ORIGINAL PAPER

Intra-seasonal variation in foraging behavior among Adélie penguins (*Pygocelis adeliae*) breeding at Cape Hallett, Ross Sea, Antarctica

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Abstract We investigated intra-seasonal variation in foraging behavior of chick-rearing Adélie penguins, *Pygoscelis adeliae*, during two consecutive summers at Cape Hallett, northwestern Ross Sea. Although foraging behavior of this species has been extensively studied throughout the broad continental shelf region of the Ross Sea, this is the first study to report foraging behaviors and habitat affiliations among birds occupying continental slope waters. Continental slope habitat supports the greatest abundances of this species throughout its range, but we lack information about how intra-specific competition for prey might affect foraging and at-sea distribution and how these attributes compare with previous Ross Sea studies. Foraging trips increased in both distance and duration as breeding advanced from guard to crèche stage, but foraging dive depth, dive rates, and vertical dive distances travelled per hour decreased. Consistent with previous studies within slope habitats elsewhere in Antarctic waters, Antarctic krill (*Euphausia superba*) dominated chick meal composition, but fish increased four-fold from guard to crèche stages. Foraging-, focal-, and core areas all doubled during the crèche stage as individuals shifted distribution in a south-easterly direction away from the coast while simultaneously becoming more widely dispersed (i.e., less spatial overlap among individuals). Intra-specific competition for prey among Adélie penguins appears to influence foraging behavior of this species, even in food webs dominated by Antarctic krill.

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Introduction

The diet composition of seabirds varies temporally and spatially (e.g., Murphy 1925; Ashmole and Ashmole 1967; Ainley and Boekelheide 1990). To cope with such variability, brought by abiotic (e.g., climate cycles, proximity to productive fronts) and biotic (e.g., prey life cycles, inter- and intra-specific competition) factors, seabirds demonstrate the ability to adjust to constraints imposed by morphological, physiological, and behavioral characteristics

(references above; also Ballance et al. 2001; Tremblay and Cherel 2003; Ballard et al. 2010a, b).

During the last 3–4 decades, increased variability, and an apparent decline in abundance and availability of mid-trophic level organisms that comprise the prey of top predators in marine food webs around the world have been linked indirectly to climate change and directly to intensive commercial fishing and other direct anthropogenic factors (Pauly et al.1998; Hilborn et al. 2003; Osterblom et al. 2006, 2007; Watermeyer et al. 2008a, b, Baum and Worm 2009; Perry et al. 2009). These changes increasingly conflict with the ability of some seabirds to successfully adapt aspects related to their foraging strategies in order to acquire sufficient food to maintain reproduction and survival (Iverson et al. 2007; Grémillet et al. 2008). Our ability to detect the impacts of changing foraging conditions on seabirds is confined largely to long- and well-studied species including Northern gannet, *Morus bassanus* (Grémillet et al. 2008), Black-legged kittiwake, *Rissa tridactyla* (Lewis et al. 2001; Daunt et al. 2002; Frederiksen et al. 2004), and Common guillemot, *Uria aalge* (Osterblom et al. 2006; Wanless et al. 2005). These studies allow comparisons with conditions that occurred during an earlier state (i.e., regime) of a system. Yet, few remaining ocean ecosystems have remained unaffected by long-term and large-scale fishing and other anthropogenic impacts (Hilborn et al. 2003; Halpern et al. 2008). The Ross Sea (a relatively anthropogenically unaffected and intact ecosystem) provides an exemplary natural laboratory to measure ecosystem variability and ecological processes in foraging and trophic relationships among species (Ainley 2002a, 2004; cf. Leopold 1949).

The Adélie penguin, *Pygocelis adeliae*, is one of two truly Antarctic penguins (the other being the Emperor, *Aptenodytes forsteri*) and is one of the most extensively studied seabirds in the world (recent research summarized in Ainley 2002b). The Adélie penguin is an obligate pack-ice species that typically forages where sea ice concentration is 20–80% (Fraser and Trivelpiece 1996; Smith et al. 1999; Ballard et al. 2010a) but can also forage in open sea (recently vacated by sea ice) and under pack ice and coastal fast ice (Ainley et al. 1998; Clarke et al. 1998; Rodary et al. 2000; Watanuki et al. 1999; Kato et al. 2003). Off the western Antarctic Peninsula, Adélie penguins concentrate foraging in waters overlying bathymetric complexity at the heads of submarine canyons (Fraser and Trivelpiece 1996; Chapman et al. 2004; Ribic et al. 2008). As central-place foragers, breeding Adélie penguins have limitations to how far they can forage and still effectively provision young (Ballance et al. 2009; Ballard et al. 2010a). To cope with dynamic sea ice conditions, varying prey distribution and availability, and the seasonal flux in potential intra- and inter-specific competitors (Ainley et al. 2004, 2006; Lescroël and Bost 2005; Friedlaender et al.

2008) requires breeding Adélie penguins to have adaptable foraging behaviors. Even so, in some regions of Antarctica (i.e., Antarctic Peninsula), where diversity among prey options may have become reduced (Emslie and Patterson 2007) and inter-specific competition has increased (Ainley et al. 2009), it appears that Adélie penguins can no longer adapt their foraging behavior to successfully cope with changing conditions (Forcada et al. 2006; Ducklow et al. 2007; Hinke et al. 2007; Ainley et al. 2010).

Ainley et al. (2004, 2006) and Ballance et al. (2009) concluded that intra- and inter-specific competition influence Adélie penguin foraging behavior differently at colonies of varying size and proximity to oceanic features (e.g., polynyas, ocean fronts). Ballance et al. (2009) demonstrated that Adélie penguin colony size positively correlated with foraging trip duration and proposed that competition-induced reduction in prey availability resulted in greater energy expenditure for birds foraging in the prey depletion halo that forms as a result around large colonies (such as Cape Crozier, 135,000 breeding pairs; Ballance et al. 2009). To compensate for the halo-effect, a bird must increase its foraging distance and thereby use more energy. The combination of sea ice conditions, oceanography, prey availability, and intra- and inter-specific competition experienced by Adélie penguins determines their seasonal foraging patterns and diet (Kato et al. 2002; Ballance et al. 2009), short-term- and long-term fluctuations and trends in demographic parameters, and ultimately abundance (Weimerskirch 2001). The ability to cope with such variability indicates a certain degree of phenotypic plasticity (e.g., Forcada et al. 2008; Lescroël et al. 2010).

Here, we investigate the degree to which Adélie penguins breeding at Cape Hallett, northwestern Ross Sea (northern Victoria Land coast) altered their foraging behavior during the 2004/2005 and 2005/2006 chick-rearing periods. Whereas the foraging behavior of this species has been well studied in continental shelf ecosystems of the Ross Sea (Clarke et al. 1998; Ainley et al. 2003, 2004; Lescroël et al. 2010), this is the first Ross Sea study to examine penguins foraging in a continental slope-dominated ecosystem, a condition that is similar to most other (non-Ross Sea) investigations. Northern Victoria Land also supports the greatest abundance of Adélie penguins throughout its range. Previous work demonstrated that Adélie penguins at a large colony (Cape Crozier) extended foraging trip duration and diving depth, whereas these patterns were not evident at smaller colonies (Capes Royds and Bird; Ballard 2010). We consider evidence to evaluate the following three hypotheses. First, in the absence of intra-specific prey competition we expected that foraging parameters (foraging trip distance, duration, dive depth, and dive frequency) would not increase as the chick-rearing phase progresses because of Cape Hallett's relatively smaller colony size (19,744 breeding

pairs; Lyver and Barton unpublished data) as compared with large colonies such as Cape Crozier (cf. Ballard 2010). Second, consistent with other studies in the southern Ross Sea and East Antarctica, we expected that the proportion of fish in chick meals at Cape Hallett would increase as the season progresses (Puddicombe and Johnstone 1988; Clarke et al. 2002; Ainley et al. 2003, 2006). Third, we determined the degree to which Adélie penguin foraging areas correlate with characteristics of the physical environment (bathymetry and sea ice). We expected that as sea ice conditions allow, space sharing would decrease as foraging areas expanded and shifted northwards toward zones of heterogeneous bathymetry and relatively greater productivity, such as the Ross Sea Continental Slope and Shelf-break Front (Ainley et al. 1984; Fraser and Trivelpiece 1996; Chapman et al. 2004; Ribic et al. 2008).

Materials and methods

We conducted all field work at Cape Hallett, Ross Sea (72°19′S, 170°12′E; Fig. 1) between 20 December and 15 January 2004–2005 and 2005–2006. We attached Smart Position or Temperature Transmitting Tags (SPOT4; $n = 26$; Wildlife Computers, Redmond, WA, USA, 52 g, dimensions: $88 \times 25 \times 12$ mm) or Time Depth Recorders (TDR–Mk9; $n = 26$; Wildlife Computers, 30 g, dimensions: $67 \times 17 \times 17$ mm) to breeding Adélie penguins using Tesa® tape (see Wilson and Wilson 1989 and Ballard et al. 2001 for details on attachment). We randomly selected adult Adélie penguins and captured them by hand or with the aid of a landing net during pair change-over during the guard period (i.e., when one or both parent birds are present at the nest; 20–31 Dec) and crèche period (i.e., when chicks group together generally in the absence of parent birds; 1–15 Jan) of the chick-rearing season (Table 1). To aid relocation of birds we also attached a small VHF transmitter (TX-Sirtrack, NZ, 15 g, dimensions: $43 \times 20 \times 10$ mm) to the penguin's back feathers just above the SPOT or TDR (see Wilson and Wilson 1989; Wilson et al. 1997). We attempted to recover devices from each bird after they completed one foraging trip, but several individuals (19%) completed multiple trips at sea (Table 1).

