Articles

Testing assumptions of central place foraging theory: a study of Adélie penguins *Pygoscelis adeliae* in the Ross Sea

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We investigated central place foraging (CPF) in the context of optimal foraging theory in Adélie penguins *Pygoscelis adeliae* of the southern Ross Sea by using satellite tracking and time-depth recorders to explore foraging at two spatio-temporal scales: within the day-to-day (sub-mesoscale: single foraging trip, 10s of km²) and the entire breeding season (mesoscale: trips by multiple individuals across the collective foraging area, 100s of km²). Specifically, we examine whether three basic assumptions of the Orians–Pearson CPF model, shown to occur in other CPF species, are met: 1) within a patch, the rate of prey acquisition declines with time spent in that patch; 2) food is distributed in discrete patches and is not available between those patches; and 3) CPF species have knowledge of the potential (or average, at least) feeding rate within their universe of patches, and use this knowledge to determine their foraging strategy when planning or engaging in a foraging trip. We found that prey consumption rates did not decline with time spent in patches, and penguins foraged to some degree most of the time when at sea. Food availability, as measured by foraging dive rate, appeared to be predictable within the same day at the same location, but predictability broke down after 2 d at distances > 10 km away. We conclude that the assumptions of the Orians–Pearson CPF model are not a good fit to the circumstances of Ross Sea penguins, which clearly are central place foragers.

The positive correlation between colony size and the foraging area of colonial, central place foraging (CPF) species has been well-researched in birds (Storer 1952, Ashmole 1963, Diamond 1978, Furness and Birkhead 1984, Brown and Brown 1996). This relationship results from the foraging-driven decline in prey availability, which is a process most intense nearest to the colony, decreasing with distance away, either by exploitative (Birt et al. 1987, Elliott et al. 2009) or interference competition among colony members (Lewis et al. 2001, Ainley et al. 2003a, Ford et al. 2007, Ballance et al. 2009). The corresponding increase in overall foraging effort as the area of high prey availability becomes more distant can negatively affect reproductive success (Hunt et al. 1986, Brown and Brown 1996, Hipfner et al. 2007, Boersma and Rebstock 2009), colony choice by recruits (Brown et al. 1990, Danchin and Wagner 1997) and, ultimately, population size (Furness and Birkhead 1984, Elliott et al. 2009).

Despite the fact that CPF occurs widely in the animal world, investigating its implications for natural history patterns is often difficult. Penguins, however, can be easy to work with given easy access, large size and visibility. Therefore, previously we broadly explored the consequences of CPF (sensu Orians and Pearson 1979) as it applies to Adélie penguins *Pygoscelis adeliae* nesting at colonies of

different size. We found that, owing to intra- and interspecific competition for food: 1) foraging area size is directly related to colony size (Ainley et al. 2004); 2) for largest colonies, foraging area expands further within a breeding season as more parents forage for increasingly larger (more demanding) chicks as well as themselves (Ainley et al. 2004, Lyver et al. 2011); 3) food loads brought back to chicks decrease at large colonies as parental trip duration (a consequence of expanding foraging area) reaches above an asymptotic level (Ainley et al. 1998); 4) the arrival of trophic competitors (whales) increased foraging effort (Ainley et al. 2006); and 5) energetic cost (calories invested) of foraging is high at large colonies (Ballance et al. 2009).

Expanding this work, herein, we address the relevance of optimal CPF to Adélie penguins in the Ross Sea at two spatio-temporal scales: within the day-to-day (sub-mesoscale – single foraging trip, 10s km², multiple prey patches) and within the entire breeding season and collective foraging area of the colony (mesoscale – trips by multiple individuals within the preyscape, 100s km²). In doing so we investigate the implications of CPF (and optimal foraging theory) at the next larger scales compared to those investigated by Watanabe et al. (2014), who investigated single dives (prey capture rate within a dive) and a series of dives (diving

bout) within a patch. While it would be ideal to have had coincident information on actual prey distribution at the sub-meso- and mesoscales during our field work, much can still be learned about seabird foraging behavior in the absence of such extremely difficult-to-acquire information (Fauchald and Tveraa 2003, Weimerskirch et al. 2007, Boersma et al. 2009 and dozens of other seabird foraging papers also lacking real-time information on prey availability). As described in Methods, we use the foraging dive rate (as opposed to other types of diving: exploration, traveling) as an indicator of local food accessibility, following the lead of Watanabe et al. (2014), who had the means as well to evaluate single patch quality (prey density, capture rate using penguin-borne video, and diving rate).

In its most general sense, optimal foraging entails the prediction of animal behavior based on the assumption that individuals are foraging in ways that maximize or minimize some fitness-related criterion, such as trip time, load size, rate of energy uptake (prey capture rate) or energy expenditure (cf. Mori 1998 for exploitation of single patches by divers). The Orians–Pearson model formalized this concept for CPF species that return regularly to their nest sites to feed and protect their offspring, and made predictions as to these birds' foraging behavior. In so doing, they expanded on the marginal value theorem of Charnov (1976, Watanabe et al. 2014). The Orians–Pearson model has been applied to a range of species including penguins (Boersma et al. 2009), and in many cases has proven to be a useful tool for interpreting and potentially predicting foraging behaviors (Ropert-Coudert et al. 2004).

Nonetheless, optimal foraging has generally proven to be a difficult theory to test and to improve on in the real world. To definitively reject a hypothesis based on CPF theory, a researcher would need to know the exact metabolic and nutrient requirements of the foraging population, as well as the relationship between load size and travel cost for each kind of prey. In terms of the preyscape, they would need to know the distribution, availability, and nutrient content of all the potential prey species within the entire foraging area. Even with advances in measurement technology, data of this scope are unlikely to become available in the near future. Since such an approach to model testing was not practical, we used two different methods for evaluating model applicability: 1) do southern Ross Sea penguins and their prey fit the assumptions used to define the Orians–Pearson model, and 2) can we identify particular behaviors which logically would not occur in a system that functioned strictly according to OP–CPF rules?

The Orians–Pearson model assumptions are quite specific and do not necessarily apply to all circumstances above the single-patch scale, as we will elaborate in our Discussion. Penguins, given their relatively slow movement rate (i.e. swimming as compared to flying), the difficulty of detecting clues regarding prey availability, and the often rapid changes of prey availability in the ocean at mesoscales (100 km^2) and especially below, are limited more than many other CPF species in terms of their real-time ability to assess the likely variable distribution of prey (i.e. the preyscape).

In regard to the availability of prey in the Ross Sea, we know that the principal food of southern Ross Sea penguins, crystal krill *Euphausia crystallorophias* and Antarctic silverfish *Pleuragramma antarcticum*, occur in discrete, dense swarms and 'loose' shoals, respectively (Pakhomov and Perissinotto 1996, Fuiman et al. 2002). Southern Ross Sea penguins feed on these two prey in an approximate 50:50 ratio of mass, though with krill predominating early and fish later in the nesting season (Ainley et al. 1998, 2003b, Ainley 2002), and do so in our study area, sometimes diving to 114 m (deepest recorded in this study, though elsewhere to 180 m; Watanuki et al. 1997). Swarms and schools of these prey would constitute prey patches, and have been detected in the study area using hydroacoustics and video (Fuiman et al. 2002, Sala et al. 2002). These prey are generally taken in loosely pack-ice covered habitat, with little connection to bathymetry, the ocean everywhere being deeper than 400 m (to 800 m; Ainley et al. 2003b, Lescroël et al. 2014).

