

1 Accepted Manuscript distributed under the terms of a Creative Commons Attribution 4.0 [CC-BY Licence](https://creativecommons.org/licenses/by/4.0/)

2 <https://doi.org/10.1098/rspb.2022.0535>

3 **Long walk home; Magellanic penguins have strategies that lead them to areas where they can**
4 **navigate most efficiently**

5

6 Flavio Quintana,^{1*} Agustina Gómez-Laich,² Richard M. Gunner,³ Fabián Gabelli,⁴ Giacomo Dell'
7 Omo,⁵ Carlos Duarte,⁶ Martín Brogger¹ and Rory P. Wilson³

8

9 ¹ Instituto de Biología de Organismos Marinos (IBIOMAR), CONICET. Boulevard Brown 2915,
10 U9120ACD, Puerto Madryn, Chubut, Argentina.

11 ² Departamento de Ecología, Genética y Evolución & Instituto de Ecología, Genética y Evolución
12 de Buenos Aires (IEGEB), CONICET, Pabellón II Ciudad Universitaria, C1428EGA, Buenos
13 Aires, Argentina.

14 ³ Swansea Lab for Animal Movement, Biosciences, College of Science, Swansea University,
15 Singleton Park, Swansea, Wales SA2 8PP, United Kingdom.

16 ⁴ Cátedra de Biología del Comportamiento, Facultad de Psicología, Universidad de Buenos Aires,
17 Av. Hipólito Yrigoyen 3242, C1207ABR, Buenos Aires, Argentina.

18 ⁵ *Ornis Italica*, Piazza Crati 15, 00199 Rome, Italy.

19 ⁶ Red Sea Research Centre, King Abdullah University of Science and Technology, Thuwal 23955,
20 Saudi Arabia

21

22

23 *Correspondence: quintana@cenpat-conicet.gob.ar

24

25

26 **Summary**

27

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

40

41 **Keywords:** *Spheniscus magellanicus*, movement speeds, movement direction, energy saving.

42

43

44

45

46 **Introduction**

47

48 Birds are renowned for their spectacular feats of navigation, with an impressive number of species
49 displaying trans-globe movements (e.g. [1, 2, 3]). Understandably, this has incited extensive
50 research into how they might manage this, with researchers looking at multiple cues that may be
51 relevant for such long-distance movement, including the use of stars, the sun, magnetic senses, and
52 olfaction [4, 5, 6]. But navigational tasks performed by birds include much shorter movement
53 trajectories, for example those associated with central place foraging as well as other more local
54 movements within familiar areas, such as cache recovery in food-storing species and, ultimately, the
55 fine-scale movement of even long-distance migrating birds as they approach their final nesting
56 destination [7]. This has received much less attention than long-distance migration, partly due to the
57 difficulties of resolving such movement, although the consequences of it are no less important.

58

59 Seabirds are all central place foragers [8] and so must find their nest on land after feeding at
60 distance out at sea. It has been suggested that many use route-based navigation for this [9, 10], a
61 process which generally describes homing navigation performed on the basis of information
62 perceived during the outward journey from its beginning to the point at which the return is begun.
63 Once the nesting area is visible, however, the flight height of birds is presumed to allow them to
64 hone in on visual cues relating to the location of their nest [11, 12].

65

66 This visual advantage is obviously reduced in penguins because, in losing the ability to fly, they
67 have sacrificed the capacity to see far (e.g. [13]). They also travel much more slowly and with
68 increased costs of transport than flying birds [14, 15, 16] which has profound consequences for the
69 efficiency of their navigation because small errors in trajectory can result in greater time and energy
70 investment than would be the case in flying birds. The situation is particularly extreme in
71 Magellanic penguins *Spheniscus magellanicus*, because, unlike many highly visible colonial surface

72 nesting penguins such as Adélie *Pygoscelis adeliae* [17] and King *Aptenodytes patagonicus* penguins
73 [18, 19, 20], they may breed in colonies (of up to 500,000 pairs [21, 22]) that can extend to 1 km
74 inland, with nests among high shrubs within a complex vegetation matrix [23]. Thus, these
75 penguins cannot generally see their nests until they are a few metres from them and apparently have
76 no line-of-sight information although it is possible that they recognise fine-scale visual cues and
77 vocal cues may play a role when they are close to their partners ([24] and references therein). The
78 navigational challenge for Magellanic penguins is, therefore, how to move efficiently between the
79 sea and their nest under such conditions, particularly given how mistakes will affect their energy
80 expenditure, their allocation of time to the process, and the efficiency of brood provisioning. The
81 challenge for scientists in determining the movement strategies of these birds at this time is how to
82 elucidate these critical fine-scale movements undertaken by this otherwise far-ranging species [25].

83

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

94

95 To address this, we used animal-attached technology consisting of GPS and tri-axial accelerometers
96 as well as dead-reckoning units to give unprecedented resolution in determining the fine-scale paths
97 of adult breeders moving from the nest to the sea and back to the nest after their foraging incursions

98 at sea. Although our approach was intended to examine movement strategies rather than being
99 conceived to relate to mechanisms of animal navigation, we hoped that our work might provide
100 insight for future studies investigating mechanisms that these birds might use to navigate through
101 their challenging vegetation matrix.

102

103 **Methods**

104

105 *Study site*

106

107 All work was conducted during November and December 2018 at the San Lorenzo Magellanic
108 penguin colony (42° 05' S, 63° 52' W), Peninsula Valdés (World Heritage Site, UNESCO), Chubut,
109 Argentina on birds (sex and age unknown but all birds would have been > three years old) that were
110 provisioning small chicks <10 days old. San Lorenzo holds more than 200,000 penguin pairs [22,
111 28]. The colony extends along the beach in a swathe that is almost 4 km long, reaching *ca.* 800 m
112 inland, covering an area of more than 145 ha. The whole colony consists of a homogeneous
113 landscape composed of pebble beaches with gentle slope and a dense vegetated environment with
114 an average covering of 40-80 %, dominated by 1-3 species of shrubs (more than 80 cm height) with
115 no substantial differences of topography [23]. The colony receives tourist visitors to a small area
116 (only 2% of the area of the colony) under a management plan approved by the Government of
117 Chubut Province.

118

119 For the study period, our defined hours of 'light' occurred between 03:30 h (astronomical dawn) and
120 22:30 h (astronomical dusk) (<https://meteogram.es/sol/argentina/>), after which the sky was not
121 illuminated by the sun. However, at the time of our study (i.e. November 21 to December 2, 2018,
122 electronic supplementary material, table S1) there was a full moon, with partial cloud cover and

123 extensive starlight, which can be presumed to provide a partially illuminated landscape for walking
124 penguins.

