be in travel times. This is supported in Chapter 5, where I explored how the energetic costs of flight might vary under different wind conditions and demonstrated that fulmars flew with relatively constant power input, despite variation in airspeed.

6.2 Limitations, challenges and future directions

Project-specific challenges of tracking methods

This study was dependent on an extensive geolocator dataset, which has been collected over many years, and greatly benefits from the repeated tracking of multiple individuals. As in many tracking studies, at some points a lack of power limited inference, which was surprising considering the raw number of tracks. Once loggers that failed before retrieval were accounted for and the sample was split across the ten study years, I was somewhat limited in my ability to make meaningful comparisons of consistency between years.

The limitations of geolocation as a tracking method are well known (Lisovski *et al.*, 2020), with each location accompanied by a difficult to quantify, sometimes biased and often sizeable, margin of error. Throughout this study I were cautious of over-interpreting location estimates and used methods that were as robust as possible to highly erroneous locations and bias. In other geolocator studies, nearest-neighbour distance (Fayet *et al.*, 2017b; Van Bemmelen *et al.*, 2017; Merkel *et al.*, 2020) and earth mover's distance (Franklin *et al.*, 2022) have been successfully utilised to quantify individual consistency. However, due to the variation in the spatial scales covered by fulmars, and movement close to the colony being constrained by the land mass of mainland Europe, these approaches were not suitable for quantifying the behaviours of interest here.

This study was also limited by high numbers of missing locations, which were mainly due to large northwards movements or colony attendance. Identifying a signal for colony attendance from combined light and immersion data would have greatly aided the interpretation of the sex differences in trip-taking behaviour described in Chapter 4. I explored shading events during the day that are combined with the logger remaining dry, but there was no clear clustering in these signals. Additionally, fulmars are known to both fly and attend the colony at night, making the interpretation of night-time dry periods particularly difficult.

Fulmars are also relatively sensitive to disturbance, meaning that experimental manipulations such as handicapping (Gillies *et al.*, 2021) are unlikely to be successful and so observational studies must be relied on. This sensitivity also partly limited the sample size in Chapter 5, where the combination of a small sample size and stable wind conditions during the tracking period resulted the reduced range of behaviours observed.

Interpreting individual differences

Much attention is given in the literature to the role of inter- and intra-specific competition in shaping at sea distributions of seabirds. This is particularly apparent in the breeding season, when segregation between colonies was reported in 79% of reviewed studies (Bolton *et al.*, 2019), with increasing colony size and local proximity of other colonies predicting segregation, and highly productive areas predicting overlap. It is notable, however, that Procellariiformes are over-represented in the "overlap" and "partial segregation" categories of this review, suggesting that competition might be less important in species with lower flight costs. During the non-breeding period, the mechanisms of how competition might shape distributions is less obvious, especially in highly mobile species, although there is evidence of non-breeding separation, for example in Atlantic puffins (*Fratercula arctica*) (Fayet *et al.*, 2017a) and common guillemots (*Uria aalge*) (Buckingham *et al.*, 2022). This study is based on a single colony, but given the individual-level consistency, but colony-level variation in strategies observed within this small population, fulmars may be a good model to further study how individually consistent movement strategies arise. I suggest that genetic differences, arising from natal philopatry (Wynn *et al.*, 2020), and previous experience, where environmental conditions in the years between fledging and recruitment might shape preferred strategy (Guilford *et al.*, 2011; Campioni *et al.*, 2019), would also be valuable avenues of further research. Understanding the ontogeny of individual movement patterns remains challenging (Wynn *et al.*, 2021) and is somewhat biased by often only observing birds that successfully recruit. However, these lost years may be formative for a bird's knowledge of the seascape and represents an important research area for understanding how experience shapes movement patterns.

Future development of tracking technology

As a relatively low-cost and low-impact method for tracking seabirds, light-level geolocation remains valuable but challenging, with particular limitations for species that frequent high latitudes (Fauchald *et al.*, 2021) and highly transitory species that translocate large distances in a single day (Lisovski, 2018). By incorporating information from multiple sensors (Merkel *et al.*, 2016) it was possible to include equinox locations (Chapter 3), but further work to reduce the run-times and computing capacity needed for template-fit methods such as FlightR (Rakhimberdiev *et al.*, 2017) would be helpful in maximising the value of existent data. The integrated salt-water immersion logger remains a rich source of behavioural information, which should not be neglected.

