



Research



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Emergence of functional prey depletion halo through penguin–krill behavioural dynamics

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Predators can influence prey through both consumption and non-consumptive effects arising from their behaviour. In colonial central-place foraging systems, repeated predator activity near breeding sites can generate spatial gradients in prey availability, termed prey-depletion halos (Ashmole's halo). However, it remains unclear whether these patterns are driven primarily by numerical (abundance) or functional (accessibility) depletion of prey. We addressed this question using fine-scale behavioural data from breeding Adélie penguins (*Pygoscelis adeliae*) feeding on krill in East Antarctica. Combining GPS tracking, three-dimensional dive paths and feeding events, we quantified prey accessibility and patch quality across foraging scales. Penguins foraged most intensively near the colony, where dive depths and under-ice feeding distances were greater, indicating reduced accessibility without corresponding changes in patch quality. Within bouts, penguins progressively exploited deeper or more distant portions of the same patch while maintaining similar feeding rates, consistent with krill redistribution as an escape response. These within-bout processes can accumulate near the colony, generating colony-scale gradients in accessibility. Our results suggest that predator-induced changes in prey accessibility can contribute to the emergence of a functional prey depletion halo around the colony, supporting a role of non-consumptive behavioural processes.

1. Introduction

Predators can influence the spatial distribution and behaviour of prey not only through direct consumption but also via non-consumptive effects arising from their presence and behaviour [1,2]. Such effects are widely documented in terrestrial ecosystems, particularly in the context of the landscape of fear [2–4], where predator-induced changes in prey behaviour and space use can have cascading consequences for population dynamics [5,6]. In marine ecosystems, however, empirical evidence remains comparatively limited (but see [7,8] in controlled settings), largely because interactions between free-ranging predators and mobile, patchily distributed prey are difficult to observe and quantify under natural conditions [2,4].

Colonial breeding seabirds are typical central-place foragers, whose foraging decisions are constrained by the need to return to a fixed place to incubate eggs or feed chicks [9–12]. Optimal foraging theory predicts that such constraints can generate spatial gradients in foraging effort as individuals balance travel costs against prey profitability [12,13]. Within this framework, localized foraging pressure around colonies may generate zones of

reduced prey availability, known as prey-depletion halos (Ashmole's halo) [14]. Such reductions, reflecting both prey abundance and accessibility, may arise through direct consumption and/or behavioural redistribution of prey. These spatial gradients may increase foraging distances and energetic costs, with potential negative consequences for reproductive success and individual fitness [14–19]. Ashmole's halo has long served as a conceptual framework for understanding density-dependent regulation in colonial animals, particularly seabirds constrained by central-place foraging during breeding [14,15,17,20].

The spatial patterns consistent with Ashmole's halo have been reported in several seabird species [15,21], typically inferred from increased foraging trip distance, duration or dive depth, and reduced prey availability near large colonies [22–25]. However, the behavioural mechanisms generating these spatial gradients remain poorly resolved [26]. In particular, it remains unclear whether the reduction in prey availability arises primarily from decreases in prey abundance caused by cumulative consumption or from behavioural and spatial redistribution that reduce prey accessibility without necessarily reducing overall prey abundance [25,27]. Both mechanisms may also operate simultaneously, with some prey being removed while others escape or disperse in response to repeated disturbance. Determining the relative importance of these processes requires linking predator movements, feeding events and prey availability at fine temporal and spatial scales—an approach that has rarely been applied in marine predator–prey systems.

In systems involving mobile and patchily distributed prey, reductions in prey availability do not necessarily require reductions in prey abundance but may arise when prey become less accessible owing to behavioural responses and spatial redistribution. Here, we distinguish between numerical depletion (a reduction in prey abundance) and functional depletion (a reduction in prey accessibility). We define prey accessibility as the ease with which predators encounter and exploit prey, an emergent property of predator–prey–environment interactions that can be expressed across spatial and temporal dimensions of foraging effort. Importantly, numerical and functional depletion are expected to generate distinct signatures in predator foraging behaviour. Numerical depletion should increase search effort and reduce patch quality through cumulative removal. By contrast, functional depletion should increase search effort without necessarily reducing patch quality once prey are encountered.

In this study, we examine whether spatial patterns commonly attributed to Ashmole's halo reflect reductions in prey availability driven solely by prey consumption or whether they are also consistent with reduced accessibility arising from behavioural redistribution. We address this question using fine-scale behavioural data from breeding Adélie penguins (*Pygoscelis adeliae*) at an East Antarctic colony. These central-place foragers in this region primarily feed on Antarctic krill (*Euphausia superba*) [28,29], a mobile and patchily distributed prey species [30,31], and typically perform dive bouts consisting of repeated dives associated with intense foraging activity [32]. We analysed three-dimensional (3D) dive paths and identified feeding events using acceleration and video data to quantify prey accessibility and patch quality. Prey accessibility was characterized by maximum dive depth, under-ice feeding distance and mean time to feeding events, with greater values indicating reduced accessibility. Patch quality was defined operationally as the profitability of a prey patch once encountered and measured as the feeding rate within a patch. Under a consumptive (numerical depletion) mechanism driven by reductions in prey abundance, reduced accessibility should be accompanied by reduced patch quality owing to cumulative prey removal. By contrast, under a non-consumptive (functional depletion) mechanism driven by behavioural redistribution, accessibility-related metrics should change without a corresponding decline in patch quality. We quantified these metrics at two nested spatial scales: (i) a colony scale (<5 km, across foraging trips) and (ii) a within-bout scale (<200 m, across repeated dives), and examined how they varied with distance from the breeding colony and across foraging dive bouts. This approach allows us to evaluate whether spatial gradients in foraging effort, often interpreted as evidence of prey depletion through direct consumption, may also be consistent with behavioural processes that reduce prey accessibility.

