



Adjustment of foraging trips and flight behaviour to own and partner mass and wind conditions by a far-ranging seabird

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Many animals are highly adapted to cover vast distances in search of ephemeral food resources. Pelagic seabirds have particularly wide-ranging foraging trips, made possible through efficient use of wind. During incubation, partners alternate long periods of fasting and so should adjust foraging and flight decisions according to the condition of the pair, as well as wind conditions experienced at sea. Here, we tracked incubating Juan Fernández petrels, *Pterodroma externa*, with GPS and immersion loggers, assigned at-sea behaviours using hidden Markov models, and weighed birds and their partners, to investigate the roles of wind and mass on flight and foraging behaviour, and the link between wind use and trip success. Birds conducted long anticlockwise looping trips, on average lasting 20.4 days and covering 10 741 km. They reached a region in the southeastern Pacific Ocean where prey search behaviour was concentrated, typically about 3400 km west of the colony. Outbound and return journeys appeared to broadly benefit from predictable southeasterly trade and westerly winds, respectively. Over finer scales, departure bearings were influenced by wind directions. Across trips, birds oriented predominantly with quartering tail winds which maximized ground speeds. Individuals experienced variable support from tail winds, and those that benefited more on outbound journeys (when winds were generally weaker) travelled faster, reached foraging areas more quickly and, over the entire trip, had higher mass gain per day at sea. Additionally, birds that were lighter on departure gained more mass and birds with heavier partners ranged further from the colony. Our results suggest that decisions involving where to go and how far, respectively, are based on prevailing wind patterns and an assessment of the condition of the pair. Consequently, while birds sought to benefit from wind assistance, those encountering greater tail wind support had more successful foraging trips, indicating that wind use may have direct fitness consequences.

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Foraging animals should favour strategies that minimize costs (e.g. travel time, energy expenditure) while maximizing benefits (e.g. energy gain; MacArthur & Pianka, 1966). For predators foraging on ephemeral or patchily distributed prey, the optimal searching strategy may be to increase the probability of finding prey (Andersson, 1981; Sims et al., 2008) by maximizing the distance covered and minimizing energy costs per unit distance travelled (Pyke, 1981). In pelagic ocean environments beyond coastal and continental shelf waters, the distribution of prey is

considered to be particularly patchy or sparsely distributed, at least at the (sub)mesoscale (1–100 km), compared to coastal or continental shelf waters (Robinson et al., 2021; Weimerskirch, 2007). Faced with these constraints, oceanic predators that routinely commute between breeding and foraging areas often have morphological, behavioural or physiological adaptations that allow them to cover vast distances to forage successfully (e.g. Au & Pitman, 1986; Ballance et al., 1997; Sims et al., 2008).

Pelagic seabirds such as albatrosses and petrels (Order: Procellariiformes) are extremely well adapted for low-cost flight and many species routinely conduct transhemispheric migrations (Bonnet-Lebrun et al., 2021) and travel over 10 000 km in a single foraging trip (e.g. Clay et al., 2019; Taylor et al., 2020; Weimerskirch

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et al., 2000). Their high wing aspect ratios (long, narrow wings; Spear & Ainley, 1997a) and dynamic soaring flight style allow them to exploit vertical wind speed gradients near the sea surface (Kempton et al., 2022; Richardson, 2011; Sachs et al., 2013). Consequently, their flight performance is shaped by wind patterns over a range of spatiotemporal scales, from migration routes (e.g. González-Solís et al., 2009) to finer-scale flight decisions within foraging trips (e.g. Clay et al., 2020). Generally, procellariiform seabirds orient with tail or cross-winds (Spear & Ainley, 1997a) allowing them to maximize achieved ground speeds (i.e. flight speeds relative to the ground; Spear & Ainley, 1997b; Ventura et al., 2020; Wakefield et al., 2009) and reduce the energetic costs associated with flapping flight (Weimerskirch et al., 2000). Morphological traits such as body mass and associated wing loading (body mass per unit wing area) strongly influence flight performance and so optimal flight and foraging strategies vary among and within species (Pennycuik, 1982; Spear & Ainley, 1997a; Wakefield et al., 2009). When breeding, many seabirds commute between breeding and often distant foraging sites, constraining where and for how long they can forage before having to return to incubate the egg or care for the chick. Thus, optimal foraging strategies vary over short timescales as a function of variable wind conditions encountered as well as changes in body mass that occur as food is ingested and energy used (Alerstam et al., 2019; Wakefield et al., 2009). This reliance on wind likely has important energetic consequences. While changes in wind influence foraging strategies and breeding success (Thorne et al., 2016; Weimerskirch et al., 2012), the extent to which wind use influences trip success (duration or mass gained) remains poorly understood.

Seabirds are monogamous and the majority exhibit biparental care, meaning that breeding success is dependent on the decisions of both an individual bird and its partner. Research on species with long-lasting pair bonds shows that cooperation between the pair is important to manage the costs of current and future reproduction, and parents often adjust their behaviour in response to their partner (Griffith, 2019; Lessells & McNamara, 2012). Since most seabirds share incubation, the foraging bird must gather not only enough food for its immediate needs but also an additional amount sufficient for its forthcoming incubation stint. Therefore, birds have to trade spending sufficiently long at sea to recover lost body condition against returning before the partner leaves, which may result in egg neglect and nest failure (Chaurand & Weimerskirch, 1994; Ronconi & Hipfner, 2009). The optimal strategy should take into account the condition of the partner, and experiments have shown handicapped Manx shearwaters, *Puffinus puffinus*, and Antarctic petrels, *Thalassoica antarctica*, return quicker if their partner is in poorer condition (Gillies et al., 2021; Tveraa et al., 1997). Most studies of pair coordination have focused on species with short (e.g. several hours to a day) trips, where regular change-over and communication facilitate an assessment of the partner's efforts and condition (Gillies et al., 2022; Kavelaars et al., 2019). For practical reasons, this is much more difficult for species with long (and few) incubation shifts.

Gadfly petrels, *Pterodroma* spp., have extremely long (up to ca. 20 days) and few incubation bouts (Warham, 1990). While the 35 species have generally been poorly studied, recent tracking studies have shown that birds undertake some of the widest-ranging foraging trips of any seabird, ranging up to 5000 km from breeding colonies (e.g. Clay et al., 2019; Taylor et al., 2020). The vast distances covered by individuals are facilitated by the small (5–10%) amount of time spent resting on the sea surface (Bonnet-Lebrun et al., 2021; Clay et al., 2017; Ramírez et al., 2013). These birds are highly dependent on winds for their gliding flight (Spear & Ainley, 1997b), and appear to take advantage of ocean basin-scale wind circulation patterns to facilitate long trips (Adams & Flora,

2010; Clay et al., 2019; Ventura et al., 2020). Indeed, subtropical Desertas petrels, *Pterodroma deserta*, also adjust movements to finer-scale variation in winds, resulting in faster trips than predicted if birds just followed basin-scale wind patterns (Ventura et al., 2020).

We present the first tracking study of Juan Fernández petrels, *Pterodroma externa*, a large gadfly petrel endemic to Isla Alejandro Selkirk (33°46'S, 80°47'W), Juan Fernández Islands, Chile, in the southeast Pacific Ocean. Through combining GPS data with mass measurements of each tracked bird and its partner, we examined the effects of (1) pair mass and (2) wind on the flight behaviour and routes taken by birds, as well as (3) the effect of wind use on overall trip success (trip duration, mass gain). The species is one of the most commonly sighted seabirds in the subtropical southeast Pacific Ocean (Miranda-Urbina et al., 2015) and is abundant in its nonbreeding range in the eastern tropical Pacific Ocean (based on at-sea surveys; Ballance et al., 1997; Spear & Ainley, 1998), but little is known about its movements and foraging behaviour during breeding. It has long (19.5-day) incubation shifts (Brooke, 1987; Warham, 1990), and by analogy with other similarly sized congeners (Clay et al., 2019; Ventura et al., 2020) is predicted to range far from its colony; however, data from temperature loggers attached to chick-rearing adults suggested most foraging is within 1000 km of the colony (Smith, 2008).

We used hidden Markov models (HMMs) to classify major behavioural states at sea (directed flight, area-restricted search [ARS], rest) and overlaid tracks with maps of averaged wind conditions to test the prediction that birds conduct large-scale anti-clockwise looping trips that broadly follow prevailing wind patterns in the southeast Pacific Ocean (sensu Clay et al., 2019; Ventura et al., 2020; hypothesis 1a; H1a). We examined the extent to which birds fine-tuned their routes and flight behaviour to wind they encountered. First, if wind strongly dictated the travel paths of birds, they should adjust initial departure directions to orient favourably with wind directions experienced (H1b). Second, across trips, birds should orient with quartering tail winds (<90° angle between the bearing of the bird and wind direction), facilitating higher ground speeds (H1c; Spear & Ainley, 1997a). Moreover, given adults presumably have some prior knowledge of both the distribution of prey and synoptic winds at the macroscale (100 km to thousands of km; Ventura et al., 2020), detours taken from the most direct route to foraging areas should serve to take advantage of finer-scale variation in wind and allow birds to maximize overall distance travelled (H1d), presumably at low energetic cost. We also examined whether bird and partner mass influence trip decisions; specifically, we expected that birds departing at a lower mass would gain more mass at sea (e.g. Kim et al., 2018; Weimerskirch, 1995; H2a) and those with partners in better condition would travel further and/or take longer trips (Tveraa et al., 1997; H2b). Lastly, we determined whether a more efficient use of tail winds, which presumably promotes faster ground speeds (see H1c) or increased distance covered (see H1d), results in increased trip success, either a shorter trip and/or increased mass gain (H3).

