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Recent prey capture experience and dynamic habitat quality mediate short-term foraging site fidelity in a seabird

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Foraging site fidelity allows animals to increase their efficiency by returning to profitable feeding areas. However, the mechanisms underpinning why animals 'stay' or 'switch' sites have rarely been investigated. Here, we explore how habitat quality and prior prey capture experience influence short-term site fidelity by the little penguin (*Eudyptula minor*). Using 88 consecutive foraging trips by 20 brooding penguins, we found that site fidelity was higher after foraging trips where environmental conditions were favourable, and after trips where prey capture success was high. When penguins exhibited lower site fidelity, the number of prey captures relative to the previous trip increased, suggesting that switches in foraging location were an adaptive strategy in response to low prey capture rates. Penguins foraged closer to where other penguins foraged on the same day than they did to the location of their own previous foraging site, and caught more prey when they foraged close together. This suggests that penguins aggregated flexibly when prey was abundant and accessible. Our results illustrate how foraging predators can integrate information about prior experience with contemporary information such as social cues. This gives insight into how animals combine information adaptively to exploit changing prey distribution in a dynamic environment.

1. Introduction

Foraging site fidelity enables animals to increase their foraging efficiency by returning to locations where productivity was previously high (e.g. [1]). However, this strategy is only efficient if prey distribution is predictable at the spatial and temporal scales at which animals forage [2]. Under predictable conditions, an animal should return to a location where it was previously successful and choose an alternative site if it was unsuccessful: a 'win–stay, lose–switch' strategy [3–5]. Conversely, if the environment is unpredictable, an animal should not base its decision to return to a site on its past success there, as the probability of experiencing the same outcome again is low [3]. However, animals might be expected to return to the same site even in unpredictable conditions if there are fitness benefits of site familiarity [6] or if the mean quality of all available sites is similar, meaning that there is no advantage to switching [3]. In cases where the environment is both unpredictable and heterogeneous in quality, animals might be expected to show lower site fidelity, but greater use of environmental cues that help them to adaptively locate prey [7,8].

Understanding what constitutes predictability and heterogeneity on scales that are meaningful to animals making foraging decisions is challenging. For example, environments can be relatively unpredictable at fine spatial and temporal scales, but contain features that provide reliably enhanced productivity at larger scales. This is true in the open ocean, for example, where water circulation patterns result in a dynamic distribution of organisms at the base of the food web [9]. However, at the meso-scale (1–100 km), features of the ocean environment such as bathymetric structures, fronts and upwelling zones enhance productivity, and consequently aggregate prey for mobile marine predators [2,10,11]. An increasing number of studies have shown that foraging animals repeatedly 'commute' to these areas, and learn to be faithful to them within and between years [12–16].

Even 'predictable' areas can be dynamic through the lifetime of an animal, and in many systems, animals are forced to respond adaptively to changes in the distribution of their prey [7]. However, it is often unknown how different factors influence an animal's decision about where to forage relative to their previous location, especially in highly dynamic environments. Animals are likely to combine different types of information at different spatial and temporal scales, and the degree to which their decision-making reflects prior experience at a site rather than contemporary information such as prey encounter, social or environmental cues may vary under different conditions [17]. Most studies that have assessed site fidelity were unable to incorporate information on prey consumption (but see [18]), and the mechanisms underpinning site fidelity and its fitness consequences in complex systems are therefore usually unknown [6,15].

In this study, we assess foraging site fidelity by the little penguin (*Eudyptula minor*), a marine predator that feeds on forage fish in dynamic coastal environments [19,20]. We tracked penguins during brooding when individuals undertake single-day trips every second day, and are limited to foraging within approximately 25 km of their colony off southeast Australia. Under these constraints, penguins must find prey that is distributed patchily [21], in a complex marine environment dominated by rapid incursions of the warm, nutrient-poor East Australian Current [22], a water mass that has been associated with low foraging success by penguins [20].

Here, we first describe the environment and its average predictability over a 2-day window—the temporal scale at which penguins leave the colony to forage. We use a prey capture signature derived from the movement profiles of penguins [23] to determine when and where penguins catch prey. We then assess whether penguins exhibit greater site fidelity under different environmental conditions, or when different numbers of prey captures were recorded on the previous trip. We also determine whether penguins catch more prey when they are more faithful to their previous foraging site. Additionally, we examine whether penguins forage in locations that are more similar to their own previous site or are closer in proximity to the locations of other tagged penguins foraging on the same day. By systematically testing predictions of site fidelity in relation to environmental predictability on a trip-by-trip basis, we aim to shed light on how animals use different types of information at short time scales to maximize prey intake in changeable environments.

2. Material and methods

(a) Penguin tracking

The study was conducted on Montague Island (36.253° S, 150.227° E), 9 km off the southeast coast of New South Wales, Australia over 44 days from 18 September to 31 October 2016. The study was designed to coincide with the peak of the period when little penguins were brooding small chicks (less than two weeks old). During this stage of the breeding cycle, one parent remains at the nest to guard the chicks, while the other goes to sea for a single-day foraging trip, returning after sunset. Consequently, individuals at this breeding stage usually undertake foraging trips every second day. Penguins undertaking single-day trips are restricted to foraging within a maximum distance of approximately 25 km from the colony. By selecting only birds at this breeding stage for tracking, we were able to remove the effect of differential habitat selection strategies caused by the varying foraging ranges and energetic requirements of birds at different breeding stages [24].

