

Environmental conditions and life history constraints determine foraging range in breeding Adélie penguins

Judy Clarke^{1,*}, Louise M. Emmerson¹, Petr Otahal²

¹Department of the Environment and Heritage, Australian Antarctic Division, 203 Channel Hwy, Kingston, Tasmania 7050, Australia

²35 Seventh Ave, West Moonah, Tasmania 7009, Australia

ABSTRACT: Foraging movements of Adélie penguins are constrained both by environmental conditions (e.g. sea ice cover) and life history factors (e.g. regular offspring provisioning). We describe within season changes in foraging range, trip duration and body condition of Adélie penguins nesting at Béchervaise Island, East Antarctica, in the context of these constraints. Penguins were satellite tracked over multiple seasons during the incubation, guard, crèche and pre-moult phases of their annual cycle. They ranged farthest during incubation when sea ice was extensive and shortest during the guard stage when chicks were small and sea ice limited in extent. Prior to their annual moult the birds foraged hundreds of kilometres to the west and east of their breeding sites. A recurrent polynya facilitated access to the sea early in the season when ice cover was extensive. Kernel analyses showed that penguins foraged most intensively close to the colony, along submarine canyons and at the continental shelf break. Increases in foraging range, as the chick rearing period progressed, were consistent with changing energy requirements of adults and chicks and likely intraspecific competition. Whilst provisioning their offspring, penguins adopted a variable combination of time minimising and food maximising foraging behaviour in which choice of foraging rule was determined largely by adult body condition.

KEY WORDS: Satellite tracking · *Pygoscelis adeliae* · Foraging range · Chick provisioning · Body condition · Kernel analysis · Polynya

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INTRODUCTION

Foraging strategies of breeding seabirds involve tradeoffs between self maintenance and offspring provisioning (Ydenberg et al. 1994). Penguins are central place foragers (Orians & Pearson 1979) whose foraging range is constrained during the breeding season by a variety of extrinsic and intrinsic factors (Stephens & Krebs 1986). Extrinsic constraints include physical barriers such as sea ice, proximity of prey concentrations to nesting sites and competition with other species and individuals. Intrinsic constraints include physiological capabilities, the requirement to return to the colony regularly to carry out incubation and chick feeding duties, and the basic necessity of maintaining body condition above certain threshold levels.

There are 2 currencies by which foraging behaviour can maximise the overall net rate of energy gain: (1) minimising the time taken to obtain a fixed amount of energy (time minimisation) and (2) maximising the amount of energy gained in a fixed amount of time (energy maximisation) (Schoener 1971, Stephens & Krebs 1986). While the 2 currencies are equivalent in terms of overall rate maximisation (Pyke et al. 1977), the currency appropriate to a given situation depends on whether time or energy is most constrained. Central place foragers may aim to: (1) minimise time away from the colony when food is available nearby, thereby allowing regular feeding of offspring, or (2) maximise energy intake regardless of time away, thus enabling access to distant dense prey resources. A combination of both strategies may facil-

*Email: judy.clarke@bigpond.com

itate partitioning of resources between reproduction and self maintenance in environments where the location and accessibility of prey resources are variable or when intra-specific competition for food is a limiting factor. A dynamic penguin-krill modelling study by Alonzo et al. (2003) demonstrated that penguin foraging rules (food maximising vs time minimising) can strongly affect their predicted at-sea distribution in a system where prey is available both inshore and offshore. In this dynamic predator-prey model, penguins adopting a time-away-from-colony minimising strategy foraged close to the colony while penguins maximising food intake were more likely to forage further away.

In this paper we show how Adélie penguin foraging ranges vary as the breeding season progresses and discuss these changes in the context of environmental conditions and life history constraints. We demonstrate a strong correlation between foraging trip duration and foraging range, and use an extensive multi-year set of foraging duration and weight data to further investigate foraging strategies during the guard and crèche stages when penguins must finely balance chick provisioning and self maintenance. We investigate whether Adélie penguins adopt time minimising and/or food maximising foraging rules during chick rearing and discuss how flexible use of these strategies helps this species to survive in a variable physical environment.