METHODS

Data Collection

Fieldwork was conducted on Isla Alejandro Selkirk between December 2019 and February 2020 where most birds nest in a mixed colony with Stejneger's petrels, *Pterodroma longirostris*, on the southern half of the island at an altitude of around 850 m (Brooke, 1987). The majority of study burrows were situated in a grassy area overlooking the pinnacles known as Tres Torres on the northern fringes of the colony (33°46'48"S, 80°47'24"W). Burrows

were opened in mid-December using a standard procedure involving cutting a flowerpot-shaped sod (ca. 20 cm in maximum diameter) roughly above the nest chamber, allowing the temporary removal of the incubating bird. The sod was replaced, and a capping stone was put atop for safety. From the bird's perspective the nest was not altered. The procedure permitted regular checks of the nest chamber over the laying period, daily from 18 December until 9 January and thereafter on alternate days until 19 January. The first egg was laid on 17 or 18 December and the median lay date was 31 December ($N = 47$). After laying, the female, identified by her lower mass (<530 g on day after laying) and distended cloaca, remained in the burrow for several days (range 1–12, $N = 19$) until relieved by her partner, with a greater mass (>550 g on first day after return) and normal cloaca. The incubating bird, found shortly after laying, was ringed, weighed using a Pesola spring balance, and its wing length (maximum chord) measured. To assess daily mass loss of incubating birds for the purpose of estimating departure and return masses, females were weighed again roughly 5 days after laying if still present, while males were also weighed intermittently during their first long incubation stint. Overall, we obtained measurements of mass loss across 21 intervals for 18 birds. The balance was only able to measure masses up to 600 g, so for six focal birds and 13 partners which were measured on return with a mass >600 g, we waited a few days to weigh the bird, and then estimated its return mass using a daily mass loss estimate (see below). Of these, five focal birds could not be reweighed either because the field season had ended or because the birds ($N = 2$) had deserted by the second visit.

Birds were tagged prior to departure and the majority (23 of 33) of loggers that were successfully retrieved were from females, since males could only be tracked after their first long (ca. 20-day) incubation bout. Twenty-four nanoFix-GEO GPS loggers (30 × 14 mm and 19 mm high, 9 g; PathTrack, Otley, U.K.) and seven FastLoc GPS devices (38 × 13 mm and 12 mm high, 10 g; PathTrack; Clay et al., 2019) were attached to the four central tail feathers using Tesa tape and programmed to obtain a position every 20 min (nanoFix-GEO) or 40 min (FastLoc GPS) (Table 1). In addition, geolocator-immersion loggers (Intigeo C65-SUPER: 14 × 8 mm and 6 mm high, 1 g; Migrate Technology Ltd, Cambridge, U.K.) were attached to a Darvic plastic ring on the tarsus of 34 birds and programmed to sample wet/dry status every 6 s, providing a score out of 50 every 5 min.

Ethical Note

All capture, handling and tagging procedures were in accordance with permits provided by Servicio Agrícola y Ganadero, Chile (permit no. 9793/2019). Ethical approval was provided by the Department of Zoology, University of Cambridge and the Corporación Nacional Forestal (CONAF; certificate 009/2019) provided authorization to work in the Archipiélago de Juan Fernández National Park. Birds were caught by hand in their burrows and the attachment of devices, always carried out in decent weather by a licensed bird ringer (BTO A 1871MP), took about 15 min. Device

retrieval took 5 min. The total mass of the GPS and immersion loggers, rings and attachment materials (ca. 12 g) represented $2.7 \pm 0.2\%$ (range 2.2–3.1%) of birds' departure mass (446 ± 41 g, range 387–534 g). There were no detectable differences in trip duration (GPS: 19.6 ± 2.7 days, $N = 24$; no GPS: 19.4 ± 4.4 days, $N = 5$; t test: $t_{27} = 0.12$, $P = 0.903$) or mass gain (GPS: 117.5 ± 30.8 g, $N = 22$; no GPS: 126.7 ± 35.7 g, $N = 3$; $t_{23} = -0.48$, $P = 0.637$) between birds equipped with both a GPS and immersion logger and those carrying just an immersion logger, although we acknowledge the sample size for the latter group is particularly small.

Data Processing

Data processing and statistical analyses were conducted in R v. 4.0.3 (R Core Team, 2020). We assigned departure and return dates based on nest monitoring, specifically the day after the nights when the bird departed and returned, respectively. If daily burrow checks were not made at the time of departure or return, departure and return dates were verified based on either immersion or GPS data. Mass gain was calculated for each bird by subtracting the departure from the return mass (day after the nights of departure and return, respectively), which we estimated based on the mass at weighing, the time difference (if any) between capture and departure or return and capture and an estimated daily mass loss (Table 2). Daily mass loss while incubating was assumed to be constant (Brooke, 1995) and calculated based on a linear regression applied to multiple measurements of the same individuals (slope $\pm$ SE = 6.8 ± 2.1 g/day). Indeed, the slope was remarkably similar among individuals (Fig. A1). The mass of the partner taking over incubation duties from the departing bird was also adjusted upwards if it was not weighed the first day after the night of its return. As the majority (13 of 25) of partners were initially weighed at >600 g and had to be reweighed and the return mass estimated, we consider partner mass to be an estimate and may not be the precise return mass. There was slight variation in wing length among individuals (5.9% difference between smallest and largest) in contrast to departure (38.0%) and return mass (19.5%) and mass gain (172.9%), and wing length did not correlate with mass variables (Spearman rank correlation: departure mass: $r_s = 0.22$, $P = 0.281$; return mass: $r_s = 0.24$, $P = 0.287$; mass gain: $r_s = 0.05$, $P = 0.819$); thus we use mass as a proxy for body condition.

GPS data were run through an iterative forwards/backwards speed filter (90 km/h) in the 'trip' package (Sumner, 2020) to remove locations ($N = 2$, <0.01% of total) associated with unrealistic flight speeds. We used the 'track2kba' package (Beal et al., 2021) to remove incomplete trips and remove locations at or around the breeding colony, based on a distance buffer of 10 km, and to calculate the maximum range (maximum distance from the colony) and cumulative distance travelled (sum of straight-line distances between consecutive locations). Trip duration was based on data from birds monitored at the colony.

We linked GPS data to hourly wind data downloaded from the European Centre for Medium Range Weather Forecasts (ECMWF) ERA5 reanalysis data set (<https://doi.org/10.24381/cds.adbb2d47>; accessed May 2020) at a spatial resolution of 0.25°. Zonal (V_u) and meridional (V_v) wind components nearest in time to each interpolated tracking location were extracted using the 'raster' package (Hijmans et al., 2021) from which wind speed (V_w) and direction (θ_w) were computed using the following equations:

$$V_w = \sqrt{V_u^2 + V_v^2}$$

$$\theta_w = \left(\frac{180}{\pi}\right) \text{atan} 2\left(\frac{V_u}{V_w}, \frac{V_v}{V_w}\right)$$

Table 1
Sample sizes for different device combinations

	Deployed	Retrieved	Complete trips
GPS + immersion	27	20	13
GPS	4	6 ^a	5
Immersion	7	7	14 ^a
Total	38	33	32

Immersion = geolocator-immersion logger.

^a Individuals from the GPS + immersion category were moved to the GPS category if the immersion logger fell off while the GPS data were retained or to the immersion category if the GPS recorded an incomplete trip and so was discarded.

Table 2
Summary of mass measurements

	Departure mass (g)	Return mass (g)	Mass gain (g)	Mass gain (% of departure mass)	Mass gain (g/day)
Mean ± SD	450.1 ± 39.5	558.7 ± 34.6	117.0 ± 30.6	26.9 ± 30.6	6.2 ± 2.0
Range	387–534	502–632	70–191	15.4–46.7	2.9–10.1
N	33	28	28	28	27

Note that the sample sizes for return mass and mass gain are lower as five individuals could not be reweighed before fieldwork ended (see [Methods](#)).

For each location we calculated relative wind direction ($\Delta\theta$), which was the absolute difference between the bearing of the bird and wind direction, scaled to between 0° (tail wind) and 180° (head wind). We calculated tail wind support (i.e. wind speed in the direction of travel; V_{tw}) using the formula: $V_{tw} = V_w \cos\Delta\theta$, after converting $\Delta\theta$ from degrees to radians. To determine wind conditions experienced at the colony, we extracted the mean hourly wind speed and direction within a 5 km buffer around the colony.

We fitted multivariate hidden Markov models (HMMs) to interpolated tracks within the ‘momentuHMM’ package (McClintock & Michelot, 2018) to identify behavioural states at sea (e.g. Clay et al., 2020; Halpin et al., 2022; Tarroux et al., 2020). Trips were projected to an azimuthal equal area projection and linearly interpolated to 40 min intervals using the ‘adehabitatLT’ package (Calenge, 2006). We considered the following three states using two input variables, step lengths and turning angles: directed flight (high speeds, shallow turning angles), area-restricted search (ARS; moderate speeds, moderate to wide turning angles) and rest (low speeds, shallow to moderate turning angles; [Appendix Table A1](#)). A gamma distribution was chosen for step lengths and a von Mises distribution for turning angles. We initially incorporated wet events from the immersion data (as a proxy for prey capture on the

sea surface) as a third input variable, and also tested whether searching behaviour could be split into dry and wet searching behaviour (the latter indicative of foraging; [Carneiro et al., 2022](#); see [Appendix](#) for details). The inclusion of wet events did not improve model fit, and since birds are known to sometimes aerially pursue volant prey (meaning foraging may not be associated with wet activity; [Spear & Ainley, 1998](#)), we opted for the more parsimonious three-state model without immersion data. We used the Viterbi algorithm to estimate the most likely sequence of behavioural states from the fitted model ([Rabiner, 1989](#)) and initial values of step and angle distributions were chosen based on 100 iterations of random values within a biologically realistic range ([Clay et al., 2020](#)). The final HMM was assessed for goodness of fit and autocorrelation using QQ, pseudoresidual and autocorrelation plots.

