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Long walk home: Magellanic penguins have strategies that lead them to areas where they can navigate most efficiently

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Understanding how animals move in dense environments where vision is compromised is a major challenge. We used GPS and dead-reckoning to examine the movement of Magellanic penguins commuting through vegetation that precluded long-distance vision. Birds leaving the nest followed the shortest, quickest route to the sea (the 'ideal path', or '*I-path*') but return tracks depended where the birds left the water. Penguins arriving at the beach departure spot mirrored the departure. Most of those landing at a distance from the departure spot travelled slowly, obliquely to the coast at a more acute angle than a beeline trajectory to the nest. On crossing their *I-path*, these birds then followed this route quickly to their nests. This movement strategy saves birds distance, time and energy compared to a route along the beach and the into the colony on the *I-track* and saves time and energy compared to a beeline trajectory which necessitates slow travel in unfamiliar areas. This suggests that some animals adopt tactics that take them to an area where their navigational capacities are enhanced for efficient travel in challenging environments.

1. Introduction

Birds are renowned for their spectacular feats of navigation, with an impressive number of species displaying trans-globe movements (e.g. [1–3]). Understandably, this has incited extensive research into how they might manage this, with researchers looking at multiple cues that may be relevant for such long-distance movement, including the use of stars, the sun, magnetic senses and olfaction [4–6]. But navigational tasks performed by birds include much shorter movement trajectories, for example, those associated with central place foraging as well as other more local movements within familiar areas, such as cache recovery in food-storing species and, ultimately, the fine-scale movement of even long-distance migrating birds as they approach their final nesting destination [7]. This has received much less attention than long-distance migration, partly due to the difficulties of resolving such movement, although the consequences of it are no less important.

Seabirds are all central place foragers [8] and so must find their nest on land after feeding at distance out at sea. It has been suggested that many use route-based navigation for this [9,10], a process which generally describes homing navigation performed on the basis of information perceived during the outward journey from its beginning to the point at which the return is begun. Once the

nesting area is visible, however, the flight height of birds is presumed to allow them to hone in on visual cues relating to the location of their nest [11,12].

This visual advantage is obviously reduced in penguins because, in losing the ability to fly, they have sacrificed the capacity to see far (e.g. [13]). They also travel much more slowly and with increased costs of transport than flying birds [14–16] which has profound consequences for the efficiency of their navigation because small errors in trajectory can result in greater time and energy investment than would be the case in flying birds. The situation is particularly extreme in Magellanic penguins *Spheniscus magellanicus*, because, unlike many highly visible colonial surface nesting penguins such as Adélie *Pygoscelis adeliae* [17] and king *Aptenodytes patagonicus* penguins [18–20], they may breed in colonies (of up to 500 000 pairs [21,22]) that can extend to 1 km inland, with nests among high shrubs within a complex vegetation matrix [23]. Thus, these penguins cannot generally see their nests until they are a few metres from them and apparently have no line-of-sight information although it is possible that they recognize fine-scale visual cues and vocal cues may play a role when they are close to their partners ([24] and references therein). The navigational challenge for Magellanic penguins is, therefore, how to move efficiently between the sea and their nest under such conditions, particularly given how mistakes will affect their energy expenditure, their allocation of time to the process, and the efficiency of brood provisioning. The challenge for scientists in determining the movement strategies of these birds at this time is how to elucidate these critical fine-scale movements undertaken by this otherwise far-ranging species [25].

The main goal of the present study was to describe the outgoing and incoming terrestrial paths of adult breeding Magellanic penguins during the early chick-rearing period to determine their movement strategies and to examine the efficiency of their movements within the colony with respect to time and energy expenditure (cf. [26,27]). Given that vision is so important for penguins (see above), we predicted that birds would move more efficiently travelling towards the sea than returning to the nest because the nest area is familiar and outgoing penguins should be able to navigate between recognized features along a well-travelled path. Against this, penguins returning from the sea may not land at an ideal spot on their featureless and changeable beach, which is all they can see from the water. We also predicted that penguins would move faster during light because visual cues can be perceived more easily.

To address this, we used animal-attached technology consisting of GPS and tri-axial accelerometers as well as dead-reckoning units to give unprecedented resolution in determining the fine-scale paths of adult breeders moving from the nest to the sea and back to the nest after their foraging incursions at sea. Although our approach was intended to examine movement strategies rather than being conceived to relate to mechanisms of animal navigation, we hoped that our work might provide insight for future studies investigating mechanisms that these birds might use to navigate through their challenging vegetation matrix.

2. Methods

(a) Study site

All work was conducted during November and December 2018 at the San Lorenzo Magellanic penguin colony (42°05' S, 63°52' W),

Península Valdés (World Heritage Site, UNESCO), Chubut, Argentina on birds (sex and age unknown, but all birds would have been greater than 3 years old) that were provisioning small chicks less than 10 days old. San Lorenzo holds more than 200 000 penguin pairs [22,28]. The colony extends along the beach in a swathe that is almost 4 km long, reaching approximately 800 m inland, covering an area of more than 145 ha. The whole colony consists of a homogeneous landscape composed of pebble beaches with gentle slope and a dense vegetated environment with an average covering of 40–80%, dominated by 1–3 species of shrubs (more than 80 cm height) with no substantial differences of topography [23]. The colony receives tourist visitors to a small area (only 2% of the area of the colony) under a management plan approved by the government of Chubut Province.

For the study period, our defined hours of 'light' occurred between 03.30 (astronomical dawn) and 22.30 (astronomical dusk) (<http://users.softlab.ntua.gr/~ipanag/fromnetmode/scripts/suntime.htm>), after which the sky was not illuminated by the sun. However, at the time of our study (i.e. 21 November to 2 December 2018; electronic supplementary material, table S1) there was a full moon, with partial cloud cover and extensive starlight, which can be presumed to provide a partially illuminated landscape for walking penguins.