2. Materials and methods

(a) Study site

We conducted the fieldwork between 26 December 2018 and 8 January 2019 at the Hukuro Cove colony (69.21°S, 39.63°E; a relatively small colony comprising 217 breeding pairs) in the Lützow-Holm Bay, East Antarctica. During the study period, the bay was covered by landfast sea ice, and penguins accessed the water through narrow tidal cracks and leads (channels of open water formed by breaks in the sea-ice cover) around a small island near the colony (figure 1a–c). Tidal cracks were typically a few metres wide and extended for several hundred metres along the coast. By contrast, leads, scattered within 5 km of the colony, ranged from several metres to a few kilometres in length and were typically < 5 m in width (figure 1b,c). These limited openings were repeatedly and simultaneously used by multiple individuals—often by more than 10 birds [33]—resulting in substantial spatial overlap in diving activity. Penguins forage in waters approximately 50–300 m deep, with no systematic deepening of the seabed with distance from the colony [34,35]. While tidal cracks open in shallow water, the seabed descends steeply within a short horizontal distance [34,35], meaning that penguins reach typical foraging depths almost immediately. Thus, bathymetry is unlikely to influence the spatial patterns in dive behaviour.

(b) Data logger experiments

To obtain data on penguins' 3D diving and feeding behaviours, we conducted two behavioural experiments using different data logger combinations (hereafter, experiments A and B, respectively).

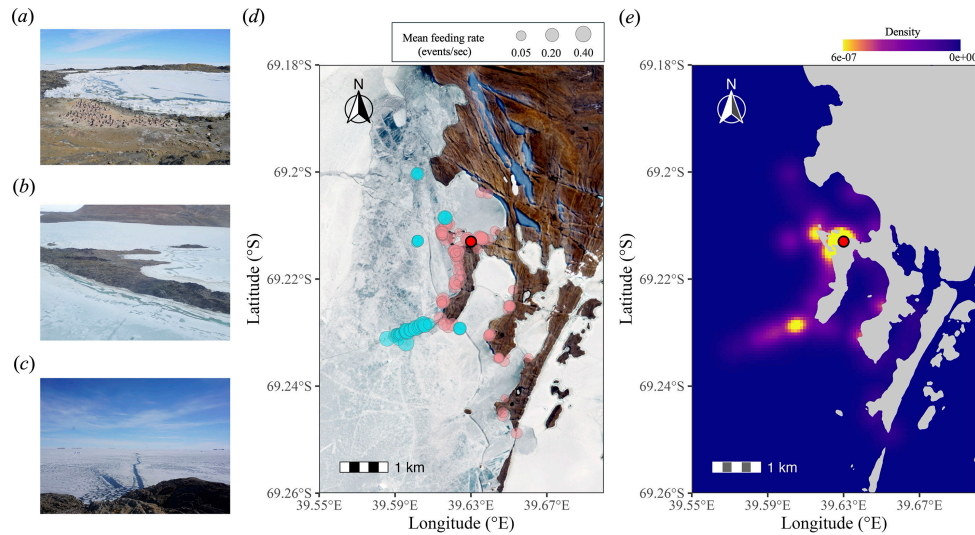


Figure 1. Sea-ice conditions within the foraging areas used by breeding Adélie penguins and the spatial distribution of dive locations and mean feeding rates during dive bouts. (a–c) Representative sea-ice microhabitats: (a) thick land-fast ice near the breeding colony; (b) a tidal crack formed by tidal movement; and (c) a lead formed in the sea-ice cover away from the coastline. (d) Spatial distribution of mean feeding rates during dive bouts ($n = 163$ bouts from 23 birds). Circle size denotes the relative mean feeding rate. Pink and light blue points indicate dive bouts occurring along tidal cracks and leads, respectively. Panel (d) was created using a Sentinel-2 satellite image acquired on 8 January 2019. (e) Kernel density distribution of dive locations ($n = 6307$ dives from 23 birds). The red circle with a thick black border marks the location of the colony.

(i) Experiment A: 3D diving behaviour

Sixteen chick-rearing Adélie penguins were captured before their departure for foraging trips, and three types of loggers were attached using waterproof tape and instant glue: (i) a multi-channel data logger on the upper back, (ii) a GPS logger on the lower back, and (iii) an accelerometer on the head. The multi-channel data logger (ORI-3MPD3GT; Little Leonardo Co., Tokyo, Japan; diameter, 16.5 mm; length, 84 mm; mass, 42.5 g) was set to record depth, swim speed, ambient temperature at 1 Hz and triaxial acceleration and magnetism at 20 Hz. The GPS logger (Axy-Trek; TechnoSmArt, Rome, Italy; $43 \times 21 \times 10$ mm, 18 g) was set to record positions every 1 min and triaxial acceleration at 25 Hz. The accelerometer (LoggLaw-C6; Biologging Solutions Inc., Tokyo, Japan; $40 \times 15 \times 12$ mm, 8 g) was set to record triaxial acceleration at 25 Hz. All loggers were retrieved after either one or two foraging trips.

(ii) Experiment B: Observation of feeding behaviours based on the video footage

Sixteen chick-rearing penguins were equipped with three types of loggers: (i) an animal-borne video logger on the upper back, (ii) a GPS logger on the lower back, and (iii) an accelerometer on the head. The video logger (DVL400M130SW; Little Leonardo, Japan; $65 \times 20 \times 22$ mm, 46 g) was attached to observe prey capture events underwater directly. The video logger was set to record videos at 30 frames per second with a resolution of 1280×960 pixels. To ensure that video footage captured the foraging period at sea, we set a start-delay timer (0–12 h) and activated a saltwater switch, which triggered recording upon the penguin's entry into the water. The sampling intervals for the GPS logger (Axy-Trek) and the head-mounted accelerometer (LoggLaw-C6) were set as in experiment A. All loggers were retrieved after their one or two foraging trips. We do not have information on the sex of our study birds, but a previous study in this colony [36] reported no sex differences in diving and foraging trip parameters.