125

126 *Deployment of devices*

127

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

149

150 *Track analysis*

151

152 Since penguin walking behaviour can be easily distinguished from other behaviours by acceleration
153 data [30], the information obtained from the tri-axial acceleration sensors was used to determine
154 how long it took for each animal to walk from the nest to the sea and *vice versa*. GPS locations of
155 stationary objects are subject to greater error [31] so we considered the start of trajectories from the
156 nest only when birds had moved >5 m from the site and were clearly engaged in transit between the
157 nest and the sea.

158

159 All track analyses were conducted using R version 3.6.1 [32]. To characterize each track the
160 following parameters were calculated; 1) the total duration of the track (calculated as the difference
161 in time between the first and last point), 2) whether the track started during ‘dark’ or ‘light’ hours
162 (see above), 3) the distance between the nest and the coast by means of the *gDistance* function from
163 the *rgeos* package, 4) the linear distance between the first and last point of each trajectory using the
164 *spDistsNI* function from the *sp* package, 5) the distance between the last point of the outgoing trip
165 (defined as the moment at which the animal reached the coastline and entered the water) and the
166 first point of the associated return trip (defined as the point at which the animal exited the sea
167 following foraging) - this distance also being computed using the *spDistsNI* function from the *sp*
168 package, 6) the total distance travelled by means of the *TrajLength* function from the *trajr* package,
169 7) the overall heading of each track computed using only the first and last positions of each track by
170 means of the *dl* function from the *adehabitatLT*, 8) the outgoing angle computed using the nest, the
171 bird departure position and the closest coastal point to the nest (electronic supplementary material,
172 figure S1A) by means of the *Angle* function from the *LearnGeom* library, 9) the incoming angle (i.e.
173 corresponding to a beeline to the nest) computed with the nest, the landing position and the closest
174 coastal point to the nest (electronic supplementary material, figure S1B), 10) the initial angle for *Y*-

175 *shape* inbound trajectories (see below) computed between the start of the *I-segment* of the path (see
176 below), the landing position, and the closest coastal point to the nest (electronic supplementary
177 material, figure S1C) and 11) the initial angle for the rest of inbound trajectories (see below)
178 computed between the position after the birds walked 100 m after landing, the landing position and
179 the closest coastal point to the nest (electronic supplementary material, figure S1D).

180

181 *Statistical Analysis*

182

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

193

194 Return tracks were visually classified into five different types based on their overall pattern in
195 space: 1) straight *I-paths* were defined by having >80% of the positions of the inbound track falling
196 within 15 m of the bird's outbound pathway, 2) *Y-paths*, where birds walked obliquely to the
197 coastline until they reached the regularly used outward *I-path*, at which point they followed it,
198 perpendicular to the coast, until they reached the nest. These tracks were defined by having >30%
199 <80% of the positions of the inbound tracks falling within 15 m of the outbound pathway, 3) *V*
200 *tracks*, where birds walked obliquely to the coastline in a direct line until they reached their nest, 4)
201 *L-paths*, where birds returned from the sea obliquely until they reached a point where their distance

202 from the sea was roughly equivalent to that of the nest, whereupon they travelled parallel to the sea
203 until they reached their nest and 5) *U-paths*, where penguins travelled inland for some period before
204 returning to the coast (electronic supplementary material, figure S2).

205

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

213

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

223

224 All statistical analyses were carried out using R version 3.6.1 [32]. Values are reported as mean ±
225 standard deviation.

226

227 **Results**

228

229 We obtained a total of 108 terrestrial paths and 18 at-sea paths that immediately preceded them. Of
230 these, 89 paths (52 outgoing and 37 incoming), were from 22 penguins instrumented with Axy-
231 Treks with the remaining 19 (12 outgoing and 7 incoming) from nine birds instrumented with DDs.
232 There were no apparent differences in movement behaviour between penguins equipped with Axy-
233 Treks or DDs. In two of the return trips registered by the Axy-Treks, the complete track was not
234 recorded. Overall, there were 24 individuals (77.4% of the studied birds) where we achieved one or
235 more completed terrestrial paths (i.e. both outgoing and incoming) with 7, 15 and 2 individuals with
236 1, 2 and 3 completed terrestrial paths, respectively.

237

238 Sixty-six percent of movements between nest and sea took place during the light, with 34%
239 occurring during the dark hours. The percentage of departures did not differ between light and dark
240 hours (outgoing paths $\chi^2 = 3.25$, $P = 0.07$). However, most arrivals took place during the light hours
241 (incoming paths $\chi^2 = 5.29$, $P = 0.02$, Figure 1). Overall, penguins walked faster during the light
242 hours than during darkness (0.5 ± 0.1 m/s, range: 0.2 - 0.6 m/s vs 0.4 ± 0.1 m/s, range: 0.3 - 0.6 m/s,
243 respectively, LMM, $L_{ratio} = 7.97$, $P < 0.01$).

244

245 *Track metrics and specific pathways*

246

247 All penguins travelled roughly NNW on their way to the sea and travelled in approximately the
248 opposite direction (SSE-SSW) on their way back to the nest (Figure 2). All outbound birds followed
249 well-defined routes from their nests that took the form of an *I-path*, running essentially
250 perpendicular to the sea edge with consistent intra- and inter-individual patterns (Figure 2A and B).
251 The headings taken during outbound legs by birds in which at least one complete land trip was
252 recorded, accorded with a route that took them in a direct line to the closest point of the sea, which

253 we define as the *I-point*. Accordingly, outgoing angles deviated little from perpendicular (Figure
254 3A).

255

256 Inbound tracks from these same birds, however, were sometimes markedly different to the outbound
257 tracks, both in space-use and in track metrics, showing much more variation (Figures 2 and 3A).

258 Thus, during the land phase, inbound birds walked overall further than outgoing birds (603 ± 293 m
259 vs 470 ± 39 m, respectively, LMM $L_{ratio} = 11.2$, $P < 0.01$) and took more time to do so (46.3 ± 54.8
260 min vs 19.8 ± 7.3 min., respectively, LMM $L_{ratio} = 13.7$, $P < 0.01$). In addition, penguins walked
261 faster when heading out to the sea than when returning (mean walking speed: 0.5 ± 0.1 m/s, range:
262 $0.2 - 0.6$ m/s vs 0.4 ± 0.1 m/s, range: $0.2 - 0.6$ m/s, respectively, LMM, $L_{ratio} = 36.12$, $P < 0.01$).