(b) Deployment of devices

Twenty-two penguins brooding small chicks were removed from their nest and fitted with Axy-Trek tags (64 mm length, 39 mm width, 19 mm height, 55 g; TechnoSmArt, Rome, Italy; electronic supplementary material, table S1). The tags were programmed to register position (lat/long) at 1 Hz when birds were not in the water and acceleration at 25 Hz for the full length of the tag deployment period. In addition, another nine animals were fitted with Daily Diary (DD) bio-logging units (75 mm length, 30 mm width, 12 mm height, 31.7 g; Wildbyte Technologies, Swansea, Wales; electronic supplementary material, table S2). DD devices recorded acceleration and magnetic field strength (each in three orthogonal axes) at 40 Hz. We gently (i.e. manually) removed the penguins from their nest and attached the loggers to their lower back (midline) following Wilson *et al.* [29] using overlapping strips of tape. Loggers were attached using four strips of Tesa tape 4651. We first placed the tape under a few dorsal feathers with the glue facing up, then placed the logger and wrapped the tape around it. The process took less than five minutes, after which the birds were replaced on their nest. We removed all devices after a single, or a maximum of two, foraging trips (electronic supplementary material, table S1 and table S2) and Axy-Treks and DDs were left on the birds for 50.1 ± 14.2 h and 92.5 ± 21.1 h, respectively. Axy-Trek's data were downloaded by using the *AXY MANAGER 2* software (TechnoSmArt, Rome, Italy) and DD's data were accessed by downloading from the micro-SD card on which the data were stored. Following device removal, we monitored all nests where animals had been every 3 to 5 days until the end of December (late chick-rearing period) to ascertain that they all continued to breed normally. All nests used for instrumented birds were randomly chosen from an area located away from (greater than 200 m) the zone where tourists were allowed at an average distance of approximately 400 m to the sea.

(c) Track analysis

Since penguin walking behaviour can be easily distinguished from other behaviours by acceleration data [30], the information obtained from the tri-axial acceleration sensors was used to determine how long it took for each animal to walk from the nest to the sea and vice versa. GPS locations of stationary objects are subject to greater error [31] so we considered the start of trajectories from the nest only when birds had moved greater than

5 m from the site and were clearly engaged in transit between the nest and the sea.

All track analyses were conducted using R v. 3.6.1 [32]. To characterize each track the following parameters were calculated: (1) the total duration of the track (calculated as the difference in time between the first and last point); (2) whether the track started during 'dark' or 'light' hours (see above); (3) the distance between the nest and the coast by means of the *gDistance* function from the *rgeos* package; (4) the linear distance between the first and last point of each trajectory using the *spDistsN1* function from the *sp* package; (5) the distance between the last point of the outgoing trip (defined as the moment at which the animal reached the coastline and entered the water) and the first point of the associated return trip (defined as the point at which the animal exited the sea following foraging)—this distance also being computed using the *spDistsN1* function from the *sp* package; (6) the total distance travelled by means of the *TrajLength* function from the *trajr* package; (7) the overall heading of each track computed using only the first and last positions of each track by means of the *dl* function from the *adehabitatLT*; (8) the outgoing angle computed using the nest, the bird departure position and the closest coastal point to the nest (electronic supplementary material, figure S1A) by means of the *Angle* function from the *LearnGeom* library; (9) the incoming angle (i.e. corresponding to a beeline to the nest) computed with the nest, the landing position and the closest coastal point to the nest (electronic supplementary material, figure S1B); (10) the initial angle for *Y-shape* inbound trajectories (see below) computed between the start of the *I-segment* of the path (see below), the landing position, and the closest coastal point to the nest (electronic supplementary material, figure S1C); and (11) the initial angle for the rest of inbound trajectories (see below) computed between the position after the birds walked 100 m after landing, the landing position and the closest coastal point to the nest (electronic supplementary material, figure S1D).

(d) Statistical analysis

Differences between the proportion of animals that left the nest during the light and dark hours were tested using the Fisher exact probability test using the *prop.test* function in R. The same function was employed to test if there were differences in the proportion of animals that return to the colony during light and dark hours. In these analyses, all the recorded tracks were considered. For the following statistical analyses, only those penguins from which at least one outgoing and returning track had been recorded were considered. To compare the total distance travelled, track duration and travel speed between the outgoing and incoming tracks, we employed linear mixed effect models (LMMs) using the *nlme* package [33]. All models included the animal ID as random effect. The significance of the parameters included in the models was examined by assessing the effect of removing the parameter of interest on the fit of the model using likelihood ratio tests.

Return tracks were visually classified into five different types based on their overall pattern in space: (1) straight *I-paths* were defined by having greater than 80% of the positions of the inbound track falling within 15 m of the bird's outbound pathway; (2) *Y-paths*, where birds walked obliquely to the coastline until they reached the regularly used outward *I-path*, at which point they followed it, perpendicular to the coast, until they reached the nest. These tracks were defined by having greater than 30% less than 80% of the positions of the inbound tracks falling within 15 m of the outbound pathway; (3) *V tracks*, where birds walked obliquely to the coastline in a direct line until they reached their nest; (4) *L-paths*, where birds returned from the sea obliquely until they reached a point where their distance from the sea was roughly equivalent to that of the nest,

whereupon they travelled parallel to the sea until they reached their nest; and (5) *U-paths*, where penguins travelled inland for some period before returning to the coast (electronic supplementary material, figure S2).

For those trajectories showing a *Y-path* shape, the relationship between the initial angle and the distance between the landing point on the beach and the closest coastal point to the nest (or *I-point*) (electronic supplementary material, figure S1) was tested by means of a linear model using the function *lm* where the intercept was forced through 90°. The relationship between the incoming angle (corresponding to a beeline to the nest—see above) as a function of the distance between the landing point and the *I-point* was also tested using the *lm* function, incorporating distance both as a single and quadratic term.