Satellite telemetry

SPOT tags were set to transmit every 45 s for the first 8 transmissions and then once every 90 s thereafter and programmed to turn off after being dry for 23 h in order to conserve batteries. All transmissions were received and processed using the ARGOS system (CLS Corporation, Ramonville Saint-Agne, FR). Before analysis, we excluded data collected from one SPOT tag that was attached to an
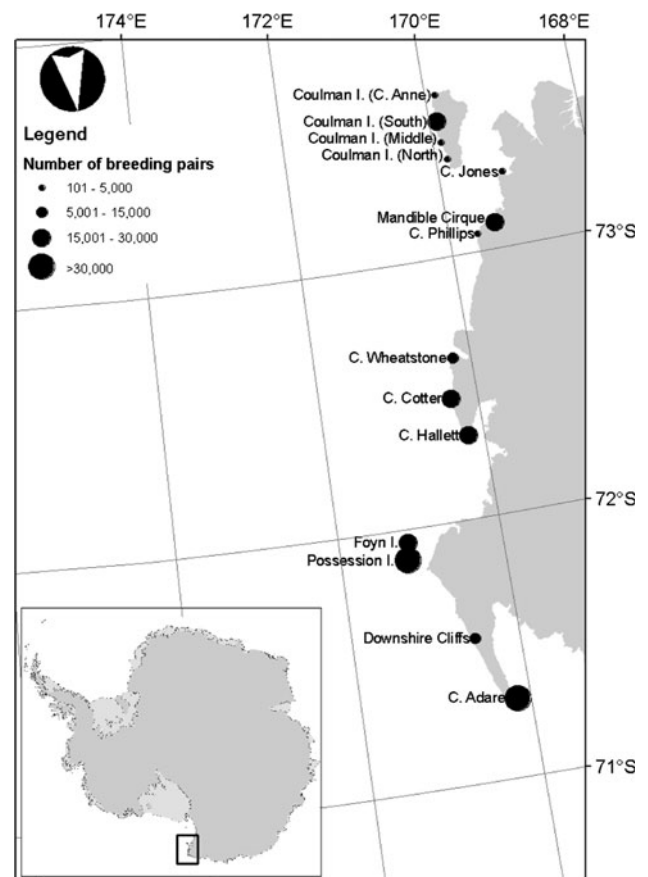

Fig. 1 Location and relative size of Adélie penguin colonies in the northern Ross Sea, Antarctica

individual that failed to return to the colony. We also removed all locations overlapping land/ice shelves or ice tongues outside the colony area. We removed duplicate ARGOS location records (i.e., multiple location records for the same individual recorded within the same minute); in each case we retained the higher-quality location record. To remove potentially erroneous locations for individuals with >4 locations, we used a speed-distance-angle ARGOS filter (SDAfilter function, argosfilter package version 0.5; Freitas et al. 2008) in the statistical program R (version 2.6.1; R Development Core Team 2007). We specified a maximum speed threshold of 2.2 m s^{-1} (Ainley 2002b) and used default settings for distance and angle (Freitas et al. 2008). Because the first two and last two locations (i.e., end locations) along each track were retained automatically by the SDAfilter, we then used a purpose-built function to remove potentially erroneous end locations from the track when the maximum speed threshold 2.2 m s^{-1} was exceeded.

We used the filtered data and a custom function in MATLAB (MathWorks 2007) to create linearly interpolated locations (Tremblay et al. 2006) every half an hour along each individual track line. To avoid misrepresentation of an individual's location, we did not interpolate track-line

Table 1 Summary satellite tracking data collected from 27 Adélie penguin adults tagged at Cape Hallett breeding colony Ross Sea, including the dates that tags were deployed and retrieved

Bird ID	Breeding season	Stage	Deployment (Julian day)*	Retrieval (Julian day)*	No. of locations for complete track			No. of foraging trips	1st foraging trip	
					Pre-filter	Post-filtered	Interpolated		No of locations	Final location within 3 km of colony
1	2004/2005	Guard	356	359	17	12	22	1	21	n
2	2004/2005	Guard	357	360	45	30	56	1	26	y
3	2004/2005	Guard	360	363	66	51	97	2	45	y
4	2004/2005	Guard	361	362	38	26	60	2	29	y
5	2004/2005	Guard	362	363	12	7	25	1	23	y
6	2004/2005	Guard	363	365	52	38	94	1	69	y
7	2004/2005	Guard	363	365	34	27	70	1	48	y
8	2004/2005	Guard	366	2	45	33	74	1	38	y
9	2004/2005	Guard	366	2	34	23	68	1	41	y
10	2004/2005	Crèche	6	9	39	29	61	1	35	n
11	2004/2005	Crèche	6	10	107	81	188	1	151	y
12	2004/2005	Crèche	11	16	36	27	53	1	43	y
13	2004/2005	Crèche	11	16	76	51	184	1	177	y
14	2005/2006	Guard	354	357	65	44	86	2	19	y
15	2005/2006	Guard	354	358	95	74	168	2	16	y
16	2005/2006	Guard	357	360	56	46	74	2	38	y
17	2005/2006	Guard	358	360	62	40	86	1	83	n
18	2005/2006	Guard	360	363	81	51	118	1	112	y
19	2005/2006	Guard	360	362	79	54	94	1	82	y
20	2005/2006	Guard	362	364	59	41	93	1	83	y
21	2005/2006	Guard	363	365	47	31	87	1	77	y
22	2005/2006	Guard	364	2	33	27	41	1	20	y
23	2005/2006	Crèche	1	4	106	52	80	1	78	y
24	2005/2006	Crèche	2	5	142	85	154	1	144	y
25	2005/2006	Crèche	4	7	112	92	157	1	150	y
26	2005/2006	Crèche	9	14	152	113	195	1	167	n
27	2005/2006	Crèche	15	18	4	NA	NA	NA	NA	NA

(* Julian days calculated based on Greenwich Mean Time) and the number of locations retained pre- and post-filtering and interpolation for the complete track and 1st foraging trip (see Methods)

sections when the interval between filtered locations was ≥6 h. Interpolated locations provided us with a temporally uniform distribution of locations for analysis that, unlike the raw ARGOS locations are not biased by satellite orbital parameters and the penguin's latitudinal position (Georges et al. 1997; BirdLife International 2004).

To simplify analyses and avoid pseudo-replication associated with repeated measures from the same individual, we selected only location data for the first foraging trip for each individual. Therefore, we distinguished independent foraging trips as those tracks which ranged >3 km from the colony and were >6 h in duration (Ballard et al. 2001; Ainley et al. 2004; Ballard 2010). Only tracks with >4 locations post-filtering were retained (n = 26 individuals). Nicholls et al. (2007) reported a mean accuracy of <1

and <5 km for high (LC 3, 2, 1) and low (LC 0, A, B) quality ARGOS locations, respectively.

Foraging trip duration and distance

Using the interpolated location data, we estimated three parameters for the first foraging trip of each individual: duration, total distance travelled, and maximum straight-line distance from the colony. When calculating total distance travelled for each trip for individuals where a >6-h interval occurred between locations, we assumed a straight-line distance between these locations. When the last known location was away from the colony and the return time to the colony was unknown, we calculated the straight distance to the colony from the last known location and

assumed a maximum travel speed of 2.2 m s^{-1} to estimate the travel duration for this segment. All distance estimates were calculated using the great circle distance function in the ARGOS-filter package (Freitas et al. 2008).

Dive parameters

We used Mk9 TDRs to measure the depth (range: 0–1,000 ± 0.5 m) and temperature (range: −40–60 ± 0.05°C) every 10 s. Because a 10-s sampling interval was too coarse to accurately measure maximum dive depth, we only use these data for comparisons within this study, and care should be taken when comparing with other studies where sampling frequency on similar TDRs was typically higher.

We used program *Divesum* (v.7.5.5; G. Ballard unpublished computer script) to process raw diving data. This program corrected the recorded surface pressure and computed five dive parameters for each dive: (1) dive duration (s); (2) maximum depth (m); (3) depth change rate (m s^{-1}; calculated as a running average for each 5-s block of the dive duration; slow [<1 m s^{-1}] and fast [>1.5 m s^{-1}] dives with depth change rates ≥4 m s^{-1} were indicative of instrument error and excluded from subsequent analyses; (4) rate of ascent and descent (m s^{-1}; sustained rate of depth change in same direction from surface to bottom and from bottom to surface; we defined bottom as any depth within 60% of the maximum depth recorded); and, (5) bottom time (s; the duration within 60% of the maximum depth and with no change in depth exceeding 0.5 m s^{-1}). For analyses, only dives ≥5-m deep and ≥30 s in duration were considered.

Because of the 10-s sampling interval of TDRs, we used a 30-s filter in analysis which prevented reliable classification of "foraging" versus "exploratory" dives, so we combined these into a single class (F/E). F/E dives were ≥10 m and had either ≥15 s bottom time, 30% of the dive duration spent in slow depth change rate and 30% with fast depth change rate, or <15 s bottom time and rapid (≥1 m s^{-1}) ascent/descent phases. All other dives were categorized as "other" (O) and are thought to be primarily commuting dives. Although we could not quantify fine-scale dive parameters (cf. Lescroël et al. 2010), we used our data to determine the following five dive parameters: (1) mean dive duration (2) mean maximum depth during F/E dives (3) mean bottom time during F/E dives (4) number of dives per hour for all types combined and for F/E dives separately, and (5) hourly vertical distance (m) for all dives combined and F/E dives separately.