We partitioned outbound, middle and return stages of trips ([Fig. 1](#)) using a methodology similar to [Wakefield et al. \(2009\)](#) based on distance and time thresholds as well as the proportion of time in ARS (see [Appendix](#) for details; [Fig. A2](#)). For outbound and return stages, we calculated sinuosity (S) as a measure of detours taken by birds from the most direct straight-line route to and from middle stages of trips, using the equation $S = 1 - \frac{D_1}{D_2}$, where D_1 is the great-circle beeline distance between the first and last location of the

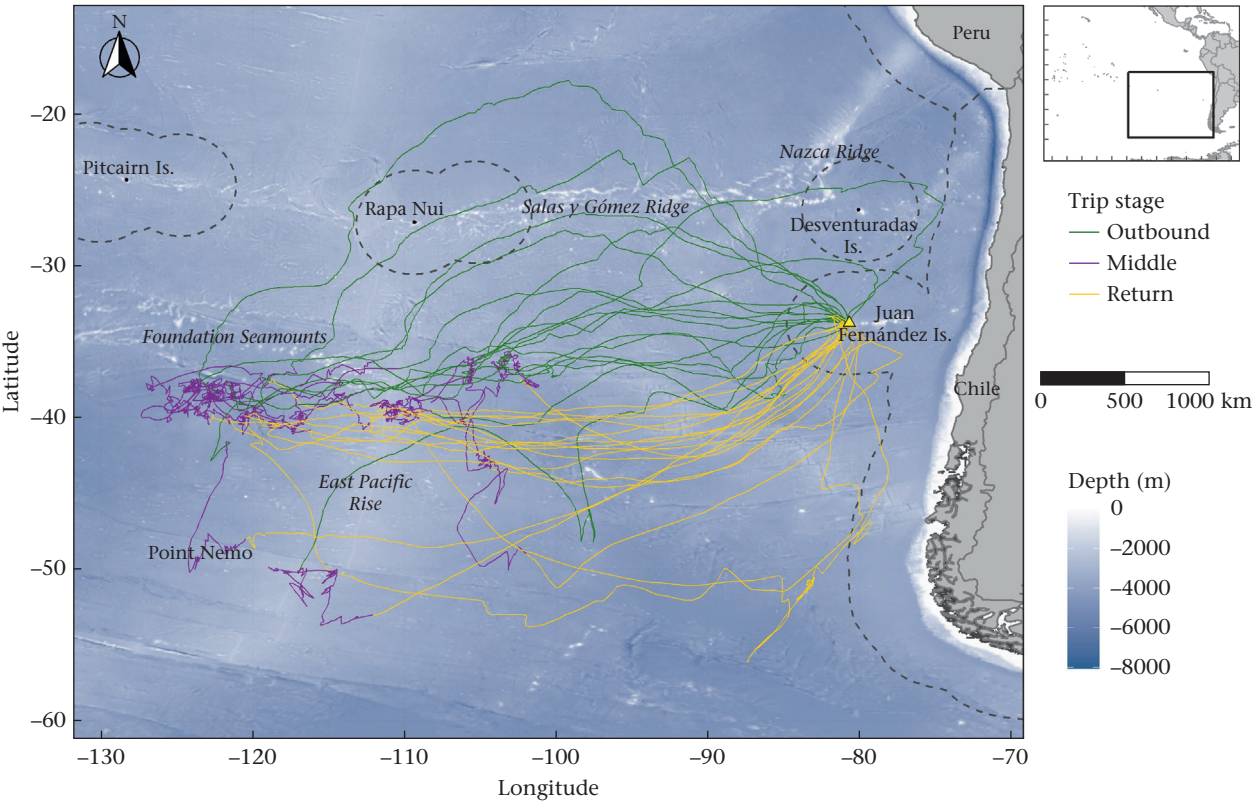


Figure 1. Map of the study region and 18 complete foraging trips of Juan Fernández petrels tracked with GPS loggers during incubation from Isla Alejandro Selkirk, Juan Fernández Islands (yellow triangle). Trips are coloured according to trip stage. National jurisdictions and their exclusive economic zones (EEZ) in the southeast Pacific Ocean are shown by dotted grey lines for the Pitcairn Islands (UK), Rapa Nui (Easter Island, Chile), Desventuradas Islands (Chile), Chile and Peru. Bathymetry is shown by blue shading and topographical features are labelled in italics. Point Nemo represents the point in the world's oceans furthest from land. The scale bar represents distances at the latitude of the breeding colony.

entire outbound and return stage, and D_2 is the sum of straight-line distances travelled between consecutive locations for each trip stage, both calculated using the ‘fields’ package (Nychka et al., 2021). A high value indicates that the bird has taken a substantial detour.

Statistical Analysis

Effects of wind on foraging and flight behaviour

We plotted trips and core foraging areas in relation to the average values and predictability of wind speed and direction over the study period (Fig. 2) to examine whether trips took advantage of persistent wind fields (H1a). Predictability was based on the inverse of scaled (between 0 and 1) coefficient of variation values of hourly wind speed and direction in each grid cell. We defined core foraging areas as 50% kernel utilization distributions (UDs) of ARS locations calculated in the ‘adehabitatHR’ package (Calenge, 2006). UD were calculated for each trip using a smoothing factor (h) of 50 km and cell size of 5 km and averaged across trips.

We tested whether the average θ_w experienced during the first 3 h of each trip explained bird departure bearings using circular–circular regression in the ‘circular’ package (Lund et al., 2017). Generalized additive mixed models (GAMMs) were then applied to all locations assigned as directed flight to model the potentially nonlinear effects of V_w and $\Delta\theta$ on ground speeds (H1c), using the

‘mgcv’ package (Wood, 2022). Ground speed (m/s) was calculated from step lengths and took a Gaussian error distribution. We included the factor DayNight to test for differences by day and night, calculated using the ‘maptools’ package (Bivand et al., 2021) with civil twilight (6° below horizon) included as day. Both wind variables were found not to be collinear and were standardized by subtracting from the mean and dividing by the standard deviation. We included an individual identity random intercept as a smooth term and an autoregressive moving average (ARMA) autocorrelation term to control for serial autocorrelation. We compared a series of candidate models containing DayNight, the linear and smoothed effects of V_w , $\Delta\theta$ and the two combined, as well as their interaction, in the form of a tensor smooth product interaction, using the Akaike information criterion (AIC), with the best supported model that with the lowest AIC. The number of knots for smooths was set to five to reduce overfitting and smooths were produced using cubic regression splines with shrinkage, allowing variables to be penalized out of the model during fitting (Wood, 2017), to reduce the risk of overparameterization. We calculated root mean squared error (RMSE), the square root of the sum of all errors divided by number of values as a measure of model fit. The RMSE was calculated using k -fold cross validation whereby each fold was a separate individual ($N = 18$). Models with the lowest RMSE were deemed to be the best fitting. We tested for significant differences in ground speeds by day and night using Tukey’s post

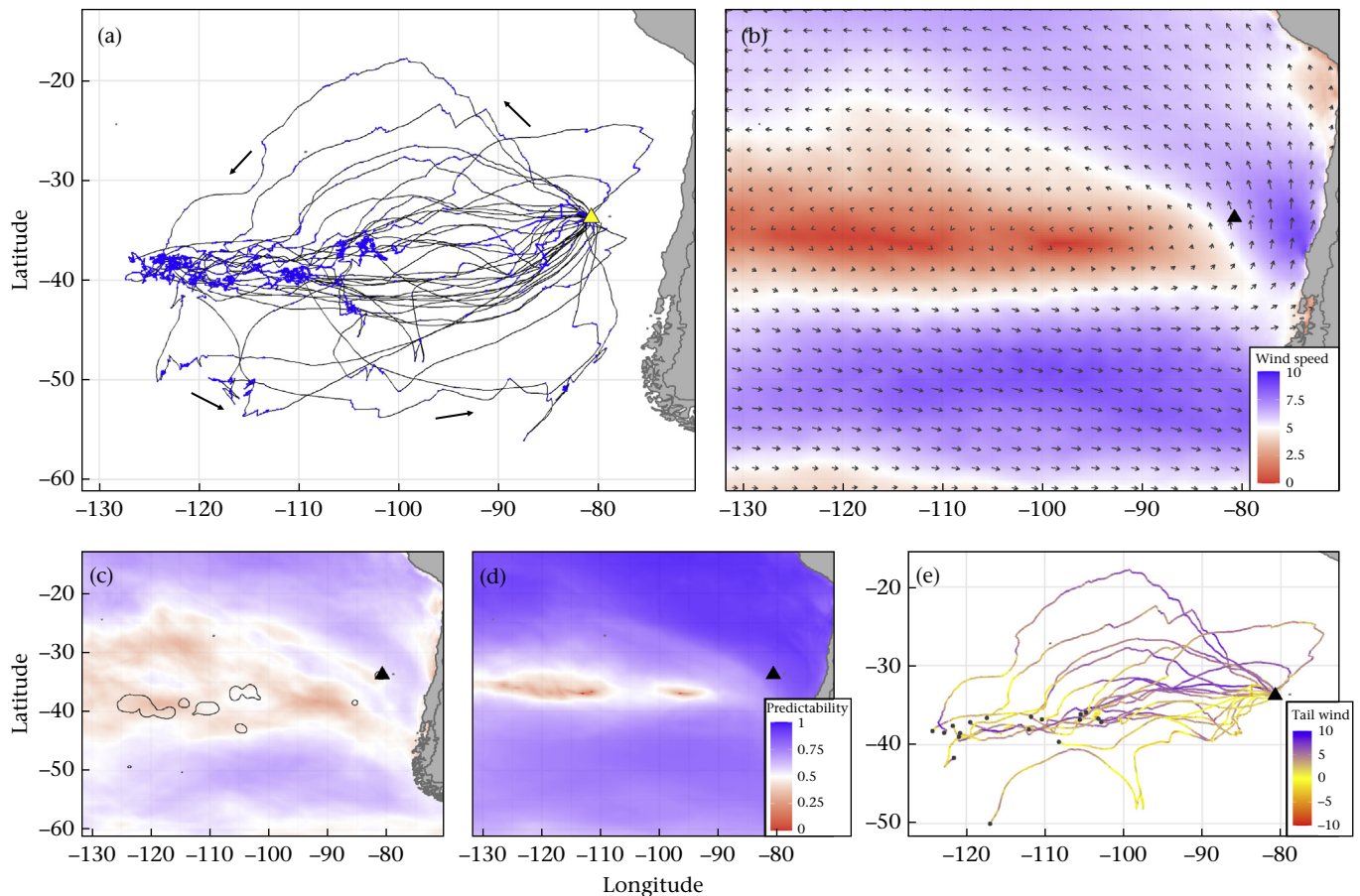


Figure 2. Use of southeast Pacific Ocean winds by foraging Juan Fernández petrels tracked with GPS loggers from Isla Alejandro Selkirk (yellow/black triangle). (a) Complete foraging trips with area-restricted search (ARS) locations in blue. The direction of travel is indicated by black arrows. (b) Wind climatology over the study period with mean wind speeds (m/s) increasing from red to blue and wind directions indicated by arrows. (c, d) Maps of predictability of (c) wind speed and (d) direction scaled between 0 and 1. High values (in blue) indicate low variation in wind speed and direction values across the study period. Core foraging areas are shown in dark grey in (c) by the 50% utilization distribution (UD) contour based on ARS locations. (e) Outbound stages of trips coloured according to the degree of tail wind support (V_{tw} , m/s; blue = positive; yellow = no support; red = contrary) showing large variation among individuals. The start of the middle stage of trips is indicated by a black dot. Note that the colour scales differ for (b–e).

hoc comparisons in the ‘multcomp’ package (Hothorn et al., 2016). We also subsequently ran a series of models on outbound and return stages of trips to test whether V_w and ground speeds of birds differed across the two stages (see Appendix for details).