Differences in travel speed between the outbound and returning path of *I-paths* and *Y-paths* were tested by means of LMM including animal ID as a random effect. The *I-segment* (electronic supplementary material, figure S1) of each *Y-path* was considered from the point at which the return path fell within 15 m of the outbound pathway. Once the *I-segment* of the *Y-paths* had been recognized, the comparison between the travel speed of this segment and the outgoing trajectory was also performed by means of LMM, including animal ID as a random effect. Finally, for *Y-paths*, the incoming travel speed while birds were walking along the *I-segment* was compared to the travel speed while birds were walking outside the *I-segment* by means of LMM, including animal ID as a random effect.

All statistical analyses were carried out using R v. 3.6.1 [32]. Values are reported as mean \pm standard deviation.

3. Results

We obtained a total of 108 terrestrial paths and 18 at-sea paths that immediately preceded them. Of these, 89 paths (52 outgoing and 37 incoming), were from 22 penguins instrumented with Axy-Treks with the remaining 19 (12 outgoing and 7 incoming) from nine birds instrumented with DDs. There were no apparent differences in movement behaviour between penguins equipped with Axy-Treks or DDs. In two of the return trips registered by the Axy-Treks, the complete track was not recorded. Overall, there were 24 individuals (77.4% of the studied birds) where we achieved one or more completed terrestrial paths (i.e. both outgoing and incoming) with 7, 15 and 2 individuals with 1, 2 and 3 completed terrestrial paths, respectively.

Sixty-six per cent of movements between nest and sea took place during the light, with 34% occurring during the dark hours. The percentage of departures did not differ between light and dark hours (outgoing paths $\chi^2 = 3.25$, $p = 0.07$). However, most arrivals took place during the light hours (incoming paths $\chi^2 = 5.29$, $p = 0.02$; figure 1). Overall, penguins walked faster during the light hours than during darkness ($0.5 \pm 0.1 \text{ m s}^{-1}$, range: 0.2–0.6 m s^{-1} versus $0.4 \pm 0.1 \text{ m s}^{-1}$, range: 0.3–0.6 m s^{-1} , respectively, LMM, $L_{\text{ratio}} = 7.97$, $p < 0.01$).

(a) Track metrics and specific pathways

All penguins travelled roughly NNW on their way to the sea and travelled in approximately the opposite direction (SSE–SSW) on their way back to the nest (figure 2). All outbound birds followed well-defined routes from their nests that took the form of an *I-path*, running essentially perpendicular to the sea edge with consistent intra- and inter-individual patterns (figure 2a,b). The headings taken during outbound legs by birds in which at least one complete land trip was

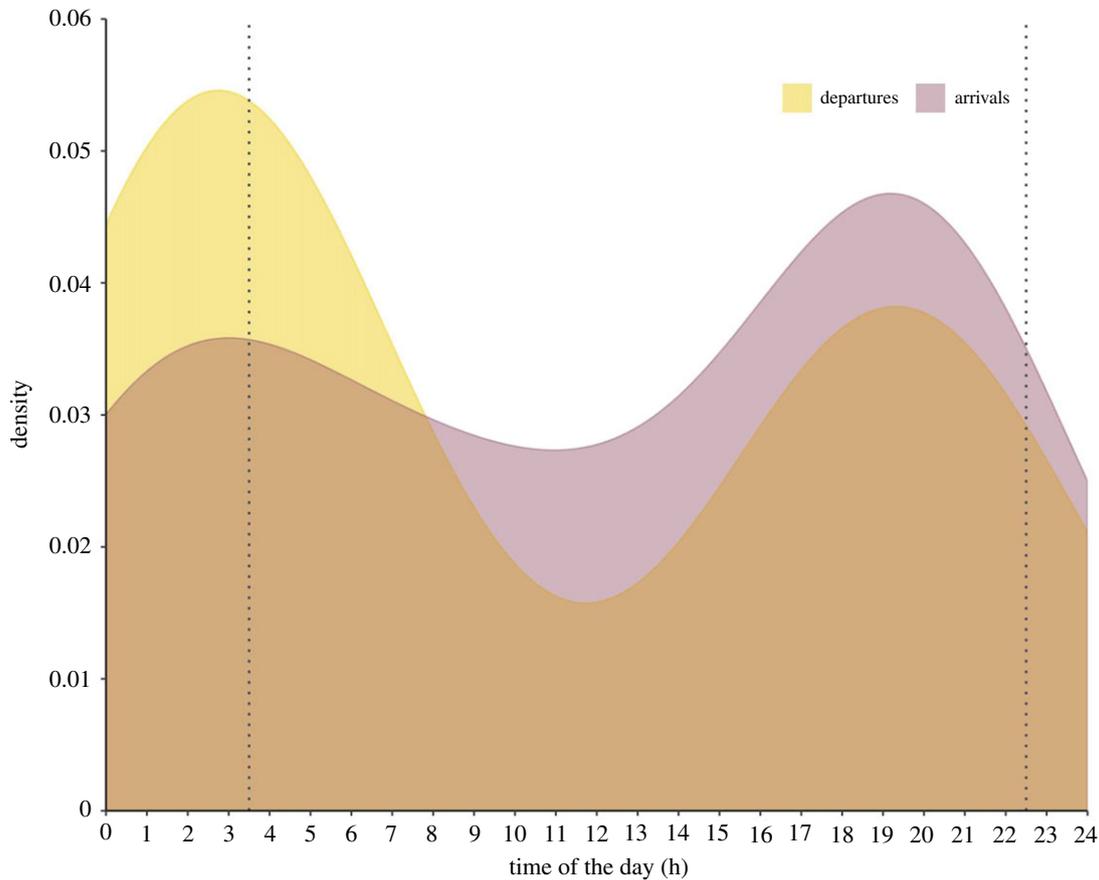


Figure 1. Departures and arrivals from and to the colony by Magellanic penguin adult breeders during the early chick-rearing period. Dashed lines indicate the astronomical dawn and dusk (see text for more details). (Online version in colour.)

recorded, accorded with a route that took them in a direct line to the closest point of the sea, which we define as the *I*-point. Accordingly, outgoing angles deviated little from perpendicular (figure 3*a*).