Although the Ross Sea is the most productive stretch of the entire Southern Ocean, contributing 28% of total primary production (Arrigo et al. 1998, 2008) and which ultimately sustains a huge biomass of mesopredators (Ballard et al. 2012, Smith et al. 2012), Adélie penguins face a complex foraging problem involving uncertainty in the spatial and temporal distribution of their prey, uncertainty in the depth of their prey, and low predictability of prey concentrations in part likely due to competing predators. At the meso- and lower spatial scales at which upper predators typically forage (i.e. within the ocean features that help to concentrate prey; Bost et al. 2009), resources are spread unevenly through space, change unpredictably through time, and are difficult or impossible to detect from the surface – particularly a problem for non-flying birds. Indeed, circulation in the southwest Ross Sea is complex, with a variety of sub-mesoscale eddies that very likely influence the distribution of prey and their food supply (Dinniman et al. 2003, 2007). From this complex preyscape, adult penguins (unlike competing cetaceans, pack ice seals and predatory fish in the area) are constrained to return to their offspring as frequently as possible to provide food and protection. The penguins' rate of food capture must be sufficient to provide for both them and their chicks (Ballard et al. 2010).

In this paper we examine whether or not three of the Orians–Pearson basic assumptions, some of which have been seen among other CPF species, are met at the sub-meso- and mesocales by populations of Adélie penguins breeding in the southern Ross Sea: assumption 1: foraging within a prey patch, the rate of prey acquisition declines with time spent in that patch; assumption 2: within a foraging trip, food is distributed in discrete patches and is not available in the interstices between those patches; assumption 3: within a season of foraging, central place foragers have knowledge of the potential feeding rate within their foraging universe, or at least know the average feeding rate within that area, which is used to inform their foraging strategy for a given trip.

If these assumptions apply to Ross Sea Adélie penguins, then two basic predictions of the model should be evident and we tested for these as well, on both single trip and seasonal foraging scales: prediction 1: central place foragers should bypass areas where prey are depleted (small, diffuse patches) and forage further from the colony where prey are more readily available (larger, denser patches); prediction 2: central place foragers should not continue to forage in areas

where the rate of prey acquisition is less than in other areas where they foraged. The foraging dive rate when a bird gives up on a patch should be similar across all the patches utilized during a foraging trip.

In the Methods and Results, we present our findings in accord with this outline of the assumptions and predictions to be tested.

Methods

Definitions of key concepts

At the spatial and temporal scale of a single trip (see below), we examine foraging dive rate during visits to places (prey patches) where birds were engaged in intense foraging behavior, evidenced by a high and continuous rate of foraging dives. These were assumed to be areas of perceived high prey concentration, and were selected using a methodology similar to that used by Watanabe et al. (2014). This definition of a resource 'patch' makes no assumption about its shape, depth, or persistence. Such patches could potentially be irregular, circular, linear or area-wide, be determined by the rise and fall of prey within the water column, or move horizontally with the prey's own movements (Watanabe et al. 2014).

At the larger spatial and temporal scale of the colony foraging area and chick-rearing period (mid-December to late January), we compare spatially explicit foraging rates recorded on trips occurring early and late in the season to determine whether birds abandon certain places in favor of others as the season progresses. We know from previous work (see above) that large numbers of penguins foraging in the same sub-mesoscale area can affect prey availability (see also Lewis et al. 2001, Elliott et al. 2009 for studies of other avian species), seemingly facilitated by the foraging of other predators as well [e.g. cetaceans (Ainley et al. 2006) and fish (Ainley 2007)]. We know from Ainley et al. (2006) that the arrival of whales leads to penguins' diet switching from crystal krill to silverfish and increased foraging effort, which then revert back once the whale density diminishes. Moreover, we know that silverfish (penguin prey), which is the main predator of krill in this system (thus a penguin competitor), become cannibalistic in the late summer conceivably as krill are depleted by predators (penguins, whales and fish; Ainley 2007). Other than a diminution of sea ice and of phytoplankton biomass (owing to nutrient limitation), no seasonal oceanographic change in circulation or water-column structure has been described in the well-studied southern Ross Sea (as summarized in Smith et al. 2012, 2014) that would force within-chick-feeding-season (6 weeks) food web alteration. Thus, it is not a change in oceanography that alters diet or foraging effort among nesting, chick-feeding Adélie penguins but rather predation.

Study sites

Data were collected at the three Adélie penguin colonies on Ross Island, southwestern Ross Sea (Fig. 1 or, for a map of study sites, see Ainley et al. 2004): Cape Crozier (77°27′S, 169°12′E; ~ 200 000 pairs), Cape Bird (77°13′S, 166°26′E;

~ 50 000 pairs), and Cape Royds (78°33′S, 166°10′E; ~ 2000 pairs), during three austral summers, 2005–2006 to 2007–2008 (colony size data from Lyver et al. (2014)). Colony sizes in our study area spanned the full range for the species, the Cape Royds colony being among the smallest and the Crozier colony, two orders of magnitude greater, is among the largest for this species; Cape Bird is mid-way in size (cf. Ainley 2002).

We defined the foraging area for each colony as the accumulation of grid cells (11.1 × 11.1 km, equivalent to 0.1 latitude degrees) containing all penguin foraging locations across all study years (Fig. 1).

During the first year of data acquisition reported herein, 2005–2006, a very large iceberg (54 × 172 km) was grounded in the western portion of the Crozier foraging area (see below for definition). Its presence forced Crozier birds to forage farther to the east, and thus not as far as usual into the Ross Sea Polynya marginal ice zone (Dugger et al. 2014, Lescroël et al. 2014). It also prevented Crozier birds from displacing penguins from the adjacent but much smaller Bird and Beaufort Island colonies toward the west, displacement otherwise being the usual pattern (Ainley et al. 2004). In the subsequent analyses, we separated 2005–2006 data from the other two years for Crozier, when the iceberg was no longer present.

Owing to differences in breeding phenology between Royds and both Crozier and Bird (earlier than Royds), the data that we report from December for Bird and Crozier are mostly from the guard stage (early season, to 24 Dec), while those from January reflect primarily the crèche stage (late season). At Royds, we do not report any results prior to 25 December since most parents do not begin provisioning chicks until late December (and there is no subsequent crèche stage at Royds).

Instrument configuration and deployment

Once chicks hatched, we equipped randomly selected parents with SPLASH tags (Wildlife Computers, Redmond, WA, USA), as well as small, streamlined cylindrical radio transmitters (Crozier; 8 g, 46 mm long × 14 mm diameter – model A2630, Advanced Telemetry Systems, Isanti, MN, USA; Bird; 15 g, 43 × 20 × 10 mm – Sirtrack, NZ, only during crèche period). SPLASH tags recorded depth, light, and temperature every second, and emitted radio signals for determining position by Doppler shift using ARGOS satellites (see below). SPLASH tags weighed 62 g (1.6% of a 4-kg Adélie penguin) and had a cross-sectional area of 3.2 × 10⁻⁴ m² (1.0–1.6% of a penguin's cross-sectional area). Radio transmitters alerted us to when birds returned to the colony. Attachment procedures have been described previously (Ballard et al. 2001). SPLASH tags were set to transmit locations every 45 s for the first eight successive transmissions and then switch to once every 90 s thereafter, with up to 1440 transmissions allowed per day. They were programmed to turn off after being dry for 6 h in order to conserve batteries.