Diet analysis

We combined four techniques to assess Adélie penguin diet during the breeding seasons (2004/2005: guard n = 17

samples; crèche n = 13; 2005/2006: guard n = 18; crèche n = 52): (1) stomach flushing (Wilson [1984]; 58% of samples); (2) spilled prey remains collected from the ground after chick-feeding regurgitations (33% of samples); (3) stomach contents of chicks found dead (7% of samples); and (4) stomach contents of chicks killed by South polar skuas (*Stercorarius maccormicki*; 2% of samples). Stomach flushing did not yield the complete contents of the stomach but rather allowed individuals to regurgitate about a quarter (~250 g) of their stomach contents. As described in Ainley et al. (2003), most of the food beneath the upper portion is a soupy mush which cannot be separated according to prey species. Furthermore, taking only the upper portion allowed the parent to provide at least some food to its chick (Lishman 1985; Ainley et al. 1998). Ainley et al. (2003) also showed that results from stomach flushing were consistent with stable isotope analysis that indicated the relative proportions of krill and fish in the diet. No data exist that indicate Adélie penguin parents feed their chicks a diet different from what they eat themselves (Ainley et al. 2003).

We obtained flushed stomach samples at 7-day intervals beginning 22 December (the beginning of the chick-rearing period) and ending 22 January, with dates closely corresponding between years. In each session, we collected samples from 8 to 10 adults just after they came ashore. To ensure we sampled breeding individuals, we caught birds at their nests just before they fed their chicks. We preserved samples with 70% ethanol for later analysis.

Within each diet sample, we separated euphausiids from fish remains and estimated the relative proportions of each. Whereas we identified euphausiids to species, we did not identify fish otoliths; therefore, the percentage of stomach content samples made up by fish likely under-estimated true dietary contribution because fish are digested more rapidly than krill. Based on previous studies of fish distribution and Adélie penguin diet, we assumed the majority of fish present in samples were Antarctic silverfish, *Pleuragramma antarcticum* (DeWitt 1970; Eastman and Hubold 1999; Donnelly et al. 2004; O'Driscoll et al. 2009). We compared the relative percentages of fish delivered to chicks during the guard and crèche stages of the breeding season. We classified guard and crèche season diet samples as those collected during 22 December–2 January and 3–22 January, respectively. Here, we used samples collected approximately 2 days later than the matching foraging trip and dive parameters (described above) to account for the length of foraging trips, which averaged 2.3 days during the crèche stage.

Individual utilization distributions

To quantify the location and area among individuals' distribution at sea, we calculated fixed-kernel utilization

distributions (UD, Van Winkle 1975) for interpolated track lines using a 3×3 km raster. We selected this cell size as it is approximately equivalent to the nominal accuracy of the combined ARGOS locations (see above; Nicholls et al. 2007). To calculate kernel values, we specified a bivariate-normal model (R: kernelUD function in the adehabitat v.1.7.1 package; Calenge 2006) and a smoothing parameter of 9 km to best represent the area used by penguins based on their estimated tracks. We arbitrarily chose three classifications to describe the at-sea distribution of individual Adélie penguins: we define *foraging* area to be the area within the 90% probability density contour (90UD; Börger et al. 2006); *focal* area to be within the 50% probability density contour (50UD area), and *core* area to be within the 25% probability density contour (25UD area). We used the adehabitat *kernel.area* function to estimate the total areas of foraging, focal, and core areas. To quantify shifts in the location of UD areas between guard and crèche stages, we calculated the latitude and longitude range limits for individuals' foraging, focal, and core areas.

Spatial overlap among individuals

To quantify space sharing among individuals within guard and crèche stages, we calculated two measures of overlap. First, we used the home range (HR) method (see Equation 1 in Fieberg and Kochanny 2005) to estimate the proportion of at-sea distribution area of animal *i* that overlapped with animal *j*. Second, to quantify space use sharing of animals *i* and *j* we estimated the volume of intersection statistic (VI index; see Equation 5 in Fieberg and Kochanny 2005). The VI method uses the UD estimates of both animals to calculate the degree to which individual *i* and individual *j* sharing space where the UD areas intersect. Both overlap indices were calculated using the *kerneloverlap* function in the adehabitat package in R (Calenge 2006). For each individual's 90, 50 and 25UD, we estimated its mean overlap (both HR and VI) with all other individuals within that stage of the season within the relevant year. Because the maximum VI estimate was determined using 90, 50, and 25UD, we scaled VI estimates to range between 0 and 1.

Comparative analysis of foraging range and trip parameters

We tested for temporal variation in foraging behavior by fitting a set of candidate linear regression models, where the foraging parameter was the response variable and year (2004/2005 and 2005/2006), the stage of the season (guard or crèche) or stage of season (nested within year) were the potential explanatory variables (Appendices 1–3). We evaluated all models in R using the *lm* function and the maximum likelihood method. We identified the best-fit model or subset of models using Akaike's information criteria corrected for small sample sizes (AICc). To normalize residuals, we log-transformed values for foraging trip distance, duration, and area estimates for foraging, focal, and core areas. We used an arcsine transformation to analyze percentage diet estimates.

Colony-level utilization distributions and hotspots of distribution at sea

For guard and crèche stages, we identified hotspots of distribution at sea (i.e. areas where the individual UD values were relatively high and also where multiple individuals overlapped in space; MacLeod et al. 2008). First, we estimated the number of individuals' 90UD areas that occupied each 3×3 km grid cell. We then summed the relevant individuals' 90UD surfaces ($\Sigma_n 90UD$) to calculate a colony-level estimate of the total proportional amount of time spent within each 3×3 km grid cell. Finally, we weighted the summed UD values for each 3×3 km grid cell according to the number of individuals that co-occupied it: $\Sigma_n 90UD/n_t^{-1}$, where n_t was the number of individual 90UD kernel surfaces which overlapped that grid cell. Thus, $\Sigma_n 90UD/n_t^{-1}$ estimates for grid cells that were only occupied by a few individuals were down-weighted relative to those visited by a greater number of penguins.

Bathymetry and sea ice coverage

We obtained sea ice imagery (250-m pixel resolution) coinciding with our study for the northwest portion of the Ross Sea from the Moderate Resolution Imaging Spectro-radiometer (MODIS) platform (http://rapidfire.sci.gsfc. nasa.gov/subsets/?RossSea). Frequent cloud cover in our study area limited our evaluations to only one image per breeding stage in each of the breeding seasons. MODIS sea ice data were presented for the following Julian days during the guard and crèche stages: 357 and 024 in 2004/2005, respectively; and 354 and 016 in 2005/2006, respectively. Bathymetric maps show the 200-, 500-, 900-, and 1,500-m contours (Data reproduced from the GEBCO Digital Atlas published by the British Oceanographic Data Centre on behalf of IOC and IHO 2003).

Results

Summary of location data filtering process

Between 20 December and 15 January, we obtained 601 locations from 13 penguins in 2004/2005 and 1089 locations from 13 penguins in 2005/2006 (Table 1). Before

track-line interpolation, we retained 71 ± 8% (SD; range = 49–82%) of locations after speed-distance-angle filtering. Among the 26 penguins tracked, 18 and 8 foraging trips occurred during the guard and crèche stages, respectively.

Foraging trip parameters

During guard stage, foraging trips averaged 22 h, 79 km, and were a maximum straight-line distance of 35 km from the colony (Table 2). The duration of foraging trips, the total distance travelled, and the maximum straight-line distance from the colony were approximately three times longer and farther during the crèche stage, respectively (Table 2). In all cases, the subset of best-fit models included season and season (nested within year), highlighting the importance of stage of season as a predictor of temporal variance in foraging trip parameters (Appendix 1).

Dive parameters

Mean maximum depth, dives per hour, and hourly vertical distance travelled for F/E dives were less during the crèche stage than during the guard stage (Table 2; Appendix 2). There was no evidence of intra-seasonal change in mean dive duration or mean bottom time for F/E dives (Table 2; Appendix 2). The hourly vertical distance travelled for all dives also was less during the crèche stage (Table 2; Appendix 2).

Foraging, focal, and core areas

Individual foraging, focal, and core areas (as determined by the 90, 50 and 25UD, respectively) doubled between the guard and crèche stages (Table 3; Appendix 3). Within each stage, individual focal and core areas were about a third and tenth the area of the corresponding foraging areas, respectively; the latter increased from an average of 2,125–4,352 km^2 between guard and crèche stages.

Latitudinal-longitudinal extent of utilization distributions

Changes in the latitudinal and longitudinal extent of the UD areas occurred and were primarily associated with the southern and eastern boundaries (Table 3; Appendix 4). The northern limits of individual foraging, focal, and core areas retreated during the crèche stage in 2004/2005 (see best-fit model in Appendix 4; Table 3). The western extent of the UD areas increased between the guard and crèche stage in 2004/2005 but decreased in 2005/2006 (see best-fit model in Appendix 4; Figs. 2, 3, 4, 5; Table 3).