263

264 Where the ‘at-sea’ phase of the bird movement could be reliably determined (the DD data because
265 the Axy-Trek units generally failed to get locations for incoming penguins close to land because the
266 birds spent almost no time at the surface), we noted that tracks often came in at an oblique angle to
267 the shore (Figure 2B) with some individuals landing at an appreciable distance from their departure
268 point at the coast (237 ± 475 m, range: 3 - 3003 m, $n = 44$ incoming paths). More than half (56%) of
269 the return paths started within 100 m of the departure point on the shore and 85.4%, occurred within
270 300 m.

271

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

275 (i) Straight *I-paths*, which were similar to the outgoing paths (9 tracks = 22.0% of all returning
276 tracks – figure 2i). During the outbound tracks, birds walked faster than during the incoming tracks
277 (0.5 ± 0.1 m/s, range 0.4 - 0.6 m/s and 0.4 ± 0.1 , range 0.2 - 0.5, respectively, LMM, $L_{ratio} = 12.5$,
278 $P < 0.01$) (table 1).

279 (ii) *Y-paths*, where birds walked obliquely to the coastline until they reached the regularly used
280 outward *I-path*, at which point they followed it, perpendicular to the coast, until they reached the
281 nest (26 tracks = 63.3% of all returning tracks – figure 2ii). *Y-paths* were initiated when birds
282 landed at greater distances from the *I-point* than birds that undertook straight *I-paths* (figure 3B). In
283 addition, in these *Y-paths*, there was a linearly decreasing relationship between the initial path angle
284 and the distance between the landing point on the beach and the *I-point* (initial angle_(for Y paths) = 90
285 – 0.225*landing distance, $r^2 = 0.84$, $P < 0.01$, figure 3B). This best fit line had an initial angle that
286 was markedly shallower than the angle necessary for birds to make a beeline from the beach to the
287 nest (figure 3B). Although inbound birds walked generally slower than outbound birds (0.5 ± 0.1
288 m/s, range 0.3 – 0.7 m/s and 0.4 ± 0.1 , range 0.2 – 0.7, respectively, LMM, $L_{ratio} = 21.38$, $P < 0.01$)
289 (table 1), there was no difference between outbound and inbound speed of travel for these birds at
290 the time they were on the *I-segment* of the trajectory (0.5 ± 0.1 m/s, range 0.3 - 0.7 m/s and $0.5 \pm$
291 0.1 , range 0.3 - 0.7 respectively, LMM, $L_{ratio} = 1.67$, $P = 0.19$), with the overall reduction in
292 inbound travel speed (see above) being due to a reduction in speed occurring when penguins were
293 off the *I-segment*. Thus, during their path to the nest, birds walked slower when they were on the
294 tangential segment of the *Y-paths* than when on the vertical (or *I-segment*) of the *Y-paths* (0.3 ± 0.1
295 s, range 0.2 – 0.6 m/s and 0.5 ± 0.1 , range 0.3 - 0.7, respectively, LMM, $L_{ratio} = 23.6$, $P < 0.001$).
296 (iii) *V-paths* where birds returned from the sea obliquely using a beeline until they reached the nest
297 (2 tracks, 4.9% of all returning tracks – figure 2iii). These birds landed at 100 and 215 m from the *I-*
298 *point*.
299 (iv) *L-paths*, where birds returned from the sea obliquely until they reached a point where their
300 distance from the sea was roughly equivalent to that of the nest, whereupon they travelled parallel
301 to the sea until they reached their nest (2 tracks, 4.9% of all returning tracks – figure 2iv). These
302 birds landed at distances > 370 m from the *I-point*.

303 (v) *U-paths*, where penguins travelled inland for some period before returning to the coast (2
304 individuals or 4.9% of all returning tracks - figure 2v). This walking strategy was used only when
305 birds arrived at the coast extensive distances from their departure location (952 and 3003 m).

306

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

312

313 **Discussion**

314

315 Our data are derived from a relatively small sample of 31 birds executing 108 paths within a large
316 colony and so may not be entirely representative of that population. However, the consistency of
317 patterns shown across individuals, resolved in fine spatial and temporal detail, has highlighted what
318 we believe are ‘strategic’ decisions in movements over time as birds navigate between the nest and
319 the sea in visually difficult terrain. This particular environment contrasts land-based movements in
320 many other colonial penguin species such as Adélie and King penguins where the colonies are in
321 open space. In these circumstances, visual cues can be used as birds move in a fairly straight line
322 towards their nests [34], with deviations round dense groups of nests and minor deviations within
323 the colony to avoid individuals in the ‘bee-line’ that are defending territories (cf. [17-20, 34, R.P.W.
324 - Pers. obs). Against this, our unprecedented resolution of Magellanic penguin pathways shows how
325 they too avoid conspecific nests, but as much as because they are generally located under thick
326 vegetation as because of territoriality. Nonetheless, despite some vegetation-linked tortuosity, it is
327 clear that Magellanic penguins are fairly efficient at finding their way to their nests despite the thick
328 vegetation precluding a line of sight to the nest. However, birds can presumably see salient

329 landmarks on their landwards horizon looking over the colony from the top of the beach. Vision is
330 important in penguins [13, 35-38] and is presumed to play a major part in their navigation between
331 the nest and the sea. We do note that some birds travelled on land at night (figure 1) where their
332 general abilities to find their way were seemingly unaffected by light, including the extent of the
333 moon. However, penguins did travel faster during the day which would underpin the importance of
334 vision in their navigation.

335

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

347

348 *I-paths* (electronic supplementary material, figure S2) enable penguins to travel energetically most
349 efficiently to reach the sea (*cf.* figure 2B) by minimizing the distance travelled on land where their
350 cost of transport (*sensu* [42]) is some 2.6 times higher than in water (derived using data from [14]
351 on costs for Adélie penguins walking at 0.45 m/s [the approximate speed of penguins in our study]
352 of 6.14 W/kg and data from [43] for costs of Humboldt penguins *Spheniscus humboldti* swimming
353 at 2.1 m/s [the normal swimming speed of commuting Magellanic penguins [44] of 11.1 W/kg as

354 rough approximations for Magellanic penguins). We note also that land travel for them is only 20%
355 the speed at which they habitually swim (see above).