Effects of bird and partner mass on trip characteristics and mass gain

We ran three linear models to investigate the effects of bird and partner mass on trip duration, maximum range and mass gain (H2a–b), with each metric taking a Gaussian distribution. We did not consider cumulative distance travelled as it was highly correlated (Spearman rank correlation: $r_s > 0.7$) with the other two variables (see Results). Bird and partner mass were not significantly correlated (Pearson correlation: $r = 0.30$, $P = 0.143$) permitting their inclusion, and their importance was assessed using backwards model selection and likelihood ratio tests using the package ‘lmtest’ (Hothorn et al., 2022).

Effects of Route Selection and Tail wind Support on trip Outcomes

A series of tests was conducted to examine links between V_{tw} , path sinuosity, trip duration and mass gain. We first ran Spearman rank correlations to test for significant correlations among route sinuosity, durations and cumulative distances travelled during outbound and return stages (H1d). As these variables were not significantly correlated (see Results), we then ran a series of linear models examining the effect of average V_{tw} on sinuosity, durations, distances travelled and average ground speeds during outbound and return stages. Second, we ran three linear models with trip duration, mass gain and mass gain/day as response variables to test the effect of V_{tw} (H3). For mass gain and mass gain/day models, bird mass was also included as a covariate (see above), as was the proportion of the trip spent in ARS, to test the alternative hypothesis that mass gain was related to foraging activity rather than wind use. Lastly, we ran a model with mass gain/day as the response and V_{tw} during outbound and return stages as separate covariates (which were not correlated). All linear models took a Gaussian distribution and likelihood ratio tests were used to select significant variables. Sinuosity during the return stage was square root transformed to conform to the assumption of a normal distribution. Unless otherwise specified, means are provided ± 1 SD.

RESULTS

We tracked Juan Fernández petrels during incubation, recording 18 complete GPS trips (13 with geolocator-immersion loggers) and another 14 with geolocator-immersion loggers only. Sample sizes were reduced as (1) several devices were lost at sea or failed to download or (2) the birds were not recaptured before fieldwork ended (Table 1). Trips based on the larger sample of colony monitoring data lasted 19.8 ± 3.4 days (range 13–30 days) and complete GPS trips lasted 20.4 ± 2.8 days (16–24 days), with birds travelling up to 13 178 km (mean $\pm$ SD = $10\,741 \pm 1672$ km) and ranging up to 4166 km (3404 ± 630 km) from the colony. Trips generally took the form of looping anticlockwise journeys across the southeast Pacific Ocean towards a large oceanic region between the Foundation Seamounts and the East Pacific Rise (ca. 35° – 45° S and ca. 130° – 100° W), with more concentrated movements at middle stages, presumably associated with foraging around the Subtropical Convergence (Figs. 1 and 2a). Two birds went further south than the rest (ca. 50° – 55° S) with one at Point Nemo, the point in the world's oceans furthest from land (Fig. 1).

Foraging Behaviour during Outbound and Return Stages

Birds spent $45.8 \pm 7.5\%$ of their time in directed flight, $40.0 \pm 4.9\%$ of their time in ARS and only $14.2 \pm 3.6\%$ of their time resting. Immersion activity data corresponded well with states assigned from GPS data, with the most ($94.3 \pm 1.1\%$) and least ($24.8 \pm 4.8\%$) time spent dry during directed flight and rest states, respectively, with high percentages ($80.9 \pm 3.1\%$) of ARS also spent dry (i.e. in flight). Somewhat surprisingly, the number of wet events/h was highest during rest (1.78 ± 0.42), closely followed by ARS (1.57 ± 0.13), and with a considerable number also occurring during directed flight (1.19 ± 0.11). This indicates that at a 40 min GPS resolution, fine-scale foraging behaviour may also be captured within the rest state, while birds also make frequent feeding attempts during more directed travel (Fig. 2a). More time appeared to be spent in ARS during the outbound ($25.2 \pm 10.8\%$) than the return ($19.3 \pm 7.0\%$) stage, although the majority of ARS ($63.8 \pm 17.6\%$) occurred during the middle stages, a period that represented $41.1 \pm 12.3\%$ of total trip time (outbound: $33.1 \pm 9.8\%$; return: $25.8 \pm 6.1\%$).

Effects of Wind on Foraging and Flight Behaviour

Birds used predictable southeasterly trade winds to assist outbound journeys in a northwesterly or westerly direction, while returning birds headed southeast into the region of stronger and predictable westerlies associated with the Antarctic Circumpolar Current (H1a; Fig. 2). In contrast, middle stages of trips occurred in the southern portion of the South Pacific Gyre where wind speeds are weaker and more variable, and directions also variable.

Wind at the colony generally blew towards the north northwest ($354 \pm 1^\circ$; Fig. 3a) and birds appeared to adjust departure bearings according to wind directions experienced (circular–circular regression: $P = 0.031$; Fig. 3b, c, d; H1b), most heading northwest (mean $\pm$ 95% confidence interval: $319 \pm 20^\circ$; Fig. 3c). Across foraging trips, birds mostly experienced low to moderate V_w (9.9 ± 2.7 m/s; Fig. 4a) and oriented predominantly with quartering tail winds ($54.4 \pm 29.5^\circ$; 88% of locations $\leq 90^\circ$) while in directed flight (Fig. 4b; H1c). Nevertheless, the degree of V_{tw} experienced among individuals varied substantially, particularly when outbound (Fig. 2e) as a result of finer-scale variation in wind conditions.

The best GAMM explaining variation in ground speeds over the whole trip included the tensor smooth of V_w and $\Delta\theta$ as well as DayNight (Table 3). Ground speeds increased with V_w and were highest (ca. 20 m/s) under the strongest winds encountered (10 – 15 m/s; Fig. 4). Ground speeds were similarly high for tail winds and cross-winds ($<60^\circ$) and lowest for head winds ($>90^\circ$; H1c). The two-dimensional tensor interaction showed the optimum conditions for fast flight were $V_w > 5$ m/s and $\Delta\theta < 50$ – 60° (Fig. 4c). Birds' ground speeds were 1.3 ± 0.1 m/s slower at night than by day (Tukey's post hoc test: $P < 0.001$). Ground speeds were slightly higher (modelled difference of 0.92 ± 0.04 m/s) during the return than the outbound stage, mainly due to the faster V_w experienced (0.75 ± 0.03 m/s), rather than because the birds flew significantly faster for a given V_w as a result of their increased return mass (see Appendix for details).

Effect of Bird and Partner Mass on Trip Characteristics and Mass Gain

Birds gained around a quarter of their departure mass while on foraging trips (Table 2). Birds that were lighter on departure gained more mass than heavier birds ($\chi^2_1 = 6.64$, $P = 0.010$, $N = 21$; Fig. 5a; H2a), yet there was no effect of partner mass on mass gain ($\chi^2_1 = 0.70$, $P = 0.403$). Lighter birds did not appear to gain more

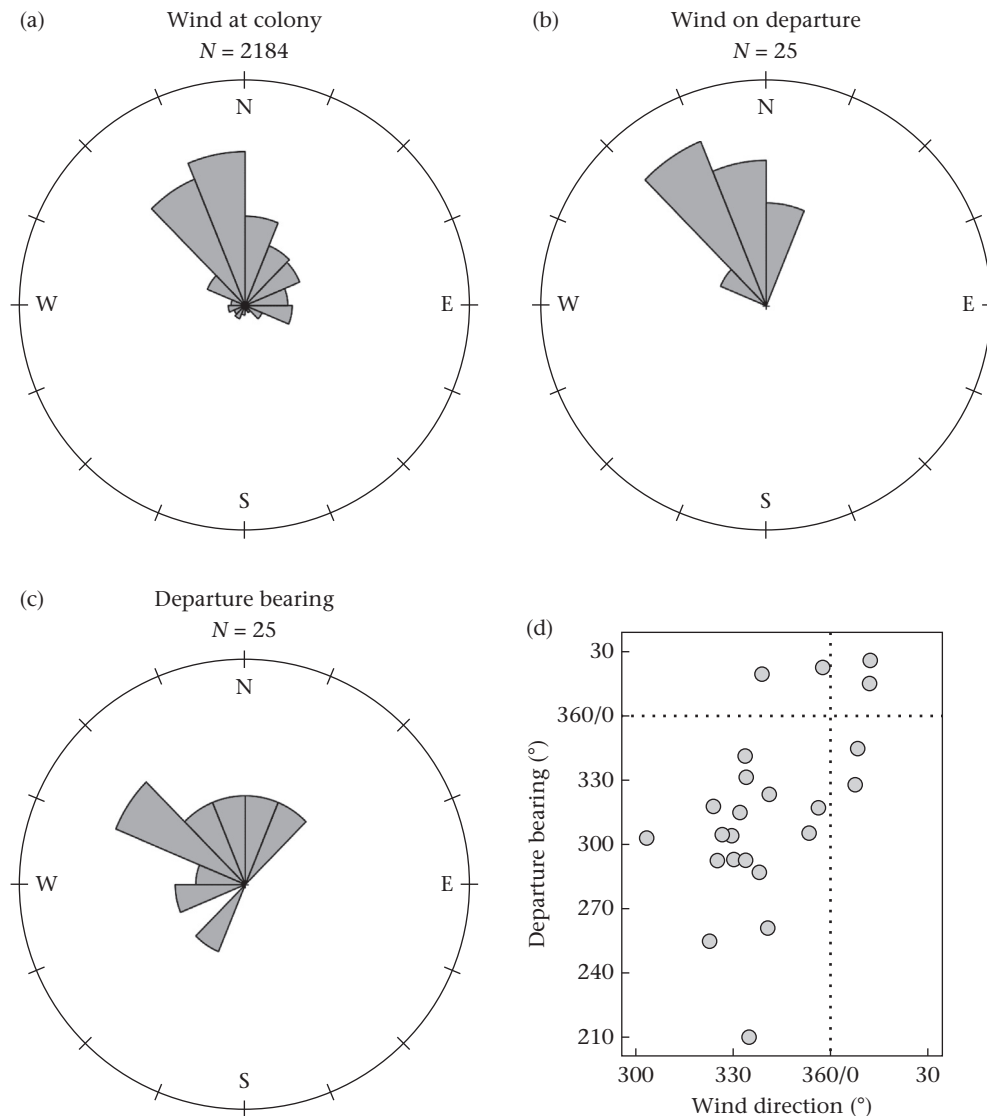


Figure 3. Effect of wind direction (i.e. direction towards which wind is blowing, °) on initial departure bearings (°). (a) Hourly wind directions at the colony over the study period, (b) wind direction experienced by and (c) departure bearings of GPS-tracked birds averaged over the first 3 h of each foraging trip. (d) The association between wind direction and departure bearing is plotted linearly but was modelled using a circular–circular regression ($P = 0.031$).