Table 2 Summary of foraging trip and dive depth parameters for breeding Adélie penguins tracked using satellite tags and time-depth recorders in the guard stage and crèche stages of two breeding seasons (2004/2005 and 2005/2006) at Cape Hallett, Antarctica

Aspect	Parameter	2004/2005						2005/2006					
		Guard stage			Crèche stage			Guard stage			Crèche stage		
		Estimate	LCL	UCL	Estimate	LCL	UCL	Estimate	LCL	UCL	Estimate	LCL	UCL
Foraging trip*	Maximum distance from colony (km)	38.6	21.0	71.0	94.6	49.1	182.6	31.8	18.6	54.4	110.6	49.5	247.4
	Total distance travelled (km)	70.6	37.3	133.7	209.4	105.1	417.3	86.6	49.3	152.1	310.6	133.5	722.8
	Total duration (h)	18.2	11.1	29.9	47.5	27.9	81.0	26.1	16.9	40.4	71.0	37.0	136.6
Foraging and exploratory dives	Mean dive duration (s)	111.2	101.1	121.3	113.5	92.1	134.9	108.4	97.7	119.1	102.9	91.4	114.3
	Mean maximum depth (m)	67.5	57.9	77.1	55.0	34.6	75.5	57.8	47.6	68.0	50.2	39.3	61.1
	Mean bottom time (s)	56.7	51.6	61.7	64.5	53.7	75.3	58.0	52.6	63.4	60.4	54.7	66.2
	Number of dives per hour	11.3	9.8	12.9	7.1	3.9	10.4	11.6	9.9	13.2	9.8	8.0	11.6
	Hourly vertical distance (m)	1,524.3	1,245.6	1,803.0	853.6	262.3	1,444.9	1,324.7	1,029.1	1,620.4	982.7	666.6	1,298.7
All dives	Number of dives per hour	16.1	14.2	17.9	14.6	10.7	18.6	16.9	14.9	18.7	16.6	14.5	18.7
	Hourly vertical distance (m)	1,617.5	1,343.7	1,891.3	996.5	415.8	1,577.2	1,428.1	1,137.7	1,718.4	1,120.1	809.7	1,430.6

The parameter estimates (with 2.5 and 97.5% confidence levels) presented were extracted from model 3 (Year/season) in Appendices 1 and 2. * Estimates have been back transformed (as data were log-transformed for analysis)

Table 3 Intra-seasonal variation in the area (km^2) and latitudinal and longitudinal extent of the foraging, focal, and core ranges (90, 50, and 25UD, respectively; UD = utilization distribution) among individual Adélie penguin adults tracked during two breeding seasons (2004/2005 and 2005/2006) at Cape Hallett, Antarctica

Variable	Range	2004/2005						2005/2006					
		Guard stage			Crèche stage			Guard stage			Crèche stage		
		Estimate	LCL	UCL	Estimate	LCL	UCL	Estimate	LCL	UCL	Estimate	LCL	UCL
UD area (km^2)*	Core	209	136	320	366	231	582	232	159	338	558	317	983
	Focal	648	417	1,008	1,217	756	1,959	736	499	1,086	1,703	950	3,051
	Foraging	2,004	1,345	2,986	3,932	2,556	6,049	2,245	1,579	3,191	4,771	2,815	8,085
North latitude (°S)	Core	72.20	72.14	72.26	72.31	72.25	72.37	72.24	72.19	72.29	72.23	72.16	72.31
	Focal	72.16	72.11	72.22	72.28	72.22	72.34	72.21	72.16	72.26	72.20	72.13	72.28
	Foraging	72.09	72.03	72.15	72.21	72.15	72.28	72.13	72.07	72.18	72.13	72.05	72.21
South latitude (°S)	Core	72.33	72.24	72.43	72.49	72.39	72.59	72.35	72.26	72.43	72.49	72.36	72.61
	Focal	72.36	72.28	72.45	72.53	72.44	72.63	72.38	72.30	72.46	72.51	72.39	72.63
	Foraging	72.43	72.34	72.52	72.59	72.49	72.68	72.44	72.36	72.52	72.56	72.45	72.68
East longitude (°E)	Core	171.06	169.96	172.16	173.37	172.18	174.56	171.61	170.64	172.58	173.66	172.21	175.11
	Focal	171.23	170.14	172.33	173.53	172.35	174.71	171.72	170.75	172.69	173.82	172.38	175.27
	Foraging	171.57	170.51	172.64	173.83	172.69	174.98	171.99	171.06	172.93	174.16	172.75	175.57
West longitude (°E)	Core	170.35	169.69	171.01	170.88	170.17	171.60	170.42	169.84	171.01	170.72	169.85	171.59
	Focal	170.19	169.58	170.80	170.70	170.04	171.36	170.20	169.66	170.73	170.36	169.55	171.17
	Foraging	169.80	169.67	169.93	169.71	169.56	169.85	169.76	169.64	169.88	169.94	169.77	170.12

The parameter estimates (with 2.5 and 97.5% confidence levels) presented were extracted from model 3 (Year/season) in Appendices 3 and 4. * Estimates have been back transformed (as data were log-transformed for analysis)
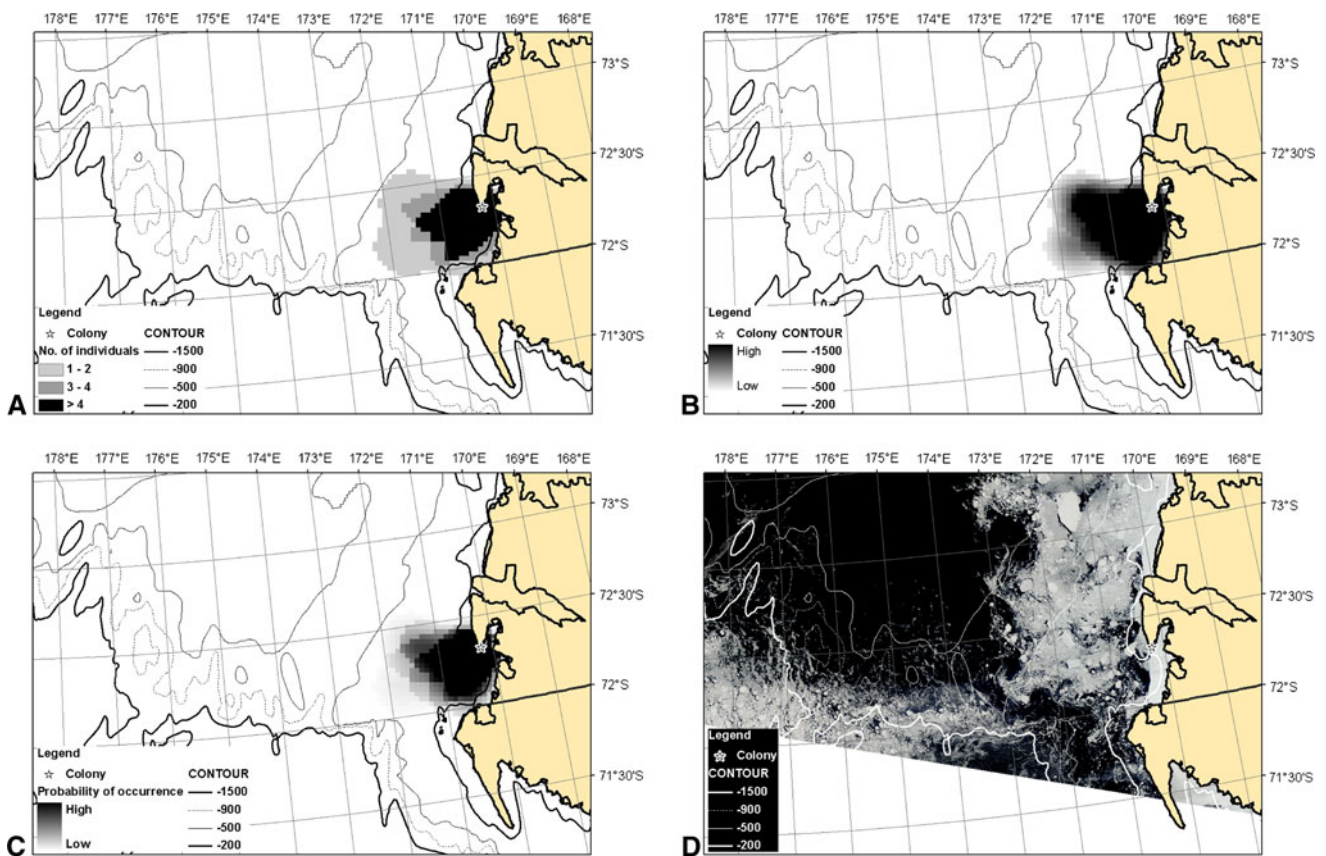
Fig. 2 At-sea distribution of satellite tracked Adélie penguins ($n = 9$) from the Cape Hallett breeding colony (as indicated by the *black star*) during the guard stage of the 2004/2005 breeding seasons : **a** the number of foraging areas (90UD) which overlapped each 3×3 km grid cell; **b** the summed Σ_n 90UD estimates; **c** the weighted Σ_n 90UD estimates, which provide a measure of the cumulative proportional time in space occupied by penguins at sea that takes into account both the number of individuals and the level of activity (time spent) in each 3×3 km grid cell; **d** the pack-ice distribution around the colony (Julian day 357). All maps show the 200, 500, 900, and 1,500-m bathymetric contours

Overlap in utilization distributions

Using the HR method, the degree of spatial overlap among individual foraging areas (90UD) decreased from 61% in the guard stage to 45% during the crèche stage, while measures of overlap among focal and core areas were approximately halved (Table 4; Appendix 5). Using the VI method, individual overlap also decreased from the guard to crèche stages (Table 4; Appendix 5). This pattern was consistent across all three area classes (i.e. foraging, focal, and core areas).

Diet composition

We identified two euphausiid species in stomach content samples ($n = 100$) collected from breeding Adélie penguins during 2004/2005 and 2005/2006: Antarctic krill (*Euphausia superba*) and Crystal krill (*E. crystallorophias*). *E. superba* was more frequent and occurred in 80% of all samples. *E. crystallorophias* occurred in only 3% of samples.