As tracking technology continues to develop and loggers reduce in size, the focus is often on bio-logging that is high-resolution, short-term or remotely downloadable. However, an archival GPS logger that could take daily fixes and be leg mounted would be invaluable in seabird tracking, where uncertainty in over-winter locations hugely limits the nature of questions that can be tackled. In fulmars, better spatial resolution from late winter and into incubation would allow more targeted questions into the function of colony visitation and its possible role as a driver of late winter distributions to be answered. Accurate locations would also permit the study of fine-scale consistency between trips and confirm whether within-season site fidelity develops throughout late winter and into pre-laying and incubation. Additionally, better understanding the spatial and temporal scales at which individual movement patterns are consistent is intrinsic to identifying possible environmental drivers of individual movement decisions.

At the opposite end of the scale for tracking resolution, the power of accelerometry to provide insight into extremely fine-scale movement is highly valuable. However, as an emerging method several challenges remain that limit how easily this data can be interpreted. As with any high-resolution data, the large size of individual files is prohibitive in both visualising and processing data. Open-source programming that permits interactive visualisation of data and is compatible across logger manufacturers would greatly assist in identifying patterns of interest. Additionally, in species that spend most of their time out of sight, and proxies cannot be observed in captivity to aid with ground-truthing, accurately identifying and classifying behaviours remains a challenge. While unobserved methods from machine-learning provide useful tools for this (Ladds *et al.*, 2017), they are dependent on enough data to have fully captured the range of behaviours and are unlikely to identify infrequent, but potentially interesting behaviours. This challenge is not easily resolved but is improved by awareness of the limitations of different methods during the initial stages of planning.

Breeding success

As part of Chapter 4, I looked for evidence of carry-over effects between late winter and the subsequent breeding season. While I were limited by a restricted sample size and incomplete information regarding partner movement decisions, I were surprised to not find evidence of either seasonal carry-over effects (Shoji *et al.*, 2015) or behavioural adjustment between years. The value of breeding success as a useful response variable is limited, as in many seabirds it is binary by nature and incorporates many potential sources of variation. The extensive failure rate in 2015, followed by extremely high breeding success in 2016, suggest that breeding success in these years had local drivers, such as extreme weather conditions, predation levels, local prey availability or disturbance, that affected almost all the tracked birds. While the probability of laying an egg might be more likely to yield insight into the relative successes of non-breeding behaviours, the rarity of observing skipped breeding means that studies that focussed on this would similarly lack statistical power. Alternatively, the high breeding success seen in 2016 might be an annual carry-over effect, with individuals able to invest highly in breeding following low investment the previous year (Fayet *et al.*, 2016), which would be an interesting avenue of further study using this dataset.

However, developing a better understanding of the drivers of breeding success in fulmars should be prioritised, as while populations have not experienced the extreme collapses seen in some boreal seabirds (Fayet *et al.*, 2021), both survival (Cordes *et al.*, 2015) and productivity (Parsons *et al.*, 2008) are gradually declining. I propose that the timing of failure might provide an interesting insight into localised drivers of breeding failure. This could be explored with existent data if colony visitation could be reliably inferred from the light and immersion patterns of geolocators (see above). Alternatively, the current methodology for JNCC monitoring involves repeated observations of active nests throughout the breeding season, which would allow the timing of failure to be inferred and compared to local conditions. While this approach has different limitations (such as uncertainty around “apparently occupied sites”), this data has been collected over many years at multiple colonies around the UK, making it a potentially rich sources of timing information.

Fulmars have variable and often high nest failure rates, with fledging success fluctuating between 0.13 and 0.64 chicks fledged per egg laid (Chapter 5), which is lower than comparable species such as Manx shearwaters (*Puffinus puffinus*) (0.43 - 0.90, Brooke, 1990). This difference may result from higher vulnerability to external causes of failure linked to exposed nesting, such as extreme weather or predation. However, it may also represent subtle differences in life-history strategies, where fulmars may have a lower threshold for initial investment, resulting in higher numbers of failed nests.