mass by foraging more ($\chi^2_1 = 0.20$, $P = 0.656$). Birds making longer-lasting trips ranged further (by 145.3 ± 45.7 km/day; $r_s = 0.65$, $P = 0.007$) and covered greater distances (by 415.7 ± 114.1 km/day; $r_s = 0.70$, $P = 0.001$), such that maximum range and cumulative distance travelled were highly correlated ($r = 0.86$, $P < 0.001$). There was no effect of own ($\chi^2_1 = 0.81$, $P = 0.369$) or partner mass ($\chi^2_1 = 3.40$, $P = 0.065$) on trip durations (H2b), yet birds with heavier partners ranged further (by 1098.6 ± 497.1 km/100 g; $\chi^2_1 = 5.34$, $P = 0.021$, $N = 17$; Fig. 5b; H2b), even though there was no effect of their own mass on maximum ranges ($\chi^2_1 = 0.56$, $P = 0.453$).

Effect of Route Selection and Tail Wind Support on Trip Outcomes

After controlling for significant effects of departure mass (above), we found no effect of average V_{tw} over the whole trip on trip durations ($\chi^2_1 = 2.31$, $P = 0.128$) or mass gain ($\chi^2_1 = 0.90$, $P = 0.342$; Fig. 6a). However, the negative relationship between V_{tw} and overall trip duration became significant when we removed one individual that experienced anomalously low (i.e. negative)

wind support on the return voyage ($\chi^2_1 = 4.62$, $P = 0.032$; Fig. 6d). There was large variability in the outbound distances travelled (range 2450–6743 km) and time taken (range 2.7–11.7 days) to complete the outbound stage (Fig. 6e, i). Birds that took looping detours covered greater distances ($r_s = 0.74$, $P < 0.001$) and took more time to do so ($r_s = 0.64$, $P = 0.004$), but did not appear to benefit more from V_{tw} ($\chi^2_1 = 0.04$, $P = 0.846$; Fig. 6i, k; H1d). Instead, birds with greater V_{tw} had shorter outbound commute durations ($\chi^2_1 = 4.51$, $P = 0.034$) due to faster ground speeds achieved ($\chi^2_1 = 19.94$, $P < 0.001$; Fig. 6e, g). Outbound V_{tw} did not influence overall mass gain ($\chi^2_1 = 1.22$, $P = 0.268$), but was associated with increased mass gain per day at sea ($\chi^2_1 = 5.02$, $P = 0.025$; Fig. 6b; H3). Return commutes were shorter and less variable in duration (range 3.3–7.5 days), mainly because birds experienced faster V_w (see above) rather than because they covered less distance (range 2715–7028 km; Fig. 6f, j). Yet, while higher V_{tw} enabled faster ground speeds ($\chi^2_1 = 6.77$, $P = 0.009$; Fig. 6h), there was no link between V_{tw} and the duration of return commutes ($\chi^2_1 = 2.67$, $P = 0.102$), overall mass gain ($\chi^2_1 = 0.42$, $P = 0.519$) and mass gain per day at sea ($\chi^2_1 = 0.50$, $P = 0.481$; Fig. 6c, f).

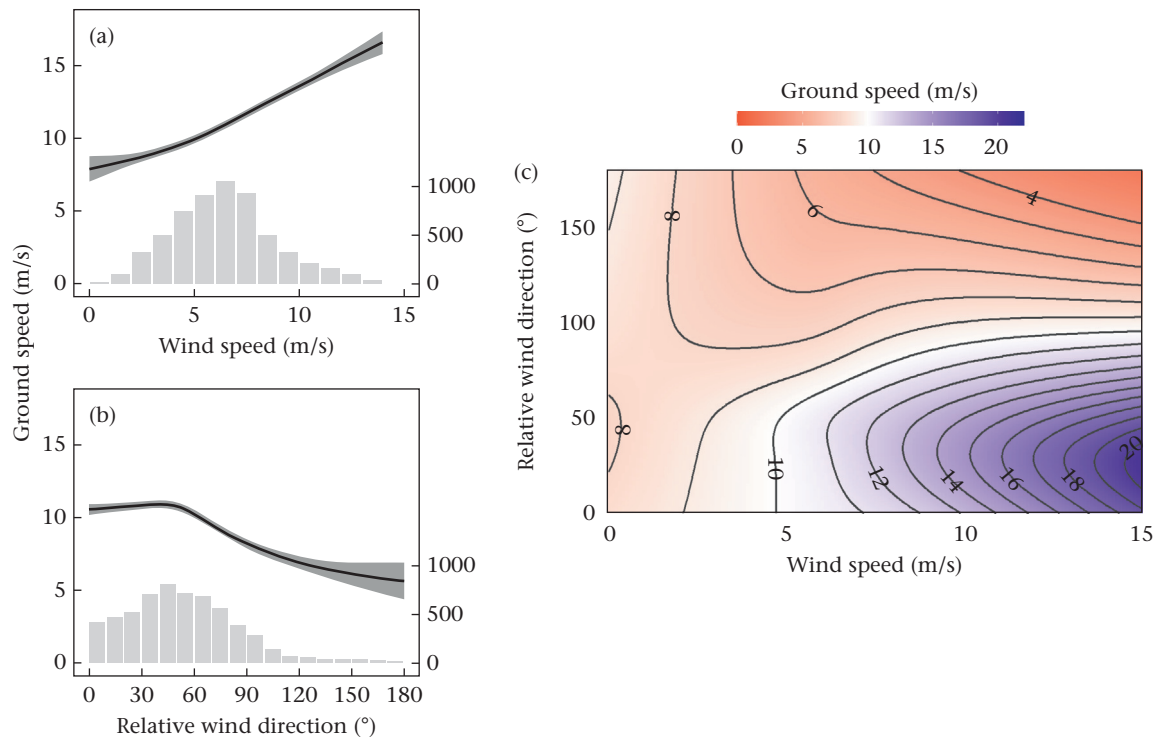


Figure 4. Predicted ground speeds (m/s) of Juan Fernández petrels in relation to (a) wind speed (V_w , m/s), (b) relative wind direction (wind direction relative to bird direction; $\Delta\theta$, °) and (c) their predicted combined effect based on the tensor smooth product modelled in generalized additive mixed models (GAMMs). (a, b) Histograms show the distribution of V_w and $\Delta\theta$ values encountered by birds, with the frequency indicated by the right-hand y axes. Predicted relationships are shown as means with 95% confidence intervals. Contours in (c) indicate changes in predicted ground speeds at 1 m/s intervals.

Table 3

Model selection for generalized additive mixed models (GAMMs) examining the effect of wind speed (V_w) and relative wind direction (wind direction relative to bird direction; $\Delta\theta$) on ground speeds

Model	Formula	AIC	Δ AIC	RMSE	R^2
18	$\sim \text{te}(V_w, \Delta\theta) + \text{DayNight}$	25205.3	0.0	2.00	0.45
16	$\sim s(V_w) + s(\Delta\theta) + \text{DayNight}$	25543.0	337.7	2.07	0.42
10	$\sim V_w * \Delta\theta + \text{DayNight}$	25686.1	480.8	2.10	0.40
17	$\sim \text{te}(V_w, \Delta\theta)$	25693.9	488.6	2.09	0.40
15	$\sim s(V_w) + s(\Delta\theta)$	26044.4	839.1	2.16	0.36
9	$\sim V_w * \Delta\theta$	26098.9	893.6	2.17	0.35
8	$\sim V_w + \Delta\theta + \text{DayNight}$	26293.9	1088.6	2.17	0.33
7	$\sim V_w + \Delta\theta$	26515.3	1311.0	2.25	0.31
12	$\sim s(V_w) + \text{DayNight}$	26612.5	1407.2	2.27	0.29
4	$\sim V_w + \text{DayNight}$	26626.3	1421.0	2.27	0.29
11	$\sim s(V_w)$	27934.6	1829.4	2.35	0.24
3	$\sim V_w$	27045.2	1839.9	2.35	0.24
14	$\sim s(V_w) + \text{DayNight}$	27053.6	1848.3	2.35	0.24
13	$\sim s(\Delta\theta)$	27429.4	2224.1	2.43	0.19
6	$\sim \Delta\theta + \text{DayNight}$	27458.9	2253.7	2.44	0.19
5	$\sim \Delta\theta$	27761.1	2555.8	2.50	0.14
2	$\sim \text{DayNight}$	27971.3	2766.0	2.54	0.11
1	~ 1	28269.1	3063.9	2.61	0.07

AIC = Akaike information criterion; Δ AIC = change in AIC from the best supported model; RMSE = root mean squared error from k-fold cross validation; Day-Night = factor encoding day or night; te = tensor smooth interaction, s() indicates a smoothed variable. The best-supported model is highlighted in bold.