Unidentified fishes and amphipods were present in 52 and 49% of samples, respectively. *E. superba* comprised 85 and 74% of the estimated stomach content material during the guard and crèche stages, respectively. However, the proportion of fish in chick diet (likely underestimated) increased fourfold between the guard and crèche stages (Parameter estimate [2.5 and 97.5% CL] from the best-fit model (Year/season) in Appendix 6; guard stage: 2004/2005, 4% [0–14%], 2005/2006, 2% [0–9%]; crèche stage: 2004/2005, 24% [10–42%], 2005/2006, 8% [4–14%]).

Colony-level UD estimates and hotspots of at-sea distribution in relation to bathymetry and pack ice

In both years, the colony-level UD area was greater during the crèche stage, when individuals also were more widely dispersed (Fig. 2: 2004/2005: guard stage = 4,158 km^2; crèche stage = 15,327 km^2; 2005/2006: guard stage = 6,408 km^2; crèche stage = 12,510 km^2). At all stages, overlap among individuals generally was greatest close to
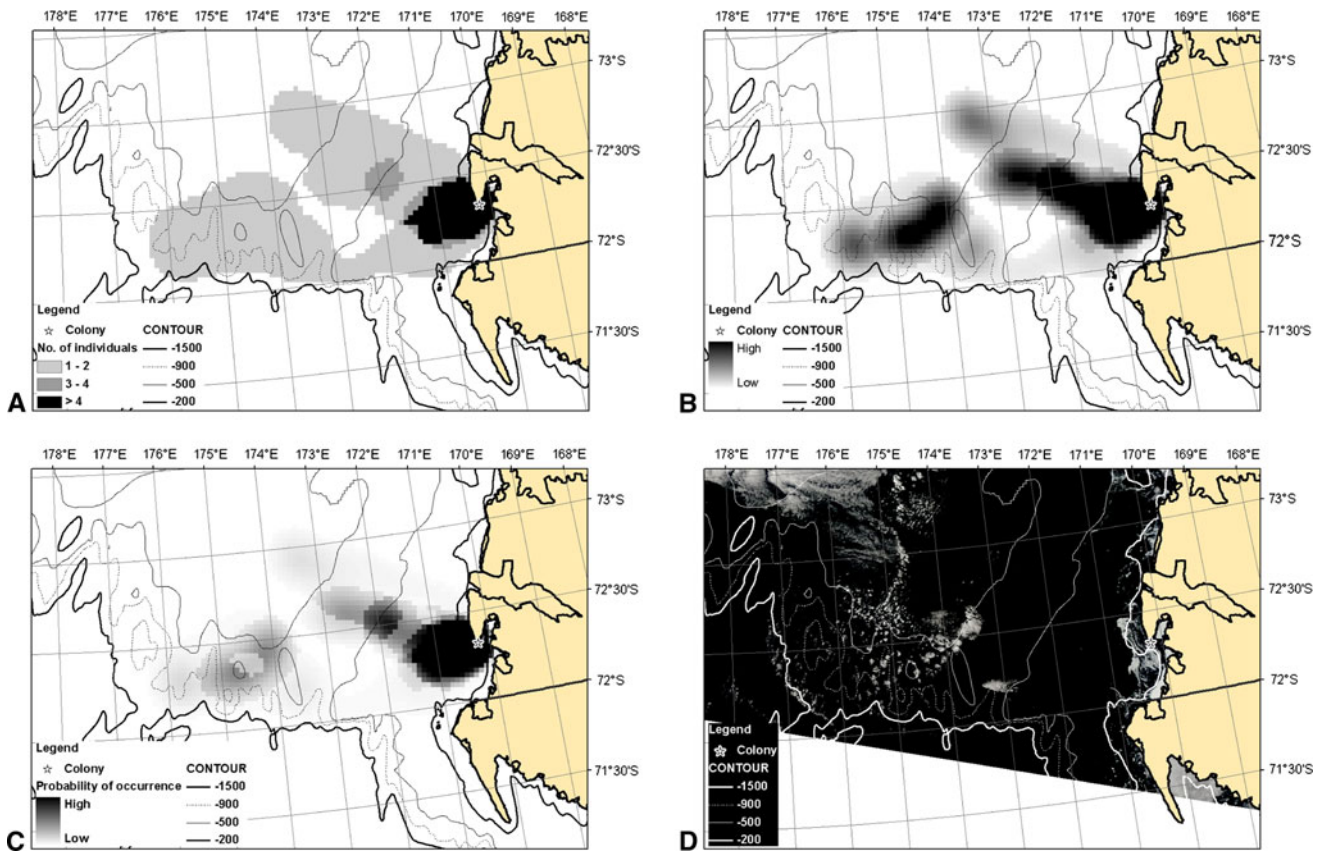
Fig. 3 At-sea distribution of satellite tracked Adélie penguins ($n = 4$) from the Cape Hallett breeding colony (as indicated by the *black star*) during the crèche stage of the 2004/2005 breeding season : **a** the number of foraging areas which overlapped each 3×3 km grid cell; **b** the summed Σ_n 90UD estimates; **c** the weighted Σ_n 90UD estimates (see caption of Fig. 2 for explanation); **d** the pack-ice distribution around the colony (Julian day 24). All maps show the 200, 500, 900, and 1,500-m bathymetric contours

the colony (Figs. 2a, 5a) and was greater overall in 2005/2006 than in 2004/2005. Overlapping distributions, especially near the colony, reflect the commuting activity of individuals. However, the more area-restricted distribution of individuals and greater occurrence (as determined by the summed UD estimates, Figs. 2b, 5b) within the vicinity of the colony during the guard stage, compared with the crèche stage, indicates that most foraging activity occurred relatively close to the colony during the guard stage. After down-weighting summed UD estimates to identify those areas visited by several individuals and where those individuals spent more time, the hotspot of at-sea distribution during the guard stage occurred close to the colony (Figs. 2c, 5c). Thus, most individuals foraged in or travelled over the relatively shallower waters (≤ 500 m deep) over or adjacent to the continental shelf break. During the crèche stage, two additional hotspots emerged: one over the Victoria Land Trough (especially in 2005/2006) and another over the edge of the Ross Sea Shelf Break (Figs. 3c, 5c).

Greater overlap between penguin foraging areas and pack ice during guard stage compared with the crèche stage

likely resulted from heavy concentrations of pack ice off Cape Hallett earlier in the season (Figs. 2, 4). However, within the areas of densest pack ice, it appeared that penguins occupied areas where pack ice was relatively more dispersed. Given the dynamic nature of the pack habitat, however, it is difficult to confirm this trend using the single satellite image from each period. It remains unknown whether penguins actively targeted pack ice as a foraging environment, or whether the association resulted because pack ice dominated the seascape immediately offshore during the guard stage.

Pack ice coverage at the scale of the colony-level UD areas decreased during the crèche stages (Figs. 3, 5). The foraging activities of a small number of birds appeared to be associated with small areas of pack ice offshore. Similar to the guard stage, the foraging areas during the crèche stage overlapped with pack ice plumes close (within 60 km) to the colony, however, the overlap (i.e. density) among penguin foraging areas were less as birds expanded foraging areas into regions of ocean with less concentrated pack ice.
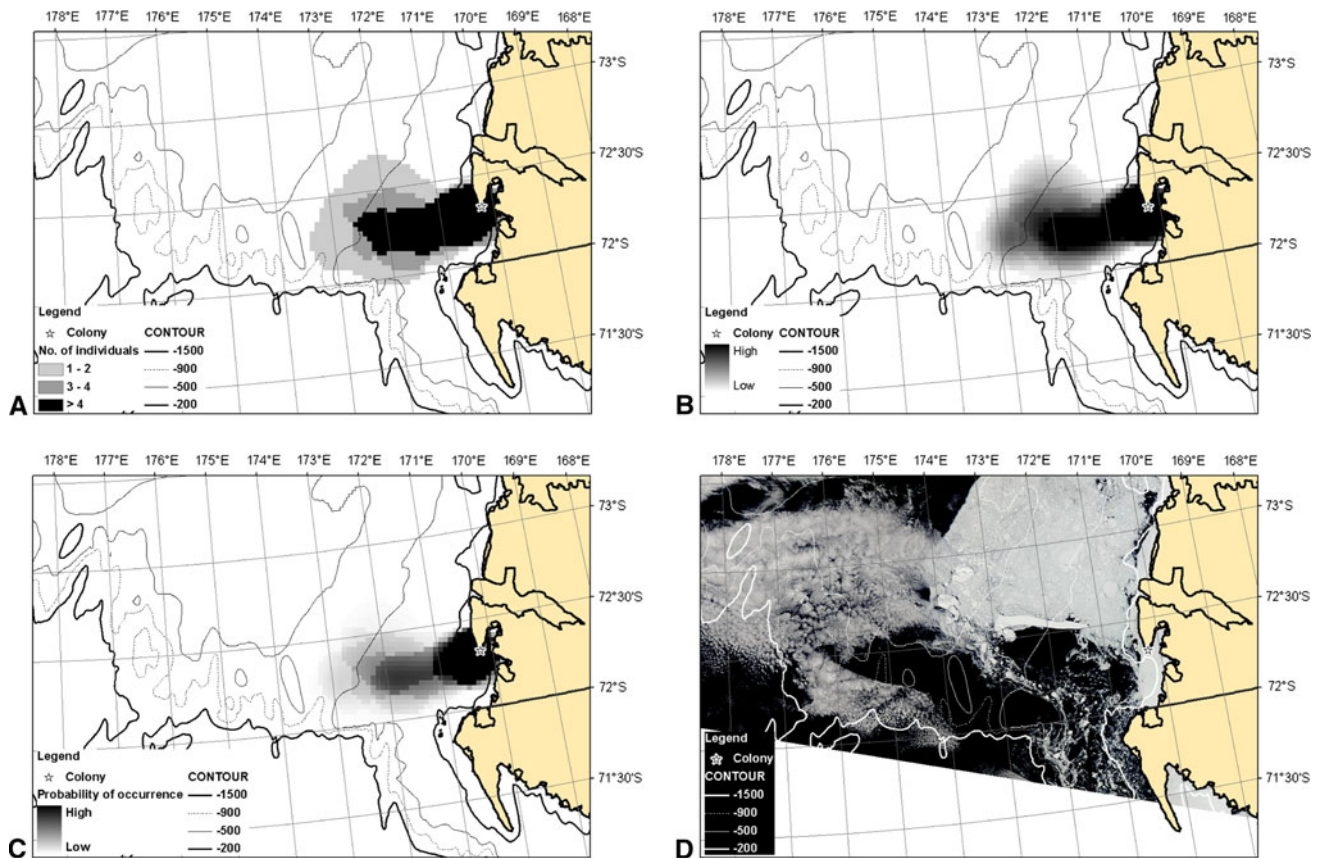
Fig. 4 At-sea distribution of satellite tracked Adélie penguins (*n* = 9) from the Cape Hallett breeding colony (as indicated by the *black star*) during the guard stage of the 2005/2006 breeding seasons : **a** the number of foraging ranges which overlapped each 3 × 3 km grid cell; **b** the summed Σ_n 90UD estimates; **c** the weighted Σ_n 90UD estimates (see caption of Fig. 2 for explanation); **d** the pack-ice distribution around the colony (Julian day: 354). All maps show the 200, 500, 900, and 1,500-m bathymetric contours