6.3 Conclusion

In this doctoral thesis I had three main aims: (i) describe and quantify individual consistency at biologically relevant timescales throughout the annual cycle; (ii) explore long distance trip-taking in the transitory late winter period and look for evidence of this behaviour affecting movement decisions into the breeding season; and (iii) characterise fine-scale flight mechanics, with respect to wind conditions.

My findings of sex-linked variation in non-breeding distributions supported previous work at this colony (Quinn *et al.*, 2016). Additionally, the finding of inter-annual individual consistency in both early winter and late winter, suggests that individual consistency is not only driven by fidelity to moulting areas. Even within this small population there was large variation in both areas visited and consistency. This diversity of strategies is likely to be important in maintaining a population that is resilient to future environmental change. Sex differences in late winter trip-taking behaviour hint at variation in the role of colony attendance, but also highlight that there is potential risk of sex-specific threats, such as interaction with fisheries. While individuals are likely to vary greatly in distances travelled, the lack of carry-over effects suggests that this does not incur a high energetic cost. I found that fulmars adjust their airspeeds in response to wind conditions, probably using dynamic wind features, as they flew with a relatively standard power output. At low wind speeds they are more dependent on flapping flight than expected, highlighting that especially during the breeding period, they may incur high flight costs. This is of particular relevance, given the prediction that mean wind speeds in the North Atlantic will decrease in the future (Ruosteenoja *et al.*, 2019).

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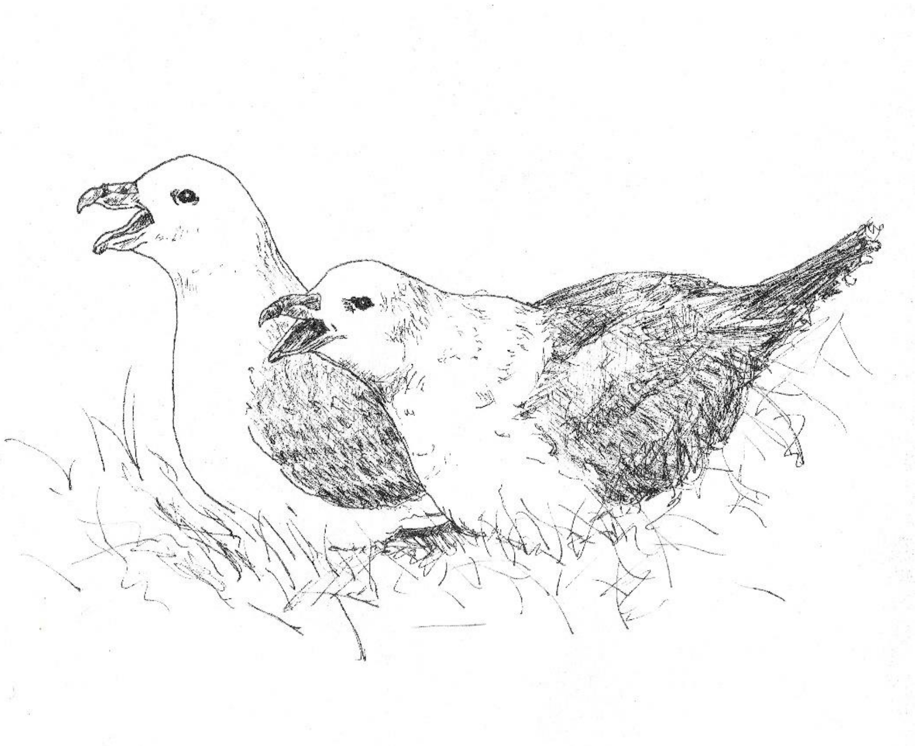
Chapter 7 (Appendix) 3D printing a fulmar decoy



7.1 Rationale

One of the challenges of working with northern fulmars (*Fulmarus glacialis*) is that they are quite sensitive to disturbance. After handling to deploy data loggers, they often leave the nest for a prolonged period (~ 1 hour), leaving the egg or young chick vulnerable to predation. On Eynhallow, the main avian predators are great skuas (*Stercorarius skua*) and Arctic skuas (*Stercorarius parasiticus*). Predation of the nest is important to avoid, not only as a direct impact of the study, but also when using archival loggers, as recapture of the tagged bird and retrieval of the logger (and data) becomes unlikely after a nest has failed. To mitigate this risk, an observer is left close to the nest to discourage any predators before the parent returns. However, this is both labour intensive and can be counterproductive, as the additional disturbance sometimes interferes with how quickly the parent returns.