Penguins were equipped with a GPS logger (CatTrack, South Carolina, USA) recording a position every 2–6 s, and an accelerometer data logger (G6a+, CEFAS Technology Pty Ltd, Suffolk, UK) recording tri-axial acceleration and depth at a frequency of 30 Hz during dives greater than 1.5 m. The combined tag weight was 62 g in air, less than 6% of the mean bodyweight (1038.7 g ± 8.9 in this study) and the proportional cross-sectional area was less than 3.5%, an important consideration for logger effects on penguins due to the influence of drag [25,26]. For further details regarding tag specifications and attachment protocols see Carroll *et al*. [20,21].

Devices were deployed for a single foraging trip and deployments were alternated between partners, with birds being equipped multiple times through the chick-rearing period to assess site fidelity. We minimized handling time and in most cases total time spent at a nest including deployment and retrieval of devices was less than 8 min. To reduce stress caused by repeated handling [27], penguin pairs were given a respite from tracking for 5–7 days in the middle of sampling, during which time the nest was not visited. Throughout the study the mass of chicks and adults were monitored, and tracking of an individual ceased if it lost more than 15% body mass over the study period (average mass change less than 10%), dropped below 900 g or changed its nest attendance patterns ($n = 2$ individuals excluded during the study).

(b) Data analysis

(i) GPS tracks and prey capture signature

We tracked 20 penguins from 10 nests during the chick-guarding period, resulting in 148 trips where both GPS and accelerometry data were successfully recorded (number of deployments per penguin ranged from 3 to 12, mean = 7.4 ± 0.54). Owing to the time that penguins spend submerged during commuting and foraging and the wave wash they experience on the surface, the actual resolution of GPS fixes was much lower than the resolution of programming (2–6 s), and often contained gaps. To regularize the tracking data and estimate locations through these gaps, we interpolated GPS positions to 30 s intervals using a state-space model in the R package *bsam* [28]. To determine where prey captures occurred along the track, we used a support vector machine algorithm that classified subsurface movement profiles of penguins from tri-axial accelerometry data as either 'swimming' or handling prey' at 0.3 s intervals [23,29]. This algorithm identified prey handling by wild penguins with a false positive rate of 0.09%, and these prey-handling observations were translated to a 'prey capture' index after applying a broken stick model to determine a time threshold separating prey-handling observations into unique prey capture events (details in [23]). Prey captures were assigned a location by matching their time signature to those of GPS tracks after interpolating the positions to a 1 s resolution. Because we did not have information on the size or type of prey captured by penguins during this study, this metric may not necessarily be an objective measure of relative 'foraging success', where this is defined by net energy intake on a foraging trip. However, the metric nonetheless offers a useful proxy for a penguin's relative prey capture experience at sea.

(ii) Predictability of foraging habitat

We used sea surface temperature (SST) as a proxy for variability in the marine environment. This is because the study region is dominated by the influence of the warm, southward flowing East Australian Current [22]. Incursions of warm, nutrient-poor tropical water onto the continental shelf are driven by the action of offshore eddies, resulting in a highly dynamic foraging area around Montague Island. A previous study showed that prey capture by penguins in this region was related to SST both spatially and temporally, with high SSTs being associated in general with lower numbers of prey captures across multiple spatial and temporal scales [20].

Day/night composite SST data (satellite, processed by L3S) at a 0.02° × 0.02° spatial resolution were sourced from the Integrated Marine Observing System's online data access portal (www.imos.org.au). Of the 44 study days, there were 22 days when satellite coverage was high (usually greater than 80%), and these were included in analyses (electronic supplementary material, figure S1). To fill in gaps associated with cloud cover on these days, we smoothed data onto a 2 km × 2 km grid using ordinary kriging, a geostatistical interpolation technique [30]. We used automated variogram fitting in the R package *gstat* [31]. From these daily SST surfaces (electronic supplementary material, figure S2), we calculated the difference between SST and SST 2 days prior (where data were available) using a sliding window, then took a mean for each cell over the study period. This represents the mean spatially explicit variability in the environment at the temporal scale at which penguins leave the colony to forage.

(iii) Spatial heterogeneity in prey captures

As measures of the relative profitability of different parts of the foraging range, we calculated the total number of prey captures recorded by penguins in each 2 km × 2 km grid cell, as well as the number of prey captures divided by the number of foraging trips on which a cell was visited. These indices give insight into the productivity of each part of the foraging range, in relation to their use by penguins.

(iv) Site fidelity

To determine the degree to which penguins returned to the same area on consecutive foraging trips, we first determined a penguin's 'foraging site' by calculating the 50% kernel utilization distribution (KUD) of state-space model-estimated GPS locations for each foraging trip using the R package *adeHabitatHR* [32]. We used a bivariate normal kernel to estimate the KUD of all trips on a grid of approximately 1 km × 1 km, and used the *href* algorithm to optimize h parameter estimation (mean h-value $= 1.01 \pm 0.03$, range $= 0.24-2.25$). Where penguins had consecutive foraging trips that were 2 days apart (separated by a day guarding chicks on the nest), we calculated the distance in kilometres between the centroid of the first foraging trip's KUD and the centroid of the second foraging trip's KUD. We selected the distance between centroids as a continuous measure of site fidelity, after also testing KUD overlap. KUD overlap contained a high proportion of zero values that were largely uninformative about the relative similarity of two trips, therefore the continuous distance measure was preferred. Throughout this paper, we use 'site fidelity' to refer to a continuous measure of spatial proximity between consecutive foraging sites, rather than a binary outcome describing return to a specific location.