Inbound tracks from these same birds, however, were sometimes markedly different to the outbound tracks, both in space-use and in track metrics, showing much more variation (figures 2 and 3*a*). Thus, during the land phase, inbound birds walked overall further than outgoing birds (603 ± 293 m versus 470 ± 39 m, respectively, LMM $L_{\text{ratio}} = 11.2$, $p < 0.01$) and took more time to do so (46.3 ± 54.8 min versus 19.8 ± 7.3 min, respectively; LMM $L_{\text{ratio}} = 13.7$, $p < 0.01$). In addition, penguins walked faster when heading out to the sea than when returning (mean walking speed 0.5 ± 0.1 m s⁻¹, range 0.2–0.6 m s⁻¹ versus 0.4 ± 0.1 m s⁻¹, range 0.2–0.6 m s⁻¹, respectively; LMM, $L_{\text{ratio}} = 36.12$, $p < 0.01$).

Where the ‘at-sea’ phase of the bird movement could be reliably determined (the DD data because the Axy-Trek units generally failed to get locations for incoming penguins close to land because the birds spent almost no time at the surface), we noted that tracks often came in at an oblique angle to the shore (figure 2*b*) with some individuals landing at an appreciable distance from their departure point at the coast (237 ± 475 m, range: 3–3003 m, $n = 44$ incoming paths). More than half (56%) of the return paths started within 100 m of the departure point on the shore and 85.4% occurred within 300 m.

We ascribed the variation in return tracks on land to five major types of movement based on their overall pattern in space (figure 2; electronic supplementary material, figure S2) although we recognize that some path types occurred only twice (defined below):

- (i) Straight *I*-paths, which were similar to the outgoing paths (9 tracks = 22.0% of all returning tracks; figure 2(i)). During the outbound tracks, birds walked faster than during the incoming tracks (0.5 ± 0.1 m s⁻¹, range 0.4–0.6 m s⁻¹ and 0.4 ± 0.1 , range 0.2–0.5, respectively, LMM, $L_{\text{ratio}} = 12.5$, $p < 0.01$; table 1).
- (ii) *Y*-paths, where birds walked obliquely to the coastline until they reached the regularly used outward *I*-path, at which point they followed it, perpendicular to the coast, until they reached the nest (26 tracks = 63.3% of all returning tracks; figure 2(ii)). *Y*-paths were initiated when birds landed at greater distances from the *I*-point than birds that undertook straight *I*-paths (figure 3*b*). In addition, in these *Y*-paths, there was a linearly decreasing relationship between the initial path angle and the distance between the landing point on the beach and the *I*-point (initial angle (for *Y* paths) = $90 - 0.225 \times \text{landing distance}$, $r^2 = 0.84$, $p < 0.01$; figure 3*b*). This best fit line had an initial angle that was markedly shallower than the angle necessary for birds to make a beeline from the beach to the nest (figure 3*b*). Although inbound birds walked generally slower than outbound birds (0.5 ± 0.1 m s⁻¹, range 0.3–0.7 m s⁻¹ and 0.4 ± 0.1 , range 0.2–0.7, respectively; LMM, $L_{\text{ratio}} = 21.38$, $p < 0.01$) (table 1), there was no difference between outbound and inbound speed of travel for these birds at the time they were on the *I*-segment of the trajectory (0.5 ± 0.1 m s⁻¹, range 0.3–0.7 m s⁻¹ and 0.5 ± 0.1 , range 0.3–0.7 respectively; LMM, $L_{\text{ratio}} = 1.67$, $p = 0.19$), with the overall reduction in inbound travel speed (see above) being due to a reduction in speed occurring when penguins were