Discussion

Limitations of methods and effects of devices

We acknowledge that externally attached devices can have an effect on swimming ability, reducing speed (Wilson et al. 1986, 1997), and generally increasing energy expenditure (Bannasch et al. 1994; Kato et al. 2003). In this study, a VHF tag also was deployed on each bird to maximize instrument recoveries. It is possible that the addition of the VHF tag could further compromise the streamlining of the birds, although we do not think this is likely given the lack of effect found for such configurations from our previous work (Ballard et al. 2001).

Human disturbance also can affect penguin behavior and breeding success (Giese 1996). Although we did not collect foraging or breeding behavior data on non-instrumented birds, other studies have shown that similar devices and level of researcher disturbance did not affect foraging trip duration (Ballard et al. 2001; Kato et al. 2003), chick growth, chick survival, meal mass (Watanuki et al. 1992, 1997) nor breeding success of Adélie penguins (Wilson

et al. 1989, 1991). Therefore, we believe the foraging behaviors observed in this study are representative of the species.

Adélie penguin foraging patterns likely are affected by a range of prey-related factors including the type and size of prey available, daily vertical migration, prey density, and the dispersion of prey patches (Watanuki et al. 1993; Endo et al. 2002) and also by abiotic factors including sea ice dynamics and oceanic productivity. Since we were not able to measure prey-related parameters directly, we based our interpretations on observed foraging patterns.

Do foraging trips indicate competition for prey?

Competition for food arises from two sources: (1) an increase in predator abundance or (2) a decrease in food resource availability driven by factors other than predation (e.g., persistent summer sea ice coverage). Our first prediction that intra-specific competition would not affect penguins from the Cape Hallett colony was challenged by the tendency for breeding adults to travel farther, for longer, and over a greater area later in the breeding season.
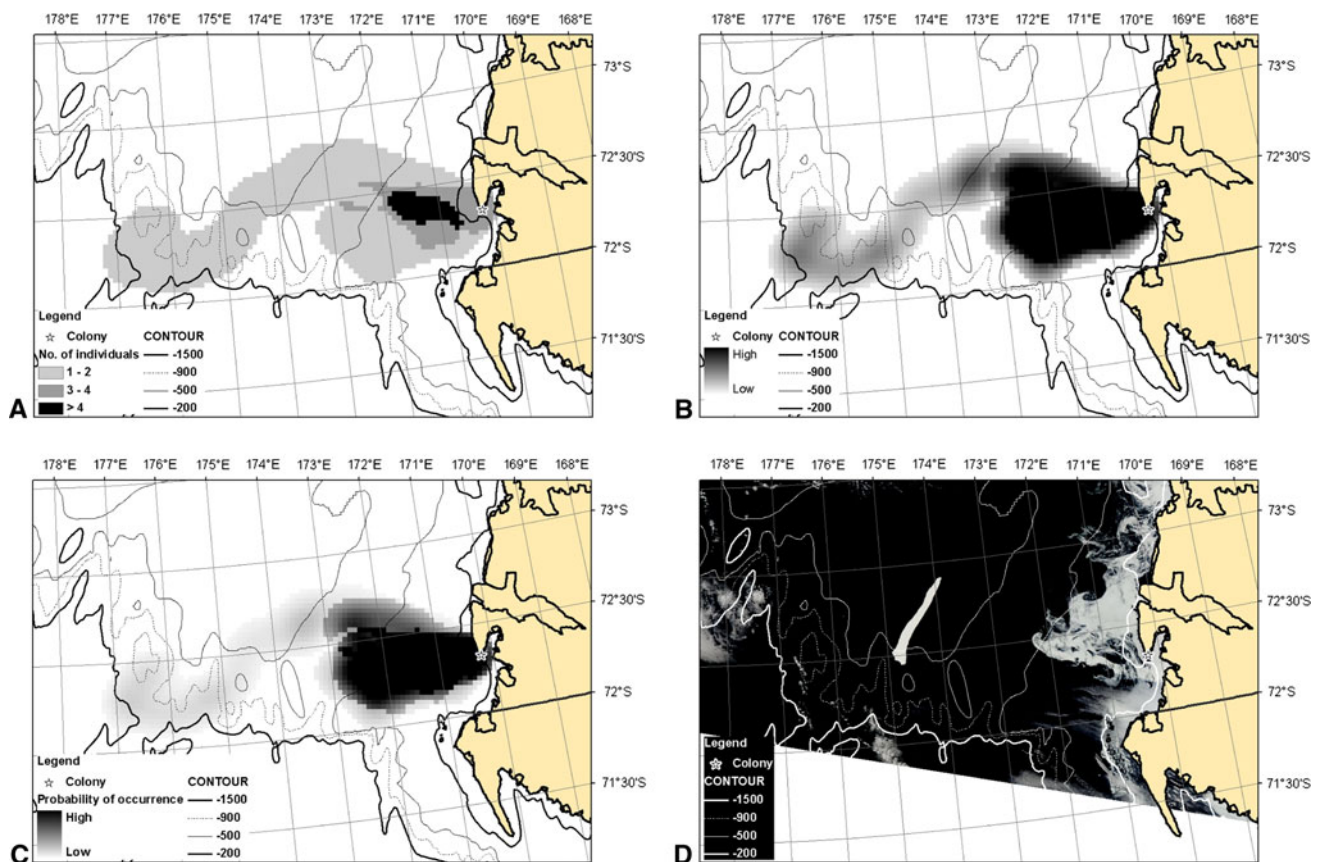
Fig. 5 At-sea distribution of satellite tracked Adélie penguins ($n = 4$) from the Cape Hallett breeding colony (as indicated by the *black star*) during the crèche stage of the 2005/2006 breeding season: **a** the number of foraging ranges which overlapped each 3×3 km grid cell; **b** the summed Σ_n 90UD estimates; **c** the weighted Σ_n 90UD estimates (see caption of Fig. 2 for explanation); **d** the pack-ice distribution around the colony (Julian day: 16). All maps show the 200, 500, 900, and 1,500-m bathymetric contours

Table 4 Intra-seasonal variation in the degree of spatial overlap among individuals foraging, focal, and core areas (90, 50, and 25UD, respectively; UD = utilization distribution)

Overlap measure	Range	2004/2005						2005/2006					
		Guard stage			Crèche stage			Guard stage			Crèche stage		
		Estimate	LCL	UCL	Estimate	LCL	UCL	Estimate	LCL	UCL	Estimate	LCL	UCL
HR	Foraging	0.62	0.48	0.74	0.45	0.31	0.60	0.60	0.49	0.72	0.43	0.26	0.61
	Focal	0.31	0.19	0.46	0.17	0.07	0.30	0.32	0.20	0.44	0.16	0.05	0.33
	Core	0.17	0.06	0.32	0.08	0.01	0.21	0.18	0.08	0.31	0.04	0.00	0.17
VI	Foraging	0.75	0.70	0.80	0.53	0.47	0.59	0.68	0.64	0.73	0.58	0.51	0.65
	Focal	0.53	0.43	0.64	0.32	0.21	0.44	0.49	0.40	0.59	0.36	0.22	0.50
	Core	0.38	0.24	0.51	0.22	0.07	0.36	0.37	0.25	0.49	0.18	0.00	0.36

Home range (HR) is a measure of the proportion of the area of each UD class that overlaps with all other individuals. Volume of intersection (VI) provides a relative measure of the proportional time of two individuals overlapping within the area of overlap within each UD area class. The back-transformed parameter estimates (with 2.5 and 97.5% confidence levels) presented were extracted from model 3 (Year/season) in Appendices 5 (where data were arcsin-transformed for analysis)

This indicates that there is a change in prey availability throughout the season as a function of distance to Cape Hallett. Our results are consistent with Ainley et al. (2004) and Ballance et al. (2009) who suggested that intra-specific

foraging competition affects penguins among colonies on Ross and Beaufort islands, where at the larger colony (Cape Crozier, c. ~135,000 breeding pairs; Ballance et al. 2009) breeding penguins foraged farther and for longer

later in the season than during the early season (see also Ainley et al. 2004, 2006). However, in contrast to our findings from Cape Hallett, parents from Cape Crozier also exhibited deeper dives, dived more frequently, and for greater durations later in the breeding season (Lescroël et al. 2010). Although prey resources were not directly measured by Lescroël et al. (2010), they attributed this pattern to intra-specific foraging competition as prey stocks were gradually depleted as the breeding season progressed (see also Ballance et al. 2009). Among other colonies on Ross Island in the southern Ross Sea, the opposite patterns were observed. At both Cape Bird and Cape Royds, foraging ranges and dive depths decreased through the chick-rearing stage (Ballard et al. 2006) indicating that either intra-specific competition has less effect on colonies with similar size or smaller than Cape Hallett, or that prey availability changes differently off these colonies.