(v) Site fidelity and environmental conditions

To examine whether short-term site fidelity was influenced by environmental conditions on the previous trip, we related the distance between the centroids of two consecutive trips to SST at the closest pixel to the centroid of the penguin's foraging trip on the first day. We used a likelihood ratio (LR) test to test whether a linear mixed-effects model (LMM) containing a spatial term (interaction between latitude and longitude), SST and random effect of penguin ID outperformed the null model, which contained only the spatial term and random effect. This tests the alternative hypothesis that SST has an effect on the degree of site fidelity exhibited by penguins, beyond variation due to individual behaviour and other unmeasured attributes of foraging habitat. The response variable was log-transformed and the LMM contained Gaussian errors.

(vi) Site fidelity and foraging experience

To assess whether site fidelity was influenced by a penguin's foraging experience on the previous trip, we related the distance between the centroids of two consecutive trips to the number of prey caught on the first foraging trip, using an LMM with penguin ID as a random effect. An LR test was conducted to compare this model with a null model containing only the random effect, testing the alternative hypothesis that the distance between two sites was related to the number of prey captures experienced on the first trip, and not just individual variation in behaviour. The response variable was log-transformed and the LMM contained Gaussian errors.

To determine how successfully penguins foraged as a function of their prior prey capture experience and their fidelity to the previous foraging site, we related the difference in the number of prey captures between two consecutive trips to the distance between the two foraging sites, using an LMM with penguin ID as a random effect. An LR test was conducted against a null model containing only the individual random effect, testing the alternative hypothesis that the difference in prey captures between two consecutive trips was related to the distance between foraging sites, not just individual variation in behaviour. This model contained Gaussian errors.

(vii) Proximity of other penguins

We paired the distance between a penguin's own consecutive KUD centroids and the mean distance between its centroid and the centroids of all other tagged penguins foraging on the same day. We took the difference of these two values, and used a one-sample t-test to test whether the differences were not equal to zero, after checking for normality. We then determined whether the mean distance separating penguins foraging on the same day was related to how successful they were that day (mean number of prey caught that day), using a generalized linear model with Gaussian errors, and used an LR test to test this model against a null model with no covariates.

All LMMs containing log-transformed response variables with Gaussian errors were fitted after inspecting residuals and determining that this distribution resulted in a better fit than alternative distributions (e.g. Gamma). LMMs were all performed using the R package *lme4* [33]. The R package *MuMIn* was used to calculate marginal and conditional R^2 values [34,35]. Plotted relationships between response variables and fixed effects of interest are presented without random effects for clarity, but LMM results are described in the text. Data presented are means ± standard error. All analyses were performed in R v. 3.3.2 [36].

3. Results

(a) Predictability of the foraging environment

Over the study period, SST was generally lowest inshore, and highest offshore where the flow of the warm East Australian