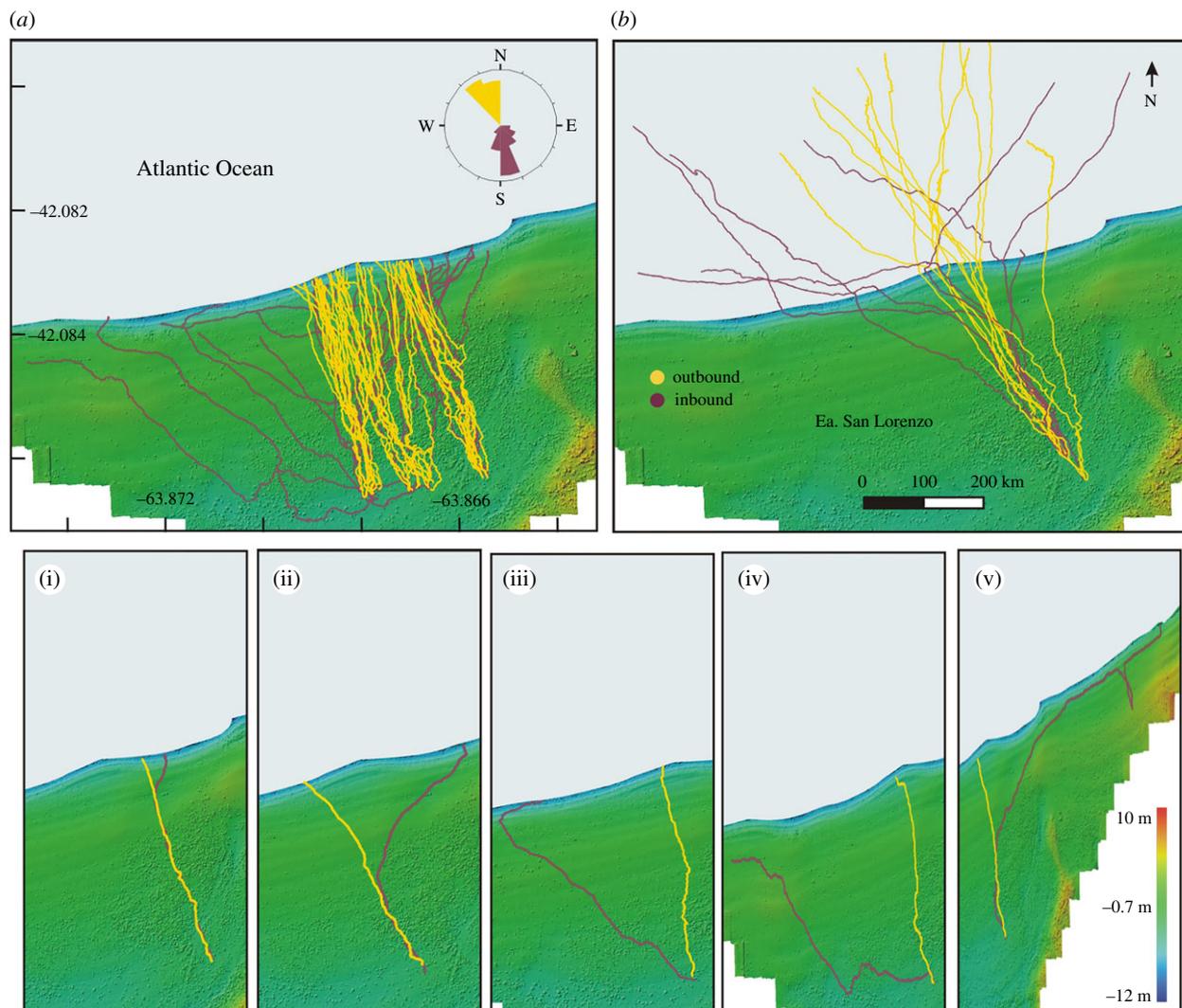


Figure 2. Tracks taken by Magellanic penguins commuting between their nests and the sea (outbound and inbound tracks) at San Lorenzo colony, as determined by (a) Axy-Trek (land trajectories) and (b) dead-reckoning tags (sea and land trajectories). The directionality of the land-based travelling phases is also shown (a). Examples of specific track features are highlighted in (i) the *I-path*, (ii) the *Y-path*, (iii) the *V-path*, (iv) the *L-path* and (v) the *U-path* (see text for more details). The direction taken by penguins on their way to the sea and on their way back to the nest is also shown. Note: the white background indicates no topographic data. (Online version in colour.)

off the *I-segment*. Thus, during their path to the nest, birds walked slower when they were on the tangential segment of the *Y-paths* than when on the vertical (or *I-segment*) of the *Y-paths* (0.3 ± 0.1 s, range 0.2–0.6 m s^{-1} and 0.5 ± 0.1 , range 0.3–0.7, respectively; LMM, $L_{\text{ratio}} = 23.6$, $p < 0.001$).

- (iii) *V-paths* where birds returned from the sea obliquely using a beeline until they reached the nest (2 tracks, 4.9% of all returning tracks; figure 2(iii)). These birds landed at 100 and 215 m from the *I-point*.
- (iv) *L-paths*, where birds returned from the sea obliquely until they reached a point where their distance from the sea was roughly equivalent to that of the nest, whereupon they travelled parallel to the sea until they reached their nest (2 tracks, 4.9% of all returning tracks; figure 2(iv)). These birds landed at distances greater than 370 m from the *I-point*.
- (v) *U-paths*, where penguins travelled inland for some period before returning to the coast (2 individuals or 4.9% of all returning tracks; figure 2(v)). This walking strategy was used only when birds arrived at the coast

extensive distances from their departure location (952 and 3003 m).

The incidence of the various incoming path types appeared to vary systematically according to the angle between the landing spot and the nest relative to the coast. *L-paths* had the most acute angles, followed by *V-paths*, then *Y-paths* and finally *I-paths* (figure 3b). The relationship between distance to the *I-point* and the incoming angle if birds were to take a beeline directly to the nest would be; incoming angle (for all but *U* tracks) = $0.0002x^2 - 0.20x + 91.86$ ($r^2 = 0.97$, $p < 0.01$; figure 3b).

4. Discussion

Our data are derived from a relatively small sample of 31 birds executing 108 paths within a large colony and so may not be entirely representative of that population. However, the consistency of patterns shown across individuals,