So, why did penguins from Cape Hallett, a colony of similar size to Cape Bird and larger than Cape Royds, display patterns consistent with the prey depletion hypothesis observed at Cape Crozier? We suggest that the close proximity of three additional large Adélie penguin breeding colonies (Cape Adare, Foyn Is. And Possession Is.; combined $\sim$449,858 breeding pairs; Woehler 1993) to the north of Cape Hallett and two immediately to the south (Cape Cotter and Cape Wheatstone; together $\sim$46,235 breeding pairs; Fig. 1) exposed the birds from Cape Hallett to a lower relative level of intra-specific competition than previously observed at Crozier, yet significant enough to alter foraging patterns. We suggest that Adélie penguins from Cape Hallett increased their foraging areas to source adequate prey, but not so much as to increase aspects of their diving behavior. By foraging farther, for longer, and over a greater area, breeding Adélie penguins from Cape Hallett could have adjusted in response to intra-specific competition with the large Adélie penguin colonies to the north. The seasonal shift more to the southeast also could be a response to avoid competition with the large numbers of penguins associated with colonies to the north, which likely also would be seasonally expanding their foraging ranges, much as the Cape Crozier colony causes a seasonal shift in the foraging area of the adjacent Beaufort Island colony (Ainley et al. 2004).

Ainley et al. (2006) also suggest that other large krill eating species such as Minke whales (*Balaenoptera bonaerensis*) could contribute to prey depletion and contribute in part to the observed increase in foraging effort among breeding Adélie penguins around Ross Island. Minke whales are most abundant in the Ross Sea along the shelf break (Ainley 1985), but unfortunately we lack observations of cetacean abundances within the foraging area of the penguins breeding at Cape Hallett.

Is intra-specific competition mitigated by prey type?

In the Antarctic marine ecosystem, *E. superba* dominate prey biomass that support most of the upper-trophic-level predators, including Adélie penguins (Barrera-Oro 2002; Watanuki et al. 1994). *E. superba* comprised the majority of food delivered to chicks at Cape Hallet. This contrasts with higher latitude colonies on Ross Island where the smaller *E. crystallorophias* is the more important krill species taken (Ainley et al. 2003). *E. crystallorophias* was infrequently delivered during both seasons at Cape Hallett. These findings are consistent with krill distribution patterns observed by Sala et al. (2002), Azzali et al. (2006), and Taki et al. (2008) who determined using acoustics and net sampling that *E. superba* were the most abundant euphausiid along the Ross Sea shelf break and in the northern Ross Sea region. Presumably, penguins foraging farther offshore from Cape Hallett would be less likely to encounter *E. crystallorophias* as evidenced in the stomach samples. It is possible also that the greater mean relative biomass of *E. superba* (9.3 g/1,000^3 of filtered water) in surface waters overlying the continental shelf break compared with lesser *E. crystallorophias* (3.0 g/1,000^3 of filtered water) over the continental shelf south of 74 S (Sala et al. 2002), buffered the Cape Hallett penguins from the effects of more intense intra-specific competition with large neighboring colonies—a situation perhaps more likely to occur within the Ross Island metapopulation (Ainley et al. 2004, Ballance et al. 2009).

Seasonal changes in diet

Besides krill, fishes are the second most important dietary component for top predators in Antarctic waters (Fischer and Hureau 1985) and particularly, energy-rich pelagic myctophid species in open waters of the Southern Ocean and *Pleuragramma* over the shelf (Barrera-Oro 2002). Based on the fish distribution patterns reported by (DeWitt 1970, Eastman and Hubold 1999, Donnelly et al. 2004; see also O'Driscoll et al. 2009) and our measured penguin distributions, Adélie penguins from Cape Hallett were most likely to encounter and have consumed *Pleuragramma* while foraging over the continental shelf. No myctophids (*Electrona* sp.) were detected in net hauls over the Ross Sea continental shelf (references above); therefore, the probability that myctophids would have been encountered and taken by Hallett penguins was low.

As predicted, the amount of fish in adult Adélie penguin diet samples increased significantly as the season progressed, consistent in pattern but not amount with observations at Ross Island Adélie penguin colonies. In the southern Ross Sea, fish can comprise almost 100% of the diet at times (Ainley et al. 2006). Although, large aggregations of

Pleuragramma have been detected over the deeper waters of the Victoria Land Trough (O'Driscoll et al. 2009) given the relatively low percentages detected in our samples, Adélies from Hallett did not appear to specifically target *Pleuragramma* but may take *E. superba* when sufficiently abundant and available.

Unfortunately, we cannot yet disentangle whether adult penguins from Cape Hallett were targeting *Pleuragramma* or were opportunistically catching these fish as they encountered them more frequently farther off-shore. Although fish are more energy dense, Adélie penguin chicks can be sustained on pure krill diets (Salihoglu et al. 2001; Ainley et al. 2003). In some years in parts of East Antarctica, Adélie penguins switch to fish species' other than *Pleuragramma* (such as *Trematomus* sp. and *Pagothenia borchgrevinki;* Watanuki et al. 1993; Clarke et al. 2002).

Effects of prey availability and physical habitat

The at-sea UD areas of Adélie penguins from Cape Hallett indicated that provisioning adults were closely associated with coastal fast and pack ice during the guard stage; however, this association lessened somewhat during the crèche stage as penguins increased their foraging areas and the sea ice dispersed. During the crèche stage, a greater proportion of Adélie penguin foraging areas were characterized by lesser pack ice concentrations.

Ainley et al. (1984) determined that the most important feature affecting Adélie penguin distribution in the Ross Sea after the presence of pack ice and proximity to breeding areas was the Antarctic Slope Front (the region herein referred to as the Ross Sea Slope Front (RSSF); see Ainley and Jacobs 1981; Ainley 1985; Jacobs 1991). They also suggested that penguins preferred pack ice to open-ocean habitats and that the biological activity in the water column beneath the ice probably was more important in determining where in the ice Adélie penguins occurred (i.e. the degree to which the ice co-occurred with the RSSF). Greater densities of Adélie penguins were observed by Ainley et al. (1984) across an area extending southeast from Cape Adare in the pack ice over the Ross Sea Slope, and their concurrent absence from the pack ice to the north and in the open polynya waters to the south also was obvious (Ainley et al. 1984, 2006). In our study, when chick-rearing demands increased with the crèche stage, we found that Cape Hallett penguins began to aggregate spatially in the vicinity of the RSSF. This habitat feature also is important for penguins from other colonies in East Antarctica (Clarke et al. 1998). We found little evidence that penguins specifically targeted canyons, as is the case off the western Antarctic Peninsula. Rather, they gradually expanded foraging areas in one direction to eventually overlie the Victoria Land Trough and the continental slope.

Flores et al. (2009) found densities of post-larval *E. superba* were greater under sea ice than the open ocean because of enhanced conditions for ice algal and phytoplankton production. From a predator's perspective, this would support our observations that focal and core foraging areas among penguins were associated with pack ice and that small hot-spots of activity later in each season appeared to overlap with small pack ice patches over highly productive waters offshore. Alternatively, it is possible that concentrations of pack ice around Cape Hallett earlier in the breeding season created a temporary barrier and prevented penguins from accessing more prey-rich waters offshore. Once the pack ice began to break up during the crèche stage and become increasingly dispersed, penguins were able to swim to feeding areas (which is energetically less demanding than transiting across sea or pack ice); this would allow penguins to expand their foraging areas into areas presumably with less depleted prey stocks. And in doing so, the birds seemingly were able to maintain a relatively low level of diving effort during the crèche stage.

Crucial to understanding the foraging behavior of Adélie penguins (and other predator species') is knowledge about the abundance and distribution of their different prey species'. Concurrent prey abundance and distributions surveys would be advantageous for better interpreting how these predators use the seascape and employ different foraging strategies.

Appendix 1

See Table 5.