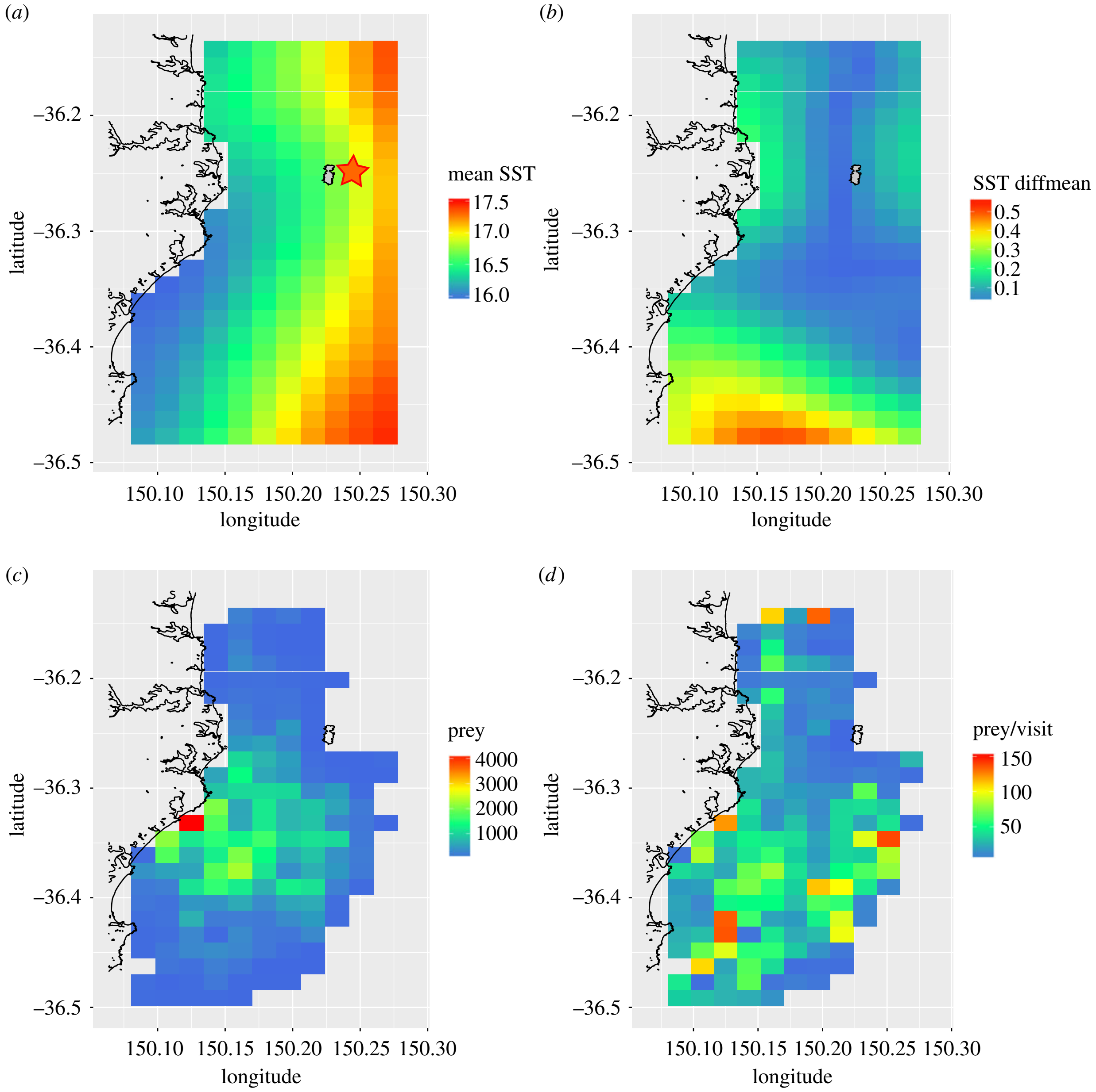

Figure 1. (*a*) Mean sea surface temperature (SST) over the 30-day study period. (*b*) Mean difference in SST over a 2-day rolling window. (*c*) Total number of prey captures recorded by little penguins in each cell. (*d*) Number of prey captures divided by number of cell visits. Montague Island is indicated by the red star on panel (*a*).

Current is strongest (figure 1*a*) [22]. At the 2 day temporal scale at which penguins forage, SST in the penguins' foraging range was variable, and this variability was spatially heterogeneous. The mean difference in each cell's SST over a 2 day window showed that the most predictable area at this scale was immediately to the south of Montague Island, where temperatures changed on average less than 0.1°C over 2 days. The area of highest variability was to the far south of the penguins' foraging range, where average temperature variability was 0.5°C (figure 1*b*). The absolute magnitude of change in SST over the 2-day time scale was 0.01−5.98°C.

(b) Spatial heterogeneity in prey captures

The total number of prey caught in each part of the foraging range varied, with penguins catching most prey items in the area inshore and southwest of Montague Island (figure 1*c*). When the number of times that a site was visited was taken into account, the number of prey captures per cell was more diffuse with no clear hotspot (figure 1*d*). However, the area to the south of the island was still generally of higher quality than the area to the north.

(c) Site fidelity

Of the 148 foraging trips recorded by the 20 birds during this study, 88 had a consecutive trip occurring 2 days later. On these 88 paired trips, the mean distance between the centroids of each pair of 50% KUDs was 7.38 (±0.54) km (range = 0.77 km – 21.3 km). In general, the degree to which penguins foraged in proximity to their previous trip was variable at this time scale (electronic supplementary material, figure S3), and it did not appear that there were divergent strategies among individuals.

(d) Site fidelity and environmental conditions

The proximity of two consecutive foraging trips varied as a function of SST at the centroid of the first trip's foraging site ($LR_2 = 6.21$, $p = 0.01$). This supports the hypothesis that the degree of site fidelity was a function of the SST, beyond

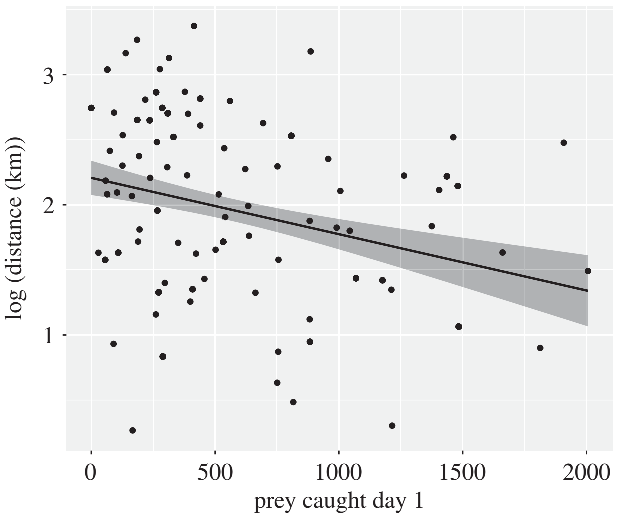

Figure 2. Relationship between the number of prey caught on a foraging trip and the log distance between the centroid of that trip and the trip 2 days later.

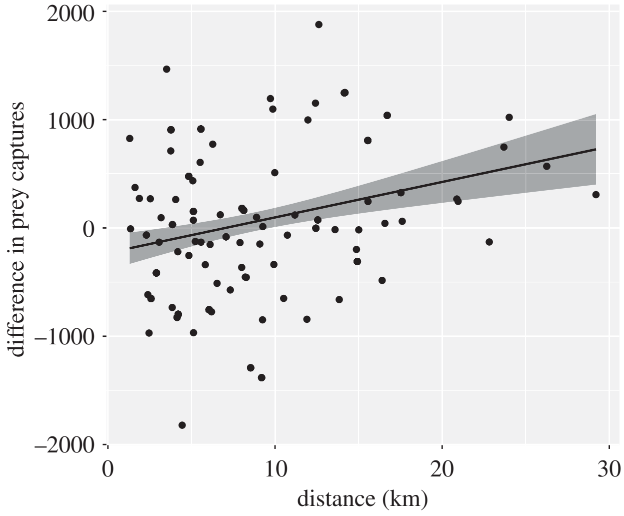

Figure 3. Relationship between the distance (kilometres) between centroids of consecutive foraging trips by penguins and the difference in prey captures between the two trips.

individual differences and other unmeasured habitat characteristics. The SST had a positive effect on the distance between two sites, with the full model showing that the distance between sites increased by 35% for every degree increase in the SST (e.g. from 5 km to 6.75 km), given the spatial term. The marginal R^2 for this model was 0.10 and the conditional R^2 was 0.13.