Diving data were downloaded from the tags after retrieval. For this analysis, we used data from all trips for which both dive data and location data were available. This included data for 137 tag recoveries comprising 178 foraging trips (see Table 1 for sample sizes by colony).
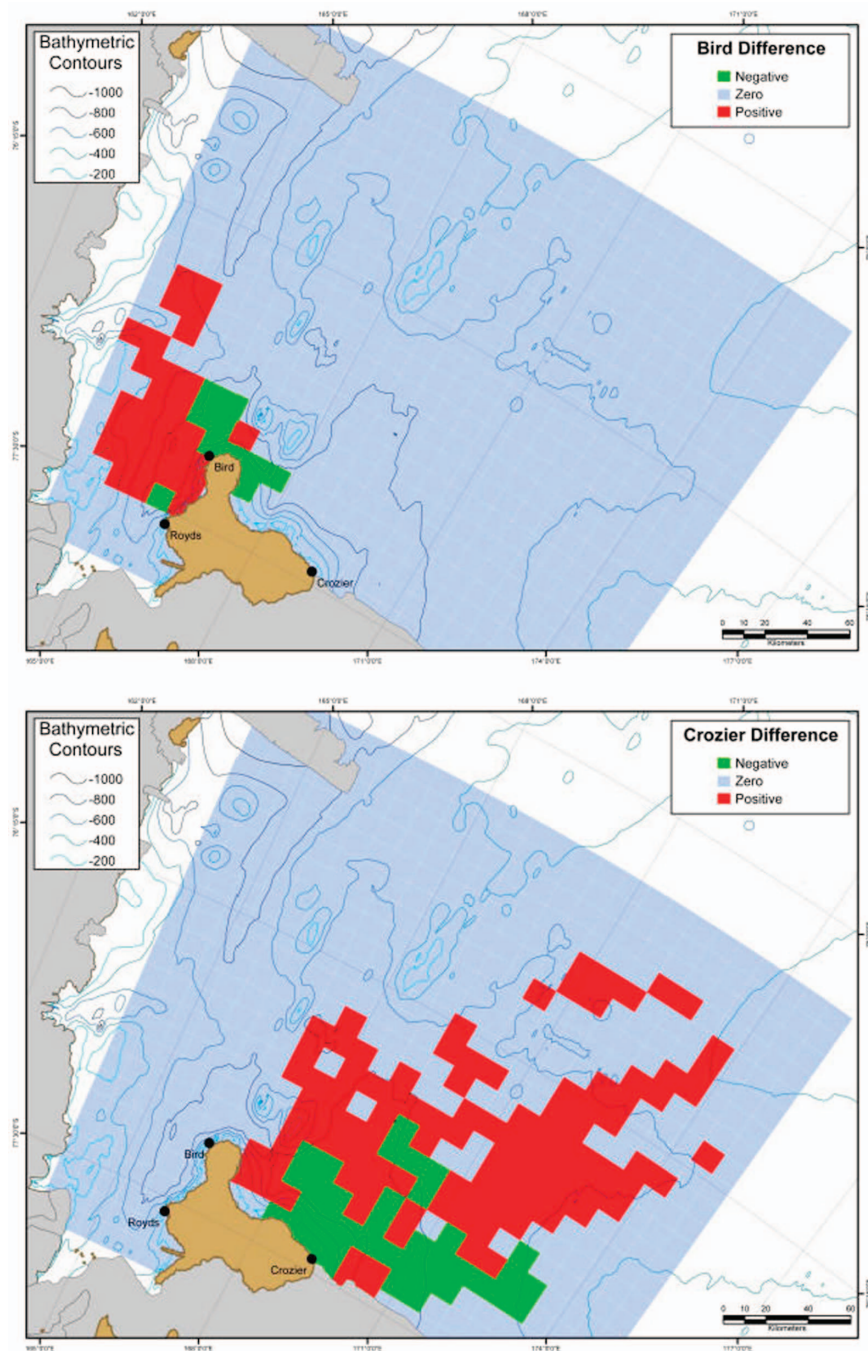
Figure 1. Change in area usage between early season and late season among penguins at Cape Bird (top) and Cape Crozier (all years; bottom). Green cells (all cells are 11.1 × 11.1 km) denote areas where the proportion of foraging dives decreased, and red cells denote areas where the proportion of foraging dives increased. The foraging area for Cape Bird is based on 19 trips in the early season and 20 in the late season. The foraging area for Cape Crozier is based on 49 trips in the early season and 32 during the late season.

Many individuals made more than one trip before their tags were removed, and the trip database contains instances of multiple trips by the same individual. Since foraging behavior potentially varies in a consistent fashion among individuals, multiple trips by the same individual could potentially alter the results of linear regressions involving these data, and we ran these regressions both including and excluding multiple trips by the same individual.

Data collection

All transmissions were received and processed within the ARGOS system (CLS Corporation, Ramonville Saint-Agne, France). The resulting satellite location data still contained positions that were clearly inaccurate, often involving movement 'spikes', during which a bird appeared to suddenly move kilometers or tens of kilometers from its last position,

returning shortly thereafter to a location close to this original position. We utilized two simple one-pass filters to remove these spikes: 1) if distance moved between three consecutive fixes resulted in a movement rate > 5.6 m s^{-1} (20 km h^{-1}), the central point of the three fixes was deleted; and 2) if the angle formed by three consecutive fixes was $< 45°$, the middle point of the three fixes was deleted.

Definition of foraging dives and foraging success

Depth profiles have been widely used as a basis for classifying dives in terms of their intent, e.g. foraging, exploration, or travel (see for example Lescroël et al. 2010). Typical U-shaped 'foraging' dive profiles include relatively long periods of time spent near the bottom of the dive, whereas in 'exploratory' V-shaped profiles the bird swam steadily downward and then immediately upward. Using esophageal temperature sensors, Ropert-Coudert et al. (2001), found that 73% of prey are caught during the bottom-phase of U-shaped dives, with the remaining 27% of prey captures during descent and (especially) ascent phases. Others have found that the number of prey captured per dive was distributed according to a power function (Watanabe et al. 2014), indicating that similar-looking dive profiles could result in different outcomes in terms of prey capture (see also Watanabe and Takahashi 2013). During U-shaped dives, the time spent at deeper depths is often punctuated by vertical undulations (changes in vertical direction), each of which represents a possible prey capture event (Ropert-Coudert et al. 2001, Bost et al. 2007, Halsey et al. 2007, Watanabe et al. 2014; Fig. 2), and this has been used as an additional means by which to classify foraging dives and as an index of foraging success (Lescroël et al. 2010).

For the purposes of this study, especially on the basis of the findings by Watanabe et al. (2014), however, we do not assume that dive profiles provide a measure of foraging success, but rather that they provide a measure of foraging effort. In other words, using diving rate, we measure the penguin's perception of prey accessibility and presume the intention to capture that prey. Our basic premise is that foraging dives, and especially successive ones, occur when and where food is available. We use time spent in the bottom phase of U-shaped dives as a measure of effort, rather than counting the number of undulations (Watanabe et al. 2014 did not find a strict relationship between undulation and prey capture), and we explain our method and compare to assessment of undulations in Supplementary material Appendix 1.