In the past, papier-mâché decoys have been used to make cliffs look more occupied and disguise that nests were unattended. These decoys are delicate, cannot be used in the rain and lack realism. For this project 3D scanning and printing were used to create a hyper-realistic decoy, which was tested throughout the 2018 and 2019 field seasons.

7.2 Methods

I based the decoy on a recently deceased fulmar specimen that was loaned from the British Trust for Ornithology (BTO), as it was not possible to find a suitable museum specimen. The bird was positioned using wire to look as if it was sat at the nest, then re-frozen so that the wire could be removed (**Figure 7-1 A**).

Multiple high-resolution 3D scans of the frozen specimen were performed using an Artec Space Spider 3D scanner to capture geometry and texture. This results in a point cloud representation (**Figure 7-1 B**), which was then combined using *Artec Studio 12* (Artec 3D, 2017). Frames with high maximum error of more than 0.3 were deleted. Where necessary common features between scans were used to perform manual alignment. I performed outlier removal, manually erased erroneous sections, then used global registration and sharp fusion, to combine all scans into a single 3D model. The defeature brush and hole filling algorithm were used to improve the scan, then mesh simplification was applied to reduce the number of polygons before exporting the digital model as a .stl file.

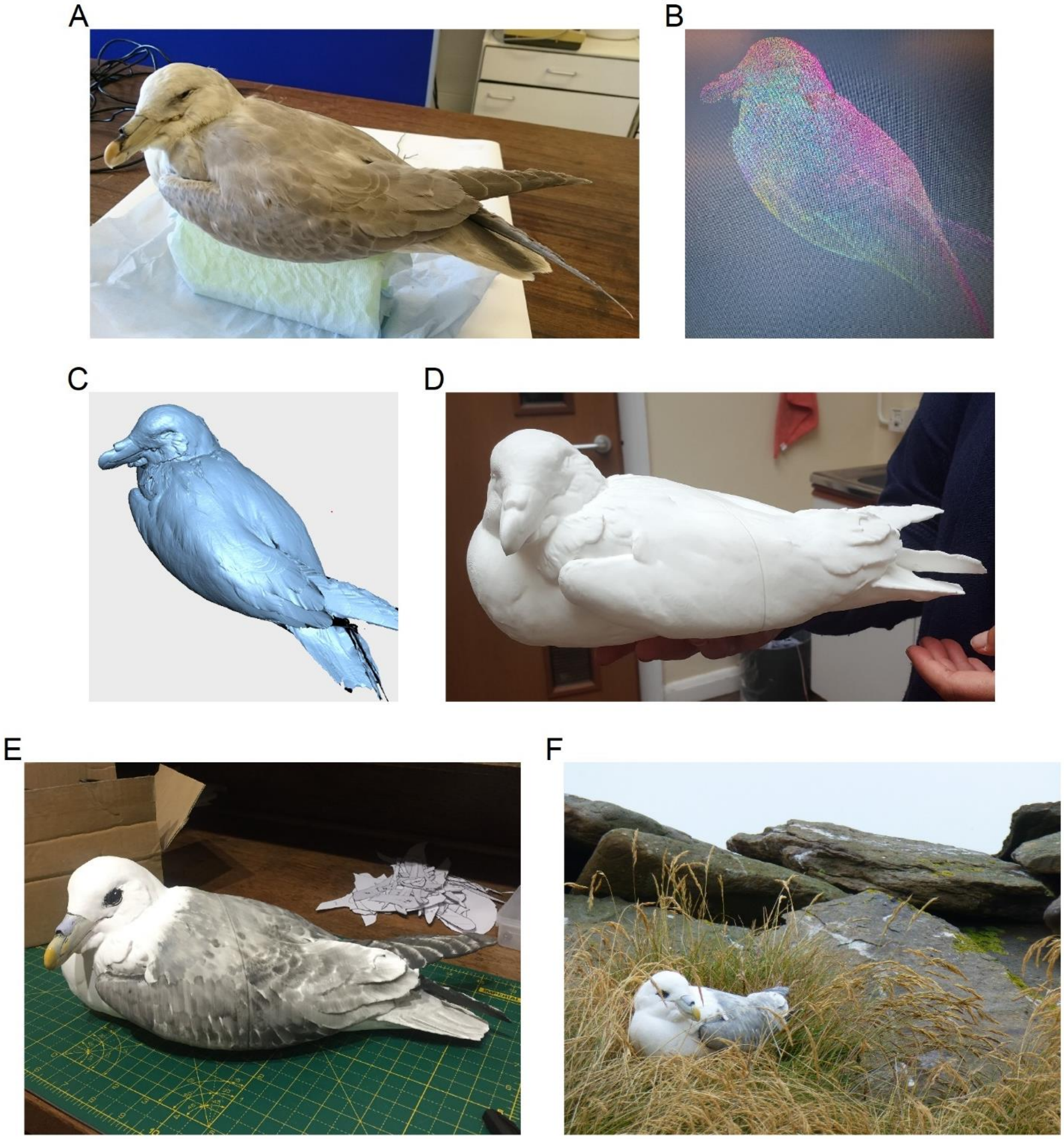


Figure 7-1: Photos detailing the process of making a 3D printed fulmar decoy. (A) Deceased specimen positioned ready for 3D scanning. (B) Point cloud showing individual scans in different colours. (C) Digital 3D model, following editing to make watertight ready for printing. (D) Model printed in PLA (Polylactic acid) showing seam where model was split into two halves for printing. (E) Painted model. (F) Complete model in-situ on a nest after the parent had been caught.

Further edits to the mesh were performed in *Meshmixer* (Autodesk, 2017) in order to remove errors and patch areas such as the primary feathers which the scanner struggled to track. To repair small holes and ensure that the model was watertight the mesh was processed using the program *MakePrintable* (Mixed Dimensions, 2017) (**Figure 7-1 C**). I imported the .stl file into the program *Cura* (Ultimaker, 2018) to set the printing parameters. The layer height was

0.06 mm, wall thickness was 1.6 mm and internal supports were not used. The model was split in half diagonally, as it was too long to print, which also meant that the two halves were self-supporting during printing. The model was printed using an Ultimaker 2+ 3D printer, using white PLA (Polylactic acid) in 2.75 – 3.00 mm diameter (**Figure 7-1 D**).