(e) Site fidelity and foraging experience

The distance between the centroids of two consecutive trips was significantly related to the number of prey caught on the first day ($LR_2 = 11.44$, $p < 0.001$). This model showed that for every 250 additional prey caught by penguins on the first trip (range of prey captures = 29–2006 in this study), the distance separating the two trips decreased by 7% (e.g. from 20 km to 18.6 km; figure 2). The marginal R^2 for this model was 0.08 and the conditional R^2 was 0.19.

The number of prey that penguins caught on the second trip relative to the first trip was related to the distance between sites ($LR_2 = 15.07$, $p < 0.001$). This model showed a positive relationship between the difference in prey captures between trips and distance, with the number of prey captures increasing by 34 ± 8.5 for every kilometre increase in distance (figure 3). The marginal R^2 for this model was 0.07 and the conditional R^2 was 0.16.

(f) Proximity of other penguins

The mean distance between the centre of a penguin's foraging site and the centres of the sites of other penguins foraging on the same day was 5.40 (±0.33) km. Distances between foraging sites by different penguins on the same day were significantly lower than the distances separating consecutive foraging sites by individual penguins, which was 7.38 (±0.54) km (mean difference = 2.74 (±0.70) km, one-sample *t*-test: d.f. = 46, $t = 3.66$, $p < 0.001$).

The mean number of prey captures by tracked penguins on a given day was related to the proximity of penguin foraging sites on that day ($LR_2 = 5.89$, $p = 0.02$). The closer together that tracked penguins foraged on the same day, the higher the mean number of prey captures across all individuals. The model showed that for every kilometre further apart penguins foraged on average, the mean number of prey captures decreased by 9% (e.g. from 500 to 455 prey items; figure 4). The marginal R^2 for this model was 0.17 and the conditional R^2 was 0.30.

4. Discussion

The degree of foraging site fidelity exhibited by animals is expected to vary as a function of the predictability of resource distribution. In this study, we found that little penguins exhibited relatively low absolute site fidelity at the scales that we examined. This is in line with findings of other seabirds foraging in dynamic tropical environments, where foraging plasticity is an adaptive response to highly variable resource distribution [7]. However, we found some evidence that the degree of site fidelity (i.e. the proximity of consecutive foraging sites) was mediated by changes in habitat quality and prior prey capture experience, showing that penguins foraged closer to their previous site when the mean SST on the first trip was low, and when the number of prey captures on the first trip was high. However, penguins foraged closer to the site of conspecifics foraging on the same day than they did to their own previous site, suggesting that *in situ* conditions are perhaps more important determinants of foraging location in this system.

Cooler mean conditions on the previous trip increased the degree of site fidelity on consecutive trips by foraging penguins. Cooler conditions indicate the presence of higher-quality foraging habitat in this system, as forage fish tend to prefer relatively cool waters in western boundary current systems [21,37]. Changes in the degree of site fidelity in response to changing habitat quality have been observed in browsing herbivores, in which a decline in the quality of resources during winter results in animals being less faithful to a site during consecutive foraging intervals [38]. Plasticity in foraging location in relation to prior experience of environmental conditions allows animals to exploit an environment where habitat quality is both spatially heterogeneous and dynamic at short and intermediate time scales [7,8].

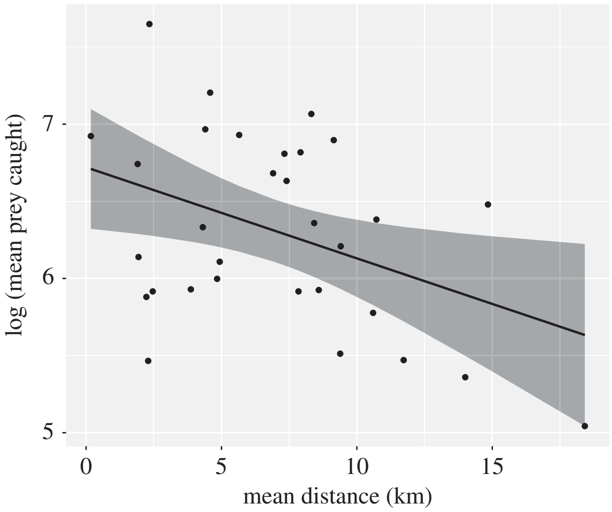

Figure 4. Relationship between the mean number of prey caught by penguins on a day and the mean distance between the centroids of all penguins' foraging sites on that day.