The total weight of the attached devices represented approximately 1.6% of body mass. Devices were attached following established protocols designed to minimize drag and behavioural impacts [37–39], and a previous study at this colony reported no detectable effects of larger devices on foraging performance [40] (details are provided in electronic supplementary material, Extended Methods 1).

(c) Data analysis

Data analysis was performed using IGOR Pro 8 (WaveMetrics, USA) with the program package Ethographer [41] and R software [42].

(i) Analysis of GPS data

GPS positions were linearly interpolated to 1 min intervals to compensate for missing fixes during extended dives. The raw fix interval averaged 1.2 ± 2.4 min (median = 1.0 min), with occasional long gaps reflecting periods of underwater activity. Penguins walking across landfast sea ice moved slowly (0.45 ± 0.43 m s⁻¹; median = 0.29 m s⁻¹), corresponding to a horizontal displacement of only 20–30 m per minute. Given these near-linear movements, 1 min interpolation introduced negligible spatial bias in trip

metrics. A foraging trip was defined as the period between successive departures from and returns to within 100 m of the colony, from which trip duration and maximum distance were calculated.

To illustrate the spatial concentration of diving activity around the colony, we estimated a utilization distribution (UD) based on all recorded dive locations using kernel density estimation (KDE; *adehabitatHR* package [43]). The UD was computed using the default "href" bandwidth estimate on a 200×200 grid (pooled across individuals). Because penguins repeatedly dived through narrow sea-ice openings near the colony that were only a few to several metres wide, conventional contour levels (e.g. 50% or 95% UD) were not biologically meaningful. We therefore used the full density raster as a heatmap to depict relative diving intensity, which was qualitatively robust to $\pm 25\%$ variation in bandwidth (electronic supplementary material, figure S1).

(ii) Analysis of diving data

A dive was defined as a swimming period with a depth of ≥ 0.5 m and a duration of ≥ 3 s. A dive bout was defined as ≥ 10 consecutive dives separated by surface intervals of ≥ 250 s. We retained the 250 s threshold because it corresponded to the peak in surface-interval distributions in our dataset and was also used for the same colony in [32], ensuring comparability. Although a data-driven bout ending criterion (BEC) can be estimated (e.g. via the R package *diveMove* [44]), the fixed threshold was sufficient for our purposes. The ≥ 10 consecutive dives requirement ensured that bout-level behavioural trends could be meaningfully assessed; shorter sequences (12% of all dives) were excluded.

Behavioural states were identified from depth and triaxial body acceleration data recorded by the loggers. Using depth to detect diving and overall dynamic body acceleration (ODBA) [45] to distinguish locomotion on the ice, we classified each second of data into diving, walking/tobogganing or resting (detailed thresholds and validation procedures are provided in electronic supplementary material, Extended Methods 2).

(iii) Extraction of feeding events using acceleration and video data

Feeding events were identified from characteristic head movements, defined as brief periods of elevated vectorial acceleration, and validated using concurrent video observations [46]. Video footage showed that penguins fed only after entering the water through cracks or leads, and all observed feeding occurred beneath the fast ice. Because all birds foraged within the continuous fast-ice zone, we inferred that individuals without video loggers (from experiment A) also fed under the ice. At depths > 50 m, prey type was sometimes unidentifiable owing to low light, but characteristic feeding motions (head shaking and rapid bill movements) remained visible. To determine the acceleration threshold for detecting prey capture, we analysed video footage of 11 birds in experiment B (18.1 h, 713 dives) and manually counted the number of prey captures during each dive. Thresholds for head-only acceleration were estimated for each individual by matching acceleration peaks to the number of video-confirmed prey captures (electronic supplementary material, figure S2), and the mean value (0.21 ± 0.05 g) was adopted to define a feeding event. This threshold was then applied uniformly to all 23 individuals. Further details of acceleration processing, including smoothing and filtering procedures, are provided in electronic supplementary material, Extended Methods 3.

(iv) Analyses of 3D diving with feeding events

Three-dimensional dive paths were reconstructed at 1 Hz using a dead-reckoning method based on triaxial acceleration, triaxial magnetism, swim speed and dive depth [47,48]. The method was implemented via the open-source *ThreeD_path* macro (<https://sites.google.com/view/threedpath/>, [49,50]) and incorporated geomagnetic declination at the colony (-51.1°). Pitch, roll and heading were derived from filtered acceleration and magnetometer data following previously described procedures [50]. Details of signal processing and calibration are provided in electronic supplementary material, Extended Methods 4.

Path straightness was calculated for each reconstructed 3D dive path as the ratio of the horizontal straight-line distance between dive start and end points to cumulative horizontal distance (0 = highly tortuous, 1 = linear) [51]. Dives with path straightness ≤ 0.4 were classified as foraging dives (electronic supplementary material, figure S3)—a threshold that was validated against acceleration-confirmed feeding events (area under the ROC curve (AUC) = 0.86; electronic supplementary material, Extended Methods 4). We defined a foraging dive bout as a series of ≥ 10 consecutive foraging dives, during which penguins typically remained at the same dive location with minimal horizontal displacement (figure 2c). A dive bout represents a temporal sequence of dives, within which one or more foraging dive bouts may occur (figure 2b), with one to three observed per bout in this dataset.

(d) Definition of foraging metrics

We quantified four metrics from reconstructed 3D dive paths and feeding event data (figure 2d): (i) maximum dive depth, computed as the deepest point reached during each dive; (ii) under-ice feeding distance, calculated as the mean 3D distance from the dive start point to each feeding event; (iii) mean time to feeding events, defined as the mean elapsed time from the start of the dive to each feeding event occurring within that dive; (iv) feeding rate within a patch, calculated as the number of feeding events divided by the time elapsed between the first and last feeding events within the dive.