356

357 But efficient use of distance *via I-paths*, which we propose requires familiarity with the route, is
358 compromised when penguins land on the beach at a distance from the (ideal) *I-point*. This
359 presumably occurs because the birds have to deal with an unfamiliar environment (and certainly
360 areas which they frequent much less than the *I-path*). Nonetheless, birds that land on the beach
361 away from the *I-point* still seem able to determine whether their nest is to the East or West of them.
362 This is because all individuals in this position (bar the two individuals that exhibited *U-paths*
363 (4.9%) – see later) moved towards their nest, albeit initially obliquely. It is notable that no
364 individuals landed on the beach and walked along it parallel to the sea until their path bisected the *I-*
365 *path* before using it to reach their nests. Instead, the birds cut the corner, moving at an angle to the
366 sea line (*Y-paths* – electronic supplementary material, figure S2), presumably operating in less
367 familiar territory than they would on the *I-path*. They did this until they reached the *I-path* when
368 they changed trajectory to follow it (electronic supplementary material, figure S2). That the area
369 outside the *I-path* is less familiar is supported by lower movement speeds. There was, however, a
370 relationship between the initial path angle with respect to the coastline (i.e. initial angle, see
371 methods) and the landing distance from the *I-point*: Penguins walked at more acute angles with
372 increasing distance (figure 3). This implies that birds either know roughly how far from the *I-point*
373 they have landed and/or how far away their nests are from the landing point and in which general
374 direction. That their chosen path angle only led directly to the nest in two cases (*V-shaped* tracks)
375 suggests that this knowledge is imperfect. We suggest that this may be due to unfamiliarity with the
376 areas outside the *I-path*. However, adopting a path angle that is systematically less than the beeline
377 angle to the nest (figure 3B) means that almost all penguins landing away from the *I-point* will
378 cross the *I-path*. By doing this, they benefit from the certainty of finding familiar terrain. They also

379 reduce the risk that an overly obtuse path angle leads them to a point farther inland than their nest
380 and a trajectory that does not cross the *I-path*.

381

382 There were only two birds that under undertook *L-paths* so consideration of their movement
383 strategies must be considered accordingly. We include them, and the other two birds engaged in
384 other rarer strategies to provide comprehensive coverage. The return angles taken by *L-path* birds
385 meant that they never crossed the *I-path* (figure 3B). Despite this, both individuals walked in a
386 fairly constant direction (as with the *Y-path* individuals) until they reached a (direct) distance from
387 the sea that was approximately equal to that of their nest. They then changed direction and
388 proceeded approximately parallel to the shore until they reached their nests (figure 2iv). Landing at
389 such distances from the *I-path* should put the birds in unfamiliar terrain. However, like the *Y-path*
390 *birds*, they nonetheless chose the correct East or West direction (figure 3A). Beyond this, their
391 change in direction at an appropriate distance from the sea would indicate that they have some sort
392 of navigation system, such as dead-reckoning [cf. 45, 46], that stops them overshooting. We
393 speculate that *L-paths* are little more than *Y-paths* with overly obtuse angles. Modification of path
394 trajectory is required once it is clear that a certain distance from the sea has been travelled without
395 the *I-path* (or the nest) being encountered.

396

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

403

404 *Consequences of return strategy on movement efficiency*

405

406 The initiator for the *L-* or *Y-path* strategy would seem to be the distance of the landing point on the
407 beach from the *I-point*. Travel along the beach until birds reach the *I-point* before moving in the
408 colony on the *I-path* would presumably give them navigational certainty. The cost of this is
409 represented by the length of two sides of a right-angled triangle. *Y-path* birds benefit in distance and
410 time by cutting the corner. However, they travel slower and run the risk of not encountering the *I-*
411 *path* if their return path angle is too large (see the *L-path* strategy). The distance (and therefore
412 time) costs of the strategy can be readily modelled using simple trigonometry. This clearly shows
413 the extent to which penguins adopting a beeline path to the nest would benefit in terms of
414 minimized distance (figure 4A): The difference between the two strategies is maximum at landing
415 distance of *ca.* 100 m from the *I-point*. However, both strategies are markedly better than a path that
416 runs along the beach before cutting in along the *I-path*. But the advantages change when time is
417 considered because penguins off the *I-path* travel slower than birds on the *I-path*. As a result, the
418 advantageous situation for the beeline path with respect to the *Y-path* is reversed, at least for birds
419 landing at distances of up to <250 m from the *I-point* (figure 4B). Finally, assuming that Magellanic
420 penguin walking energetics [47] can be derived from other penguins species, as indicated by
421 Pinshaw et al. [14], the advantage of the *Y-path* over the beeline strategy is maintained if the
422 energetics is considered (figure 4C).

423

424 It therefore seems that a key determinant for efficient movement between the landing point on the
425 beach and the nest is the distance between the landing spot and the *I-point*. Birds that successfully
426 navigate to the *I-point* have minimized distance, time and energy to travel to their nests. The
427 consequences of not landing on the *I-point* rapidly lead to increased distances, journey durations
428 and energies expended (figure 4). However, the slower passage of penguins off the *I-path*, which we
429 assume is due to processing navigation cues, means that it is strategically advantageous to maintain
430 an acute angle to the *I-path*. The speed and energy advantages of following the *I-path* however, are

431 not so great that birds benefit by walking along the beach to the *I-point* before moving into the
432 colony. Finally, penguins that land at great distances from the *I-point* (*L-path* birds) may not be able
433 to modulate their return-to-nest angles correctly (as the *Y-path* individuals do). As a result, these
434 birds have their whole extended trajectory in the colony off the *I-path*, incurring reduced travel rates
435 and increased energetic costs.

436

437 *Navigation capacities and strategies affect movement efficiency*

438

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

457 compared to one on the ground, particularly in dense vegetation, is huge. We identified that the
458 specific landing point on the beach was critical in affecting return distances, times and energies in
459 Magellanic penguins. The challenge for the future will be to determine at what point flighted birds
460 choose to land, how that relates to distance from the nest and the time and energetic consequences
461 this has for them (cf. [49]). Given the efficiency of flight for movement, it may be that the last few
462 meters of their path home may prove to be much more telling than we have previously thought.

463

464 **Acknowledgments**

465

466 This work was funded by grants from the Agencia Nacional de Promoción Científica y Tecnológica
467 (PICT 2013 - 1229) to F.Q. and by the CAASE project funded by the King Abdullah University of
468 Science and Technology (KAUST) under the KAUST Sensor Initiative to C.M.D. and R.P.W. We
469 express our gratitude to people from Ea. San Lorenzo for logistical support. We also thank the
470 Instituto de Biología de Organismos Marinos (IBIOMAR) – CONICET and the CCT CENPAT-
471 CONICET for institutional and logistical support. We thank the Ministerio de Desarrollo Territorial
472 y Sectores Productivos and the Secretaría de Turismo de la Provincia de Chubut, Argentina for the
473 permits to work at Península Valdés natural protected area (permit: 05/2018 - DFyFS-MP).

474

475 **Author's contributions**

476

477 Conceptualization: F.Q. and R.P.W.; Methodology: F.Q., R.P.W. and G.D.; Formal Analysis: A.G.-L.
478 and R.G., Investigation: F.Q. and R.P.W.; Writing Original Draft: F.Q. and R.P.W.; Writing Review
479 & Editing: F.Q., A.G.-L., C.M.D. and F.G., Visualization: F.Q., R.P.W., M.B. and A.G.-L.; Funding
480 Acquisition: F.Q., R.P.W. and C.M.D.; Supervision: F.Q.