Penguins showed weak evidence of a 'win–stay, lose–switch' foraging strategy in response to prior success [3], with the proximity of two consecutive trips increasing by 7% with every 250 additional prey caught on the first trip. Although the effect size of this finding is relatively small, this result suggests that penguins may be able to use some assessment of their own prior success to mediate their foraging location. There remains much uncertainty surrounding the degree to which prey distribution is predictable in pelagic environments, and the capacity of animals to respond adaptively at relevant spatial and temporal scales to this variability [2,7,18]. Our finding that the proximity of consecutive trips was related to prey capture experience suggests that prey distribution was sufficiently correlated over a 2-day window to provide this central place forager with some useful information with which to make foraging decisions at short time scales [3,39].

Penguins tended to be more successful relative to their first trip the further they foraged further from the previous trip's site. This suggests that penguins can mediate their foraging location in response to low success on the previous trip. That penguins were more successful when they made large changes in foraging location between trips indicates that any costs of switching sites through lost familiarity [6] were offset by encountering favourable conditions at the alternative site [40]. It is unclear how penguins gain insight into habitat quality in other parts of their range, if their own success is their primary measure of quality [41]. It is possible that penguins switch randomly to a new location in response to poor prey capture success at their previous site, or use information about habitat quality gained during foraging or exploratory movements at time scales longer than the 2-day window that we examined here [42,43]. Alternatively, penguins may encounter prey, or strong environmental cues of prey presence such as local enhancement or physical cues, as they leave the colony. Following these cues from the start of a trip may substantially alter their foraging trajectory towards alternative, profitable foraging areas. Independent information on the spatio-temporal dynamics of prey availability and its influence on foraging behaviour is required to resolve these uncertainties.

Generally, penguins foraged closer to where other penguins foraged on the same day than they did to their own previous foraging site. Despite only a small proportion of the population being tracked during this study, the proximity of these penguins to one another during foraging suggests that *in situ* conditions may be a more important determinant of foraging location than prior experience. This could be a result of local enhancement [44], cooperative foraging increasing opportunities for prey encounter [45] or penguins independently using the same signals in the environment to locate prey, such as SST or olfactory cues [46]. Like some terrestrial birds and bats [47], penguins use contact calls at sea, and several studies have identified a social component to their foraging behaviour [45,48,49]. That penguins were more successful on average when they foraged closer together indicates that social information may be an important driver of prey capture in this species, and that patterns of aggregation by penguins were related to variability in the abundance and accessibility of prey [21,50–52].

Animals are likely to combine different types of information at different spatial and temporal scales. In this study, we explored foraging site fidelity only at the scale of two consecutive trips that were 2 days apart. While this is one relevant temporal scale for measuring behavioural consistency in this species [43] and gives new insight into mechanisms underlying short-term foraging plasticity, animals are likely to use information in different ways across different time scales (e.g. [53]). It is difficult to test the relative importance of different types of sensory information, or the role of memory in free-ranging animals [54,55]. However, the way that animals perceive their environment and how this information shapes behavioural strategies are important questions in behavioural ecology. Future work in this field could examine spatially explicit temporal correlation in dynamic environments, and link this to behavioural responses by foraging animals at nested time scales. This would provide deeper insight into the relative value of information about prey availability and the environment, and how this information may degrade through time.

Ethics. Animal research protocols were approved by the Macquarie University Animal Ethics Committee (Animal Research Authority 2014/057), and work was conducted under Office of Environment and Heritage NSW Scientific Licence SL100746.

Data accessibility. Tracking data used in this study are available from the Dryad Digital Repository (http://dx.doi.org/10.5061/dryad.g24c6b6 [56]) and environmental data are available from the Integrated Marine Observing System's online data access portal (www.imos.org.au).

Authors' contributions. The study was designed by G.C., R.H., I.J., D.S. and B.J.P. Fieldwork was conducted by G.C., B.J.P., I.J. and D.S. Statistical analyses were performed by G.C. The manuscript was drafted by GC with contributions and final approval from all authors.