Assumptions and predictions

Note: in the Results we will be abbreviating these assumptions as titles of sections in the interest of saving space.

Assumption 1 – foraging within a prey patch: the rate of prey acquisition declines with time spent in that patch

Testing this assumption requires that we define 'patch' in a measurable way, a difficult task since the penguins in this study foraged nearly continuously as they travelled (see Results) and we didn't have actual measures of prey occurrence. Furthermore, we suspect that prey patches, judging from observations of fish and krill schools, come in a wide
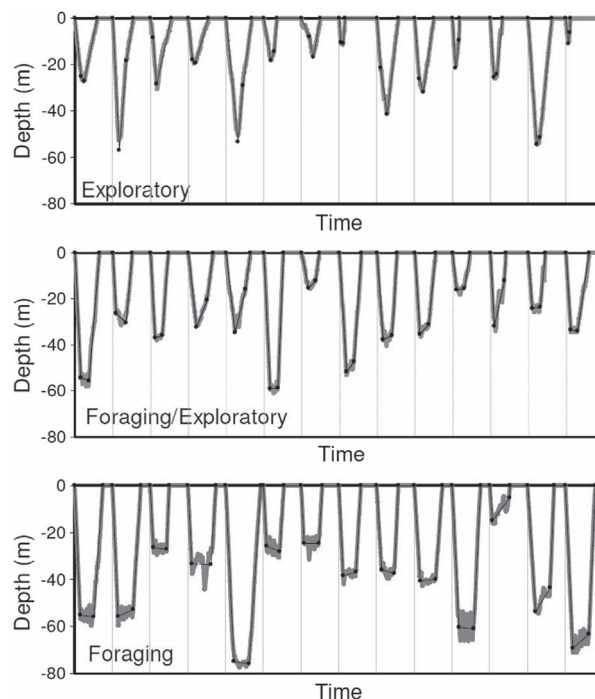

Figure 2. Sample dive type classifications based on the piecewise regression: (top) exploratory dives, (middle) mixed foraging and exploratory dives, and (bottom) foraging dives. Dives were randomly selected, two of each category from each colony/season combination. Thicker gray lines represent the actual dive profile based on depth at 1 s intervals. The thin black line and associated black dots are the results of the piecewise regression fitted to the dive.

array of shapes and sizes (Sala et al. 2002), with some portions accessible to penguins and others not. We therefore used periods of intense foraging activity (≥ 1 foraging dive every 15 min) as an indicator that a penguin was functionally within a foraging patch. We further stipulated that these periods of intense foraging activity last at least 30 min and be preceded and followed by at least 30 min with no foraging activity. The 30 min criterion for the length of intense foraging activity was subjectively chosen, as was the 1 dive/15 min requirement, and other selection criteria could have been used, but these choices were supported by evaluation of the data. For instance, results were not substantially altered by varying the period of intense foraging activity between 15 and 90 min. Similarly, the minimum dive rate used in selecting a patch was varied between 1 dive/3 min and 1 dive/15 min without affecting results.

Foraging bouts were then divided in half based on time, and the foraging dive rate in the first and second halves of the bout compared using linear regression. If the assumptions of the Orians–Pearson model are met and resource depletion is occurring in this time frame, then the foraging dive rate should decrease with time spent in a patch, and fewer foraging dives would occur during the second half of the bout.

Assumption 2 – within a foraging trip: food is distributed in discrete patches and is not available in the interstices between those patches

This assumption is logical for animals such as frugivorous birds that do not forage on the wing, and can either

forage or fly but cannot do so simultaneously. To investigate, we used a variation of the technique described by Boersma et al. (2009), dividing each foraging trip into 10 equal temporal segments (quantiles) and binning behavioral measures accordingly (see also Ropert-Coudert et al. 2004, who partitioned foraging trips though not as finely). In this way we could characterize the dive rate and distance from colony over the course of a foraging trip. For each colony, the number of foraging dives per quantile (i.e. the foraging dive rate) was plotted as a function of mean distance from the colony, distinguishing between the outgoing and incoming portions of the trip.

Assumption 3 – within a season of foraging, central place foragers have knowledge of the potential feeding rate within their foraging universe, or at least know the average feeding rate within that area, which is used to inform their foraging strategy for a given trip

For optimal foragers, it is expected that the spatial and temporal allocation of foraging effort would be altered by the predictability (based on previously obtained knowledge) of prey in both time and space (see Discussion). We measured predictability using spatial and temporal autocorrelation to determine the degree to which the foraging dive rate at a particular time and place was predictive of the foraging dive rate at every other time and place. To do this, we first estimated the foraging dive rate in all 11.1×11.1 km $\times$ 0.5 h blocks for each colony. For all pairs of bins separated by a given time and distance, we regressed the foraging dive rate in one bin on that of the other bin. The result of this procedure was the R^2 value, which in this context is a measure of the degree to which the foraging dive rate at one time and place can be used to predict the foraging dive rate at another time and place.

Now for the predictions that are based on these assumptions.

Assumption 2, predictions 1, 2 – food is distributed in discrete patches and the penguin, within a foraging trip, must choose where to forage: changes in foraging location and rate

If the assumptions of the Orians–Pearson model are met by foraging Adélie penguins, then intervals of foraging activity should be interspersed with intervals without foraging, and there should be periodic declines in foraging dive rates as patches are depleted of prey (prediction 2). Patches nearest to the colony, which were likely to have been heavily exploited by penguins previously, would be expected to become depleted most quickly and would be bypassed by birds moving outward to forage in higher quality but more distant patches (prediction 1). The foraging dive rate would therefore be expected to be low initially on the outbound portion of the trip, plateau at the outer boundary of the trip, and decline steeply as the birds pass back through the depleted zone nearer the colony.

To determine the temporal allocation of foraging activity during the course of a trip, we used the technique of Boersma et al. (2009) described above (assumption 2).

Assumption 3, prediction 1 – penguins have prior knowledge of the preyscape, so within a season what affects foraging behavior and distance from colony?

As discussed above, a logical conclusion of the Orians–Pearson model is that patches near a colony would tend to be depleted and therefore be bypassed by birds moving outward to forage in less depleted areas. We tested this prediction by examining foraging behavior as a function of distance from the colony.

For each colony and season, we calculated the number of foraging dives and the proportion of foraging dives that occurred within 1.85×1.85 km cells (1.85 km = 1 min of latitude). Proportion of foraging dives was estimated as the number of foraging dives occurring within a particular distance band during a particular season divided by the total number of foraging dives during that season. To analyze the effect of distance from colony on diving rate and success, these cells were then binned into 11.1 km (6 min or 0.1 degrees of latitude) distance bands around each colony, plotting the foraging dive rate and the proportion of all foraging dives as a function of distance from the colony for all colonies and seasons (i.e. before 25 December compared to after 25 December). The proportion of all foraging dives was normalized by dividing the number of foraging dives in a distance band by the sum of the all foraging dives for that colony. Distance bands containing 3 or fewer foraging dives were excluded.

Assumption 3, prediction 1 – penguins have prior knowledge of the preyscape, so within a season what explains spatial shifts in usage of foraging areas?