481

482 **Declaration of interests**

483

484 The authors declare no competing interests.

485

486 **References**

- 487 1. Egevang C, Stenhouse, IJ, Phillips RA, Petersen A, Fox JW, Silk JRD. 2010. Tracking of
488 Arctic terns *Sterna paradisaea* reveals longest animal migration. *Proc. Nat. Academy of Sci-*
489 *ences* **107**, 2078–2081
- 490 2. Conklin JR, Battley PF, Potter MA, Fox JW. 2010. Breeding latitude drives individual
491 schedules in a trans-hemispheric migrant bird. *Nat. Commun.* **1**, 67
- 492 3. Croxall JP, Silk JRD, Phillips RA, Afanasyev V, Briggs DR. 2005. Global circumnaviga-
493 tions: tracking year-round ranges of non-breeding albatrosses. *Science* **307**, 249–250
- 494 4. Foster JJ, Smolka J, Nilsson DE, Dacke M. 2018. How animals follow the stars. *Proc. R.*
495 *Soc. B: Biol. Sci.* **285**, 20172322
- 496 5. Nevitt GA, Bonadonna F. 2005. Sensitivity to dimethyl sulphide suggests a mechanism for
497 olfactory navigation by seabirds. *Biol. Lett.* **1**, 303-305
- 498 6. Putman NF. 2020. Animal navigation: seabirds home to a moving magnetic target. *Curr.*
499 *Biol.* **30**, R802-R804
- 500 7. Able KP. 2001. The concepts and terminology of bird navigation. *J. Avian Biol.* **32**, 174-183
- 501 8. Orians GH, Pearson NE. 1979. On the theory of central place foraging. In *Analysis of Eco-*
502 *logical Systems* (eds DJ Horn, RD Mitchell, GR Stairs), pp. 155–177. Columbus: Ohio State
503 University Press
- 504 9. Baker RR. 1981. Human Navigation and the Sixth Sense. Hodder & Stoughton, London
- 505 10. Baker RR. 1984. Bird Navigation: the Solution of a Mystery. Hodder & Stoughton, London
- 506 11. Goto Y, Yoda K, Sato K. 2017. Asymmetry hidden in birds' tracks reveals wind, heading,
507 and orientation ability over the ocean. *Sci. Adv.* **3**, e1700097

- 508 12. Shiomi K, Sato K, Katsumata N, Yoda K. 2019. Temporal and spatial determinants of route
509 selection in homing seabirds. *Behaviour* **156**, 1165-1183
- 510 13. Howland HC, Sivak JG. 1984. Penguin vision in air and water. *Vis. Res.* **24**, 1905-1909
- 511 14. Pinshow B, Fedak MA, Schmidt-Nielsen K. 1977. Terrestrial locomotion in penguins: it
512 costs more to waddle. *Science* **195**, 592-594
- 513 15. Griffin T, Kram R. 2000. Penguin waddling is not wasteful. *Nature* **408**, 929
- 514 16. White CR, Alton LA, Crispin TS, Halsey LG. 2016. Phylogenetic comparisons of pedestrian
515 locomotion costs: confirmations and new insights. *Ecol. Evol.* **6**, 6712-6720
- 516 17. Emley JT, Penney RL. 1964. Distance navigation in the Adélie Penguin. *Ibis* **106**, 417-431
- 517 18. Nesterova AP, Mardon J, Bonadonna F. 2009. Orientation in a crowded environment: can
518 king penguin (*Aptenodytes patagonicus*) chicks find their creches after a displacement? *J.*
519 *Exp. Biol.* **212**, 210-216
- 520 19. Nesterova AP, Le Bohec C, Beaune D, Pettex E, Le Maho Y, Bonadonna F. 2010. Do pen-
521 guins dare to walk at night? Visual cues influence king penguin colony arrivals and depar-
522 tures. *Behav. Ecol. Sociobiol.* **64**, 1145-1156
- 523 20. Nesterova AP, Chiffard J, Couchoux C, Bonadonna F. 2013. The invisible cues that guide
524 king penguins chicks home: use of magnetic and acoustic cues during orientation and short-
525 range navigation. *J. Exp. Biol.* **216**, 1491-1500
- 526 21. Schiavini A, Yorio P, Gandini PA, Raya Rey A, Dee Boersma P. 2005. Los pingüinos de las
527 costas argentinas: estado poblacional y conservación. *Hornero* **20**, 5-23
- 528 22. Pozzi LM, Borboroglu PG, Boersma PD, Pascual MA. 2015. Population Regulation in Mag-
529 ellanic Penguins: What Determines Changes in Colony Size? *PLoS ONE* **10**, e0119002
- 530 23. Yorio P, Frere E, Gandini P, Harris G. 1998. Atlas de la distribución reproductiva de aves
531 marinas en el litoral Patagónico Argentino. Plan de Manejo Integrado de la Zona Costera Pa-
532 tagónica. Buenos Aires: Instituto Salesiano de Artes Gráficas

- 533 24. Favaro L, Gili C, Da Rugna C, Gnone G, Fissore C, Sanchez D, McElligott AG, Gamba M,
534 Pessani D. 2016. Vocal individuality and species divergence in the contact calls of banded
535 penguins. *Behav. Processes* **128**, 83-88
- 536 25. Nathan R, Monk CT, Arlinghaus R, Adam T, Alós J, Assaf M, Baktoft H, Beardsworth CE, Bertram
537 MG, Bijleveld AI, et al. (2022). Big-data approaches lead to an increased understanding of the ecol-
538 ogy of animal movement. *Science* **375**, eabg1780
- 539 26. Martin JF. 1983. Optimal foraging theory: A review of some models and their applications.
540 *Am. Anthropol.* **85**, 612-629
- 541 27. Parker GA, Maynard Smith J. 1990. Optimal foraging theory: A review of some models and
542 their applications. *Nature* **348**, 27-33
- 543 28. BirdLife International. 2020. *Spheniscus magellanicus*. *The IUCN Red List of Threat-*
544 *enedSpecies* 2020:e.T22697822A157428850. [https://dx.doi.org/10.2305/IUCN.UK.2020-](https://dx.doi.org/10.2305/IUCN.UK.2020-3.RLTS.T22697822A157428850.en)
545 [3.RLTS.T22697822A157428850.en](https://dx.doi.org/10.2305/IUCN.UK.2020-3.RLTS.T22697822A157428850.en). Downloaded on 05 October 2021
- 546 29. Wilson RP, Pütz K, Peters G, Culik B, Scolaro JA, Charrassin JB, Ropert-Coudert Y. 1997.
547 Long-term attachment of transmitting and recording devices to penguins and other seabirds.
548 *Wildl. Soc. Bull.* **25**, 101–106
- 549 30. Shepard EL, Wilson RP, Quintana F, Laich AG, Liebsch N, Albareda DA, Halsey LG, Gleiss
550 A, Morgan DT, Myers AE, et al. 2008. Identification of animal movement patterns using tri-
551 axial accelerometry. *Endanger. Species Res.* **10**, 47-60
- 552 31. Gunner RM, Holton MD, Scantlebury MD, Hopkins P, Shepard E, Fell A, Garde B, Quin-
553 tana F, Gómez-Laich A, Yoda K, et al. (2021). How often should dead- reckoned animal
554 movement paths be corrected for drift? *Anim. Biotelemetry* **9**, 43
- 555 32. R Core Team. (2019). R: A language and environment for statistical computing. R Founda-
556 tion for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- 557 33. Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team. 2021. *nlme: Linear and Nonlinear*
558 *Mixed Effects Models*. R package version 3.1-152, [https://CRAN.R-project.org/pack-](https://CRAN.R-project.org/package=nlme)
559 [age=nlme](https://CRAN.R-project.org/package=nlme).

