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Albatrosses can memorize locations of predictable fishing boats but favour natural foraging

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Human activities generate food attracting many animals worldwide, causing major conservation issues. The spatio-temporal predictability of anthropogenic resources could reduce search costs for animals and mediate their attractiveness. We investigated this through GPS tracking in breeding black-browed albatrosses attracted to fishing boats. We tested for answers to the following questions. (i) Can future boat locations be anticipated from cues available to birds? (ii) Are birds able to appropriately use these cues to increase encounters? (iii) How frequently do birds use these cues? Boats were spatially persistent: birds searching in the direction where they previously attended boats would encounter twice as many boats compared with following a random direction strategy. A large proportion of birds did not use this cue: across pairs of consecutive trips ($n=85$), 51% of birds switched their foraging direction irrespective of previous boat encounters. Still, 15 birds (27%) were observed to closely approach (approx. 0.1–1 km) where they previously attended a boat while boats were no longer there. This is less than the distance expected by chance (approx. 10–100 km), based on permutation control procedures accounting for individual-specific spatial consistency, suggesting individuals could memorize where they encountered boats across consecutive trips. We conclude albatrosses were able to exploit predictive cues from recent boat encounters but most favoured alternative resources.

1. Introduction

The predictability of resources is increasingly suggested as central to understanding animal foraging ecology [1,2]. Resources that are predictable in space and/or time may reduce searching costs for foragers [2,3]. In species where resource encounter rate is a limiting factor for resource acquisition [4], individuals may thus favour spatio-temporally predictable resources, although this could trade off with other factors like resource quality [4,5]. Predictability may partly explain why so many animals are attracted to anthropogenic food resources such as artificial feeders, open dumps or fishing boats [1], despite important conservation issues such as direct additional mortality [6], dependency on human activities [7], and/or lower nutritional quality of some these food resources [8]. However, testing the specific influence of spatio-temporal predictability on wildlife attraction is challenging, especially under observational and uncontrolled natural situations [2,9]. Indeed quantitatively defining and testing 'predictability' *per se* has proved difficult [2].

Here we aim to decompose the question of resource predictability into two quantifiable, forager-dependent components. First, can resource properties, such as their future location, be reliably predicted by a cue available to the foragers themselves? In other words, can we show that appropriately using such cues could significantly increase encounter rates with this resource compared to a strategy ignoring these cues? Second, can we show that foragers have the

(e.g. cognitive) abilities to process and use these cues in the appropriate manner? Importantly, these two questions can be tested independently of whether or not using these ‘informative cues’ and exploiting these resources would ultimately increase fitness of the individual [10]. Indeed, some anthropogenic resources might be attractive especially because of their spatio-temporal predictability [1], but may still constitute ecological traps with deleterious fitness consequences [1,8,11]. This decomposition also enables us to quantify the link between a resource’s predictability and its attractiveness to foragers, by looking at how frequently the ‘predictive cues’ are effectively used to make foraging decisions. Indeed even if animals were able to use predictive cues to increase their encounter rate with anthropogenic resources, they may still favour alternative strategies and resources (e.g. see [12]).

Here we used this approach on a breeding population of black-browed albatrosses (*Thalassarche melanophrys*, hereafter albatrosses), in which birds can feed on fish brought to the surface by longliners operating around the colony (e.g. see [13]). This population is known to be strongly attracted to fishing boats once within perception distance (approx. 30 km [13]), as revealed by simultaneous GPS tracking of birds and boats. We do not know however if birds had cues to anticipate where they would be more likely to encounter boats and if they oriented their search accordingly, before they could perceive boats’ presence. This population displays high levels of individual-specific foraging site consistency, persistent across years [14,15]. As one plausible predictive cue, boats may be persistent in their fishing locations across consecutive bird foraging trips. Finding a boat during a foraging trip may then reliably predict that a boat would likely still be present there on the next foraging trip (hypothesis 1 on the existence of predictive cues). Birds might then memorize where they encountered boats and use this cue to orient their search there on their next foraging trip (hypothesis 2 on the birds’ abilities of appropriately using these informative cues). Yet birds may favour alternative resources to boats, and mainly use other foraging strategies, even if informative cues exist and even if birds are able to use them (hypothesis 3 on the extent to which these cues are effectively used by foraging birds).

To test hypothesis 1, we predicted that based on the average boat spatial behaviour, birds returning towards where they encountered boats on their previous trip would increase their probability of encountering boats again compared with birds not using this strategy (informative cue prediction). To test hypothesis 2 on bird’s ability to memorize recent boat encounters, we needed to distinguish between potential alternative explanations for both high individual site consistency and frequent attraction to boats [13,16,17]. Irrespective of boat spatial consistency, birds could display foraging site consistency, even if they were not able to memorize where they recently encountered boats and/or even if they favoured other resources than boats. For instance birds may have innate or early acquired individual preferences for some foraging sectors or habitat cues [15,18], and/or birds may use other predictive cues than memory to infer current boat locations beyond perception range (e.g. social information, scent traces, etc.). If long-term bird preferences coincide with boats’ fishing grounds [19], for instance because both birds and boats target similar habitats or prey, or there was a persistent network of foraging seabirds converging towards a distant boat, we may wrongly attribute a causal memory explanation to their repeated co-occurrence. To rule out

these alternative cognitive hypotheses, we examined the chronological sequence of events and the occasional bird ‘cognitive mistakes’, two classical methods in cognitive and mathematical studies of memory [20,21] that are largely under-exploited in wild observational studies [3,20,22].

To test if birds used memory of where they recently encountered boats (hypothesis 2), we made three testable predictions. First, we predicted albatrosses would show higher site consistency between consecutive trips after attending a boat than after not attending a boat (chronological sequence prediction). Second, we predicted that birds could go back where they previously found boats even on occasions where the boat had since left the area (mistake prediction). Such ‘cognitive mistakes’ are useful markers of memory [20] because they rule out direct perception of boats and/or indirect indices of boat presence (trail of traces, social information, etc.). Third, we also predicted that these ‘mistakes’ should be individual-dependent, i.e. individuals would more closely approach boat-free locations where they previously attended a boat than where others previously attended a boat (personal-information prediction). This test helps ruling out that birds might be attracted by traces (e.g. prey left-overs, seabird aggregations, oil slicks, etc.) persisting long after boats moved away. Indeed we assume that these traces should be attractive to most birds around, not just those with a previous experience with boats at this place. Finally, to assess hypothesis 3 (preference for alternative resources other than boats), and to distinguish it from hypothesis 2 (memory abilities), we quantified the proportion of instances when birds used informative boat-based cues. We predicted that a non-zero but relatively low proportion of decisions using these cues on boats would suggest an ability to use them but a preference for alternative strategies. We tested these predictions using simultaneous GPS tracking of black-browed albatrosses and fishing boats during a breeding season, in a population of the Southern Indian Ocean.