We interpreted behavioural metrics within a conceptual framework that distinguishes prey accessibility from patch quality as emergent properties of predator–prey interactions during foraging. While a foraging dive bout represents a continuous period of foraging effort typically occurring at a single sea-ice opening, a prey patch is defined as a discrete spatiotemporal encounter with krill during an individual dive. Prey accessibility describes the ease with which penguins can encounter and

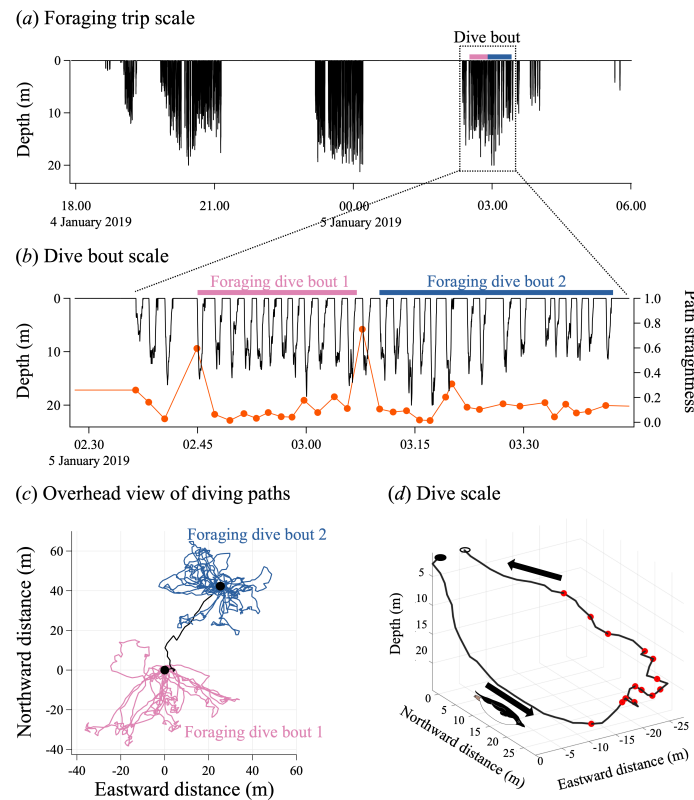


Figure 2. Example of a dive bout and foraging dive bouts during a foraging trip. (a,b) Dive bouts and foraging dive bouts in relation to the time-series changes in depth and path straightness for each dive. A foraging dive bout was defined as a continuous period of at least 10 successive foraging dives (a path straightness of 0.4 or less). A dive bout represents a temporal sequence of dives, within which foraging dive bouts (behaviourally defined subsets) occur. (c) Two foraging dive bouts viewed on a horizontal plane. Black circles indicate the start locations of individual foraging dive bouts, plotted as representative points to improve visual clarity. (d) Reconstructed three-dimensional dive path during a foraging dive. Closed and open circles represent the start and end of the dive, respectively. Arrows indicate travelling directions. The red circles indicate feeding events.

reach prey patch once a dive begins, reflecting the combined effects of prey distribution, prey behaviour and constraints imposed by the under-ice environment. We operationally defined prey accessibility using three complementary metrics: maximum dive depth (vertical accessibility), under-ice feeding distance (horizontal accessibility) and mean time to feeding events (temporal accessibility). By contrast, patch quality reflects the profitability of prey once encountered and was indexed by the feeding rate within a patch. Together, these metrics allowed us to assess whether spatial and temporal variation in foraging behaviour primarily reflected changes in accessibility (increased costs of locating or reaching prey) or changes in patch quality (profitability after encounter).

(e) Analysis of stomach contents

Stomach contents were collected from the other 10 birds using the standard stomach-flushing method [52] at the same periods as in experiments A and B, and prey species were morphologically identified. Mass-based prey composition was measured for each stomach sample (electronic supplementary material, table S1).

(f) Statistical analysis

To examine whether the behavioural parameters exhibited spatial autocorrelation, we performed Moran's I test using the *spdep* package in R [53]. The results indicated significant positive spatial autocorrelations for all behavioural parameters. Therefore, to account for spatial autocorrelation, we incorporated spatial random effects in all generalized linear mixed models (GLMMs), based on the stochastic partial differential equation (SPDE) approach implemented in the *INLA* package in R [54].

We fitted GLMMs to examine how distance from the colony and time since the start of foraging dive bouts affected maximum dive depth, under-ice feeding distance, time to feeding events and feeding rate within a patch. Explanatory variables included distance from the colony, time since the start of the foraging dive bout and elapsed days since 26 December 2018 (start of the study period). This parameter was included as a proxy for temporal changes in breeding stage, including potential variation in prey availability [55] and cumulative foraging pressure as the breeding season progresses [56,57]. Sea-ice microhabitat type (tidal crack or lead; figures 1b,c and electronic supplementary material, S4, see Extended Methods 5) was also included as an explanatory variable. Random effects included Bird ID, Bout ID and Foraging Dive Bout ID. GLMMs for maximum dive depth, under-ice feeding distance and mean time to feeding events assumed gamma distributions with log link functions. By contrast, feeding rate within a patch (number of feeding events per dive, with duration between the first and last feeding events within a dive as an offset) was modelled with a Poisson distribution and log link function. For graphical illustration (figures

3 and 4), regression lines and confidence intervals were generated from simplified non-spatial GLMMs that included the same fixed effects and random intercepts as the INLA models but excluded the spatial random field. These lines therefore represent marginal (population-level) predictions rather than conditional predictions for specific individuals or bouts.

To test whether maximum foraging distance changed over time during the chick-rearing period, we fitted a linear mixed model (LMM) with maximum distance (km) as the response variable and date (days since 26 December 2018) as a fixed effect, using Bird ID as a random intercept (lme4 package [58]). Model residuals satisfied normality assumptions and no data transformation was required.