DISCUSSION

Our study reveals that incubating Juan Fernández petrels have long and extremely wide-ranging foraging trips which are adjusted according to regional and local winds as well as the condition of the bird and its partner. Birds travelled between 2000 and >4000 km from Isla Alejandro Selkirk to forage in one of the most remote regions on Earth (Point Nemo). To do so, they exploited predictable

trade and westerly winds on outbound and return stages of trips, respectively, allowing them to maximize ground speeds and reduce the time spent travelling to and from foraging areas. Despite the broad similarity in foraging areas used by most individuals, there was substantial variation in the routes taken to and from those areas. The individuals that experienced greater tail wind support on outbound journeys reached foraging areas quicker and, on returning to the colony, had achieved a higher mass gain per day spent at sea. Moreover, birds that were lighter on departure gained more mass at sea and those with heavier partners ranged further from the colony. These results suggest that the decision of how far to go on foraging trips is based on the condition of the pair and on wind patterns, but that the success of trips is linked to how birds use winds on foraging commutes.

Large-scale Foraging Behaviour and Use of Prevailing Winds

Through GPS tracking, we have shown that incubating birds took long (16–24 days) foraging trips westwards and ranged much further than previously documented by limited at-sea surveys (Miranda-Urbina et al., 2015; Shiriha et al., 2015), to a region of concentrated search behaviour in the central South Pacific Ocean (35–45°S, 130–100°W). No tracked birds headed east to productive waters associated with the Humboldt Upwelling (<850 km away), matching other evidence that gadfly petrels often do not exploit productive areas closest to their breeding colonies (Taylor et al., 2020; Ventura et al., 2020). This probably reduces competition with other seabirds (e.g. Ballance et al., 1997) such as pink-footed shearwaters, *Ardenna creatopus*, and sooty shearwaters, *Ardenna grisea*, that feed off mainland Chile (Carle et al., 2019; Miranda-Urbina et al., 2015), and is possible because the petrels' greater mobility allows them to exploit areas too distant for other seabirds

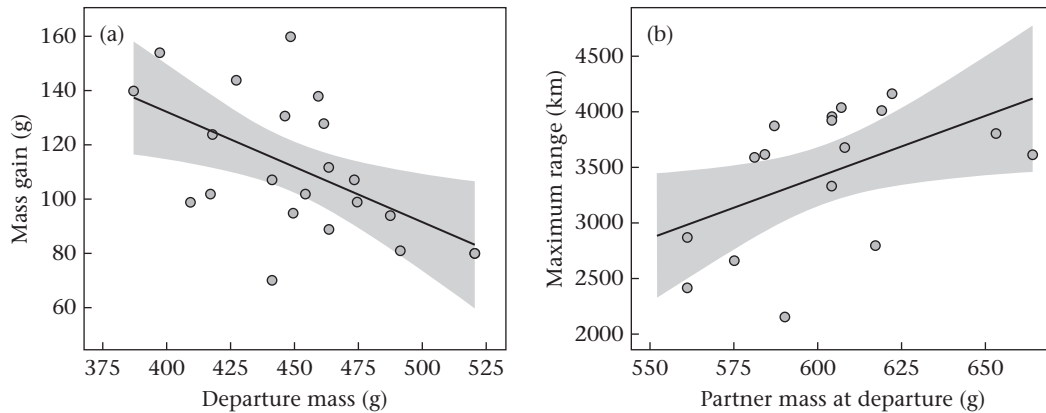


Figure 5. The relationship between (a) departure mass (g) and mass gain (g) and between (b) mass of partner at departure (g) and maximum range (km) of foraging trips. Significant modelled relationships are shown by black lines with 95% confidence intervals in grey shading.

to reach. As we predicted (H1a), birds took long looping anti-clockwise routes, matching those of Murphy's petrels, *Pterodroma ultima*, and wandering albatrosses, *Diomedea exulans*, which orient with prevailing anticyclonic winds in the South Pacific and Southern Oceans, respectively (Clay et al., 2019; Weimerskirch et al., 2000). By initially heading northwest, birds take advantage of predictable trade winds. Similarly, by taking a southerly route back, birds can use winds associated with the Antarctic Circumpolar Current (below 40°S, the 'Roaring Forties') which persistently blow west to east. In contrast to other subtropical gadfly petrels that on looping trips do not appear to concentrate searching in particular areas but instead intermittently forage during travel (Clay et al., 2019; Halpin et al., 2022; Ventura et al., 2020), Juan Fernández petrels had long periods of ARS behaviour in the middle portions of trips (representing ca. 40% of their time), during which landing rates were substantially higher than during directed travel. We note though, at the scale of our interpolated (40 min) GPS resolution, many wet events also occurred during the rest state, which indicates the HMM may be misclassifying some finer-scale foraging behaviour as resting. Regardless, our results suggest birds shared a foraging region, although individuals' foraging areas were spread over a wide longitudinal band and did not appear to target a particular topographical feature.

Juan Fernández petrels are known to be social foragers, and in their nonbreeding grounds in the eastern tropical Pacific Ocean they often feed in multispecies flocks in association with subsurface predators such as oceanic dolphins (Delphinidae) or tuna (Scombridae), which make schooling fish available to aerial predators (Au & Pitman, 1986; Ballance et al., 1997; Ribic et al., 1997). While little is known about the marine predator community in the central South Pacific Ocean where ARS activity clustered (e.g. Clay et al., 2017), this region is not used by commercial longline fisheries and so presumably does not have high tuna abundance (Lehodey et al., 2015). This suggests that breeding birds may be using alternative strategies to feed, such as targeting oceanic frontal zones around the Sub-tropical Convergence where subsurface upwelling supports greater primary productivity, to feed on fish or squid that migrate to the sea surface (Weimerskirch, 2007). Moreover, these foraging areas in the southern arc of the South Pacific Gyre are associated with low and variable wind speeds, which may facilitate manoeuvrability, while the flatter sea surface may help birds locate floating prey.

Effects of Wind on Flight Behaviour and Route Selection

Given their high aspect ratios, gadfly petrels are arguably the seabirds best adapted for efficient flight (Spear & Ainley, 1997a). In

line with our predictions, birds tended to orient on departure with the prevailing wind directions (H1b) and across trips oriented favourably with tail and cross-winds to maximize achieved ground speeds of ca. 20 m/s (ca. 70 km/h; H1c). Birds had the highest ground speeds (10–20 m/s) in moderate-to-high wind speeds (above 5 m/s) and with a relative wind direction of less than ca. 60°. Almost 90% of bird locations were oriented within 90° of the wind direction indicating that birds avoided head winds where possible. Gadfly petrels, which have lower wing loading and greater profile drag than albatrosses, may be less able to fly into head winds (Pennycuik, 1982; Spear & Ainley, 1997b), demonstrated here by the extremely low ground speeds attained by birds into head winds. Birds generally oriented with quartering tail winds (ca. 55°), similar to Desertas petrels (Ventura et al., 2020), likely because at finer scales they tack back and forth across the tail wind component, turning into cross- and head winds to gain lift and then using tail winds to maximize ground speeds during the longer descent phase (Kempton et al., 2022; Sachs et al., 2013). Indeed, Spear and Ainley (1997b) noted that unlike albatrosses that rely on energy from waves for slope soaring (Pennycuik, 1982), gadfly petrels likely use a dynamic soaring flight strategy whereby they gain energy from tilting from one side to another with wind perpendicular to their wings like a sailboat, aided by their large wing areas relative to their mass. By flying across the wind, birds likely also increase the chance of locating prey visually and enhance their sampling of air currents for odour plumes associated with prey (Nevitt et al., 2008).

Despite initially orienting favourably with tail winds, individuals varied widely in the degree of tail wind support they received across outbound journeys. Those individuals taking a more northerly outward journey appeared to orient more with tail winds. However, in contrast to our prediction (H1d), birds that took long detours from the most direct route did not appear to use winds more favourably (i.e. using tail winds) and tail wind support did not explain the distances travelled between the colony and foraging areas.

Changes in Mass and Pair Coordination of Foraging Trips

On average, foraging birds increased their mass by 25% of departure mass. As predicted (H2a), birds with a lower mass at departure gained more mass, in line with previous studies (e.g. Kim et al., 2018; Weimerskirch, 1995). However, they did not do this by taking longer trips, ranging further from the colony or spending a greater proportion of time in ARS behaviour. This contrasts with other seabird studies where birds departing at a