2. Material and methods

(a) Bird data collection

In December 2011 and January 2012, GPS devices (iGotU Mobile Technology; approx. 1% of average adult body mass) were attached to the back feathers of breeding black-browed albatrosses ($n = 86$ individuals) at Kerguelen (70.24°E, 49.68°S). Birds were handled twice for GPS deployment and recovery (generally < 10 min). Devices were left to record several trips before recovery and recorded a location every 3 min. At the time of GPS attachment, birds were either on their late incubation phase ($n = 8$) or on their brood-guarding phase ($n = 78$). Due to the low number of consecutive incubation trips recorded for a same individual ($n = 3$), we did not analyse incubation and brood-guarding separately. Long-term monitoring on this population suggests space use was similar across years (electronic supplementary material, figure S1) [14,15]. The sex of birds was known for most individuals from the long-term demographic database [14,15,23].

(b) Boat data

Only seven longliners targeting Patagonian toothfish (*Dissostichus eleginoides*) are legally operating within the French Exclusive Economic Zone of the Kerguelen Plateau. Illegal fishing boats are now extremely rare in the area [24]. During the bird tracking period in 2011–2012, we had access to vessel monitoring system (VMS) data. VMS data provides hourly GPS locations of all legally

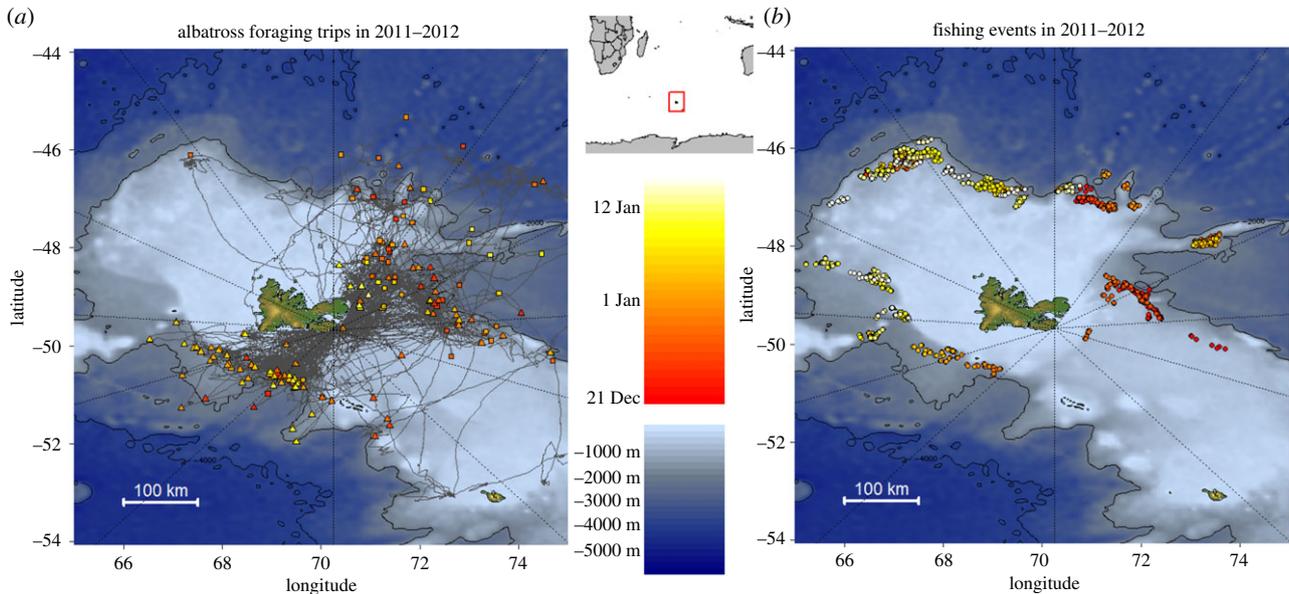


Figure 1. Dynamics of space use in (a) albatrosses and (b) fishing boats in December 2011–January 2012. (a) Albatrosses' foraging trips (grey lines) with point of maximum range indicated by a square (females) or a triangle (males) and date of departure indicated by colour. (b) Boats' fishing events with date indicated by colour. Dashed lines indicate the artificial partitioning in 30°-wide sectors centred on the albatross' colony for boat predictability analyses. Blue shades indicate bathymetry; isobaths are shown every 2000 m (black lines). (Online version in colour.)

operating boats. In addition, we had access to the Pecheker database hosted at the Museum National d'Histoire Naturelle de Paris [25]. This database records the GPS timings and locations of all legal longline settings and haulings in the area, every year since 2002 (see electronic supplementary material, figure S2–S4). We combined these datasets in 2011–2012 and then we linearly interpolated boat locations every 10 min to match the higher bird GPS frequency (further detailed in [13]).

(c) Characterizing bird interactions with boats

We calculated for each bird location the respective distances to all the fishing boats present in Kerguelen waters at the same time (± 5 min). Following [13], bird GPS locations within 3 km of a boat and with apparent speed less than 10 km h^{-1} were classified as 'attending' this boat. Indeed, we previously showed that in 80% of cases where albatrosses flew within perception distance of a boat (approx. 30 km), they ended up attracted within 3 km of boats, where they remained recorded on average at 500–800 m from boats for 3–12 h, at average apparent speeds less than 10 km h^{-1} [13]. These low speeds are suggestive of foraging attempts (albatrosses need to sit on the water to catch their prey), and we previously found that within the shelf-break habitat where boats operate, such low speeds mostly occurred when birds were close to boats and much more rarely when boats were absent [13]. Yet boats target deep species that are naturally unavailable to surface-feeding albatrosses [13]. We are therefore confident that we correctly identified boat attendance behaviour and not just fine-scale co-occurrence; however, we have no measure of foraging success, whether at or away from boats.