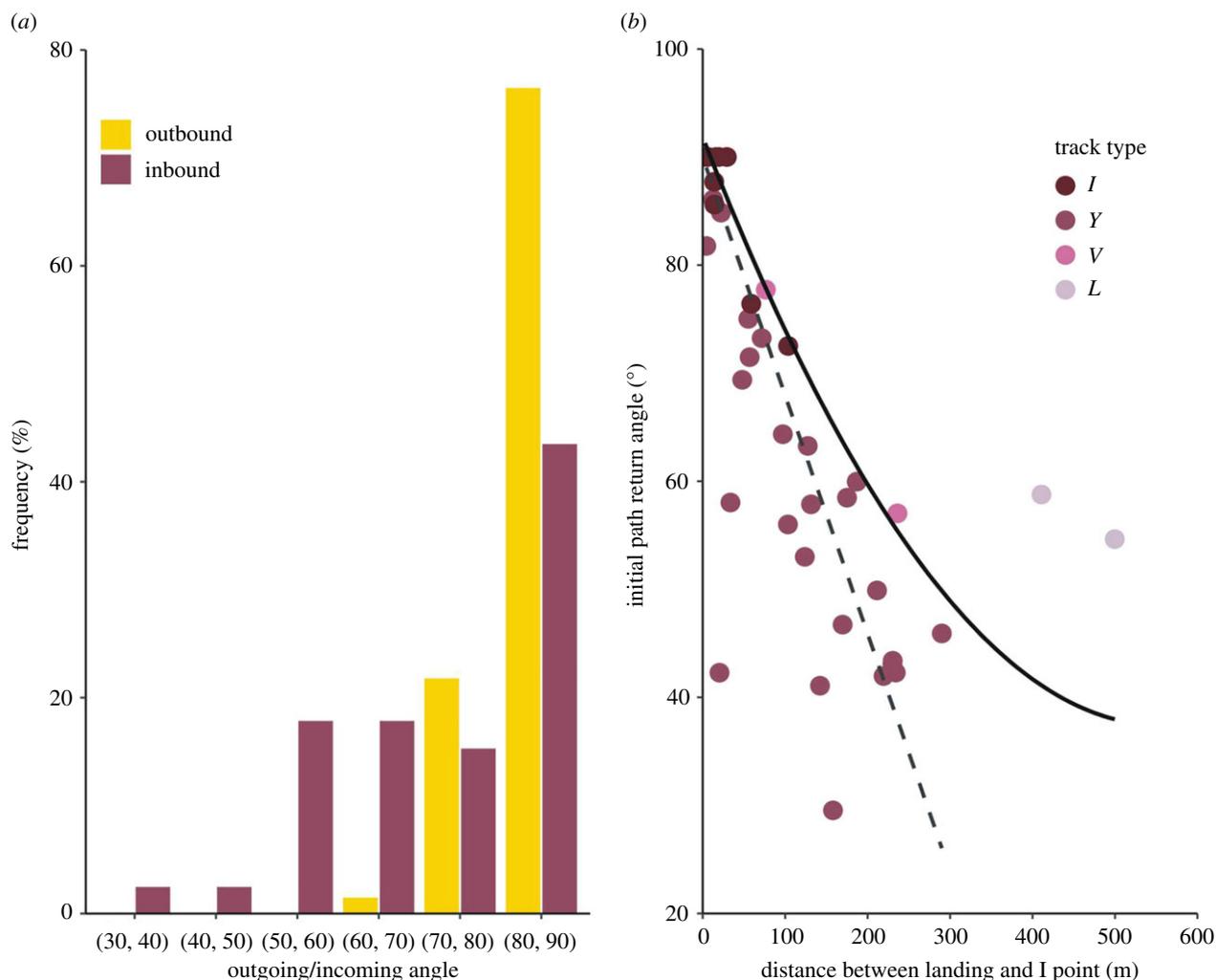


Figure 3. (a) Frequency distribution of the angles between Magellanic penguin landing points and their nests for birds commuting between their nest and the sea (expressed as a deviation from a perpendicular track, i.e. 90°). (b) Relationship between the initial angle (with respect to the coastline, see text) and the distance between landing point on the beach and the *I*-point taken by the penguins displaying *Y*-paths in their return pathways (dashed line regression forced through 90°). The black line indicates the path angle birds should have taken if they were to head directly to the nest (*I*, *V* and *L* incoming paths were also included, see text). (Online version in colour.)

resolved in fine spatial and temporal detail, has highlighted what we believe are 'strategic' decisions in movements over time as birds navigate between the nest and the sea in visually difficult terrain. This particular environment contrasts land-based movements in many other colonial penguin species such as Adélie and king penguins where the colonies are in open space. In these circumstances, visual cues can be used as birds move in a fairly straight line towards their nests [34], with deviations round dense groups of nests and minor deviations within the colony to avoid individuals in the 'bee-line' that are defending territories (R.P.W. 1988, personal observation; cf. [17–20,34]). Against this, our unprecedented resolution of Magellanic penguin pathways shows how they too avoid conspecific nests, but as much as because they are generally located under thick vegetation as because of territoriality. Nonetheless, despite some vegetation-linked tortuosity, it is clear that Magellanic penguins are fairly efficient at finding their way to their nests despite the thick vegetation precluding a line of sight to the nest. However, birds can presumably see salient landmarks on their landwards horizon looking over the colony from the top of the beach. Vision is important in penguins [13,35–38] and is presumed to play a major part in their navigation between the

nest and the sea. We do note that some birds travelled on land at night (figure 1) where their general abilities to find their way were seemingly unaffected by light, including the extent of the moon. However, penguins did travel faster during the day, which would underpin the importance of vision in their navigation.

With regard to movement strategy, we suggest that birds leaving the nest are familiar with their specific pathway leading directly to the sea. Such pathways do not take the form of well-used major highways for large numbers of birds. They are rather composed of a dense lattice of parallel trails leading through the colony (figure 2) with only a few individuals using any one route regularly. Our data though show consistency in these individual-specific *I*-paths during outbound travel (figure 2), so breeding penguins will use the same route dozens of times during any breeding season. Although the ocean is located approximately due north, so that use of a simple compass system (e.g. [39–41]) would take the birds directly to the sea, there are indications from returning birds that penguins actually recognize their *I*-path route, or features of it. For example, we note that all birds on their *I*-paths, whether outbound or inbound, travelled faster than incoming birds engaged in other path forms away from the *I*-path.

Table 1. Summary statistics (means \pm s.d., range) of the different path types performed by walking Magellanic penguins during the way from the nest to the sea (outbound) and from the sea to the nest (incoming). n = number of tracks (including outgoing and incoming paths).

| path type | speed (m s^{-1}) | | duration (min) | | distance traveled (m) | |
|----------------|-----------------------------|-------------------------|----------------------------|-----------------------------|------------------------|--------------------------|
| | outbound | incoming | outbound | incoming | outbound | incoming |
| I ($n = 9$) | 0.5 ± 0.1 [0.4–0.6] | 0.4 ± 0.1 [0.2–0.5] | 17.6 ± 2.0 [15.1–20.4] | 26.4 ± 6.6 [18.1–36.1] | 467 ± 34 [400–508] | 473 ± 27 [422–519] |
| Y ($n = 26$) | 0.5 ± 0.1 [0.3–0.7] | 0.4 ± 0.1 [0.2–0.7] | 18.8 ± 5.3 [12.5–33.7] | 32.7 ± 12.8 [14.9–63.2] | 462 ± 38 [409–541] | 547 ± 133 [381–1019] |
| V ($n = 2$) | 0.6 [0.5–0.6] | 0.3 [0.3–0.3] | 16.1 [15.9–16.3] | 43.5 [36.2–50.8] | 475 [452–497] | 606 [499–713] |
| L ($n = 2$) | 0.3 [0.2–0.4] | 0.3 [0.2–0.5] | 39.5 [27.1–51.8] | 120.4 [40.7–200.0] | 544 [27–52] | 1238 [1098–1378] |
| U ($n = 2$) | 0.4 [0.3–0.5] | 0.3 [0.2–0.3] | 27.1 [18.9–35.4] | 289.1 [196.6–381.5] | 504 [479–528] | 3147 [1972–4322] |

I-paths (electronic supplementary material, figure S2) enable penguins to travel energetically most efficiently to reach the sea (cf. figure 2*b*) by minimizing the distance travelled on land where their cost of transport (*sensu* [42]) is some 2.6 times higher than in water—derived using data from [14] on costs for Adélie penguins walking at 0.45 m s^{-1} (the approximate speed of penguins in our study) of 6.14 W kg^{-1} and data from [43] for costs of Humboldt penguins *Spheniscus humboldti* swimming at 2.1 m s^{-1} (the normal swimming speed of commuting Magellanic penguins [44]) of 11.1 W kg^{-1} as rough approximations for Magellanic penguins. We note also that land travel for them is only 20% the speed at which they habitually swim (see above).