The final model was painted with water-based acrylic and sealed with clear matt lacquer (**Figure 7-1 E**). A tether was attached through two holes drilled in the base of each decoy, to allow it to be pegged in place.

7.3 Outcome

Four decoys were created, which were regularly used during routine nest checking in incubation and when deploying loggers during chick-rearing. Decoys were left close to, but not directly on the nest, after a bird had been handled (**Figure 7-1 F**) and removed after the bird returned and settled.

It was not possible to formally test efficacy, as work is always focussed on reducing impact and this could have unnecessarily endangered nests. Anecdotally, I found that the observer was able to watch from further away and that in general birds came back quickly and were not put off by the decoy. There was one instance of a nest which was predated after it had been left with a decoy, although this occurred after the tagged bird deserted the breeding attempt. This bird was the only bird that was tagged during this study while still incubating, as at this point the egg was unlikely to hatch. At this colony I suspect that decoys are useful for artificially increasing the number of birds present on each sub-colony, and so discouraging "fly-by" predation by skua species but are less effective at protecting nests that are empty for a prolonged period of time. There were two instances of interaction directly between living and decoy fulmars recorded: one decoy was retrieved with a scratch in the paint across its bill, while the second was vomited on by a chick. Both of these responses would be expected if an intruder was found at the nest, suggesting that the decoys were suitably realistic.

As a method for decoy creation for non-game species, 3D scanning and editing was time-consuming, but very effective at producing a realistic representation of the study species. Once the digital mesh model was complete, it was simple to produce multiple decoys, although the speed of 3D printing means that it would not be suitable for producing large numbers. Following the creation of this decoy, I collaborated with BTO Cymru to help create a spoon-billed sandpiper (*Calidris pygmaea*) decoy, for conservation purposes. More recent papers have also used 3D printed decoys to test hypotheses relating to nest predation (Biagolini-Jr & Perrella, 2020) and female aggression (Bentz *et al.*, 2019), highlighting the potential of this process for multiple applications in fieldwork, research and conservation.

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