MATERIALS AND METHODS

Field site and study animals. The Adélie penguin colony on Béchervaise Island (67° 35' S, 62° 49' E) near Mawson station East Antarctica, has been monitored annually since 1990–91 (Kerry et al. 1997, Clarke et al. 2002, 2003). This colony of 2000 breeding pairs is among a complex of colonies totalling approximately 55 000 pairs located along a 10 km stretch of the coastline (Woehler 1993, Woehler et al. 2001). Much of the work on this island has been carried out using a custom built Automated Penguin Monitoring System (APMS) that records the weights and times of departure and arrival of individually tagged penguins from the colony (Kerry et al. 1993, Clarke & Kerry 1998).

Satellite tracking of foraging Adélie penguins has been carried out over a number of years, covering all stages of the breeding season (incubation, guard, crèche and pre-moult). Here we collate tracking data collected during the 1991–92 to 2002–03 austral summers to obtain an overview of foraging movements during each of these periods. We also analyse coincident APMS data collected during the guard and crèche stages to determine relationships between adult body

condition and foraging trip duration. Individual penguins were tracked over multiple foraging trips during the guard and crèche periods but only for single trips during incubation and pre-moult stages (Table 1).

A small number of penguins tracked during the late crèche period failed to return in some seasons and instead remained at sea prior to carrying out their annual moult. Tracks from these birds were collated separately as an indication of pre-moult foraging movements post-breeding. It was acknowledged that the behaviour of these birds might not be fully representative of successful breeders, which commence pre-moult foraging trips later in the season. All birds tracked prior to the moult stage were observed alive and breeding in subsequent seasons.

Trip durations and departure weights of foraging penguins were determined from APMS data as described in Clarke et al. (2002). Only foraging trips from known-sex adults that were feeding chicks were included, and data were restricted to trips commencing prior to the end of January each year (to be compatible with the tracking data set). Sex was determined by cloacal examination (Sladen 1978) at the time of initial tag implantation.

Instrument deployment and processing of location data. All penguins were tracked using platform terminal transmitters (PTTs) of three different makes and models. Toyocom T-2038 and Telonics ST-6 and ST-10 PTTs were used between 1991 and 1999, weighing 100 and 120 g, respectively, and with frontal cross-sectional areas of approximately 7 cm². From 2000 onwards Kiwisat 101 PTTs (Sirtrack) were utilised; these weigh 90 g and have a frontal cross-sectional area of 3.75 cm². All PTTs were packaged by Sirtrack to withstand diving to 200 m, and shaped to minimise hydrodynamic drag.

Table 1. Number of penguins tracked from Béchervaise Island each year at each stage, and the number of foraging trips undertaken in each category

	Incubation		Guard		Crèche		Pre-moult	
	Birds	Trips	Birds	Trips	Birds	Trips	Birds	Trips
1991–92	3	3	2	6	4	12		
1992–93			8	9	2	5		
1993–94			8	23	7	20	4	4
1994–95			7	12				
1995–96			6	12			1	1
1996–97			6	48	5	18		
1997–98	4	4	5	18				
1998–99	4	4	7	13	5	7		
1999–00	3	3	8	21	4	4	1	1
2000–01	7	7	21	67	13	15	3	3
2001–02			9	20	2	3	1	1
2002–03			10	27	6	6	3	3

Instruments were attached to the penguins' lower back using glue (Loctite 401®) and cable ties as described by Kerry et al. (1995a), except that transmitters were glued directly to the feathers after 1993. Devices were deployed on penguins of known breeding status and sex and removed at the end of the tracking period (except pre-moult birds). Durations of attachment ranged from 12 to 34 d during incubation (single trips), 1 to 31 d during chick rearing (median 2 trips, range 1 to 26 trips) and 9 to 31 d during the pre-moult period (single trips).