We looked for evidence of prey depletion as the season progressed by examining changes in the usage of different parts of the foraging area as time progressed. We plotted the distribution of foraging dives in *XYZ* coordinates where the *XY* value was the position of a cell on the 11.1×11.1 km grid, and the *Z*-value was the number of foraging dives occurring within that cell. To facilitate inter-colony comparisons, the number of foraging dives in each cell was normalized by dividing the number of foraging dives by the sum of the foraging dives in all cells for each colony. The change in usage over the course of the breeding season was estimated by subtracting the cell values of the 'early season' distribution from the cell values of 'late season' distribution and displaying the results in *XYZ* coordinates. Data from Royds were not used for this analysis since few dives occurred there during the early season (prior to 25 December).

Assumption 3, prediction 1 – penguins have prior knowledge of the preyscape, so within a season what affects changes in trip distance and duration?

We looked for geographic evidence of prey depletion as the season progressed by examining time trends in foraging area usage among colonies. We compared usage early in the season, when we would expect prey depletion to be minimal and trip durations shortest, to usage late in the season, when we would expect prey depletion near the colony to be maximal and trip durations longest. We compared seasonal trends for two measures of foraging effort: 1) the distance of the entire trip (km), and 2) the total time required for the trip (h). Each of these metrics was plotted as a function of date, and linear regression was used to fit a trend line to the data for each colony.

Note that trip distance and trip duration are correlated, so that these two metrics are not independent measures of seasonal trends.

Results

Assumption 1 – foraging within a prey patch

Foraging bouts ranged from 10 to 102 successive dives. The foraging dive rate (dives per hour) at the beginning and at the end of foraging bouts were highly correlated (Table 1). The dive rate during the first half of the bout accounted for 86–96% of the variation in the dive rate during the second half of the bout. In 5 out of 7 colony/season combinations, the slope of the regression was slightly greater than 1.0, indicating that the foraging rate increased during the second half of the bout. This increase was significant ($p > 0.95$) for Bird in both seasons. In two cases, Royds and Crozier in early 2005–2006, the slope was significantly less than 1.0 ($p > 0.95$), indicating that the foraging rate decreased during the second half of the bout.

Assumption 2 – foraging during a trip, distribution of prey patches

Figure 3 shows the relationship between distance from colony and foraging dive rate summarized into 10 equal time periods for each trip. Distance from colony and dive rate are positively correlated in all cases, indicating that at least the penguins' perception of resource availability increases as they move outwards on a foraging trip. Birds do not seem to wait until they approach their maximum excursion from the colony to begin foraging, but rather begin foraging as soon as they leave the colony.

Assumption 3 – changed foraging strategy within the season

The predictability of food resources by colony and month within the season was measured by spatial and temporal autocorrelation (Fig. 4). A simple way to interpret this figure is to imagine that you are a penguin at a particular time and place within a colony foraging area, and that you know the resource availability (as represented by your current foraging dive rate) at that point. These graphs depict how useful that information would be regarding resource availability at other places further away in space or later in time. For example, if you knew the foraging rate at your current location, it is very likely that the foraging rate would be similar at the same place tomorrow. On the other hand, you would have almost no ability to predict the foraging rate the day after tomor-

row and 10 km away. An R^2 of 0.4 is typical for 2 d into the future at the same location, dropping to ~ 0.2 for foraging 4 d into the future. Resource patches, therefore, would be expected to persist for up to several days before fading. Knowledge of local foraging conditions would be of little value after 6 to 8 d.

The predictability of resources drops off rapidly in relation to distance. In most cases, a spatial separation of 11.1 to 22.2 km causes R^2 to drop to about 0.1, and a separation of 22.2 to 33.3 km causes R^2 to drop to nearly zero. In two cases, Crozier in 2005–2006 January and Royds in January (all years), predictability remained relatively high over greater distances. The Crozier 2005–2006 pattern during the late season reflects penguins foraging farther to the east, outside of the marginal ice zone, arguably representing the lowest resource availability in our dataset and Royds during the late season the highest. We had no direct measure, however, of prey availability during the current study, and this conclusion is based on the distance and duration of foraging trips, size of food loads and growth of chicks. Subsequently, we have deployed an acoustically equipped ocean glider to assess prey distribution but those results are not ready for publication.

Assumption 2, predictions 1, 2 – changes in foraging location and rate within a trip

The foraging dive rate increased steadily as birds moved away from the colony, consistently peaking during the second half of foraging trips (Fig. 3). The dive rate at Royds in January peaked at quantile 9 (about 90% of the way through the trip duration), and at quantiles 7 and 8 for Bird during the early and late seasons, respectively (Fig. 3 top). During normal years at Crozier, the foraging dive rate peaked at quantile 7 during both the early and late seasons, whereas during the iceberg summer of 2005–2006 the corresponding peaks were at quantile 5 (Fig. 3 bottom). With the exception of the iceberg summer, the dive rate was consistently greater during the second half of the trip, peaking at or very near the maximum distance away from the colony. Note that the peak in foraging activity did not necessarily occur at the periphery of the colony's foraging area (based on the sum of all foraging tracks), but rather at the maximum distance from the colony during a given foraging trip. Most foraging trips among individual penguins did not extend all the way out to the edge of the colony foraging area.

Table 1. The foraging dive rates of Adélie penguins during the first half and second half of intense isolated feeding bouts analyzed using linear regression. The regression is a measure of the degree to which the foraging rate during the second half of the bout can be predicted by the foraging rate during the first half of the bout. A slope of 1.0 indicates that there was no difference in foraging rates between the beginning and end of the bout. The following table is based on dive sequences selected so that that there were initially at least two 15 min intervals with no foraging dives, followed by at least two consecutive intervals each with one or more foraging dives, followed by two or more intervals with no foraging dives.