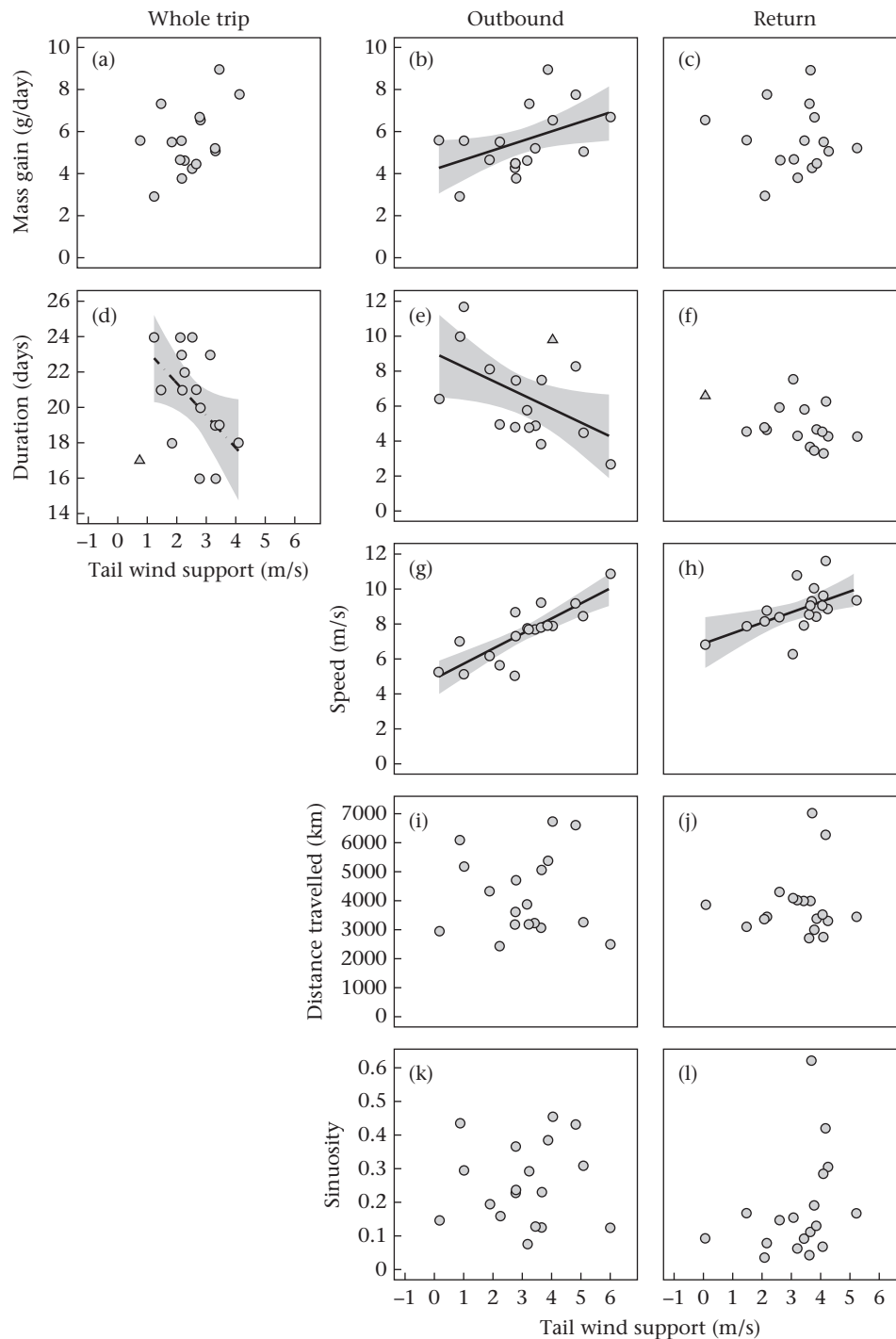


Figure 6. Relationships between average tail wind support (V_{tw} , m/s) and trip characteristics and mass gain over the whole trip and for outbound and return stages of trips, separately: (a–c) mass (g) gained per day at sea, (d–f) durations (days), (g, h) ground speeds (m/s), (i, j) cumulative distances travelled (km) and (k, l) sinuosity (an index between 0 and 1 of detours to and from middle stages of trips). Significant effects of V_{tw} on metrics are shown by a modelled black line with 95% confidence intervals in grey shading. The dotted line in (d) shows that the relationship was significant with the removal of an individual (triangle) that experienced anomalously low tail wind support during the return voyage.

lower mass spend more time at sea (e.g. short-tailed shearwaters, *Ardenna tenuirostris*: Carey, 2011; Manx shearwaters: Gillies et al., 2022) and could be explained by the fact that petrels may aim for roughly the same target mass before returning, but that their return mass (and mass gain) is influenced in an unpredictable manner by the success of outbound and return commutes (Brooke, 2004).

We also found that birds responded to their partner's condition at departure as birds with higher partner mass travelled further

from the colony (by ca. 1000 km per 100 g; supporting H2b), but did not make longer-lasting trips. Owing to logistical constraints, the majority of partner masses (birds that arrived weighing >600 g) were estimated using a daily mass loss estimate based on all individuals and not measured directly, so should be treated with some degree of caution. However, given that birds with lighter partners (<570 g) did not travel as far as those partners with moderate masses (around 600 g), and the potential error associated with back-calculating return mass was likely an issue only for the

heaviest birds (for which we had to wait several days to weigh), we believe this finding is robust to measurement constraints. This result contrasts with our prediction and the findings of a handicapping study which showed Antarctic petrels compensate for a reduction in partner condition through shorter trips (Tveraa et al., 1997). Foraging petrels with fewer time constraints (due to increased partner condition) might travel further to forage because the greater distances covered provide birds with more foraging opportunities than a direct beeline route westwards. These routes may also allow them to use more predictable, but perhaps not necessarily stronger, winds. Ultimately, our observational approach and modest sample size do not allow us to tease out between- and within-pair effects; regardless, our study reveals birds assess their partner's condition, likely to improve coordination (Gillies et al., 2021). How birds are able to assess their partner's condition when there is often very little time together in the burrow at night at change-over, remains a mystery, and future studies should explore the mechanisms through which birds reveal their physiological status, whether directly through vocalizations or indirectly through smell, touch or sight (Boucaud et al., 2016; Kavelaars et al., 2019).

Tail Wind Support and Trip Outcomes

Several studies have established direct links between foraging tactics and energy balance (Tarroux et al., 2020; Weimerskirch, 1995), yet, while wind use dictates foraging energetics (e.g. Weimerskirch et al., 2000), the effects on trip success are not well established. We did not find a direct link between tail wind support and overall mass gain, indicating that orientation with wind directions that promote the fastest travel speeds (i.e. favourable winds) at the fairly coarse scale of our study (40 min GPS resolution) does not appear to directly reduce the amount of energy stored and, by inference, energy expended. However, stronger tail wind speeds on outbound journeys substantially reduced the time taken to reach the middle stage of trips, through their direct effect on ground speeds. Those individuals that were able to reduce the time taken to reach foraging areas had increased mass gain per day at sea as a direct result of their shorter trips, which suggests that reaching core foraging areas faster provides greater rewards than a longer circuitous trip through less productive waters. In contrast, while tail wind support facilitated fast movement on return voyages, wind speeds were higher and less variable meaning that all birds returned rapidly to the colony. Ultimately, petrels seek to optimize routes according to winds, because doing so reduces time costs (Ventura et al., 2020). That said, we have shown that individuals experience variable wind which often prevents an optimal strategy being achieved, and which may have consequences for breeding success.

Conclusions

Our study provides novel insights into the mechanisms promoting and constraining the foraging strategies of gadfly petrels, including their use of private (own and partner mass) and public (wind) information. We suggest that decisions involving where to go are broadly predetermined based on knowledge of prevailing winds and the location of oceanic prey aggregations, while the decisions involving how far to go and for how long are related to the condition of the pair. Crucially, we have also shown that while gadfly petrels are extremely well adapted for efficient flight, wind speed and direction provide a stochastic set of conditions to which birds have to adapt each time they set out on a foraging trip, and which either facilitate or impede foraging journeys, with downstream consequences for the success of trips.

Author Contributions

T.A. Clay: Conceptualization, Formal analysis, Resources (supporting), Data curation (co-lead), Funding acquisition (supporting), Writing – original draft, Visualization; **P. Hodum:** Project administration (supporting), Writing – review and editing, Project administration (co-lead); **E. Hagen:** Project administration (supporting), Writing – review and editing; **M. de L. Brooke:** Conceptualization, Field Investigation (lead), Resources (lead), Data curation (co-lead), Funding acquisition (lead), Writing – review and editing, Supervision, Project administration (co-lead).

Data Availability

Raw GPS tracking data can be viewed and requested on the BirdLife International Seabird Tracking Database (http://seabirdtracking.org/mapper/?dataset_id=1661).

Declaration of Interest

The authors declare that they have no conflict of interest.

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Appendix

Deriving Wet Events from Immersion Data

We defined a wet event based on several criteria: (1) a 5 min period when at least one wet event was recorded (>0) following a 5 min period spent entirely dry (0); (2) if a 5 min period contained dry activity (1–49) and was sandwiched between periods spent entirely dry (50) then a take-off and landing event must have occurred; (3) if there were several consecutive periods when the bird was both dry and wet (1–49) we used a sliding window to assess the minimum number of take-offs and landings that must have occurred.

Incorporating Immersion Data Into Hidden Markov Models

We tested whether the inclusion of immersion data in hidden Markov models (HMMs) improved state classification (Carneiro et al., 2022) and could better explain the foraging behaviour of Juan Fernández petrels at a 40 min GPS resolution. We summed the number of wet bouts occurring 20 min either side of each interpolated GPS location and included that sum in HMMs as a third input data stream along with step lengths and turning angles derived from GPS data, taking a Poisson error distribution. We compared our simple three-state model with and without wet bouts to a four-state model whereby area-restricted search (ARS) was split into ARS with no wet bouts and ARS with wet bouts, the latter indicative of foraging on the sea surface (hereafter foraging). We also ran a four-state model without immersion data. For both four-state models, we specified slightly smaller step lengths for the foraging than ARS state. The four models were compared using the Akaike information criterion (AIC). However, as the AIC tends towards models with a greater number of states regardless of whether or not they are biologically informative (Pohle et al., 2017), we also manually screened tracks, examined pseudoresidual plots and checked model parameters and activity budgets for each state (Table A2).

As expected, the two four-state models had lower AICs than their three-state counterparts (Table A2). Although the inclusion of wet bouts resulted in models with higher AICs and did not appear to substantially change step length and angle parameters, the number of wet bouts was higher during rest for the three-state model and during foraging and ARS than rest and directed flight, indicating higher landing rates in these states. However, pseudoresidual plots indicated models with wet bouts fitted the data poorly. Lastly, the inclusion of a fourth state appeared to split directed flight into two states (i.e. two states with high step lengths), rather than split the ARS state, as intended. As such, we deemed the original three-state model without immersion data the most biologically informative and parsimonious.

Segmenting Trips Into Outbound, Middle and Return Stages

We partitioned outbound, middle and return stages of trips (Fig. 1) using a methodology similar to that in Wakefield et al. (2009) based on distance and time thresholds as well as the proportion of time in ARS. We first plotted the proportion of the maximum distance reached as a function of the proportion of total trip time for each trip (Fig. A2a), which showed that most ARS behaviour occurred at distal portions of trips. Using a 12 h moving window, we defined the start of the middle (end of outbound) stage as the first location at which at least 75% of time is spent in ARS and the distance from the colony is at least 75% of the maximal distance. The end of the middle (start of return) stage was defined as the last location within the specified criteria (Fig. A2b).

Modelling Ground Speeds and Wind Speeds Encountered in Outbound Versus Return Stages

We ran a series of generalized additive mixed models (GAMMs) in the 'mgcv' package (Wood, 2022) to test whether birds had higher ground speeds on their return than outbound stage of trips, and whether this was due to (1) stronger winds encountered on their more southerly return routes or (2) faster air speeds (ground speed minus wind speed) potentially due to an increased mass (and higher wing loading). Five models were run just on outbound and return stages with the following covariates: (1) DayNight, (2) TripStage (a factor encoding outbound or return stage) and DayNight, (3) the tensor smooth of wind speed and relative wind direction and DayNight (the best-fitting model explaining ground speeds; Table 3), (4) the same as (3) but with TripStage, and (5) the same as (4) but with TripStage as an interaction on the tensor smooth. The best models were selected using AIC and RMSE as specified in the main text. We also ran a linear mixed model (LMM) to test whether wind speeds encountered by birds differed between outbound and return stages. We compared a model with wind speed as the response (taking a Gaussian error distribution), the factor TripStage as the covariate and individual identity as a random intercept, with the null model (i.e. no covariates), using a likelihood ratio test in the 'lme4' package (Hothorn et al., 2022).