- 560 34. Shiomi K, Kokubun N, Shimabukuro U, Takahashi A. 2020. Homing ability of Adélie pen-
561 guins investigated with displacement experiments and bio-logging. *Ardea* **107**, 333-339
- 562 35. Martin GR, Young SR. 1984. The eye of the Humboldt penguin, *Spheniscus humboldti*: vis-
563 ual fields and schematic optics. *Proc. R. Soc. Lond. B. Biol. Sci* **223**, 197-222
- 564 36. Sivak J, Howland HC, McGill-Harelstad P. 1987. Vision of the Humboldt penguin
565 (*Spheniscus humboldti*) in air and water. *Proc. R. Soc. Lond. B. Biol. Sci.* **229**, 467-472
- 566 37. Suburo AM, Marcantoni M, Scolaro JA. 1988. The structure of the eye in *Spheniscus mag-*
567 *ellanicus*: Dimensions of the cornea and lens in different age groups. *Colon. Waterbird.* **11**,
568 227-233
- 569 38. Suburo AM, Scolaro JA. 1990. The eye of the magellanic penguin (*Spheniscus magellan-*
570 *icus*): structure of the anterior segment. *Am. J. Anat.* **189**, 245-252
- 571 39. Wiltschko W, Wiltschko R. 1972. Magnetic compass of European robins. *Science* **176**, 62-4
- 572 40. Wiltschko R, Wiltschko W. 1995. Magnetic orientation in animals. Berlin: Springer.
- 573 41. Muheim R, Schmaljohann H, Alerstam T. 2018. Feasibility of sun and magnetic compass
574 mechanisms in avian long-distance migration. *Mov. Ecol.* **6**, 8
- 575 42. Schmidt-Nielsen, K. 1972. Locomotion: energy cost of swimming, flying, and running. *Sci-*
576 *ence* **177**, 222-228
- 577 43. Luna-Jorquera G, Culik BM. 2000. Metabolic rates of swimming Humboldt penguins. *Mar.*
578 *Ecol. Prog. Ser.* **203**, 301-309
- 579 44. Wilson RP, Kreye JM, Lucke K, Urquhart H. 2004. Antennae on transmitters on penguins:
580 balancing energy budgets on the high wire. *J. Exp. Biol.* **207**, 2649-2662
- 581 45. Maaswinkel H, Whishaw IQ. 1999. Homing with locale, taxon, and dead reckoning strate-
582 gies by foraging rats: sensory hierarchy in spatial navigation. *Behav. Brain Res.* **99**, 143-152
- 583 46. Heinze S, Narendra A, Cheung A. 2018. Principles of Insect Path Integration. *Curr. Biol.* **28**,
584 R1043-R1058

- 585 47. Wilson RP, Locca R, Scolaro JA, Laurenti S, Upton J, Gallelli H, Frere E, Gandini P. 2001.
586 Magellanic Penguins *Spheniscus magellanicus* commuting through San Julian Bay; do cur-
587 rent trends induce tidal tactics? *J. Avian Biol.* **32**, 83-89
- 588 48. Williams TD. 1995. The penguins. Oxford University Press, Oxford, UK.
- 589 49. Shepard EL, Wilson RP, Rees WG, Grundy E, Lambertucci SA, Vosper SB. 2013. Energy
590 landscapes shape animal movement ecology. *Am. Nat.* **182**, 298-312
- 591

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 \pm 0.1 [0.4–0.6]	0.4 \pm 0.1 [0.2–0.5]	17.6 \pm 2.0 [15.1–20.4]	26.4 \pm 6.6 [18.1–36.1]	467 \pm 34 [400–508]	473 \pm 27 [422–519]
Y ($n = 26$)	0.5 \pm 0.1 [0.3–0.7]	0.4 \pm 0.1 [0.2–0.7]	18.8 \pm 5.3 [12.5–33.7]	32.7 \pm 12.8 [14.9–63.2]	462 \pm 38 [409–541]	547 \pm 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]

593

594 **Figure legends**

595

596 Figure 1. Departures and arrivals from and to the colony by adult breeders Magellanic penguins
597 during the early-chick rearing period. Dashed lines indicate the astronomical dawn and dusk (see
598 text for more details).