| Colony	Month	R^2	Number of feeding bouts	Slope	Slope: lower 95% confidence limit	Slope: upper 95% confidence limit
Bird	Dec	0.869	46	1.342	1.1836	1.5008
Bird	Jan	0.962	84	1.080	1.0332	1.1273
Crozier	Dec	0.960	127	1.021	0.9846	1.0583
Crozier	Jan	0.943	237	1.011	0.9792	1.0433
Crozier 2005–2006	Dec	0.879	92	0.952	0.8785	1.0262
Crozier 2005–2006	Jan	0.855	36	1.037	0.8877	1.1858
Royds	Jan	0.881	32	0.691	0.5967	0.7858
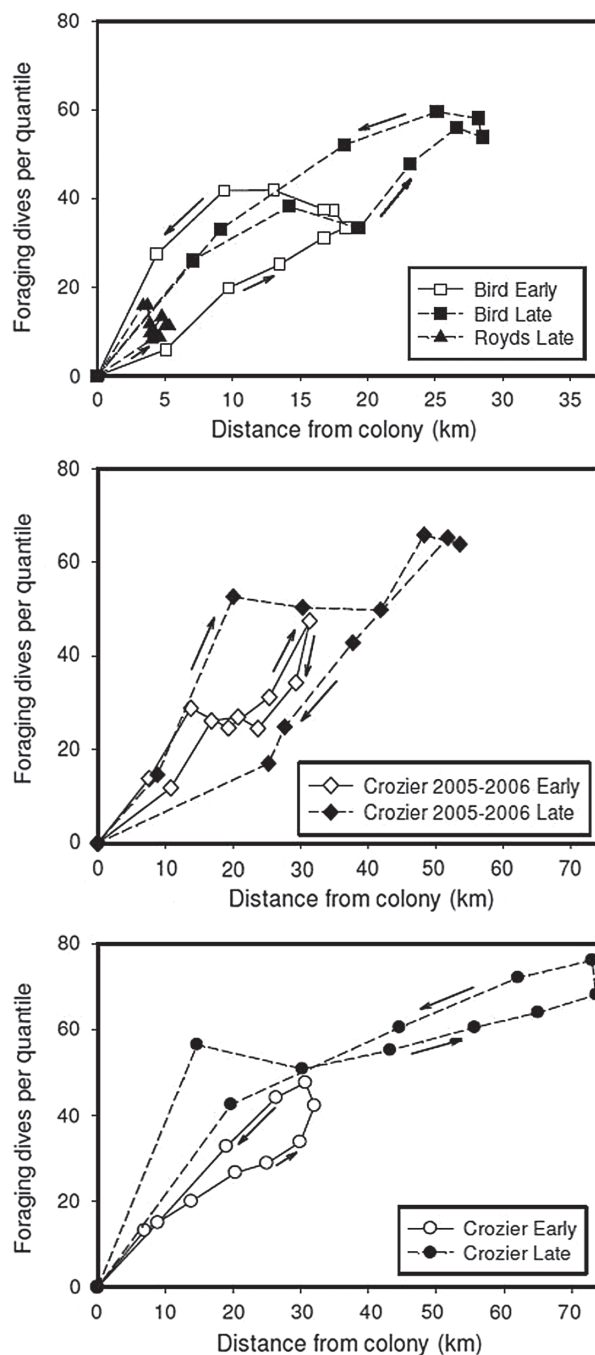
Figure 3. Average foraging dive rate versus average distance from the colony and season for Royds and Bird (top), Crozier during 2005–2006 (middle), and Crozier during other years (bottom). Each data point represents a quantile (10% of a foraging trip based on time), and successive quantiles are connected by straight lines. Arrows indicate the passage of time, heading out on and returning from a foraging trip. Early refers to trips where recorders were recovered before 25 December, and late refers to trips where recorders were recovered after 25 December.

Assumption 3, prediction 1 – within a season: changing foraging behavior

The proportion of foraging dives versus distance from colony for each season and colony combination is shown in Fig. 5. The proportion of foraging dives showed a pattern similar

to the geographic pattern of usage shown in Fig. 1, with the number of foraging dives tending to decrease more near the colony than at the periphery.

Assumption 3, prediction 1 – within a season: spatial shifts in foraging areas

Changes in the spatial distribution of foraging effort were evident at both Bird and Crozier (Royds not analyzed, see Methods; Fig. 1). Areas with decreasing foraging activity (green cells in Fig. 1) tended to occur near colonies, and areas with increasing foraging activity (red cells in Fig. 1) away from colonies.

Assumption 3, prediction 1 – within a season: changing trip distance and duration

Trip distance and duration at Crozier increased over time, with birds exploiting areas further from the colony later in the season (Table 2, 3). These changes are evident in the positively sloped regression lines for trip time or trip length versus date for Crozier. This trend was not evident at either the Royds or at the Bird colonies, however, where the regression lines indicate little or no increase. By the end of the season, trips from Crozier greatly exceeded trips originating at Bird and Royds in terms of both length and duration. Strikingly, the regression lines for all three colonies in all years, as well as that for Crozier in 2005–2006, converge to similar values early in the season. (Fig. 6 and 7).

Discussion

We suggest from our results that the preyscape in the Adélie penguin foraging world in the Ross Sea, characterized on the basis of the assumptions that we tested (see Introduction), differs substantially and qualitatively from that envisioned in the marshes studied by Orians and Pearson. The assumption that the rate of prey capture decreases with the time spent feeding in a patch is based on the idea that prey encounter rate is positively related to the density of prey, and that the density of prey is reduced by the feeding activity of the predator. If the prey capture rate does not diminish with time spent feeding, then the Orians–Pearson model result is trivialized. Predators should commute directly and repeatedly to the patch having the highest prey capture rate (taking into account distance to that patch) and each time feed there until they have acquired the quantity of food necessary for themselves and their chicks (assumption 1). This situation resembles that described by Ropert-Coudert et al. (2004) and Boersma et al. (2009), where penguins swim long distances from their colonies to the same feeding areas, and expend relatively little foraging effort during the outbound and inbound legs of their trips.

Foraging within a patch

Unlike this assumption of Orians and Pearson, our analysis did not show a decrease in foraging dive rate (proxy for prey acquisition; Watanabe et al. 2014) over the course of a feeding bout, except to a small degree for Crozier birds
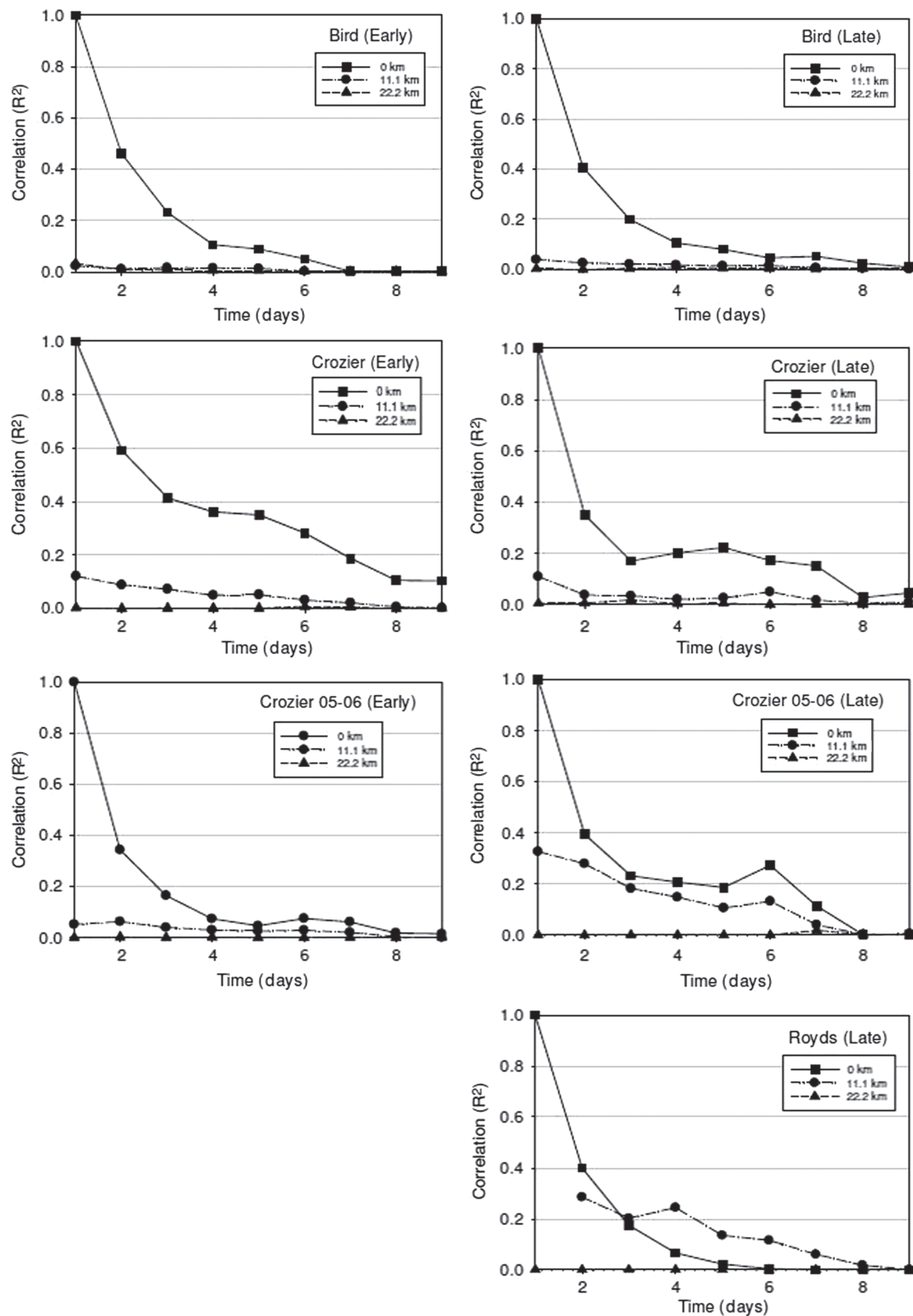
Figure 4. The predictability of food resources as measured by autocorrelation between foraging dive rate at two places separated by a given lapsed time and distance. The data are partitioned by colony and season. The vertical axis is a measure of the predictability of foraging dive rate (r^2) for two points separated by a given time and distance. Time is shown on the x-axis, and distances are shown as different point and line patterns.
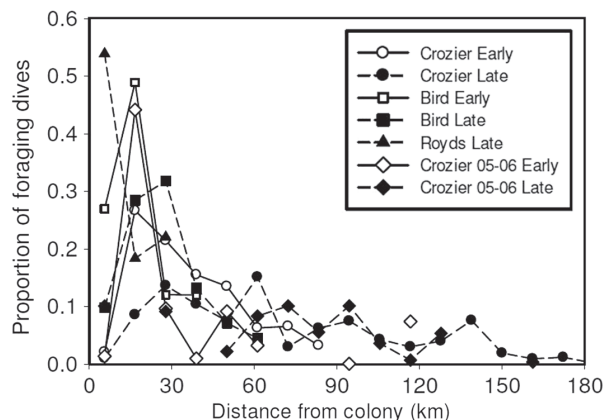
Figure 5. The proportion of all foraging dives occurring at a given distance is shown for each season and colony combination. Data are binned into 11.1 km (6 nm) annuli around each colony. The proportion of foraging dives is estimated as the number of foraging dives occurring within a particular distance band divided by the total number of foraging dives in all distance bands.