Data are shown as the mean $\pm$ standard deviation of the mean.

3. Results

(a) Data recovery and sample size

In the Experiment A (3D diving behaviours), all the parameters were successfully recorded for 12 of the 16 instrumented birds. For two birds, triaxial acceleration and magnetism data recorded by the multi-channel loggers were incomplete owing to technical issues; for the other two birds, GPS positioning data were unavailable owing to technical issues. Consequently, 12 individuals for whom all datasets were available were used for further analysis.

In the Experiment B (observation of feeding behaviours based on the video footage), all the parameters were successfully recorded for 11 of the 16 instrumented birds. For three birds, GPS positioning data were unavailable because they did not leave the colony or rarely conducted dives during the deployment periods, most probably owing to errors in identifying the departing member of the pair at the time of deployment. In addition, video data from another penguin could not be visually observed owing to insufficient illumination. For another bird, triaxial acceleration data recorded by the GPS logger were unavailable for the entire trip owing to technical issues. Eleven individuals for whom all datasets were available were used for further analysis.

(b) Foraging trip characteristics

GPS tracking yielded 30 foraging trips from 23 individuals across both experiments A and B. Trip distance and duration averaged 1.7 ± 1.0 km (range 0.41–4.2 km) and 15.6 ± 5.4 h (range 7.7–33.0 h), respectively. Penguins spent, on average, $26.6 \pm 12.8\%$ of their time diving, $46.9 \pm 8.3\%$ travelling by walking or tobogganing and $26.5 \pm 13.6\%$ resting during trips. Maximum foraging distance did not change significantly with date during the chick-rearing period (LMM: $\beta = 0.059 \pm 0.037$ km day⁻¹, $t = 1.6$, $p = 0.12$), indicating stable foraging ranges across individuals. Penguins typically walked across sea ice after leaving the colony and then dived at tidal cracks or leads located within 4.2 km of the colony (figure 1d). Once reaching a dive site, individuals tended to remain there, performing 5.5 ± 2.2 dive bouts ($n = 30$ trips), with 38.2 ± 33 dives per bout ($n = 163$ bouts).

(c) Spatial distribution of foraging activity and feeding rates

Diving activity was intensely concentrated within 3 km of the colony (figure 1e and electronic supplementary material, S5), with the highest intensity occurring near the colony itself and along a tidal crack to the northwest (0.2–0.4 km), followed by a lead to the southwest (approx. 2 km). By contrast, the number of feeding events per unit bout time (i.e. effort-standardized feeding rate) varied spatially without a clear distance-related trend (0.102 ± 0.087 events·s⁻¹, $n = 163$ dive bouts from 23 birds, figure 1d).

(d) Distance-related patterns in feeding behaviours and patch quality

Maximum dive depth decreased significantly with distance from the colony (figure 3a; table 1). Dive depth also differed among sea-ice microhabitat types, with deeper dives occurring at leads than at tidal cracks (table 1). Leads were generally located over deeper offshore areas, whereas tidal cracks often occurred along shallower coastal slopes. However, seabed depth did not show a consistent trend with distance from the colony in the area used by penguins and therefore does not account for the observed spatial pattern in dive depth. Under-ice feeding distances similarly decreased with colony distance (figure 3b; table 1). Mean time to feeding events showed a weak tendency to decline with distance, but the effect was not significant (electronic supplementary materials, figure S6; table S2). Feeding rate within a patch showed no relationship with colony distance (figure 3c), with a high rate observed even near the colony. Changes in accessibility-related metrics (e.g. dive depth and under-ice feeding distance) with distance suggest that spatial gradients in prey availability primarily reflect changes in accessibility. Elapsed days had a significant positive effect on maximum dive depth (table 1). This indicates that dives became progressively deeper ($\beta = 4.1 \pm 2.0\%$ day⁻¹) as the season advanced (electronic supplementary material, figure S7). By contrast, elapsed days showed no detectable effect on under-ice feeding distance, mean time to feeding events and feeding rate within a patch (table 1, electronic supplementary material, table S2).

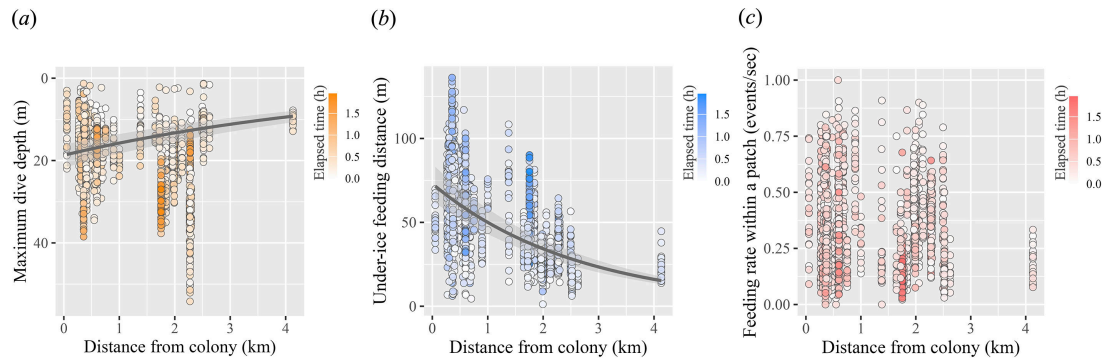


Figure 3. Relationship between distance from the colony and feeding behaviours. (a) Maximum dive depth ($n = 1545$ dives from 76 foraging dive bouts), (b) under-ice feeding distance ($n = 1503$ dives from 76 foraging dive bouts) and (c) feeding rate within a patch ($n = 1450$ dives from 76 foraging dive bouts). Each point represents measurements from a single dive. Colour scales indicate elapsed time since the start of each foraging dive bout (hours). Lines show model predictions and shaded areas indicate 95% confidence intervals. Inferential results are reported in table 1.