Table 5 Candidate models fitted to the foraging trip parameter data and best set of models identified by the model selection (highlighted in bold, based on ΔAICc threshold value <4)

Parameter	Model	Covariate	df	AICc	ΔAICc	Weight
Maximum distance (km)	m0	Null	2	65.6	11.31	0.002
	m1	Year	3	65.2	10.89	0.002
	m2	**Season**	**3**	**54.7**	**0.40**	**0.448**
	m3	**Year/season**	**5**	**54.3**	**0.00**	**0.548**
Total distance travelled (km)	m0	Null	2	68.6	11.81	0.002
	m1	Year	3	68.5	11.75	0.002
	m2	**Season**	**3**	**57.7**	**0.94**	**0.383**
	m3	**Year/season**	**5**	**56.8**	**0.00**	**0.614**
Total duration (h)	m0	Null	2	57.1	13.70	0.001
	m1	Year	3	56.6	13.11	0.001
	m2	**Season**	**3**	**46.0**	**2.54**	**0.219**
	m3	**Year/season**	**5**	**43.5**	**0.00**	**0.779**

Appendix 2

See Table 6.

Table 6 Candidate models fitted to the dive parameter data and best set of models identified by the model selection (highlighted in bold, based on ΔAICc threshold value <4)

Parameter	Model	Covariate	df	AICc	ΔAICc	Weight
Mean dive duration (s)	m0	Null	2	208.6	1.82	0.150
	m1	Year	3	207.4	0.67	0.267
	m2	Season	3	207.9	1.15	0.210
	m3	Year/season	5	206.8	0.00	0.373
Mean maximum depth (m)	m0	Null	2	211.0	6.61	0.023
	m1	**Year**	**3**	**207.1**	**2.73**	**0.162**
	m2	**Season**	**3**	**206.9**	**2.51**	**0.181**
	m3	**Year/season**	**5**	**204.4**	**0.00**	**0.634**
Mean bottom time (s)	m0	Null	2	173.8	2.69	0.116
	m1	Year	3	173.6	2.56	0.125
	m2	Season	3	171.8	0.72	0.312
	m3	Year/season	5	171.1	0.00	0.447
Dives per hour	m0	Null	2	117.4	8.07	0.013
	m1	Year	3	117.4	8.03	0.014
	m2	**Season**	**3**	**111.9**	**2.51**	**0.216**
	m3	**Year/season**	**5**	**109.4**	**0.00**	**0.757**
Hourly vertical distance (m)	m0	Null	2	388.7	9.26	0.006
	m1	Year	3	386.8	7.37	0.016
	m2	**Season**	**3**	**380.8**	**1.38**	**0.327**
	m3	**Year/season**	**5**	**379.4**	**0.00**	**0.651**
Dives per hour	m0	Null	2	120.3	1.49	0.175
	m1	Year	3	119.4	0.61	0.272
	m2	Season	3	120.2	1.40	0.184
	m3	Year/season	5	118.8	0.00	0.369
Hourly vertical distance (m)	m0	Null	2	386.8	8.27	0.010
	m1	Year	3	385.0	6.53	0.024
	m2	**Season**	**3**	**379.8**	**1.29**	**0.332**
	m3	**Year/season**	**5**	**378.5**	**0.00**	**0.634**

Appendix 3

See Table 7.

Table 7 Candidate models fitted to the UD area data for the foraging, focal and core ranges and best set of models identified by the model selection (highlighted in bold, based on ΔAICc threshold value <4)

Range	Model	Covariate	df	AICc	ΔAICc	Weight
Foraging	m0	Null	2	43.45	11.15	0.002
	m1	Year	3	43.43	11.13	0.002
	m2	Season	3	**32.93**	**0.63**	**0.42**
	m3	Year/season	5	**32.30**	**0.00**	**0.576**
Focal	m0	Null	2	47.58	10.05	0.004
	m1	Year	3	47.43	9.90	0.005
	m2	Season	3	**38.75**	**1.22**	**0.349**
	m3	Year/season	5	**37.52**	**0.00**	**0.642**
Core	m0	Null	2	46.40	10.48	0.004
	m1	Year	3	46.16	10.24	0.004
	m2	Season	3	**37.72**	**1.80**	**0.287**
	m3	Year/season	5	**35.92**	**0.00**	**0.705**

Appendix 4

See Table 8.

Table 8 Candidate models fitted to the latitudinal and longitudinal extent of the foraging, focal, and core ranges data and best set of models identified by the model selection (highlighted in bold, based on ΔAICc threshold value <4)

Extent	Range	Model	Covariate	df	AICc	ΔAICc	Weight
North	Foraging	m0	Null	2	−57.8	9.12	0.009
		m1	Year	3	−58.2	8.78	0.011
		m2	Season	3	−62.5	4.42	0.097
		m3	Year/season	5	**−67.0**	**0.00**	**0.883**
	Focal	m0	Null	2	−60.3	8.45	0.013
		m1	Year	3	−60.4	8.36	0.013
		m2	Season	3	−64.3	4.45	0.095
		m3	Year/season	5	**−68.7**	**0.00**	**0.879**
	Core	m0	Null	2	−59.7	7.65	0.019
		m1	Year	3	−59.9	7.51	0.020
		m2	Season	3	−63.2	4.15	0.107
		m3	Year/season	5	**−67.4**	**0.00**	**0.854**
South	Foraging	m0	Null	2	−37.2	10.00	0.003
		m1	Year	3	−37.5	9.74	0.004
		m2	Season	3	**−47.1**	**0.14**	**0.478**
		m3	Year/season	5	**−47.2**	**0.00**	**0.514**
	Focal	m0	Null	2	−35.3	10.49	0.003
		m1	Year	3	−35.5	10.30	0.003
		m2	Season	3	**−45.6**	**0.19**	**0.474**
		m3	Year/season	5	**−45.8**	**0.00**	**0.520**
	Core	m0	Null	2	−33.5	9.31	0.005
		m1	Year	3	−33.6	9.20	0.005
		m2	Season	3	**−42.8**	**0.05**	**0.489**
		m3	Year/season	5	**−42.8**	**0.00**	**0.502**

Table 8 continued

Extent	Range	Model	Covariate	df	AICc	ΔAICc	Weight
East	Foraging	m0	Null	2	97.6	14.22	0.000
		m1	Year	3	97.6	14.22	0.000
		m2	Season	3	**84.0**	**0.60**	**0.425**
		m3	Year/season	5	**83.4**	**0.00**	**0.574**
	Focal	m0	Null	2	98.4	13.54	0.001
		m1	Year	3	98.4	13.52	0.001
		m2	Season	3	**85.5**	**0.68**	**0.415**
		m3	Year/season	5	**84.8**	**0.00**	**0.584**
	Core	m0	Null	2	98.4	13.32	0.001
		m1	Year	3	98.3	13.29	0.001
		m2	Season	3	**85.9**	**0.81**	**0.399**
		m3	Year/season	5	**85.0**	**0.00**	**0.599**
West	Foraging	m0	Null	2	−19.2	5.23	0.058
		m1	Year	3	−20.0	4.51	0.083
		m2	Season	3	−19.4	5.08	0.063
		m3	Year/season	5	**−24.5**	**0.00**	**0.796**
	Focal	m0	Null	2	56.6	2.09	0.138
		m1	Year	3	56.2	1.72	0.166
		m2	Season	3	55.0	0.52	0.303
		m3	Year/season	5	54.5	0.00	0.393
	Core	m0	Null	2	60.3	1.96	0.140
		m1	Year	3	60.3	1.89	0.144
		m2	Season	3	58.5	0.15	0.344
		m3	Year/season	5	58.4	0.00	0.372

Appendix 5

See Table 9.

Table 9 Candidate models fitted to the UD overlap data and best set of models identified by the model selection (highlighted in bold, based on ΔAICc threshold value <4)

Overlap measure	Range	Model	Covariate	df	AICc	ΔAICc	Weight
HR	Foraging	m0	Null	2	−17.40	6.09	0.023
		m1	Year	3	−17.43	6.06	0.023
		m2	Season	3	**−23.43**	**0.06**	**0.469**
		m3	Year/season	5	**−23.49**	**0.00**	**0.484**
	Focal	m0	Null	2	−13.66	5.74	0.027
		m1	Year	3	−13.79	5.61	0.029
		m2	Season	3	**−19.39**	**0.00**	**0.472**
		m3	Year/season	5	**−19.40**	**0.00**	**0.473**
	Core	m0	Null	2	−7.11	4.77	0.047
		m1	Year	3	−7.11	4.77	0.047
		m2	Season	3	**−11.36**	**0.51**	**0.396**
		m3	Year/season	5	**−11.87**	**0.00**	**0.510**

Table 9 continued

Overlap measure	Range	Model	Covariate	df	AICc	ΔAICc	Weight
VI	Foraging	m0	Null	2	−45.69	27.03	0.000
		m1	Year	3	−45.70	27.02	0.000
		m2	**Season**	**3**	**−67.42**	**5.29**	**0.066**
		m3	**Year/season**	**5**	**−72.72**	**0.00**	**0.934**
	Focal	m0	Null	2	−26.67	10.22	0.003
		m1	Year	3	−26.77	10.12	0.004
		m2	**Season**	**3**	**−36.28**	**0.62**	**0.420**
		m3	**Year/season**	**5**	**−36.89**	**0.00**	**0.573**
	Core	m0	Null	2	−17.41	6.60	0.019
		m1	Year	3	−17.42	6.59	0.019
		m2	**Season**	**3**	**−23.85**	**0.16**	**0.462**
		m3	**Year/season**	**5**	**−24.01**	**0.00**	**0.501**

Appendix 6

See Table 10.

Table 10 Candidate models fitted to the observed diet composition data and best set of models identified by the model selection (highlighted in bold, based on ΔAICc threshold value <4)

Model	Covariate	df	AICc	ΔAICc	Weight
m0	Null	2	76.6	9.6	0.007
m1	Year	3	75.2	8.2	0.015
m2	Season	3	71.8	4.8	0.082
m3	**Year/season**	**5**	**67.0**	**0.0**	**0.896**

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