The best GAMM was that with the tensor effect of wind speed and relative wind direction and the factors DayNight and TripStage, but not the interaction between the tensor product smooth and TripStage (Table A3). Ground speeds were slightly higher (modelled difference of 1.07 ± 0.06 m/s) during the return than the outbound stage, likely because birds experienced marginally faster wind speeds on average (modelled difference of 0.72 ± 0.05 m/s) on return stages (LMM: $\chi^2_1 = 197.47$, $P < 0.001$), rather than because they flew faster for given wind conditions (due to their increased wing loading).

Table A1

Movement characteristics of behavioural states assigned to GPS tracks using a three-state hidden Markov model for Juan Fernández petrels during incubation trips

Behavioural state	Step length (km)	Ground speed (m/s)	Turning angle (radians)
Directed flight	23.5 (6.6)	9.8 (2.7)	0.010 (50.410)
Area-restricted search	10.1 (6.7)	4.2 (2.8)	0.002 (1.085)
Rest	1.0 (0.7)	0.4 (0.3)	0.113 (1.219)

Mean values are provided with standard deviations in parentheses, except for turning angles for which concentration parameters are provided in parentheses.

Table A2
Comparison of three- and four-state models with and without the inclusion of the number of wet bouts from immersion data as a third input variable along with step lengths and turning angles derived from the GPS data

Model	AIC	States	% Time in each state	Input variables		
				Step lengths (km)	Angle concentration	No. of wet bouts
Three-state without wets	101173.7	Directed flight, ARS, rest	45.7, 39.9, 14.3	23.5, 10.1, 1.0	50.4, 1.1, 1.2	–
Three-state with wets	125427.3	Directed flight, ARS, rest	41.4, 34.1, 24.5	24.3, 12.7, 2.3	59.7, 1.6, 0.9	0.76, 0.96, 1.25
Four-state without wets	97868.3	Directed flight, ARS, forage, rest	21.9, 29.2, 37.5, 11.5	28.1, 18.4, 8.8, 0.8	91.3, 26.1, 0.8, 1.6	–
Four-state with wets	122312.7	Directed flight, ARS, forage, rest	23.5, 30.6, 39.5, 6.4	27.7, 17.7, 7.5, 0.7	92.7, 21.9, 0.7, 6.1	0.69, 0.88, 1.17, 0.69

For the percentage of time in each state and input variable columns, values are presented for each state in the order that the states are listed. Step length values are means. Higher values of angle concentration represent more concentrated turning angles. AIC = Akaike information criterion; ARS = area-restricted search.

Table A3
Model selection for generalized additive mixed models (GAMMs) comparing ground speeds during outbound and return stages, while controlling for the effects of wind speed and direction and differences by day and night

Model	Formula	AIC	ΔAIC	RMSE	R ²
4	~te(V_w, Δθ) + DayNight + TripStage	21911.2	0.0	1.95	0.48
5	~te(V _w , Δθ, by = TripStage) + DayNight	22193.1	281.9	2.00	0.46
3	~te(V _w , Δθ) + DayNight	22238.8	327.5	2.01	0.45
2	~TripStage + DayNight	24168.6	2257.3	2.43	0.20
1	~DayNight	24500.4	2589.1	2.51	0.14

AIC = Akaike information criterion; ΔAIC = change in AIC from the best supported model; RSME = root mean squared error (RMSE scores represent values from k-fold cross validation); V_w = wind speed; Δθ = wind direction relative to bird direction; DayNight = factor encoding day or night; TripStage = factor encoding outbound or return stage of trips; te = tensor smooth interaction. The best-supported model is highlighted in bold.

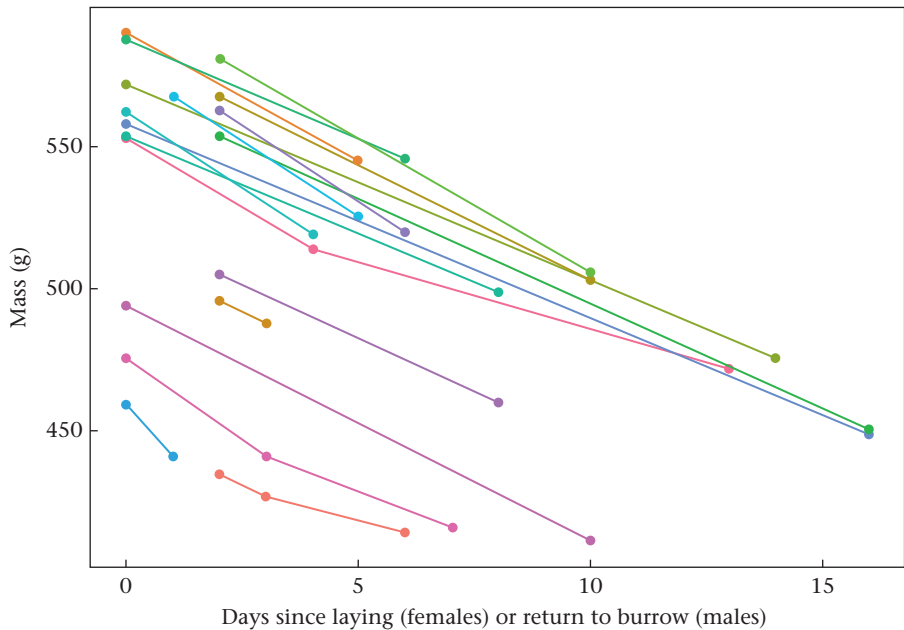


Figure A1. Mass loss over time for each individual based on multiple measurements on the nest. Each individual is a different colour and measurements are indicated by coloured dots.

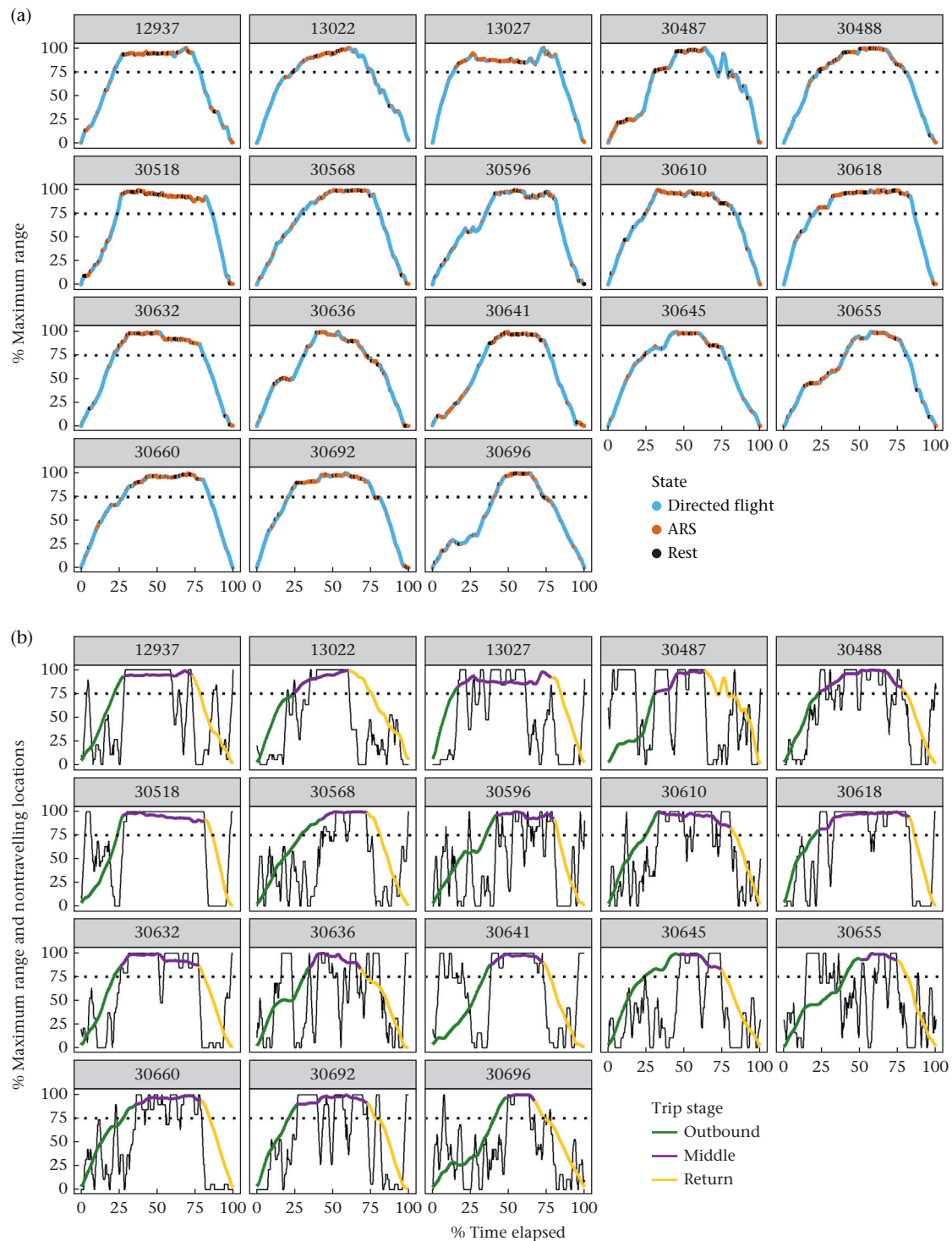


Figure A2. Visual representation of the methodology used to classify outbound, middle and return stages of trips. (a) The percentage of the maximum range achieved plotted against the percentage of trip time elapsed, coloured according to behavioural state. (b) The 12 h smoothed percentage of locations that were not travelling (i.e. directed flight) is indicated as the black line and the 12 h smoothed percentage of maximum range achieved is shown as a line coloured according to the trip stage. The start of the middle stage is identified as the first value that represents both $\geq 75\%$ of the maximum range achieved and $\geq 75\%$ nontravelling locations. Each individual, identified by a six-digit number, is shown by a separate panel.