during the late season in the 2005–2006 iceberg year. The latter might be indicative of lower food availability during that time (perhaps due to smaller or less dense prey patches), consistent with other results indicating that the iceberg shifted foraging into a less productive portion of the Ross Sea polynya MIZ (Dugger et al. 2014, Lescroël et al. 2014). The late season 2005–2006 Crozier result is consistent with what Watanabe et al. (2014) found in their system. The fact that this result only occurred then indicates that prey are usually much more available to penguins in the southern Ross Sea than they are in Lützow-Holm Bay where the latter authors conducted their study.

Foraging during a single trip

Otherwise, at the next larger scale, Ross Island penguins foraged to the extent of their maximum ability within given prey patches as determined by physiological constraints (i.e. breath-holding ability; Mori 1998) and not prey depletion. This result indicates that, on the scale of an Adélie penguin foraging trip in the southern Ross Sea, prey density is not diminished by a single penguin's feeding behavior nor by the behavior of the small flock in which it is included (Adélie penguins usually forage in flocks of 5–15 individuals; Ainley 2002). This result could occur because the quantity of food available to the foraging penguin usually is very large relative

Table 2. Results for the linear regression of foraging trip duration as a function of trip date. The table includes results for datasets that include multiple trips by the same individual and datasets that exclude multiple trips by the same individual.

Colony	Multiple trips included			Multiple trips excluded		
	Number of trips	R²	p	Number of trips	R²	p
Bird	41	0.305	0.001	39	0.274	0.001
Crozier	88	0.182	0.001	69	0.156	0.001
Crozier 2005–2006	25	0.0889	0.148	16	0.122	0.184
Royds	24	0.105	0.122	13	0.0976	0.299

Table 3. Results for the linear regression of trip length on foraging trips as a function of trip date. The table includes results for datasets that include multiple trips by the same individual and dataset that exclude multiple trips by the same individual.

Colony	Multiple trips included			Multiple trips excluded		
	Number of trips	R²	p	Number of trips	R²	p
Bird	41	0.209	0.001	39	0.201	0.004
Crozier	88	0.345	0.001	69	0.355	0.001
Crozier 2005–2006	25	0.0775	0.178	16	0.0725	0.313
Royds	24	0.067	0.222	13	0.114	0.259

to the penguin's rate of consumption, because horizontal or vertical transport of prey replenished the local food supply, or because penguins continue to move through or actively locate new prey concentrations as they feed. Penguins at Royds foraged as would be expected under circumstances of unchanging prey availability, returning again and again to the same area near the colony. At Crozier and Bird, however, foraging birds often did not return regularly to the same feeding locations, exploring much larger areas and, therefore, encountering a much wider range of prey availability.

Foraging within the chick-feeding season

The decline in the foraging dive rate immediately adjacent to the colony (Fig. 1) is consistent with what the Orians–Pearson model predicts when prey are locally depleted in the area near the colony where commuting costs are minimal. We were surprised, however, to find that the distance bands where the highest proportion of foraging dives occurred was still relatively near to the colony, from 22.2 and 33.3 km (Fig. 5). Penguins expended a higher proportion of their foraging effort in distance bands near their colonies than they did at distant sites which were many hours of travel away. Based on the logic of the OP–CPF model, this should not occur. Either the prey capture rate is higher near the colony or it is higher at distant and peripheral sites. If the capture rate is highest near the colony, then it would be sub-optimal to travel many km to reach a region with a lower prey
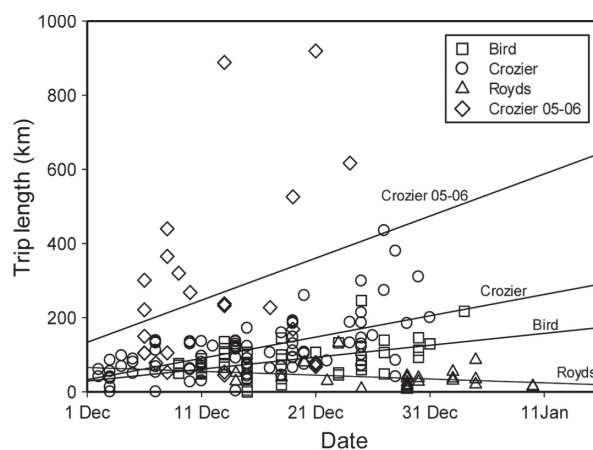

Figure 6. The distance travelled on a foraging trip (length) is shown relative to date of the beginning of the trip. Each foraging trip represents one data point. Regression lines indicate seasonal trends based on the regression of length (distance) on date.
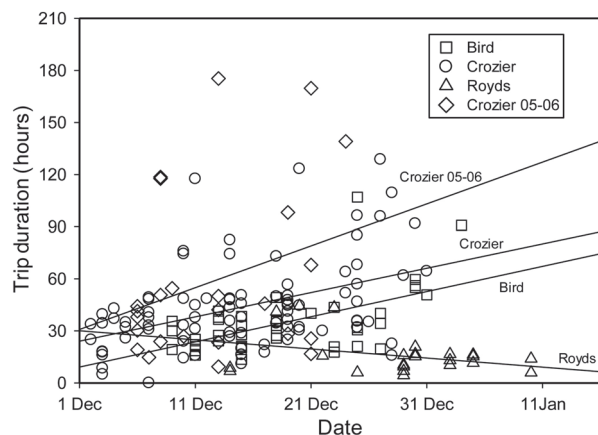
Figure 7. The time spent on a foraging trip (duration) is shown relative to date of the beginning of the trip. Each foraging trip represents one data point. Regression lines indicate seasonal trends based on the regression of time (duration) on date.