Table 1. Summary of GLMM results examining the effects of distance from the colony (corresponding to figure 3) and time since the start of the foraging dive bout (corresponding to figure 4) on maximum dive depth ($n = 1545$ dives), under-ice feeding distance ($n = 1503$ dives) and feeding rate within a patch ($n = 1450$ dives). Statistical significance was determined based on the 95% confidence interval of the slope for each covariate.

(i) maximum dive depth	estimate	SD	95% CI (lower)	95% CI (upper)	significant
intercept	1.29	0.05	1.18	1.40	yes
distance from the colony	−0.18	0.06	−0.30	−0.05	yes
the time elapsed since the start of foraging dive bout	0.08	0.03	0.03	0.13	yes
elapsed days	0.04	0.01	0.02	0.07	yes
sea-ice microhabitat type	0.33	0.10	0.13	0.53	yes
(ii) under-ice feeding distance	estimate	SD	95% CI (lower)	95% CI (upper)	significant
intercept	2.08	0.09	1.88	2.23	yes
distance from the colony	−0.26	0.08	−0.41	−0.08	yes
the time elapsed since the start of foraging dive bout	0.22	0.03	0.16	0.28	yes
elapsed days	−0.02	0.01	−0.04	0.004	no
sea-ice microhabitat type	0.03	0.11	−0.18	0.24	no
(iii) feeding rate within a patch	estimate	SD	95% CI (lower)	95% CI (upper)	significant
intercept	−0.51	2.50	−6.37	5.38	no
distance from the colony	−0.05	0.14	−0.35	0.22	no
the time elapsed since the start of foraging dive bout	0.07	0.03	0.02	0.13	yes
elapsed days	−0.04	0.03	−0.09	0.01	no
sea-ice microhabitat type	0.16	0.16	−0.14	0.47	no

*The estimates are provided on a logarithmic scale.

(e) Dive-scale patterns in a 3D space

Across all analysed foraging dive bouts ($n = 76$ bouts from 12 birds), dives had a mean depth of 18.6 ± 7.6 m and a mean duration of 78.2 ± 20.9 s ($n = 1545$ dives). Penguins travelled 118 ± 71.4 m per dive, reaching a mean furthest horizontal distance of 62.4 ± 28.2 m from the dive start point. Most feeding events occurred near the furthest horizontal point of each dive (50–100% of the maximum horizontal distance; electronic supplementary material, figure S8). While dive start locations were tightly clustered within individual foraging dive bouts, penguins probably travelled short distances of a few metres to tens of metres between successive foraging dive bouts, typically by walking or tobogganing across sea ice, although short surface swimming movements also occurred (figure 2c).