(d) Defining trips and consecutive trips

For each individual, we numbered consecutive trips chronologically (a trip is defined as a tracking period greater than 3 km from the nest). Trips showed a bimodal distribution in duration, and we discarded from further analyses trips less than 24 h (28.8%). Indeed we previously showed that among these 68 very short trips, only two boat encounters ever occurred [13], because these trips almost never reached the shelf break where boats exclusively operate (figure 1). Discarding these trips simplified our

analyses and interpretation because it was impossible for us to know if they represented a bird decision not to search for boats or an opportunistic decision to stop searching before ever reaching boats' fishing grounds. These short trips were also ignored in the numbering of consecutive trips. We show in electronic supplementary material, figure S5 that this choice is conservative and has no influence on our results and conclusions.

(e) Bird consistency in foraging direction

For each trip we extracted the direction from colony at the location of furthest distance from the colony (direction at maximum range). For any two trips (e.g. pairs of consecutive trips), we calculated the angle formed by their direction at maximum range. We used this angle to assess spatial consistency within pairs of consecutive trips (from 0° if they have identical directions and high consistency, to 180° in case of opposite directions and low consistency).

We used this angle to test the 'chronological sequence prediction'. We expected a lower angle between two consecutive trips when the bird attended a boat during the first trip of the pair than when the bird did not attend a boat during the first trip of the pair. We used a binomial GLMM to test this prediction, with the probability of having an angle less than 30° as a response variable (see electronic supplementary material, figure S6 for sensitivity analyses). Explanatory factors included a binary variable for whether or not a boat was attended during the first trip of the pair, in interaction with the sex of the bird, as we know in this population males and females can differ in site consistency strategies [14]. Bird identity was included as a random factor because multiple pairs of consecutive trips were included for each individual.

This angle measure is a reliable and easy estimate of large-scale spatial consistency across consecutive trips because most foraging trips had a 'commuting shape' [26] (i.e. exploring mainly one direction from colony; electronic supplementary material, figure S7). However, we did not test the 'mistake' and 'personal-information' predictions from the measure of angular consistency. These predictions required a more explicit measure of spatial scale (in kilometres rather than angle relative to colony), to be compared with the estimated bird perception range (30 km). In the next

section and in the Results section, we further show the angular measure of spatial consistency positively correlated with a distance-based measure of consistency.

(f) Bird consistency to sites where boats were attended

For each trip where boat attendance was observed, we extracted the bird GPS locations where a boat was attended. We then measured the minimum observed distance from these locations of boat attendance to the next foraging trip of the same individual.

This measure was less convenient to test the ‘chronological sequence prediction’ than the angular measure of spatial consistency (see previous section). Indeed, trivially, if no boats were attended during the first trip of the pair, we could not measure in the second trip a distance to where boats had been attended previously. To obtain a sensible null expectation control against which to compare our distance measure, we opted for a specific case of within-individual random permutation test. We measured the distance at which individuals during a trip approached to GPS locations recorded during their own next foraging trip where they would later be attending a boat ($n=25$). As we cannot expect birds to approach these future sites of boat attendance *because* they will later attend boats there, we use this measure as a baseline control of the distance we could expect by chance when there is some level of individual spatial consistency. We predicted a lower distance to sites of past boat attendance than to control sites of future boat attendance. To test this prediction we used a Gaussian linear mixed model, with the distance to sites of boat attendance as a response, future versus past boat attendance as a binary explanatory variable and bird identity as a random factor. Sex was not included because of low sample size.

This procedure allowed us to test as best as we could the ‘chronological sequence’ prediction at an explicit spatial scale, without making strong and speculative assumptions on the cognitive mechanisms underlying memory, search and navigation processes. Indeed we expect no significant difference between past and future sites of attendance if bird individual site consistency occurred independently from recent boat encounters, and/or if birds and boats have independent but convergent site preferences [16,17].

Note that this permutation procedure is also a test of the ‘mistake prediction’: if birds approached closer to sites of past boat attendance than to sites of future boat attendance, it would mean (i) that the boats had moved in between the two trips and (ii) that birds returned closer where boats no longer were. However, to further and explicitly demonstrate that fine-scale approaches (less than 1 km; see Results) to sites of previous boat attendance were indeed ‘mistakes’ we also report the distances between the bird and the closest boat concurrently present around, to show that boats were beyond direct perception range (approx. 30 km [13]).

Finally, to test the ‘personal-information prediction’, we used another control based on a specific inter-individual permutation test. When focal birds returned to sites of their own past boat attendance closer than expected by chance (less than 1 km; see Results), we examined whether other individuals simultaneously present at sea ($n=303$) approached as close to these sites where the focal birds but not themselves had been attending a boat previously. Again we used a Gaussian linear mixed model to test this prediction, with focal versus other individuals as a binary predictor variable, and the distance to sites of focal bird’s past attendance as a response variable, and bird identity as a random effect.

For all statistical models, we tested whether predictions were better matched when only looking at pairs of trips with similar directions at maximum range (less than 30°), to further confirm the relevance of our angular measure of large-scale spatial consistency (see section above).

(g) Boat spatial consistency and predictability

To test hypothesis 1 we worked at a spatio-temporal scale similar to our angular measure of bird consistency. We assessed if a boat would be persistent in a same given direction from colony (less than 30°, see electronic supplementary material, figure S6 for sensitivity analyses), for periods longer than the average duration in between two consecutive bird foraging trips. To do so, we used the locations of all fishing operations from 2002 to 2012 during December and January (corresponding to the stage of the breeding season where we tracked black-browed albatrosses). We used several years of boat data to assess the average predictability of boats across years that albatrosses might have regularly experienced during their breeding season.

For each GPS location of a boat fishing operation, we measured its direction from colony. We categorized these directions into 12 arc-bins radiating from the colony and of equal angular width (30°, e.g. NNE, NE, ENE, ESE, etc.; figure 1). We then assessed daily and for each of these 30° sectors around the colony the presence/absence of at least one boat. From this daily report of presence/absence of boats in each sector, we calculated two probabilities: that of average boat presence/absence in a given random sector on a given day, and that of presence/absence in a given sector on a given day knowing a boat was present k days before in this same sector, for k between 1 and 15 days.

We predicted that the probability of boat presence knowing past boat presence/absence would be larger than the probability of boat presence not knowing past boat presence/absence, for k larger than the average duration in between bird foraging excursions. To test this prediction we built for each k -value a binomial GLM, with the probability of presence as a response variable, and the year, the sector identity and a binary variable of knowing or not past boat presence/absence as explanatory variables. In the results we report the p -value for the latter factor. Standard errors illustrated in figure 2 therefore relate to year and/or sector variations in this probability.