Location data were provided by ARGOS and processed using custom software from the Australian Antarctic Division. Only class 1, 2 and 3 fixes (estimated accuracy within 1000 m; Service Argos 1996) were used for plots of foraging locations, and these were filtered to remove any fixes that required birds to swim at speeds $>12 \text{ km h}^{-1}$ between locations, as such speeds are unlikely to be maintained over long periods (Culik et al. 1994). Start and end times of foraging trips were determined by the APMS (details of transponder implantation and APMS function are provided in Kerry et al. (1993) and Clarke & Kerry (1998)). In cases where APMS data were unavailable, start and end times of trips were estimated from a combination of twice daily nest observations and ARGOS data (fixes received every $1.9 \pm 0.04 \text{ h}$).

Maximum distance reached was calculated as the straight line distance from the colony to the most distant location received during each trip. Of the 366 trips made during chick rearing 22 were not allocated a maximum distance either because the trip was too short for more than one class 1 to 3 fix to be received, or because data were received too intermittently for the bird's turn around point to be estimated with any level of certainty. The latter problem only occurred in the first few seasons due to occasional instrument malfunction or failure part way through a trip.

At sea location data were imported into Geographical Information Systems Software (ArcGIS® V8.0 and ArcView® V3.3) and plotted together with bathymetric contours and sea ice data. Bathymetry was derived from the Prydz Bay 1:500 000 Bathymetric GIS Dataset (Ryan 1999) and the General Bathymetric Chart of the Oceans (GEBCO) Digital Atlas, Centenary Edition 2003. Ice images were acquired from the Advanced Very High Resolution Radiometer (AVHRR) carried on National Oceanic and Atmospheric Administration (NOAA, USA) satellites, collated by Michael et al. (2003).

Kernel analyses and statistical models. Location data were divided into fast and slow categories depending on whether the mean speed of travel from the previous location and to the next location was >4 or $<4 \text{ km h}^{-1}$, this being low in the range of speeds utilised by Adélie penguins travelling in a swim canal

(Culik et al. 1994). Kernel density distributions were produced for location data in the $<4 \text{ km h}^{-1}$ category based on the assumption that birds travelling slowly between locations were likely to be actively foraging while those moving faster were more likely to be commuting between the colony and feeding grounds. The cut off speed of 4 km h^{-1} removed 19, 37 and 42% of fixes in incubation, guard and crèche phases respectively. Fixed kernel estimation techniques (Worton 1989) were performed using the Animal movement extension to ArcView® (Hooge & Eichenlaub 1997), available at www.absc.usgs.gov/glba/gistools/, and included ad hoc calculation of the smoothing parameter (Silverman 1986), considered robust with large sample sizes (Hooge & Eichenlaub 1997). Probability polygons of foraging density were produced showing 55, 65, 75, 85, and 95% isopleths. Kernel areas were calculated in a Lazimuth Equal Area south polar projection. ARGOS fixes closer than 40 km to the colony were omitted in the incubation stage because the birds had to cross this distance of fast ice on foot before feeding could commence.

Maximum distance-from-colony data were compared among breeding stages using individual bird means as the sampling unit to reduce the skewed nature of the distribution of maximum distances for individual trips, which was due to some birds making multiple short trips over the same time period taken by other individuals to carry out fewer longer trips. The non-parametric median test was used to analyse differences in foraging range among breeding stages because the distributions of maximal distances in both the guard and crèche stages were bimodal as well as skewed.

Statistical analyses of APMS derived data were performed on an individual trip basis to investigate: (1) the relationship between foraging trip duration and departure weight during guard and crèche phases, (2) the relationship between departure weight and chronological date of departure within the guard and crèche stages, and (3) the relationship between foraging trip duration and chronological date (relative to median hatch and crèche dates) within the two stages. In conjunction the 3 analyses were designed to disclose the rate at which parents lose or gain body condition after their chicks hatch, how this rate varies between the two stages of chick rearing, and whether the need of parents to forage for themselves in addition to their offspring affects their foraging range. Short trips and simultaneous loss of parental mass was believed to indicate use of a time minimising strategy in which investment in chick provisioning outweighs self maintenance. In contrast, food maximising behaviour was deemed more likely to manifest as longer foraging trips and an increase or maintenance of parental mass.