Competing interests. The authors have no competing interests

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References

1. González-Gómez PL, Vasquez RA. 2006 A field study of spatial memory in green-backed firecrown hummingbirds (*Sephanoides sephaniodes*). *Ethology* **112**, 790–795. (doi:10.1111/j.1439-0310.2006.01223.x)
2. Weimerskirch H. 2007 Are seabirds foraging for unpredictable resources? *Deep Sea Res. II* **54**, 211–223. (doi:10.1016/j.dsr2.2006.11.013)
3. Switzer PV. 1993 Site fidelity in predictable and unpredictable habitats. *Evol. Ecol.* **7**, 533–555. (doi:10.1007/BF01237820)
4. Schmidt KA. 2001 Site fidelity in habitats with contrasting levels of nest predation and brood parasitism. *Evol. Ecol. Res.* **3**, 633–648.
5. Chalfoun AD, Martin TE. 2010 Facultative nest patch shifts in response to nest predation risk in the Brewer's sparrow: a 'win–stay, lose–switch' strategy? *Oecologia* **163**, 885–892. (doi:10.1007/s00442-010-1679-0)
6. Piper WH. 2011 Making habitat selection more 'familiar': a review. *Behav. Ecol. Sociobiol.* **65**, 1329–1351. (doi:10.1007/s00265-011-1195-1)
7. Weimerskirch H, Le Corre M, Jaquemet S, Marsac F. 2005 Foraging strategy of a tropical seabird, the red-footed booby, in a dynamic marine environment. *Mar. Ecol. Prog. Ser.* **288**, 251–261. (doi:10.3354/meps288251)
8. Garthe S, Montevecchi WA, Davoren GK. 2011 Inter-annual changes in prey fields trigger different foraging tactics in a large marine predator. *Limnol. Oceanogr.* **56**, 802–812. (doi:10.4319/lo.2011.56.3.0802)
9. Abraham ER. 1998 The generation of plankton patchiness by turbulent stirring. *Nature* **391**, 577–580. (doi:10.1038/35361)
10. Weimerskirch H, Salamolard M, Sarrazin F, Jouventin P. 1993 Foraging strategy of wandering albatrosses through the breeding season: a study using satellite telemetry. *Auk* **110**, 325–342.
11. Scales KL, Miller PI, Embling CB, Ingram SN, Pirotta E, Votier SC. 2014 Mesoscale fronts as foraging habitats: composite front mapping reveals oceanographic drivers of habitat use for a pelagic seabird. *J. R. Soc. Interface* **11**, 20140679. (doi:10.1098/rsif.2014.0679)
12. Bradshaw CJ, Hindell MA, Sumner MD, Michael KJ. 2004 Loyalty pays: potential life history consequences of fidelity to marine foraging regions by southern elephant seals. *Anim. Behav.* **68**, 1349–1360. (doi:10.1016/j.anbehav.2003.12.013)
13. 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)
14. Arthur B, Hindell M, Bester M, Trathan P, Jonsen I, Staniland I, Oosthuizen WC, Wege M, Lea MA. 2015 Return customers: foraging site fidelity and the effect of environmental variability in wide-ranging Antarctic fur seals. *PLoS ONE* **10**, e0120888.
15. 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)
16. 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)
17. Spencer WD. 2012 Home ranges and the value of spatial information. *J. Mammal.* **93**, 929–947. (doi:10.1644/12-MAMM-S-061.1)
18. Abrahms B, Hazen EL, Bograd SJ, Brashares JS, Robinson PW, Scales KL, Crocker DE, Costa DP. 2018 Climate mediates the success of migration strategies in a marine predator. *Ecol. Lett.* **21**, 63–71. (doi:10.1111/ele.12871)
19. Hoskins AJ, Dann P, Ropert-Coudert Y, Kato A, Chiaradia A, Costa DP, Arnould JP. 2008 Foraging behaviour and habitat selection of the little penguin Eudyptula minor during early chick rearing in Bass Strait, Australia. *Mar. Ecol. Prog. Ser.* **366**, 293–303. (doi:10.3354/meps07507)
20. Carroll G, Everett JD, Harcourt R, Slip D, Jonsen I. 2016 High sea surface temperatures driven by a strengthening current reduce foraging success by penguins. *Sci. Rep.* **6**, 22236. (doi:10.1038/srep22236)
21. Carroll G, Cox M, Harcourt R, Pitcher B, Slip D, Jonsen I. 2017 Hierarchical influences of prey distribution on patterns of prey capture by a marine predator. *Funct. Ecol.* **31**, 1750–1760. (doi:10.1111/1365-2435.12873)
22. Suthers IM *et al.* 2011 The strengthening East Australian current, its eddies and biological effects—an introduction and overview. *Deep Sea Res. II* **58**, 538–546. (doi:10.1016/j.dsr2.2010.09.029)
23. Carroll G, Slip D, Jonsen I, Harcourt R. 2014 Supervised accelerometry analysis can identify prey capture by penguins at sea. *J. Exp. Biol.* **217**, 4295–4302. (doi:10.1242/jeb.113076)
24. Gales R, Green B. 1990 The annual energetics cycle of little penguins (*Eudyptula minor*). *Ecology* **71**, 2297–2312. (doi:10.2307/1938641)
25. Ropert-Coudert Y, Knott N, Chiaradia A, Kato A. 2007 How do different data logger sizes and attachment positions affect the diving behaviour of little penguins? *Deep Sea Res. II* **54**, 415–423. (doi:10.1016/j.dsr2.2006.11.018)
26. Meyer X, MacIntosh AJ, Kato A, Chiaradia A, Ropert-Coudert Y. 2015 Hydrodynamic handicaps and organizational complexity in the foraging behavior of two free-ranging penguin species. *Anim. Biotelem.* **3**, 25. (doi:10.1186/s40317-015-0061-8)
27. Carroll G, Turner E, Dann P, Harcourt R. 2016 Prior exposure to capture heightens the corticosterone and behavioural responses of little penguins (*Eudyptula minor*) to acute stress. *Conserv. Physiol.* **4**, cov061. (doi:10.1093/conphys/cov061)
28. Jonsen ID, Flemming JM, Myers RA. 2005 Robust state–space modelling of animal movement data. *Ecology* **86**, 2874–2880. (doi:10.1890/04-1852)
29. Chessa S, Micheli A, Pucci R, Hunter J, Carroll G, Harcourt R. 2017 A Comparative analysis of SVM and IDNN for identifying penguin activities. *Appl. Artif. Intell.* **31**, 453–471. (doi:10.1080/08839514.2017.1378162)
30. Cressie N. 1988 Spatial prediction and ordinary kriging. *Math. Geol.* **20**, 405–421. (doi:10.1007/BF00892986)
31. Pebesma EJ. 2004 Multivariable geostatistics in S: the gstat package. *Comput. Geosci.* **30**, 683–691. (doi:10.1016/j.cageo.2004.03.012)
32. Calenge C. 2006 The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecol. Model.* **197**, 516–519. (doi:10.1016/j.ecolmodel.2006.03.017)
33. Bates D, Maechler M, Bolker B, Walker S. 2015 Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**, 1–48. (doi:10.18637/jss.v067.i01)
34. Nakagawa S, Schielzeth H. 2013 A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods Ecol. Evol.* **4**, 133–142. (doi:10.1111/j.2041-210x.2012.00261.x)
35. Bartoń K. 2018 MuMIn: Multi-Model Inference. R package version 1.40.4.
36. R Core Team. 2016 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. See https://www.R-project.org/.
37. O'Donoghue SH, Drapeau L, Peddemors VM. 2010 Broad-scale distribution patterns of sardine and their predators in relation to remotely sensed environmental conditions during the KwaZulu-Natal sardine run. *Afr. J. Mar. Sci.* **32**, 279–291. (doi:10.2989/1814232X.2010.501584)
38. Van Beest FM, Mysterud A, Loe LE, Milner JM. 2010 Forage quantity, quality and depletion as scale-dependent mechanisms driving habitat selection of a large browsing herbivore. *J. Anim. Ecol.* **79**, 910–922.
39. Zach R, Falls JB. 1979 Foraging and territoriality of male ovenbirds (Aves: Parulidae) in a heterogeneous habitat. *J. Anim. Ecol.* **48**, 33–52.
40. Linkhart BD, Reynolds RT. 2007 Return rate, fidelity, and dispersal in a breeding population of flammulated owls (*Otus flammeolus*). *Auk* **124**, 264–275. (doi:10.1642/0004-8038(2007)124[264:RRFADI]2.0.CO;2)
41. Switzer PV. 1997 Factors affecting site fidelity in a territorial animal, *Perithemis tenera*. *Anim. Behav.* **53**, 865–877. (doi:10.1006/anbe.1996.0352)
42. Oppel S, Powell AN, Dickson DL. 2009 Using an algorithmic model to reveal individually variable movement decisions in a wintering sea duck. *J. Anim. Ecol.* **78**, 524–531. (doi:10.1111/j.1365-2656.2008.01513.x)
43. Camprasse EC, Sutton GJ, Berlincourt M, Arnould JP. 2017 Changing with the times: little penguins exhibit flexibility in foraging behaviour and low