We did not analyse boat distance from colony to keep analyses relatively simple, because we did not expect it to play a significant role. Boats operate exclusively on the shelf edge (figure 1; electronic supplementary material, figure S2), and birds rarely venture beyond the limit of the shelf edge (figure 1), despite the shelf break has a variable distance from colony. It thus seems likely that birds are able to recognize the shelf boundary habitat, and that remembering the distance at which boats were encountered would not considerably increase the probability to find them again.

(h) Computational tools

All data analyses were carried out within the R environment. Data and code have been deposited in a public repository [27]. Geographical distances and directions were calculated with the geosphere package that does not require any geographical projection but assumes great circle lines for calculations. Maps were drawn thanks to the marmap package that uses bathymetric data from NOAA servers. Circular analyses were carried with circular and CircStats packages, mixed models were calculated with nlme package. We used default parameterization of statistical models as implemented in respective packages.

3. Results

In total, 158 albatross trips were analysed. Albatrosses mostly exploited either a north-east direction from the colony (males and females) or a south-west direction (mainly males). They foraged either over neritic waters of the Kerguelen continental shelf, or over waters around the shelf break (figure 1a). These patterns have been observed every year since this colony was tracked (electronic supplementary material, figure S1).

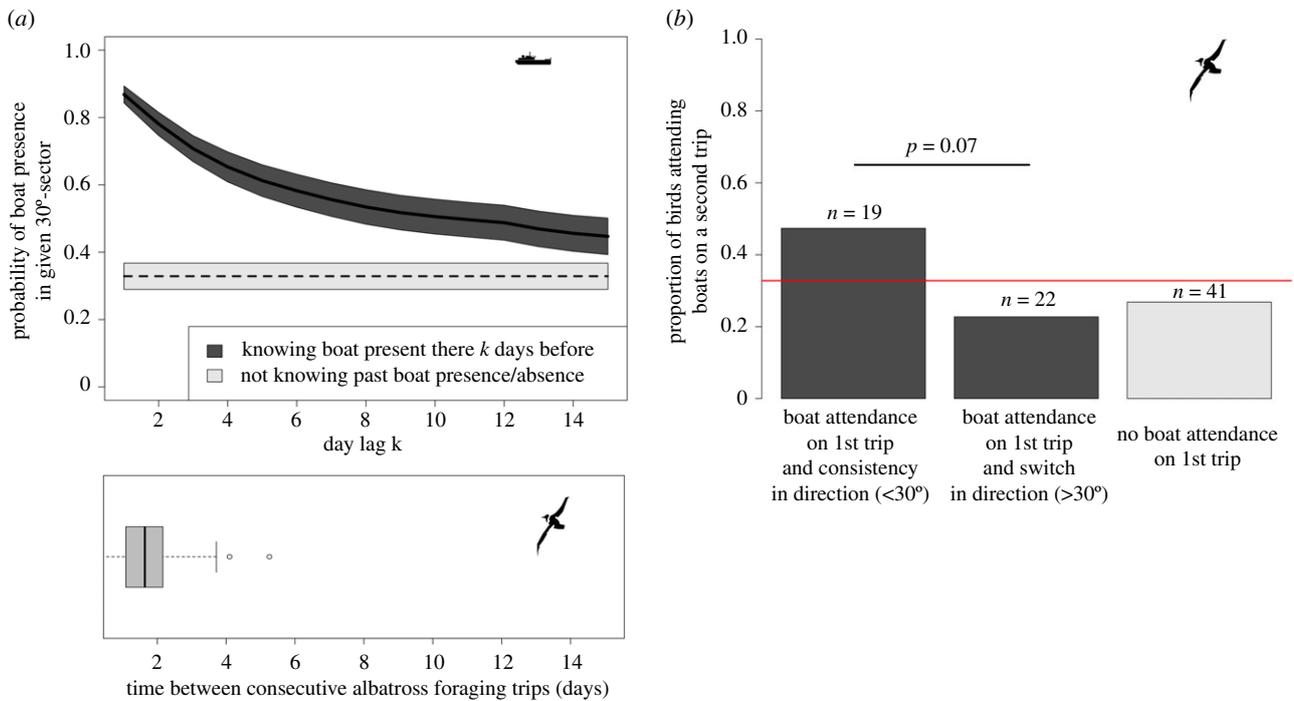


Figure 2. Informative cue prediction tested on (a) boats and (b) birds. (a) Probability of boat presence in a 30° sector depending on use/non-use of cues about previous boat presence in this same sector (top panel, mean \pm s.d.), temporal scale to be compared with bird time at nest in between foraging trips (bottom: median, interquartile, $1.3 \times$ s.d. and outlying values). (b) Observed probability of encountering boats on a second trip depending on adopted consistency strategy (red line: unconditional probability of boat presence in a 30° sector not knowing about past boat presence/absence). (Online version in colour.)

Meanwhile fishing boat operations were strictly limited to the narrow band of waters over the shelf break (1000–2000 m depth; figure 1b), situated hundreds of kilometres from the albatross colony (99% of fishing operations since 2002 occurred greater than 100 km from the albatross colony). These boats have always operated in these waters (electronic supplementary material, figure S2).

In December–January 2011–2012, boats progressively shifted their operations from various directions around the albatross colony to an area NW of the albatross colony (figure 1b, electronic supplementary material, figure S3A), but birds kept their bimodal distribution of foraging directions constant throughout (figure 1a, electronic supplementary material, figure S3B). Monthly dynamics of large-scale fishing areas in previous years revealed no obvious or repeatable trends (electronic supplementary material; figure S4).

(a) ‘Informative cue’ prediction

There was a $32.8 \pm 2.0\%$ probability that at least one boat was operating in a given sector on a given day (figure 2a). This was lower than the probability of boat presence in a sector knowing that a boat was already present in the same sector k -days before, for k up to 14 days ($p < 0.05$ when $k \leq 14$; $p = 0.06$ at $k = 15$; figure 2a). Boats therefore persisted longer in a given sector than the time individual albatrosses stayed on their nest in-between foraging excursions (1.8 ± 0.9 days; max: 5.3 days; figure 2a). Based on these average boat movements, in theory an albatross would have nearly doubled its probability of finding a boat again by returning in the same direction as where it previously attended a boat (less than 30°, see S5 for sensitivity analyses), than by foraging in a random direction (figure 2a). We found marginally non-significant empirical support for this prediction in albatrosses data from 2011 to 2012 (figure 2b). Among birds that had

attended a boat during a first trip, 47.4% of those that persisted in the same direction on their next trip ($n = 19$) encountered a boat again, against 22.7% of those that switched foraging direction on their next trip ($n = 22$, $z = 1.767$, $p = 0.07$).