Statistical models were fitted separately for the guard and crèche stages of chick rearing in all three analyses. Linear random-effects regression models were used, incorporating different intercepts and slopes for individual penguins. Sex and season were included as fixed effects and individual penguins as random effects. Correlations between successive trips by individual birds were accommodated by fitting an autocorrelation (AR1) component into each model. In all analyses the fitting of models was a sequential process in which the most complex model was fitted first and terms were progressively removed one by one until the simplest model that fitted the data was determined. Tests for interaction terms were always undertaken ahead of tests for individual effects and where interactions were retained so too were the corresponding main effects.

All analyses employed restricted maximum likelihood estimation (REML) methodology, and calculations were performed in the statistical computing package 'R' (www.r-project.org). Normality of random components was examined using QQ plots. Foraging trip duration data were log transformed to meet normality and equality of variances requirements. Consequently, group comparisons were based on ratios rather than differences among means, and linear relationships on the logarithmic scale became exponential relationships on the original scale of measurement. All variables other than foraging trip duration were untransformed.

To test for possible adverse effects of instrumentation (Watanuki et al. 1992, Hull 1997, Taylor et al. 2001), foraging trip durations of birds carrying PTTs during the chick rearing period were compared with those of a set of non-instrumented birds whose foraging trips were monitored by the APMS. To avoid differences due to sex (Clarke et al. 1998) and to randomise selection with respect to trip duration whilst controlling for date and time of day, each control trip selected was that of a bird of the same sex as the PTT carrier whose exit from the colony was recorded immediately subsequent to the departure of the instrumented bird. Trip durations of PTT carriers and controls were compared within years by Mann-Whitney rank sum tests.

RESULTS

Distribution of foraging birds in relation to sea ice and bathymetry

Clear differences in foraging range among the four stages of the breeding season were apparent and are illustrated in Fig. 1. Median maximal distances from the colony reached by foraging birds were 272, 60, 125

and 380 km in the incubation, guard, crèche and pre-moult stages of breeding respectively for all years pooled (Table 2a). Differences in maximum distances reached were significant between all pairs of breeding stages apart from incubation and pre-moult (Table 2b). Penguins from Mawson travelled to the vicinity of other major neighbouring populations (Fig. 1), especially during the pre-moult period.

The results of kernel analyses during the incubation, guard and crèche stages overlaying bathymetric contours in the region north of the colony are displayed in Fig. 2. Densities were greatest near the colony and over the steep continental shelf break. Foraging areas within the 55% isopleth covered 9977, 238 and 634 km² during incubation, guard and crèche periods respectively, while within the 95% isopleth ranges covered 79 164, 1782 and 18 039 km² for the same 3 stages of the breeding cycle.

Birds foraged furthest north during the incubation period when pack ice was extensive. Foraging was concentrated over the continental slope region northwest of the colony (Fig. 2a), as well as in ice covered areas to the north and south. Incubation stage trips were superimposed onto ice images taken when females (Fig. 3a) and males (Fig. 3b) were at sea. The position of the fast ice edge was remarkably constant between seasons (Michael et al. 2003), as was the obvious polynya situated between 60 and 62° E, which penetrates the fast ice as far south as 67° 10' S by late November each year. A striking feature of the penguin tracks, particularly females, was the birds' propensity to travel directly to the southern margin of the polynya on their outward journeys. Upon reaching the polynya the penguins travelled around its eastern edge before heading northwards into the pack ice to forage. Distances and directions of travel once in the pack ice varied among individuals. Sample sizes were too small to test whether these differences were due to season or sex or whether they were purely due to variation among individuals. Consistent among years, however, was the use of the polynya for access to the water and a preference for foraging amongst the pack ice rather than in the open water of the polynya.