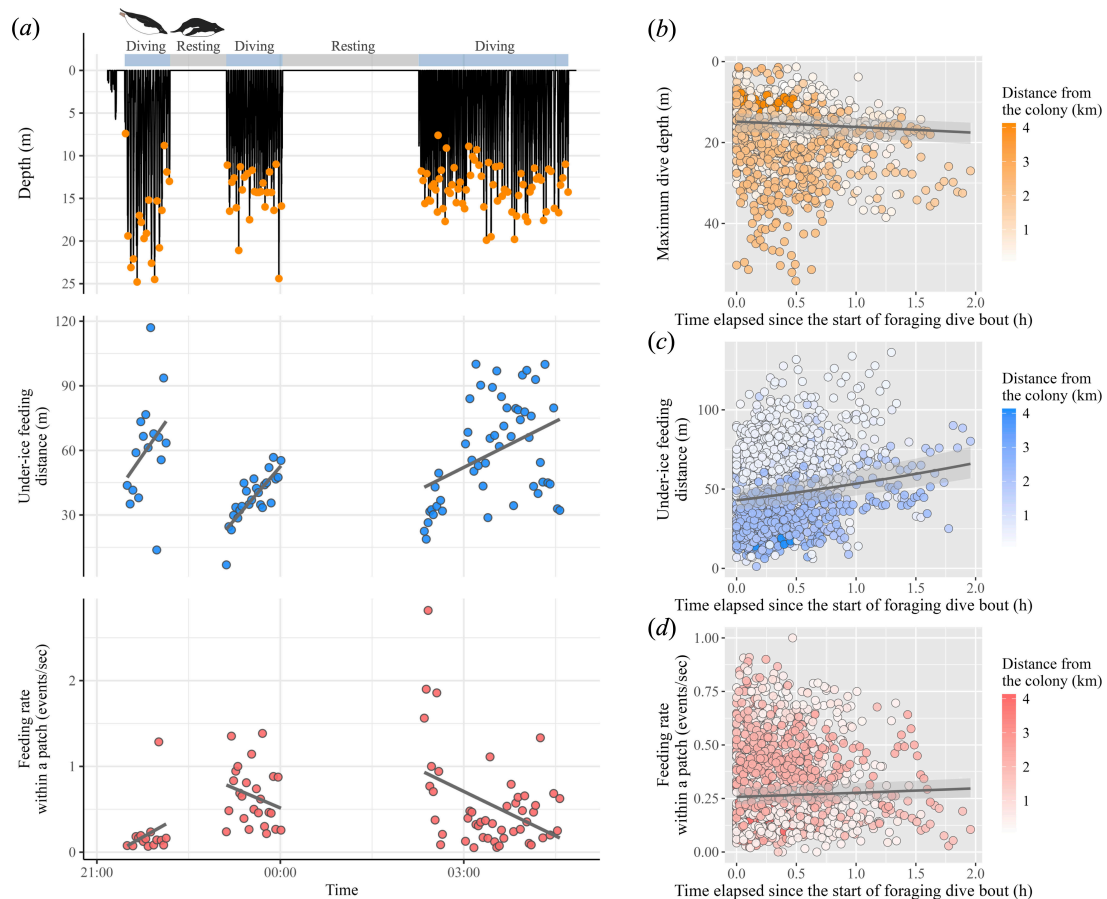


Figure 4. Time series of feeding parameters during a foraging trip and within foraging dive bouts. (a) Time series of dive behaviour during a representative foraging trip. The upper bar shows behavioural state (diving or resting) from depth and acceleration classifiers. Orange points indicate the maximum dive depth of each dive. Under-ice feeding distance and feeding rate are plotted for dives in which feeding occurred. (b–d) Relationships between the time since the start of the foraging dive bout and (b) maximum dive depth ($n = 1545$ dives from 76 foraging bouts), (c) under-ice feeding distance ($n = 1503$ dives from 76 foraging bouts), and (d) feeding rate within a patch ($n = 1450$ dives from 76 foraging bouts). Lines show model predictions and shaded areas indicate 95% confidence intervals. Inferential results are reported in table 1.

(f) Within-bout temporal changes in feeding behaviours

Within foraging dive bouts, both maximum dive depth and under-ice feeding distance increased over time, with later dives in a bout reaching greater depths and longer horizontal distances than earlier dives (figure 4a–c; table 1). Mean time to the feeding events showed no significant temporal change within bouts, although a slight increasing trend was observed (electronic supplementary material, figure S6; table S2). Feeding rate within a patch increased significantly across dives within a bout (figure 4d; table 1), but this trend varied among bouts: some bouts showed increasing rates, whereas others remained stable or declined (figure 4a). Additionally, the under-ice feeding distance at the first dive of a foraging dive bout tended to be smaller than the under-ice feeding distance at the final dive of the preceding bout (figure 4a).

(g) Prey species composition based on stomach content analysis

Stomach content analysis confirmed that the diet of Adélie penguins from this colony was dominated by euphausiids, with *Euphausia* spp. comprising $99.9 \pm 0.2\%$ of total wet mass ($n = 10$ birds; electronic supplementary material, table S1). Of the identifiable euphausiids, Antarctic krill (*E. superba*) accounted for $85.2 \pm 30\%$ of the wet mass across individuals.

4. Discussion

Our results provide clear evidence of short-term changes in prey accessibility during repeated foraging, with penguins diving progressively deeper and travelling further under the ice to reach the prey patch. These patterns indicate that prey become increasingly difficult to access at fine spatial and temporal scales, even though feeding rates within patches remained relatively stable. At larger spatial scales, penguins exhibited greater search effort near the colony, particularly in areas of repeated use. Although our results did not provide direct evidence of Ashmole's halo through quantification of prey abundance [15,21], these spatial gradients in feeding behaviour are generally consistent with Ashmole's halo [24,25]. We found that the spatial gradients in feeding behaviour were expressed primarily in metrics of prey accessibility rather than prey patch quality, indicating that reductions in prey availability were driven primarily by functional prey redistribution rather than numerical depletion.

(a) Non-consumptive effects on prey accessibility

If the observed patterns were driven primarily by numerical depletion of prey abundance owing to direct consumption, patch quality would be expected to decline closer to the colony. However, feeding rates within patches did not vary with colony distance (figure 3c; table 1), indicating that once a patch was located, its quality remained broadly consistent across space. Together with the observed increases in maximum dive depth, under-ice feeding distance and mean time to feeding events near the colony (figures 3a,b, electronic supplementary material, S6; table 1, electronic supplementary material, table S2), this spatial pattern suggests that reduced prey accessibility cannot be explained by numerical depletion alone.

Prey accessibility declined within foraging dive bouts, as maximum dive depth and under-ice feeding distance increased as bouts progressed, while feeding rate within a patch remained unchanged (figure 4; table 1). This indicates that penguins gradually exploited deeper or more distant portions of the same patch while patch quality remained relatively constant. Such patterns are consistent with local short-range escape responses of krill that lead to spatial displacement and emphasize that accessibility can decline without proportional reductions in patch quality.

These within-bout and colony-scale processes are mechanistically linked: temporary prey redistribution within bouts can accumulate over repeated bouts near the colony where predator activity is concentrated, producing colony-scale gradients in accessibility. Previous work has largely inferred Ashmole's halo from colony-scale patterns; our results identify the fine-scale processes capable of generating such spatial gradients through reductions in functional prey accessibility, even when numerical abundance remains relatively high.

(b) Fast-ice conditions promoting non-consumptive effects

Under fast ice, access to the water column was restricted to discrete tidal cracks and leads. Feeding locations under fast ice frequently reappeared around these openings across successive bouts (figure 4a, electronic supplementary material, S9). These openings provide the only access to the water column under fast ice and are repeatedly used by multiple individuals simultaneously [33], increasing the likelihood of repeated local disturbance to prey. Because krill may aggregate at such openings where light and algal production are enhanced, as reported in a previous study [59], this combination of aggregation and repeated predator use provides a plausible mechanism by which metre-scale prey redistribution could reduce functional prey accessibility. The changes in prey accessibility inferred here occur over the relatively short timescale of individual foraging dive bouts (minutes). It remains unknown whether such redistribution persists over longer periods (e.g. hours).

Several aspects of penguin foraging behaviour may facilitate such responses. Penguins forage selectively on individual krill [46] rather than through bulk filtration exhibited by baleen whales (*Mysticeti*) [60], producing repeated local predator–prey interactions that can elicit anti-predator responses of krill even among individuals not directly targeted [61] (electronic supplementary material, Video 1). Chemical cues associated with penguin guano can alter krill behaviour [62], suggesting that penguins' behavioural and chemical cues may generate non-consumptive effects on krill, thereby reducing functional prey accessibility. Such responses are broadly consistent with landscape-of-fear concepts [3,4] and probably enhanced under fast ice where movement is constrained.