(b) Chronological sequence prediction

We analysed 85 pairs of consecutive trips from birds (males: 58 pairs from 37 individuals; females: 27 pairs from 19 individuals). In 50.6% of pairs of consecutive trips ($n = 43$, 29 from males, 14 from females), a boat was attended during the first trip of the pair. The angle between the directions of consecutive individual trips was less than 30° in 50.6% of cases, with no difference between sexes ($z = -0.627$, $p = 0.53$). The probability that the angle between consecutive trips was less than 30° was not influenced by boat encounters or not during the first trip: 55.8% of birds that had attended a boat switched sector on their next foraging trip (figure 3a); while 42.9% of birds that had not attended boats switched sector on their next foraging trip ($z = -1.198$, $p = 0.23$, figure 3b).

(c) Mistake prediction

The minimum distance at which individuals ever passed from the locations where they attended fishing boats during their previous foraging trip ranged from 26 m to 411 km, with a median of 5.5 km (average: 52.6 ± 96.0 km; figure 4a,b). These were smaller distances than expected if individuals followed searching strategies independent of their previous boat encounters (figure 4a,b): minimum within-individual distance to locations of future boat attendance had a median of 38.5 km (average 51.2 ± 50 km; range: 43 m–151 km; $t = 2.732$, d.f. = 28, $p = 0.01$), better revealed on a logarithmic scale (figure 4a,b; electronic supplementary material, figure S8).

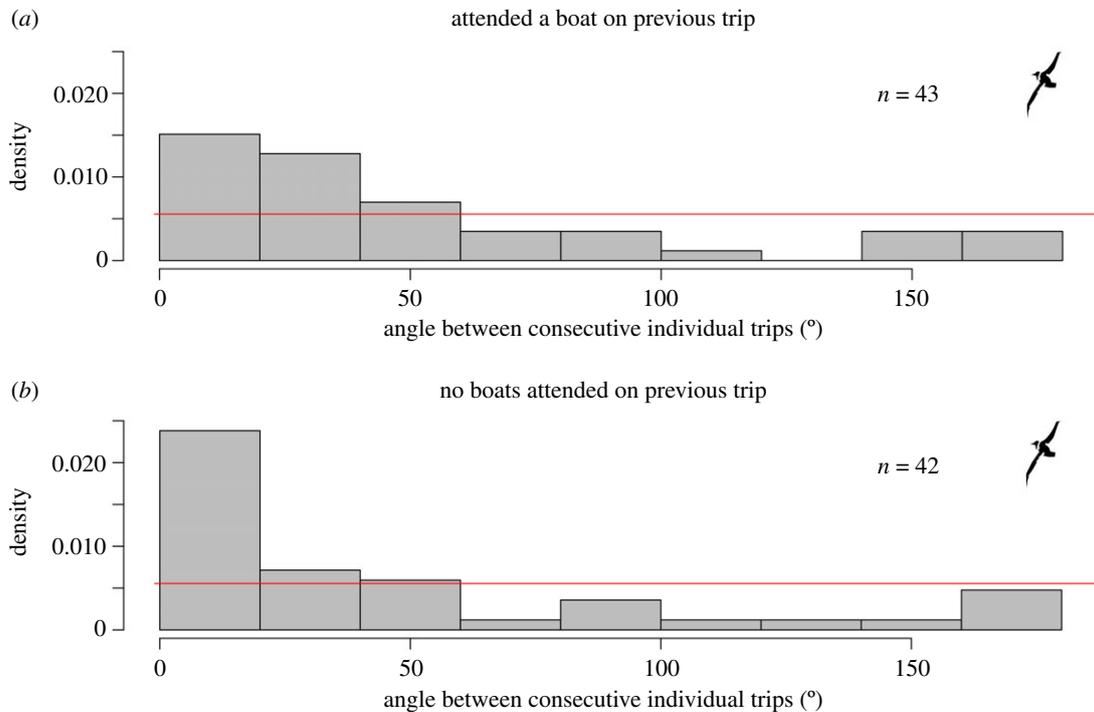


Figure 3. Chronological sequence prediction: bird consistency in direction at maximum range across pairs of consecutive trips, depending on whether (a) or not (b) a boat was attended during the first foraging trip of the pair. The probability density functions are used on the y -axis to adopt a common scale relative to sample sizes. Red lines show expectations in the absence of individual consistency in direction (uniform distribution: no privileged direction). (Online version in colour.)

Accounting for consistency in direction at maximum range (less than 30°) improved explanatory power (interaction term: $t = 2.232$, d.f. = 26, $p = 0.03$), in support of the use of a general directional measure of consistency (figure 2 and 3). As expected, distance to past sites of boat attendance was lower than distance to future sites of boat attendance only for those birds that went to the same general direction along two consecutive trips (less than 30° : $t = 4.144$, d.f. = 13, $p = 0.001$; figure 4a) but not when looking at birds that switched direction between the two consecutive trips (greater than 30° : $t = 1.077$, d.f. = 10, $p = 0.30$; figure 4b; see electronic supplementary material, figure S8 for sensitivity analyses).

Only in one case out of 25 did a bird approach at less than 1 km where it would later interact with a boat during its next foraging trip (figure 4a,b). In this instance, the bird was actually attending the boat on the same site during both trips. However the distance to previous locations of boat attendance was lower than 1 km in 14 cases out of 43 ($\chi^2 = 5.930$, d.f. = 1, $p = 0.01$; from 12 different individuals: 4 females and 8 males; figure 3a). In all these 14 cases but one (mentioned previously), no concurrent boats were within 30 km from birds (figure 4c).

(d) Personal-information prediction

As expected from the personal-information prediction, the observed distance focal birds passed from the locations where they themselves previously attended a boat (see section above) was lower than the distance other non-focal individuals present at sea at the same time passed from the sites where the focal bird previously attended a boat ($n = 303$, $t = -4.812$, d.f. = 46, $p < 0.001$). This remained true when looking only at pairs of trips (consecutive within-individuals or simultaneous between individuals) with an angle between directions at maximum range less than 30° ($n = 114$, $t = -4.593$, d.f. = 20, $p < 0.001$; figure 4a). It also remained true when further restricting the comparison with only those other individuals that we

know can be attracted to boats ($n = 28$; $t = -3.269$, d.f. = 26, $p < 0.01$) since these individuals were themselves observed in other instances returning to where they themselves previously attended a boat.