Foraging distances were shortest in the guard stage when birds travelled as far north as the continental shelf break but rarely beyond (Fig. 1, Table 2). In this period penguins return regularly to their nests to feed small chicks and swap brooding duties with their partners. The fast ice breaks out during the guard stage in most seasons, providing access to open water throughout much of the chick rearing period. Birds foraging during the guard stage concentrated most of their activity within 15 to 20 km of the colony, although some also focussed on a relatively localised

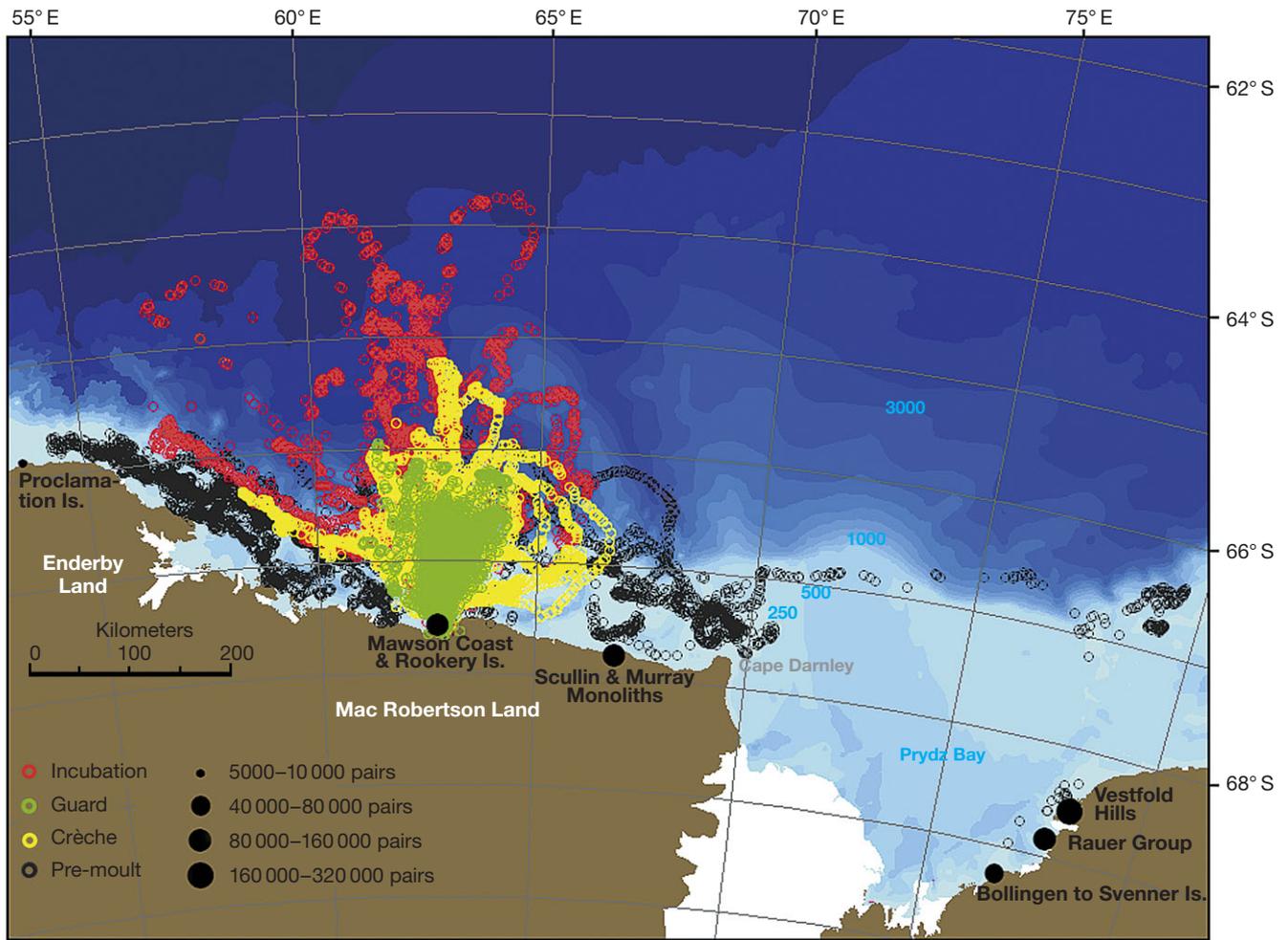


Fig. 1. *Pygoscelis adeliae*. Fixes from all birds tracked from 1991 to 2003 at Béchervaise Island. Colours indicate stage of breeding (see legend on figure). Bathymetric contours are at 250 m intervals. Major breeding populations of Adélie penguins along the coast are indicated