Similar patterns can occur in open water, where prey shift vertically in response to predator activity or predation risk, even when density remains relatively high (e.g. [63]). Such increases in dive depth have been linked to patterns consistent with Ashmole's halo in thick-billed murres (*Uria lomvia*) [24]. Thus, although fast ice constrains responses horizontally, similar mechanisms may operate vertically in open water.

(c) Scale-dependent formation of prey depletion halo

At longer temporal scales, dive depth increased with elapsed days (electronic supplementary material, figure S7, table 1), consistent with seasonal deepening of prey layers in Adélie penguins [19,23,55,64], whereas under-ice feeding distance showed little seasonal change (table 1). As the breeding season progressed, penguins' cumulative foraging effort may have further reduced prey accessibility.

Whether fine-scale behavioural processes scale up to produce colony-centred halos depends strongly on predator density, colony size and environmental structure. This scale dependence is evident in contrasting systems such as the Ross Sea, where colonies of different sizes show distinct spatial patterns in foraging behaviour. At relatively small open-water colonies such as Cape Royds (approx. 2000 pairs), within-bout foraging rates (dives per hour) decreased over the course of individual foraging bouts [65], indicating that local prey availability can decline during repeated foraging. However, no colony-scale halo was detected and prey fields appeared to recover rapidly after foraging [65]. By contrast, larger open-water colonies (e.g. Cape Crozier ~200 000 pairs; Cape Bird ~50 000 pairs) exert sufficiently high and sustained foraging pressure to outpace prey recovery, generating kilometre-scale gradients in prey availability that are probably driven by numerical depletion [56,57].

These contrasts reveal a scale-dependent continuum in which the same underlying behavioural process—local prey displacement driven by repeated predator disturbance—can remain confined to local spatial scales under fast ice or accumulate to much larger extents in open-water systems, depending on predator density, colony size and habitat structure. Consistent with this framework, our results suggest a fine-scale mechanism that can underpin broader gradients in prey accessibility, consistent with Ashmole's halo. Under fast ice, halos are expected to remain small and transient owing to spatially restricted access points and movement constraints [18,23]. By contrast, at open-water colonies, cumulative foraging pressure can extend much further from the

colony, producing halos at much larger spatial scales [56,57]. Our results further suggest that a functional prey-depletion halo can emerge at relatively small colonies when predator activity is spatially constrained and repeatedly focused on discrete access points.

(d) Integrating consumptive and non-consumptive effects

Most studies have attributed Ashmole's halo to reductions in prey availability through consumption [14–16,18,19,66]. However, an alternative perspective has long been proposed, in which predator activity alters prey distributions and accessibility through prey responses rather than through removal alone [21,22,25,27,67]. For example, repeated predator foraging may disperse prey or disrupt aggregations, reducing accessibility even when numerical abundance remains relatively high [25]. Our study provides rare empirical support for this mechanism by showing that repeated prey redistribution at the scale of individual dive bouts can accumulate near the colony, generating colony-scale gradients in accessibility, even when patch quality remains unchanged. At the same time, however, our observational data cannot fully distinguish predator-induced prey redistribution from colony-scale variation in prey accessibility owing to fine-scale environmental heterogeneity. Although our models accounted for major sea-ice microhabitat differences and residual spatial structure, unmeasured under-ice environmental heterogeneity, including fine-scale variation in currents, light conditions or prey aggregation dynamics, could also contribute to the observed spatial gradients.

Here, we propose an expanded framework for the formation of Ashmole's halo that explicitly incorporates predator-induced prey redistribution alongside consumptive removal, and recognizes how habitat structure and predator density, including colony size, constrain both predator and prey behaviour. This framework explains variation in halo scale across environments—from metre-scale accessibility gradients under fast ice to kilometre-scale depressions in open water—and emphasizes the role of behavioural coupling between predators and prey. Reduced prey accessibility may be functionally equivalent to reduced availability for central-place foragers, with potential consequences for foraging costs and individual fitness. This distinction is therefore important to avoid misinterpretation of behavioural effects as indicating low prey abundance.

5. Conclusion

Non-consumptive effects can strongly influence prey distribution, behaviour and ecosystem functioning [5,6]. While marine studies have documented predator effects on prey behaviour [68,69], their consequences remain poorly understood owing to challenges in resolving fine-scale interactions [70–73]. By integrating high-resolution 3D movement data with direct observations of feeding events, our study provides empirical evidence that repeated foraging activity by free-ranging Adélie penguins can behaviourally displace prey, thereby reducing local prey accessibility even when numerical prey abundance remains relatively high. This highlights the need to incorporate both consumptive and non-consumptive processes into ecological models that link predator behaviour to population- and ecosystem-level dynamics [74]. Our inferences are limited by the absence of direct prey measurements and the relatively small number of animals studied in a single year. Future work combining predator-borne sensors with simultaneous, fine-scale observations of prey distributions [75], across a wider range of colonies and habitats, will be essential to test the generality of these mechanisms. More generally, our results identify a general ecological mechanism underlying spatial gradients in prey accessibility through behavioural redistribution, with implications for central-place foraging systems across ecological scales.

Ethics. This fieldwork was conducted according to the protocol reviewed and approved by the Institutional Animal Care and Use Committee of the National Institute of Polar Research (approval no. H30-3). Fieldwork was conducted as part of the Japanese Antarctic Research Expedition (JARE) project AP0922 with permission from the Ministry of the Environment, Government of Japan.

Data accessibility. The datasets analysed during the current study are available on the Dryad digital repository [76].

Supplementary material is available online [77].

Declaration of AI use. AI-assisted technologies, including ChatGPT (OpenAI) and Grammarly, were used to assist with troubleshooting R code and language polishing of portions of the manuscript.

Authors' contributions. H.T.W.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, writing—original draft; J.T.: investigation, writing—review and editing; A.T.: conceptualization, funding acquisition, investigation, project administration, supervision, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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