599

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

607

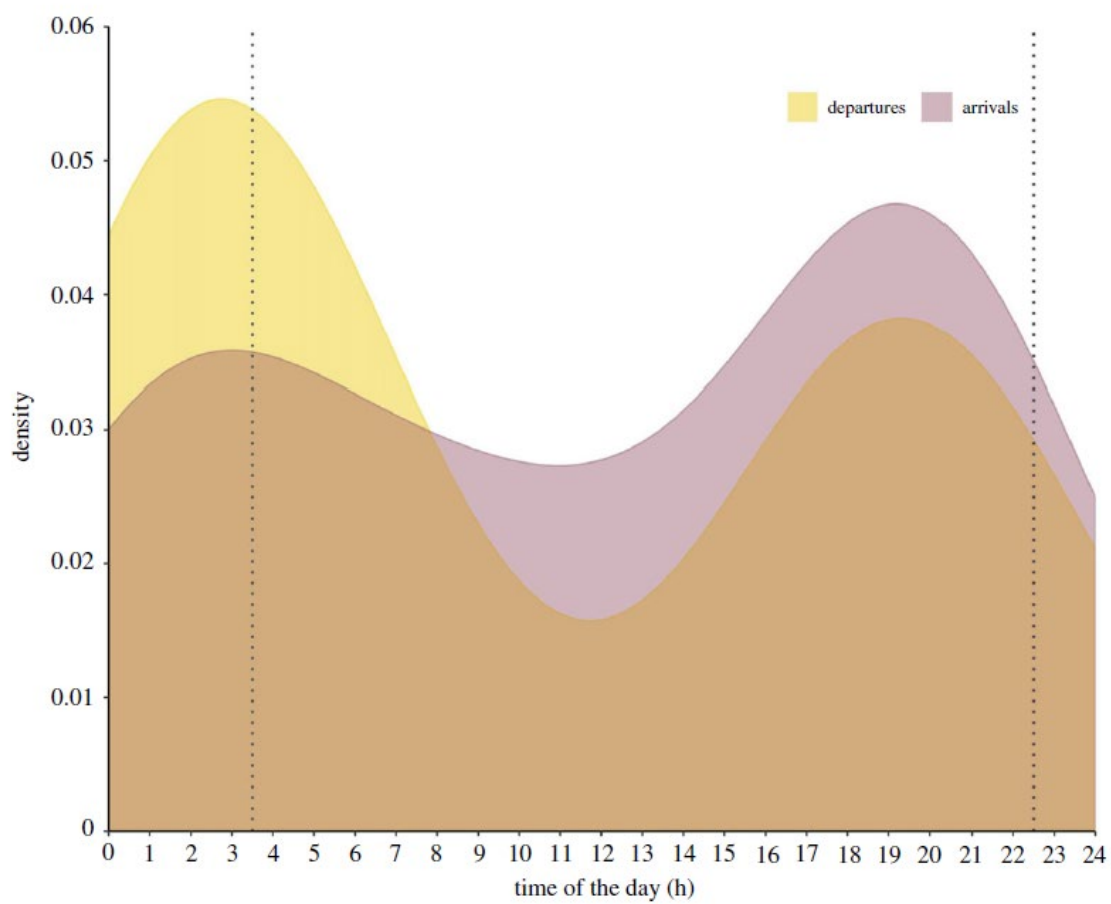
608 Figure 3. (A) Frequency distribution of the angles between Magellanic penguin landing points and
609 their nests for birds commuting between their nest and the sea (expressed as a deviation from a
610 perpendicular track (90°)). (B) Relationship between the initial angle (with respect to the coastline,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

615

616 Figure 4. Scenarios relating to (A) distance travelled, (B) time taken to cover the distance and (C)
617 energy used to cover that distance. All scenarios show (theoretical) birds that walk along the beach
618 parallel to the sea until the *I-point* before walking inland (dashed line), for birds adopting a *Y-path*

619 with the characteristics defined in figure 2 (grey line) and for (theoretical) birds that make a beeline
620 for the nest (black line). The yellow line is for reference and indicates the distance that birds would
621 travel if they landed on the *I-point*. The examples show movement from the landing spot on the
622 beach as a function of its distance from the ideal landing point (*I-point*) to the nest situated 300 m
623 inland. (A) has distances calculated using simple trigonometry, (B) converts these distances into
624 time assuming that birds on the *I-path* (and on the beach) travel at 0.5 m/s and otherwise travel at
625 0.3 m/s while (C) converts the times into energy using data in Pinshaw *et al.* [14] and Wilson *et al.*
626 [47] based on birds using a power of 11.8 W/kg on the *I-path* and 10.0 W/kg on all other paths.
627
628
629