Table 2. (a) Median foraging distances from the colony for each stage of breeding (all seasons pooled). Median, lower and upper quartile values are provided for all trips during incubation and pre-moult, and all bird means during guard and crèche when individuals made multiple trips. (b) Results of Dunn's pairwise comparisons of bird means among stages following median test (median = 99.0, Chi-square = 74.857, df = 3, $p < 0.001$)

(a) Breed stage	Sampling unit	N	Median distance	25%	75%
Incubation	Trips (1 per bird)	21	272	223	340
Guard	Bird means	93	60	8	95
Crèche	Bird means	48	125	92	147
Pre-moult	Trips (1 per bird)	13	380	301	484
(b) Bird means	Diff. of Ranks	Q	p-value		
Pre-moult vs. Guard	107.39	7.159	<0.001		
Pre-moult vs. Crèche	64.20	4.053	<0.001		
Pre-moult vs. Inc	11.65	0.652	>0.05		
Inc vs. Guard	95.74	7.822	<0.001		
Inc vs. Crèche	52.55	3.965	<0.001		
Crèche vs. Guard	43.19	4.796	<0.001		

area over the continental shelf break 100 to 110 km northeast of the colony (Fig. 2b). Instead of travelling northwest towards the edge of the polynya as they did during incubation, birds provisioning chicks travelled slightly east of north along a 200 to 500 m deep submarine canyon towards the closest and steepest region of the continental shelf break, approximately 105 km from the colony.

By the crèche stage, when free to forage simultaneously, parents ranged further to the east and west of their guard stage routes, and also foraged to the north of the continental shelf with greater frequency than was the case when chicks were small (Fig. 1). Foraging was concentrated over an area up to 30 times as large as that utilized during the guard period, with heavi-