behavioural consistency. *Mar. Biol.* **164**, 169. (doi:10.1007/s00227-017-3193-y)

44. Thiebault A, Mullers RH, Pistorius PA, Tremblay Y. 2014 Local enhancement in a seabird: reaction distances and foraging consequence of predator aggregations. *Behav. Ecol.* **25**, 1302 – 1310. (doi:10.1093/beheco/aru132)
45. Sutton GJ, Hoskins AJ, Arnould JP. 2015 Benefits of group foraging depend on prey type in a small marine predator, the little penguin. *PLoS ONE* **10**, e0144297.
46. Nevitt GA, Losekoot M, Weimerskirch H. 2008 Evidence for olfactory search in wandering albatross, *Diomedea exulans*. *Proc. Natl Acad. Sci. USA* **105**, 4576 – 4581. (doi:10.1073/pnas.0709047105)
47. Wilkinson GS, Boughman JW. 1998 Social calls coordinate foraging in greater spear-nosed bats. *Anim. Behav.* **55**, 337 – 350. (doi:10.1006/anbe.1997.0557)
48. Berlincourt M, Arnould JP. 2014 At-sea associations in foraging little penguins. *PLoS ONE* **9**, e105065. (doi:10.1371/journal.pone.0105065)
49. McInnes AM, McGeorge C, Ginsberg S, Pichegru L, Pistorius PA. 2017 Group foraging increases foraging efficiency in a piscivorous diver, the African penguin. *R. Soc. open sci.* **4**, 170918. (doi:10.1098/rsos.170918)
50. Hopcraft JGC, Sinclair ARE, Packer C. 2005 Planning for success: serengeti lions seek prey accessibility rather than abundance. *J. Anim. Ecol.* **74**, 559 – 566. (doi:10.1111/j.1365-2656.2005.00955.x)
51. Benoit-Bird KJ *et al.* 2013 Prey patch patterns predict habitat use by top marine predators with diverse foraging strategies. *PLoS ONE* **8**, e53348. (doi:10.1371/journal.pone.0053348)
52. Boyd C, Castillo R, Hunt GL, Punt AE, VanBlaricom GR, Weimerskirch H, Bertrand S. 2015 Predictive modelling of habitat selection by marine predators with respect to the abundance and depth distribution of pelagic prey. *J. Anim. Ecol.* **84**, 1575 – 1588. (doi:10.1111/1365-2656.12409)
53. Devenport L, Devenport J. 1994 Time-dependent averaging of foraging information in least chipmunks and golden-mantled ground squirrels. *Anim. Behav.* **47**, 787 – 802. (doi:10.1006/anbe.1994.1111)
54. Clayton NS, Bussey TJ, Dickinson A. 2003 Opinion: can animals recall the past and plan for the future? *Nat. Rev. Neurosci.* **4**, 685 – 691. (doi:10.1038/nrn1180)
55. Merkle JA, Fortin D, Morales JM. 2014 A memory-based foraging tactic reveals an adaptive mechanism for restricted space use. *Ecol. Lett.* **17**, 924 – 931. (doi:10.1111/ele.12294)
56. Carroll G, Harcourt R, Pitcher BJ, Slip D, Jonsen I. 2018 Data from: Recent prey capture experience and dynamic habitat quality mediate short-term foraging site fidelity in a seabird. Dryad Digital Repository. (doi:10.5061/dryad.g24c6b6)