capture rate: if the prey capture rate is highest at the periphery of the foraging area, then penguins should postpone their foraging dives until they arrive in the richer area. In the context of OP–CPF, we therefore expect that either 1) foraging dive rates will show a threshold effect as birds move outward from their colonies and postpone foraging behavior until they reach richer less depleted areas more distant from their colony, or 2) forage in the immediate vicinity of the colony. The tendency of penguins to forage continuously as they move away from their colony is also apparent in the plots of foraging dive rate versus distance from colony as shown in Fig. 3 and discussed below.

Value of prior knowledge of the preyscape

The fact that the penguins do not delay their feeding until they reach more distant patches that are not yet depleted may be related to the unpredictability of prey resources (Fig. 3), and is probably part of the reason that Bird and Crozier penguins did not regularly return to the same foraging sites near their colonies. But predictability alone is insufficient to explain differences between Royds compared to Bird and Crozier since the predictability of resources at Royds was only slightly better than at other colonies, and was comparable to predictability at Crozier in January of the iceberg year, 2005–2006.

Another explanation for the relatively small size of the foraging area at Royds, and its consistent use, could be that nearby resources do not become depleted over the course of the season, quite unlike the situation at Bird and Crozier, where there are many more penguins. This interpretation is supported by the declining usage of areas near these larger colonies, steady increases in trip distance and duration, and increasing foraging activity further away from the colony as the breeding season progresses (Table 2, 3, Fig. 1, 3; see also Lyver et al. 2011, who studied a large colony in the northern Ross Sea). Lowered prey availability near the large colony would force foraging birds to travel farther, relying on areas that they visit less frequently and therefore are less predictable in terms of the prey densities and accessibility. It is also possible that longer trips are a result of parents needing

to return less frequently to provision and guard chicks, or because the energetic demands of the chicks are increasing and more food is required.

The circumstances of an Adélie penguin foraging in the southern Ross Sea differs from the classic CPF model in the degree to which prey are distributed in discrete patches (assumption 2). Coping with the spatial heterogeneity in prey availability at the sub-mesoscale level, Adélie penguins in our study regularly made foraging dives as they traveled. The Orians–Pearson model predicts that central place foragers should not engage in foraging behavior until they arrive in a region of high prey density, typically at the periphery of their foraging area or where prey have not yet been depleted. This, too, differs from the colonies studied by Ropert-Coudert et al. (2004) and Boersma et al. (2009), in which prey in sufficient density for efficient foraging occurred only a long distance out to sea. In contrast, Ross Sea penguins clearly do not wait until they come to regions with the highest prey density or availability to begin foraging dives (Fig. 3). Under the assumptions of the Orians–Pearson model, this behavior would appear to be less than optimal since birds still must pay the energetic price of traveling far from the colony. Why then do they do this?

This deviation from Orians–Pearson model predictions could result from several factors. It is always possible that birds are foraging in a systematically non-optimal manner, unable to resist feeding even at the expense of longer term efficiency. This is not a satisfying explanation since inefficient foraging should be selected against, and the sub-optimal foraging paradigm generates few testable hypotheses. Nonetheless, sub-optimal foraging is a difficult hypothesis to reject.

One reason for the tendency of penguins to forage where prey availability is relatively low might have to do with the cost of foraging dives, and the possibility that they are especially hungry after feeding chicks. If the cost of diving were very small, it would be worthwhile to dive frequently, capturing food anywhere it was encountered. But diving is an energetically costly activity (Kooyman 1989, Williams et al. 2000), and feeding while commuting would significantly increase the time spent traveling to areas of high quality patches (Fig. 1, 3). However, diving (and capturing some prey) soon would reduce hunger and might be a physiological necessity, and would have the added advantage of providing information regarding prey availability. Given that prey capture rates are unpredictable in our study area, penguins cannot simply swim to where they know they will find a rich source of food or avoid (or swim quickly through) an intervening area where there is no food. Instead, a plausible explanation is that, based on their previous experience and knowing only that some prey is available close to the colony, it is to their advantage to assess prey availability as they commute so that they can exploit prey where ever they are encountered. In an unpredictable foraging environment at the sub-mesoscale, a strategy where feeding, assessment, and commuting are mixed is potentially advantageous.

Continuous sampling would also become useful if penguin foraging drove prey deeper than a penguins' diving capability (as noted in surface-feeding flighted seabirds: Lewis et al. 2001, Ainley et al. 2003a). Then it could be that a prey school that had not been recently harassed might have risen in the water column to exploit its own food supply

(i.e. phytoplankton needing to be near the light found near the surface) thereby renewing its jeopardy. In fact, Adélie penguins, particularly at the large colony, dive deeper as the season progresses (Lescroël et al. 2010). Penguins finding or driving prey into the darkness of deeper depths, where it might reside to reduce predation, was a phenomenon recently explored by Ainley and Ballard (2011, see also Wilson et al. 1993). Given that the ocean almost everywhere off the Ross Island colonies is on the order of 800 m deep, there is plenty of water column in which prey could avoid Adélie penguins.

The local, sub-mesoscale distribution of food likely explains much of the pattern that we saw (assumption 3, habitat quality is unpredictable) unlike that seen by Ropert-Coudert et al. (2004) and Boersma et al. (2009). In those studies, penguins were observed to commute between colony and distant foraging area, swimming through a region of sparse or nonexistent feeding opportunities to reach areas of high quality prey patches further from their colonies. As noted, the western Ross Sea is incredibly rich in food for mesopredators, the availability of their prey varying on the sub-meso – rather than meso – or larger scale. Such a food distribution also likely explains why we observed no pattern of alternation between short (acquire food for the offspring) and long (food for oneself) feeding trips (Ballard et al. 2010), as seen in many seabirds including some penguins in areas where areas of high or adequate food availability are distant (see references in Ropert-Coudert et al. 2004).

Finally, it could be, too, that a robust cetacean (and other mesopredator) population(s), unlike most oceans elsewhere, partly explains the penguins' foraging strategy (see spatial models in Ballard et al. 2012) and seeming lack of knowledge about habitat quality and the preyscape. Areas that penguins have recently visited are moderately predictable for only 4–7 d, and apparently they know almost nothing about areas just ten kilometers away. These whales can quickly and easily delete entire swarms of prey or drive them deeper than the penguins' foraging capabilities, thus, altering the preyscape radically and making it more unpredictable than it would be otherwise. Indeed, it is true that penguins are forced to increase their overall foraging effort while high numbers of whales are in their foraging areas of the southern Ross Sea (Ainley et al. 2006). In other words, because of abundant intra- and interspecific competition for resources, Adélie penguins in the Ross Sea are faced with unpredictable and sometimes sparse resources. Under these circumstances, constant sampling and opportunistic feeding may be their optimal strategy.

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