630 Fig. 1.

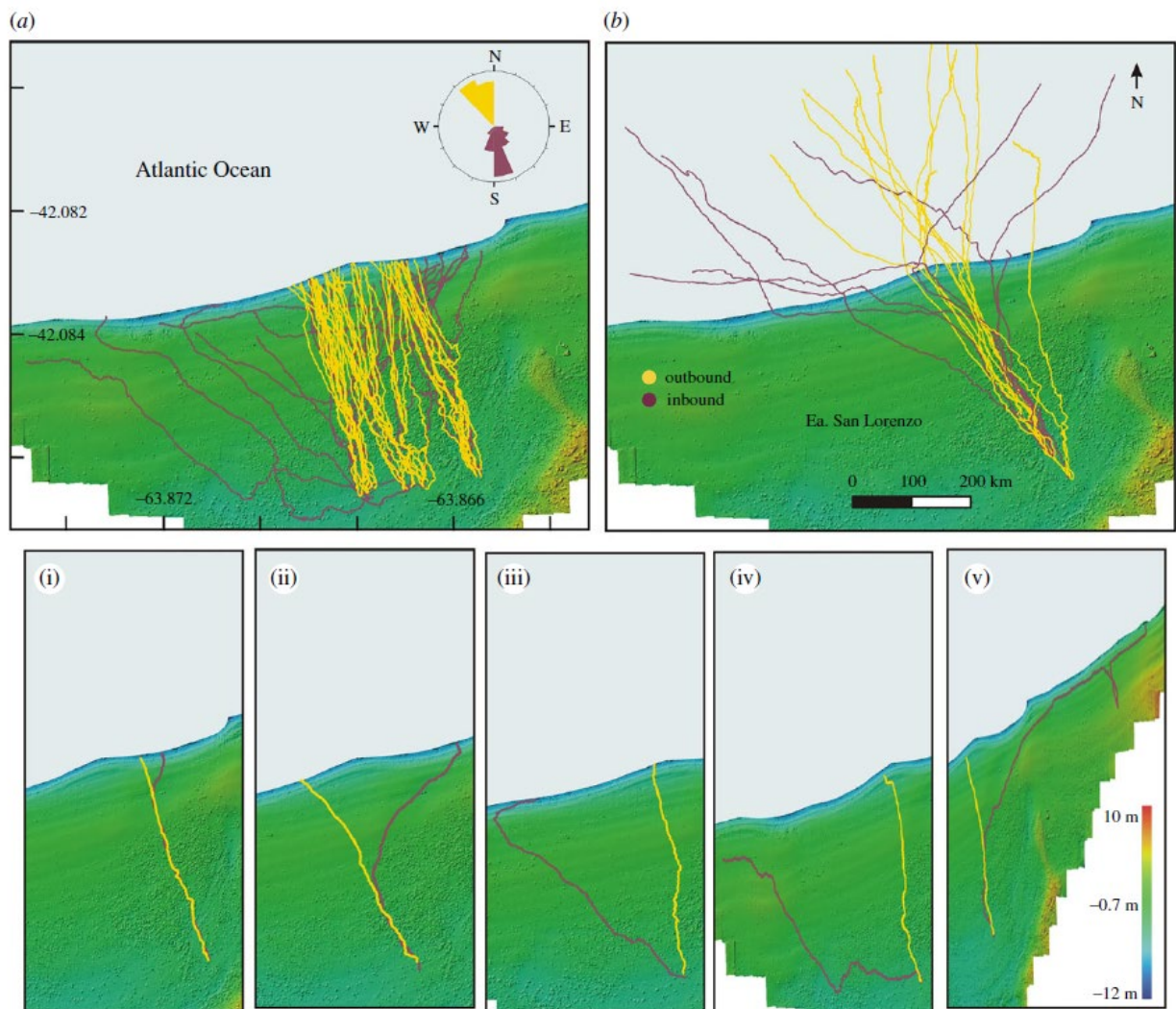


631

632

633 Fig. 2.

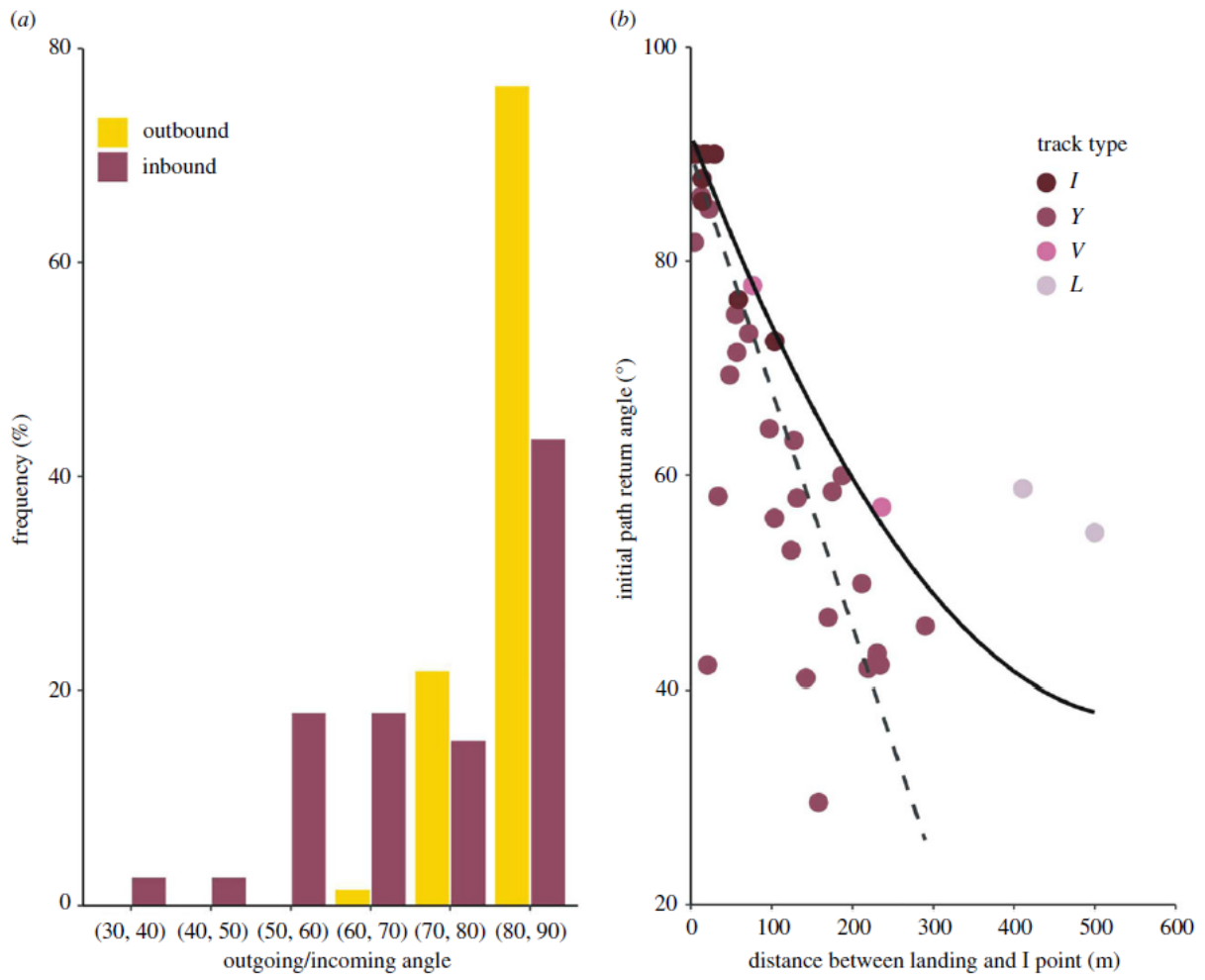
634



635

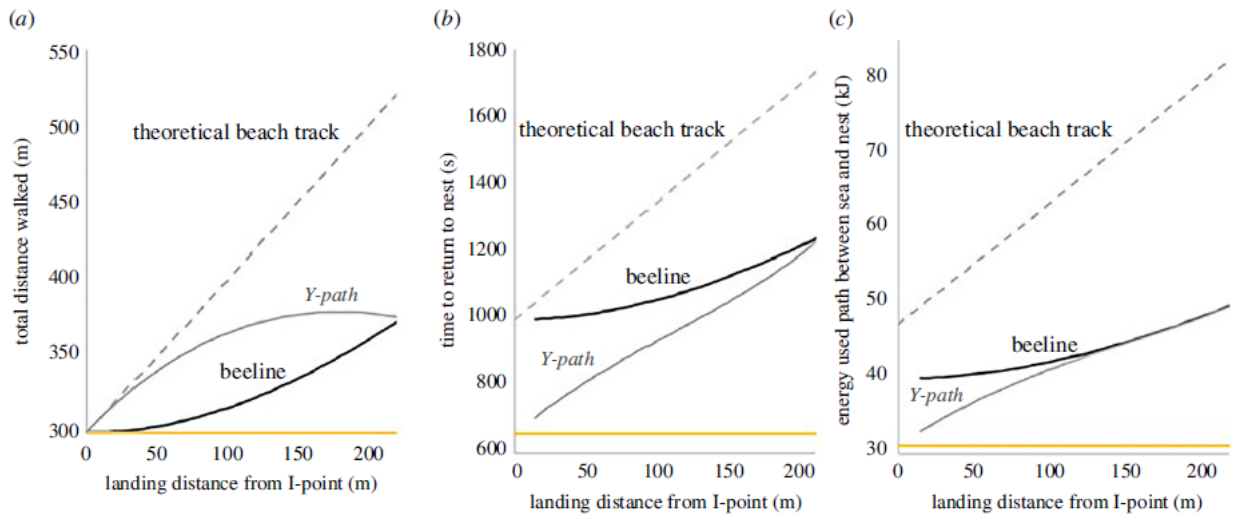
636

637



643 Fig. 4

644



645