4. Discussion

Altogether our results suggest that birds had the ability to memorize where they previously attended boats (hypothesis 2), that such strategies could have greatly increased boat encounter rates (hypothesis 1), but that birds only occasionally used this information to orient their search and rather relied on alternative resources to boats to inform their consistency strategy (hypothesis 3). Indeed we found that only a few birds accurately returned (less than 1 km) to distant locations (greater than 100 km from colony) where they attended fishing boats during their own previous foraging trip. It occurred more than expected by chance (as estimated by individual 'returns' to future sites of boat attendance), and when boats were no longer present within perception distance, matching the 'mistake' prediction. These mistakes were also individual-dependent (personal-information prediction), further lending support to hypothesis 2 that individual birds could memorize the locations where they attended boats from one trip to the next. In support of hypothesis 1 that boat locations could reliably be predicted from cues available to birds, we found that bird strategies involving consistency in trip direction after a boat encounter could nearly double the probability of encountering boats again, compared with random direction strategies (informative cue prediction). Yet, less than half of birds that attended a boat returned in the same direction on their next trip, whereas more than half of birds that had not encountered a boat did so, and consistency in direction appeared independent of recent boat encounters (against the

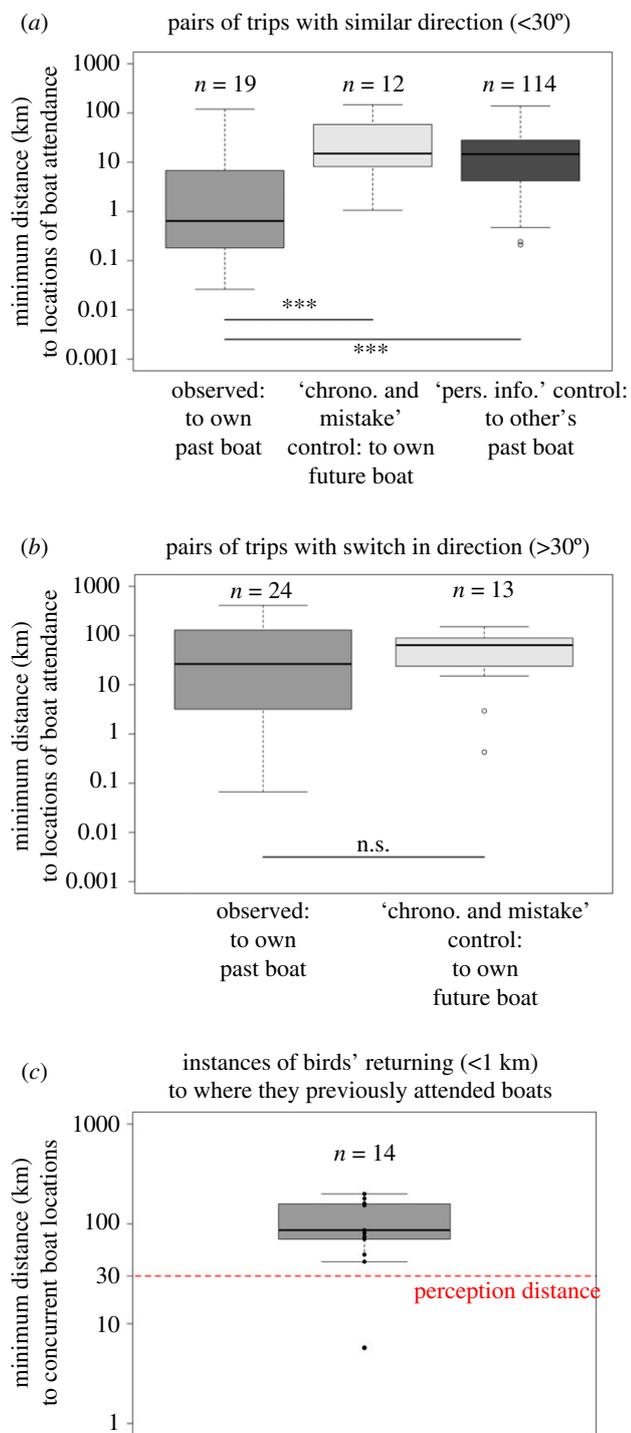


Figure 4. (a,b,c) Mistake and (a) personal-information predictions: minimum distance (logarithmic scale) to GPS locations where a boat was attended during another trip (a,b) or to GPS locations of boats concurrently present at sea (c). In a and b, distances to locations where a boat was attended by the same individual during the previous trip (left, intermediate grey) are contrasted to control distances established from specific permutation procedures (lighter and darker grey; see text for details). In b (but not in a), pairs of trips showed different directions at maximum range (greater than 30°), testing the relevance of using an angular measure of consistency (see figures 2 and 3). In c, red dashed line indicates the estimated maximum distance (30 km) at which birds can directly perceive boats. (Online version in colour.)

'chronological sequence' prediction). Overall, the fine-scale returns (less than 1 km) to sites of past boat attendance only made up to 27% of all pairs of consecutive foraging trips (hypothesis 3 on the frequency of use of predictive cues).

We know from many previous studies that large numbers of black-browed albatrosses attend fishing boats worldwide (e.g. [13,28]). Our results here suggest that at the population level, boats did not have a long-lasting influence across consecutive trips on large-scale searching decisions by breeding albatrosses. In this system, boats seem attractive mainly at a local scale, once detected (less than approx. 30 km [13]). Many of the birds observed in numbers at fishing boats may be immatures or non-breeding adults, which are more difficult to study through GPS telemetry. On the other hand, adult breeders' diet often includes fisheries-related food items [29], and we know breeding adults from this population are strongly attracted once they detect a boat [13]. It is possible that these seemingly opportunistic interactions from breeding birds may suffice to explain large number of birds behind boats when scaled up to the whole breeding population (3200 pairs [23]). Another hypothesis is that there is some individual heterogeneity in the likelihood of searching for and/or memorizing boats [14,28,30]. Boats in this fleet are implementing bycatch mitigation measures that considerably reduced the food available to attracted seabirds (see discussion in [13]), so that there might be only weak memory reinforcements for attracted seabirds. Our results might thus reflect a form of win stay, lose shift strategy [17], whereby only birds that effectively could eat from boats remembered them. We previously found that birds rearing chicks were attending boats for longer than birds in incubation [13], suggesting that constraints on foraging efficiency could influence attraction to boats. Here our sample size did not allow to test for the effects of the breeding stage. Another hypothesis that would require further testing is that the individuals accurately returning where they previously found boats were the birds that failed to find food alternatives [8,13,15].