But efficient use of distance via *I*-paths, which we propose requires familiarity with the route, is compromised when penguins land on the beach at a distance from the (ideal) *I*-point. This presumably occurs because the birds have to deal with an unfamiliar environment (and certainly areas which they frequent much less than the *I*-path). Nonetheless, birds that land on the beach away from the *I*-point still seem able to determine whether their nest is to the east or west of them. This is because all individuals in this position (bar the two individuals that exhibited *U*-paths (4.9%); see below) moved towards their nest, albeit initially obliquely. It is notable that no individuals landed on the beach and walked along it parallel to the sea until their path bisected the *I*-path before using it to reach their nests. Instead, the birds cut the corner, moving at an angle to the sea line (*Y*-paths; electronic supplementary material, figure S2), presumably operating in less familiar territory than they would on the *I*-path. They did this until they reached the *I*-path when they changed trajectory to follow it (electronic supplementary material, figure S2). That the area outside the *I*-path is less familiar is supported by lower movement speeds. There was, however, a relationship between the initial path angle with respect to the coastline (i.e. initial angle; see 'Methods') and the landing distance from the *I*-point: Penguins walked at more acute angles with increasing distance (figure 3). This implies that birds either know roughly how far from the *I*-point they have landed and/or how far away their nests are from the landing point and in which general direction. That their chosen path angle only led directly to the nest in two cases (*V*-shaped tracks) suggests that this knowledge is imperfect. We suggest that this may be due to unfamiliarity with the areas outside the *I*-path. However, adopting a path angle that is systematically less than the bee-line angle to the nest (figure 3*b*) means that almost all penguins landing away from the *I*-point will cross the *I*-path. By doing this, they benefit from the certainty of finding familiar terrain. They also reduce the risk that an overly obtuse path angle leads them to a point farther inland than their nest and a trajectory that does not cross the *I*-path.

There were only two birds that undertook *L*-paths so consideration of their movement strategies must be considered accordingly. We include them, and the other two birds engaged in other rarer strategies to provide comprehensive coverage. The return angles taken by *L*-path birds meant that they never crossed the *I*-path (figure 3*b*). Despite this, both individuals walked in a fairly constant direction (as with the *Y*-path individuals) until they reached a (direct) distance from the sea that was approximately equal to that of their nest. They then changed direction and proceeded approximately parallel to the shore until they reached their

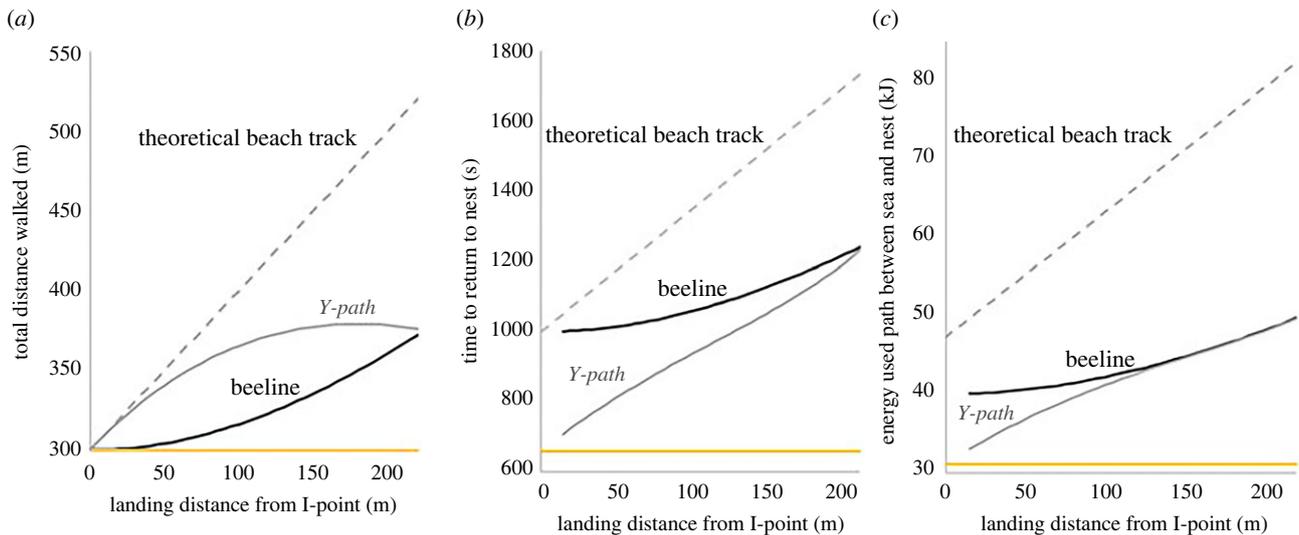


Figure 4. Scenarios relating to (a) distance travelled, (b) time taken to cover the distance and (c) energy used to cover that distance. All scenarios show (theoretical) birds that walk along the beach parallel to the sea until the *I*-point before walking inland (dashed line), for birds adopting a *Y*-path with the characteristics defined in figure 2 (grey line) and for (theoretical) birds that make a beeline for the nest (black line). The yellow line is for reference and indicates the distance that birds would travel if they landed on the *I*-point. The examples show movement from the landing spot on the beach as a function of its distance from the ideal landing point (*I*-point) to the nest situated 300 m inland. (a) has distances calculated using simple trigonometry, (b) converts these distances into time assuming that birds on the *I*-path (and on the beach) travel at 0.5 m s^{-1} and otherwise travel at 0.3 m s^{-1} while (c) converts the times into energy using data in Pinshow *et al.* [14] and Wilson *et al.* [47] based on birds using a power of 11.8 W kg^{-1} on the *I*-path and 10.0 W kg^{-1} on all other paths. (Online version in colour.)