Our results support the view that seabirds may be more sophisticated foragers than traditionally assumed. It has long been hypothesized that marine predators' ecology could largely be limited by their encounter rate with resources, and notably by the information they have on the locations of their prey, but testing this idea has proved challenging [26,31]. Our results suggest that the foraging ecology of black-browed albatrosses may in fact strongly be influenced by prior-information selection and/or resource selection processes [4]. Accounting for these cognitive processes in marine predators could help predict their responses to global changes in marine resources [8,32,33]. For instance, black-browed albatrosses are among a few investigated examples of marine predators displaying long-term foraging site consistency, across years (e.g. [14,17]). In theory, long-term consistency could arise from inherited or early acquired and then fixed preferences for some cues or foraging sites [17,18]. It could limit their flexibility in the face of changes in the environment [32]. Our results suggest that adult albatrosses may still be able to memorize much more recent experiences and adjust their search behaviour accordingly, as was suggested in species foraging in presumably more dynamic environments [34,35]. This might involve a form of win-stay, loose-shift strategy [17], integrating together foraging success from both fishing boats and more 'natural' food resources. However it is not clear whether a win-stay, loose-shift strategy alone would be sufficient to also account for the observed long-term individual spatial consistency [14,15]. Our data suggest there is no similar long-term spatial consistency in

fishing boats (figure 2; electronic supplementary material, figure S4). The long-term consistency in birds is therefore more likely to be related to their natural food resources. In summary, black-browed albatrosses display signs of both long-term consistency and fine-temporal scale memory capacities. The fine-temporal scale flexibility albatrosses seem to display may help them better cope with some rapid environmental changes (see also [32,33]), and for these albatrosses the fishing boats may not appear that different or attractive compared to alternative food resources.

The sites where boats were encountered are located at more than a hundred kilometres from the coast of Kerguelen, in an open water environment with presumably no obvious and static visible landmarks. Returning to such sites, sometimes with a precision of about a few hundreds of metres, in the absence of boats or attractive traces, would imply excellent but so far poorly understood navigation abilities (e.g. see [36,37]). Moreover, compared with homing navigation where birds repeatedly return to their nest after each foraging excursion, here it seems that only one boat encounter event may have been sufficient for accurate spatial learning. This might be easier to account for if we assume that individuals previously developed some familiarity with their local, repeatedly used environment [15,38], but this remains to be tested.

Our approach to infer memory use in observational tracking data is simple to implement as it is a specific case of within-individual random permutation. It should be relatively easy to generalize to other animal movement datasets to further test spatial memory capacities in the wild [3]. For instance nearest-neighbour distance measures are often used to evaluate within-individual spatial fidelity [16–18] but authors rarely if ever report whether they calculated

them from previous track to future track or reverse. It is highly possible that systematic asymmetries such as in the present study have been widely overlooked. This method could largely broaden our dataset for comparative cognition [3,30]. Combined (as we did) with measures of environmental predictability [2], it could also improve identification of situations where animals actually apply (or not) their cognitive capacities for their daily decisions [3], and better test whether cognitive capacities have current adaptive values [10,11,30] and how they modulate animals' behavioural responses to rapid global changes.

Research ethics. All field procedures had been ethically approved by the Prefet des Terres Australes and authorized by the Reserve Naturelle des Terres Australes. Handling time of birds was kept to the minimal.

Data accessibility. Data and code necessary to perform the analyses are available from the Dryad digital Repository: <https://doi.org/10.5061/dryad.p2ngf1vnj> [27]. Note that data on boats are confidential and cannot be published.

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References

- Oro D, Genovart M, Tavecchia G, Fowler MS, Martínez-Abraín A. 2013 Ecological and evolutionary implications of food subsidies from humans. *Ecol. Lett.* **16**, 1501–1514. (doi:10.1111/ele.12187)
- Riotte-Lambert L, Matthiopoulos J. 2019 Environmental predictability as a cause and consequence of animal movement. *Trends Ecol. Evol.* **35**, 163–174. (doi:10.1016/j.tree.2019.09.009)
- Fagan WF *et al.* 2013 Spatial memory and animal movement. *Ecol. Lett.* **16**, 1316–1329. (doi:10.1111/ele.12165)
- Schoener TW. 1971 Theory of feeding strategies. *Annu. Rev. Ecol. Syst.* **2**, 369–404. (doi:10.1146/annurev.es.02.110171.002101)
- Hills TT, Todd PM, Lazer D, Redish AD, Couzin ID. 2015 Exploration versus exploitation in space, mind, and society. *Trends Cogn. Sci.* **19**, 46–54. (doi:10.1016/j.tics.2014.10.004)
- Anderson OR, Small CJ, Croxall JP, Dunn EK, Sullivan BJ, Yates O, Black A. 2011 Global seabird bycatch in longline fisheries. *Endanger. Species Res.* **14**, 91–106. (doi:10.3354/esr00347)
- Bicknell AWJ, Oro D, Camphuysen K (C.J.), Votier SC. 2013 Potential consequences of discard reform for seabird communities. *J. Appl. Ecol.* **50**, 649–658. (doi:10.1111/1365-2664.12072)
- Le Bot T, Lescoërl A, Fort J, Péron C, Gimenez O, Provost P, Grémillet D. 2019 Fishery discards do not compensate natural prey shortage in Northern gannets from the English Channel. *Biol. Conserv.* **236**, 375–384. (doi:10.1016/j.biocon.2019.05.040)
- Cortés-Avizanda A, Jovani R, Carrete M, Donazar JA. 2012 Resource unpredictability promotes species diversity and coexistence in an avian scavenger guild: a field experiment. *Ecology* **93**, 2570–2579. (doi:10.1890/12-0221.1)
- Dunlap AS, Stephens DW. 2009 Components of change in the evolution of learning and unlearned preference. *Proc. R. Soc. B* **276**, 3201–3208. (doi:10.1098/rspb.2009.0602)
- Schlaepfer MA, Runge MC, Sherman PW. 2002 Ecological and evolutionary traps. *Trends Ecol. Evol.* **17**, 474–480. (doi:10.1016/S0169-5347(02)02580-6)
- Monsarrat S, Benhamou S, Sarrazin F, Bessa-Gomes C, Bouten W, Duriez O. 2013 How predictability of feeding patches affects home range and foraging habitat selection in avian social scavengers? *PLoS ONE* **8**, e53077. (doi:10.1371/journal.pone.0053077)
- Collet J, Patrick SC, Weimerskirch H. 2017 A comparative analysis of the behavioral response to fishing boats in two albatross species. *Behav. Ecol.* **28**, 1337–1347. (doi:10.1093/beheco/axx097)
- Patrick SC, Weimerskirch H. 2014 Consistency pays: sex differences and fitness consequences of behavioural specialization in a wide-ranging seabird. *Biol. Lett.* **10**, 20140630. (doi:10.1098/rsbl.2014.0630)
- Patrick SC, Weimerskirch H. 2017 Reproductive success is driven by local site fidelity despite stronger specialisation by individuals for large-scale habitat preference. *J. Anim. Ecol.* **86**, 674–682. (doi:10.1111/1365-2656.12636)
- Patrick SC *et al.* 2014 Individual differences in searching behaviour and spatial foraging consistency in a central place marine predator. *Oikos* **123**, 33–40. (doi:10.1111/j.1600-0706.2013.00406.x)
- Wakefield ED, Cleasby IR, Bearhop S, Bodey TW, Davies RD, Miller PI, Newton J, Votier SC, Hamer KC. 2015 Long-term individual foraging site fidelity—why some gannets don't change their spots. *Ecology* **96**, 3058–3074. (doi:10.1890/14-1300.1)
- Votier SC *et al.* 2017 Effects of age and reproductive status on individual foraging site fidelity in a long-lived marine predator. *Proc. R. Soc. B* **284**, 20171068. (doi:10.1098/rspb.2017.1068)

19. Patrick SC, Bearhop S, Bodey TW, Grecian WJ, Hamer KC, Lee J, Votier SC. 2015 Individual seabirds show consistent foraging strategies in response to predictable fisheries discards. *J. Avian Biol.* **46**, 431–440. (doi:10.1111/jav.00660)
20. Janmaat KR. 2019 What animals do not do or fail to find: A novel observational approach for studying cognition in the wild. *Evol. Anthropol. Issues News Rev.* **28**, 303–320. (doi:10.1002/evan.21794)
21. Couzin ID, Krause J, James R, Ruxton GD, Franks NR. 2002 Collective memory and spatial sorting in animal groups. *J. Theor. Biol.* **218**, 1–11. (doi:10.1006/jtbi.2002.3065)
22. Janson CH, Byrne R. 2007 What wild primates know about resources: opening up the black box. *Anim. Cogn.* **10**, 357–367. (doi:10.1007/s10071-007-0080-9)
23. Weimerskirch H, Delord K, Barbraud C, Le Bouard F, Ryan PG, Fretwell P, Marteau C. 2018 Status and trends of albatrosses in the French Southern Territories, Western Indian Ocean. *Polar Biol.* **41**, 1963–1972. (doi:10.1007/s00300-018-2335-0)
24. Weimerskirch H., Filippi D.P., Collet J., Waugh S.M., Patrick S.C. 2017 Use of radar detectors to track attendance of albatrosses at fishing vessels. *Conserv. Biol.* **32**, 240–245. (doi:10.1111/cobi.12965)
25. Martin A, Pruvost P. 2007 Pecheker, relational database for analysis and management of halieutic and biological data from the scientific survey of the TAAF fisheries, Muséum National d'Histoire Naturelle. See <http://borea.mnhn.fr/equipe4/pecheker.php>.
26. Weimerskirch H. 2007 Are seabirds foraging for unpredictable resources? *Deep Sea Res. Part II Top. Stud. Oceanogr.* **54**, 211–223. (doi:10.1016/j.dsr2.2006.11.013)
27. Collet J, Weimerskirch H. 2020 Data from Albatrosses can memorize locations of predictable fishing boats but favour natural foraging. Dryad Digital Repository. (doi:10.5061/dryad.p2ngf1vnj)
28. Granadeiro JP, Brickle P, Catry P. 2014 Do individual seabirds specialize in fisheries' waste? The case of black-browed albatrosses foraging over the Patagonian Shelf. *Anim. Conserv.* **17**, 19–26. (doi:10.1111/acv.12050)
29. Mariano-Jelich R, Copello S, Seco Pon JP, Favero M. 2017 Long-term changes in black-browed albatrosses diet as a result of fisheries expansion: an isotopic approach. *Mar. Biol.* **164**, 148. (doi:10.1007/s00227-017-3176-z)
30. Thornton A, Lukas D. 2012 Individual variation in cognitive performance: developmental and evolutionary perspectives. *Philos. Trans. R. Soc. B* **367**, 2773–2783. (doi:10.1098/rstb.2012.0214)
31. Sims DW *et al.* 2008 Scaling laws of marine predator search behaviour. *Nature* **451**, 1098–1102. (doi:10.1038/nature06518)
32. Sherley RB, Ludynia K, Dyer BM, Lamont T, Makhado AB, Roux J-P, Scales KL, Underhill LG, Votier SC. 2017 Metapopulation tracking juvenile penguins reveals an ecosystem-wide ecological trap. *Curr. Biol.* **27**, 563–568. (doi:10.1016/j.cub.2016.12.054)
33. Bost CA *et al.* 2015 Large-scale climatic anomalies affect marine predator foraging behaviour and demography. *Nat. Commun.* **6**, 8220. (doi:10.1038/ncomms9220)
34. Courbin N, Besnard A, Péron C, Saraux C, Fort J, Perret S, Tornos J, Grémillet D. 2018 Short-term prey field lability constrains individual specialisation in resource selection and foraging site fidelity in a marine predator. *Ecol. Lett.* **21**, 1043–1054. (doi:10.1111/ele.12970)
35. Carroll G, Barcourt R, Pitcher BJ, Slip D, Jonsen I. 2018 Recent prey capture experience and dynamic habitat quality mediate short-term foraging site fidelity in a seabird. *Proc. R. Soc. B* **285**, 20180788. (doi:10.1098/rspb.2018.0788)
36. Bonadonna F, Benhamou S, Jouventin P. 2003 Orientation in 'featureless' environments: the extreme case of pelagic birds. In *Avian migration* (eds P Berthold, E Gwinner, E Sonnenschein), pp. 367–377. Berlin Germany: Springer.
37. Padget O *et al.* 2019 Shearwaters know the direction and distance home but fail to encode intervening obstacles after free-ranging foraging trips. *Proc. Natl. Acad. Sci. USA* **116**, 21 629–21 633. (doi:10.1073/pnas.1903829116)
38. Wolf M, Frair J, Merrill E, Turchin P. 2009 The attraction of the known: the importance of spatial familiarity in habitat selection in wapiti *Cervus elaphus*. *Ecography* **32**, 401–410. (doi:10.1111/j.1600-0587.2008.05626.x)