nests (figure 2(iv)). Landing at such distances from the *I*-path should put the birds in unfamiliar terrain. However, like the *Y*-path birds, they nonetheless chose the correct east or west direction (figure 3a). Beyond this, their change in direction at an appropriate distance from the sea would indicate that they have some sort of navigation system, such as dead-reckoning (cf. [45,46]), that stops them overshooting. We speculate that *L*-paths are little more than *Y*-paths with overly obtuse angles. Modification of path trajectory is required once it is clear that a certain distance from the sea has been travelled without the *I*-path (or the nest) being encountered.

The two examples of *U*-paths were from individuals that left the sea at excessive distances from the *I*-point (952 and 3003 m) and indicated that the birds were probably lost although we cannot rule out that something at-sea may have induced them to land early. Interestingly, neither individual continued for any length of time in an appropriate east or west direction (as *L*- and *Y*-path birds do). This would indicate either that the birds were very inexperienced and/or that some cues are required before returning penguins engage in oblique travel.

(a) Consequences of return strategy on movement efficiency

The initiator for the *L*- or *Y*-path strategy would seem to be the distance of the landing point on the beach from the *I*-point. Travel along the beach until birds reach the *I*-point before moving in the colony on the *I*-path would presumably give them navigational certainty. The cost of this is represented by the length of two sides of a right-angled triangle. *Y*-path birds benefit in distance and time by cutting the corner. However, they travel slower and run the risk of not encountering the *I*-path if their return path angle is too large (see the *L*-path strategy). The distance (and therefore time) costs of the strategy can be readily modelled using

simple trigonometry. This clearly shows the extent to which penguins adopting a beeline path to the nest would benefit in terms of minimized distance (figure 4a): The difference between the two strategies is maximum at landing distance of roughly 100 m from the *I*-point. However, both strategies are markedly better than a path that runs along the beach before cutting in along the *I*-path. But the advantages change when time is considered because penguins off the *I*-path travel slower than birds on the *I*-path. As a result, the advantageous situation for the beeline path with respect to the *Y*-path is reversed, at least for birds landing at distances of up to less than 250 m from the *I*-point (figure 4b). Finally, assuming that Magellanic penguin walking energetics [47] can be derived from other penguins species, as indicated by Pinshow *et al.* [14], the advantage of the *Y*-path over the beeline strategy is maintained if the energetics is considered (figure 4c).

It, therefore, seems that a key determinant for efficient movement between the landing point on the beach and the nest is the distance between the landing spot and the *I*-point. Birds that successfully navigate to the *I*-point have minimized distance, time and energy to travel to their nests. The consequences of not landing on the *I*-point rapidly lead to increased distances, journey durations and energies expended (figure 4). However, the slower passage of penguins off the *I*-path, which we assume is due to processing navigation cues, means that it is strategically advantageous to maintain an acute angle to the *I*-path. The speed and energy advantages of following the *I*-path however, are not so great that birds benefit by walking along the beach to the *I*-point before moving into the colony. Finally, penguins that land at great distances from the *I*-point (*L*-path birds) may not be able to modulate their return-to-nest angles correctly (as the *Y*-path individuals do). As a result, these birds have their whole extended trajectory in the colony off the *I*-path, incurring reduced travel rates and increased energetic costs.

(b) Navigation capacities and strategies affect movement efficiency

This work indicates how Magellanic penguins navigate efficiently within their colonies to find their nest, using close to the shortest distances from the nest to the sea and back. A key part of our interpretation of this is that they have strategies to take them to familiar areas through which they can navigate efficiently. Most colonial penguin species nest in large open spaces [48] and so have line-of-sight to their nests and can simply use vision and a bee-line approach to navigate to their nests (although small deviations may take them round very densely packed areas) [19]. Although Magellanic penguins are a somewhat unusual species in nesting in dense colonies in thick vegetation (but see [48]) for Snares Island penguins *Eudyptes robustus*, the problem of short-distance movement in navigationally challenging terrain will occur in many seabird species. A good example of this is the streaked shearwater *Calonectris leucomelas*, which locates the general area of the nest by sight during flight [11], but has its visual range reduced to less than 1 m once in the undergrowth. GPS sampling regimes adapted to elucidate the long distances covered by these birds over days at sea, do not allow the temporal, and therefore spatial, resolution for them at this time. This is typical of seabird studies. Our work has overcome this for one species and suggests that the primary goal on reaching land is for birds to adopt a crude, but effective, strategy that gets them to a familiar area after some of their at-sea navigation cues are precluded. The final distance over which this happens is a few hundred metres in Magellanic penguins but we could find no comparable information for other seabirds. Certainly, the change in available information for a bird in flight compared to one on the ground, particularly in dense vegetation, is huge. We identified that the specific landing point on the beach was critical in affecting return distances, times and energies in Magellanic penguins. The

challenge for the future will be to determine at what point flighted birds choose to land, how that relates to distance from the nest and the time and energetic consequences this has for them (cf. [49]). Given the efficiency of flight for movement, it may be that the last few meters of their path home may prove to be much more telling than we have previously thought.

Ethics. All penguin handling procedures were reviewed and approved by the Dirección de Fauna y Flora Silvestre y el Ministerio de Turismo y Áreas Protegidas de la Provincia de Chubut (permit no. 05/2018-DFyFS-MP).

Data accessibility. Data and code supporting the analysis are available from the Dryad Digital Repository: <https://dx.doi.org/10.5061/dryad.4xgxd25b5> [50].

Electronic supplementary material is available online [51].

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