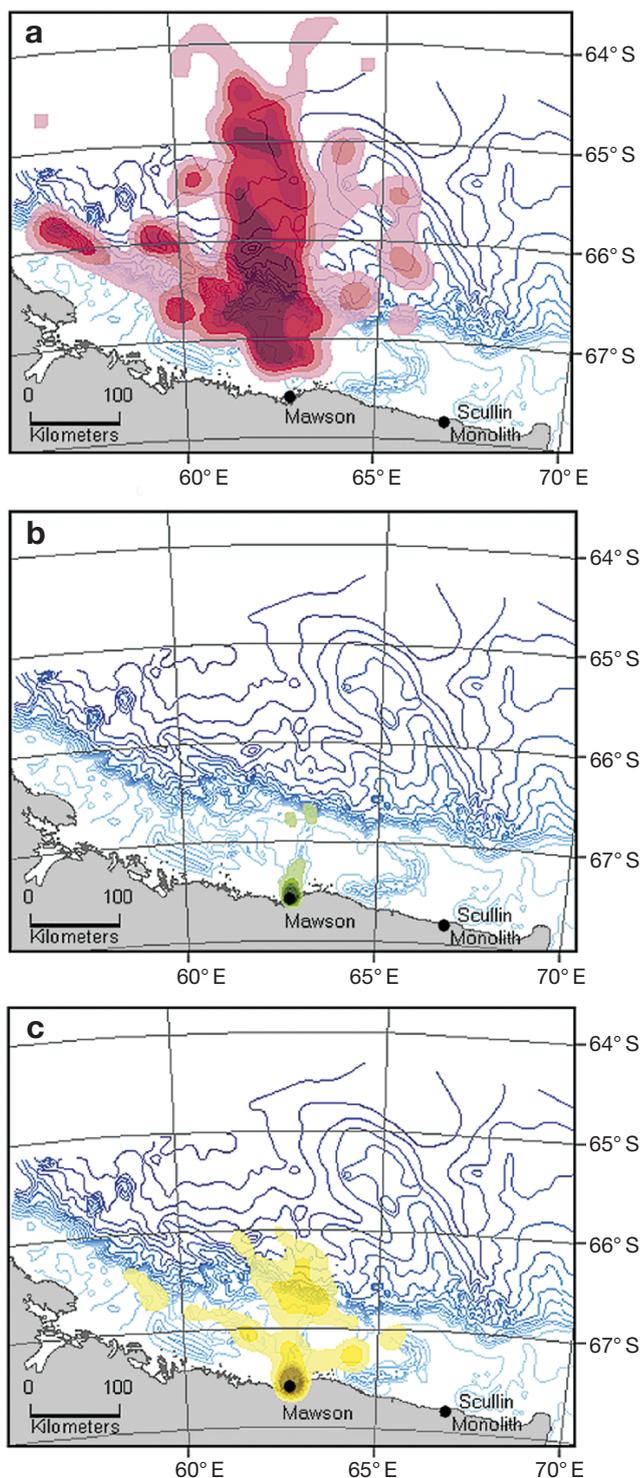


Fig. 2. *Pygoscelis adeliae*. Kernel analyses derived from penguins foraging offshore of Béchervaise Island in all years during the (a) incubation, (b) guard and (c) crèche stages of breeding. Intensity of shading indicates 55, 65, 75, 85 and 95% isopleths. Bathymetric contours are at 250 m intervals. Data were limited to fixes obtained when birds were travelling at average speeds of $<4 \text{ km h}^{-1}$. The narrow submarine canyon penetrating towards the coastline is visible at the centre of the guard and crèche maps

est intensity once again close to the colony and over the shelf break (Fig. 2c). Foraging in neritic waters over the shelf (now free of fast ice) was recorded, and penguins utilised a more extensive region of the shelf slope zone than earlier in the chick rearing period.

Prior to their annual moult penguins foraged even further from the colony, travelling east and west over the continental shelf and along the shelf break, but rarely moving far to the north of it (Fig. 1). At this stage birds were recorded almost as far west as Proclamation Island ($65^{\circ}51' \text{ S}$, $53^{\circ}41' \text{ E}$; 440 km from Mawson) and as far east as the edge of Prydz Bay (79° E ; 745 km from Mawson). PTTs carried by these individuals frequently ran out of battery power and ceased transmitting before the bird reached its location of moult; thus many of these penguins may have travelled further than determined in this study. While foraging ranges of incubation and pre-moult birds were similar, their direction of travel differed; birds foraged mainly to the north during incubation and travelled east and west over the continental shelf during the pre-moult period (Fig. 1). Fast ice is present over the continental shelf during incubation but absent during pre-moult (Michael et al. 2003).

Foraging range differences between breed stages were consistent in most years (Fig. 4), and maximum distances travelled were similar among years within the incubation, guard and pre-moult stages (Kruskal-Wallis 1-way ANOVA on ranks: $H = 4.610$, $df = 4$, $p = 0.33$; $H = 11.426$, $df = 11$, $p = 0.408$; $H = 3.731$, $df = 5$, $p = 0.589$ respectively). In the crèche stage the only unusual season was 2002–03 in which penguins travelled significantly further than they did in 1991–92 and 1993–94 (Dunn's pairwise comparisons: $Q = 3.928$, $p < 0.05$; $Q = 4.044$, $p < 0.05$ respectively; Kruskal-Wallis 1-way ANOVA on ranks: $H = 25.443$, $df = 8$, $p = 0.001$). These results indicate that the differences between breed stages demonstrated in Fig. 1 are not unduly influenced by interannual variability and unbalanced sampling design.

Foraging strategies in relation to body mass during chick rearing

A significant positive relationship between foraging trip duration and maximum distance from the colony was demonstrated for foraging trips carried out by PTT carriers during chick rearing (Spearman rank correlation, $r_s = 0.907$, $p < 0.001$, $n = 344$). The relationship is shown graphically in Fig. 5 for all seasons combined. The two variables were also significantly correlated within each of the guard and crèche stages ($r_s = 0.886$, $p < 0.001$, $n = 261$ and $r_s = 0.874$, $p < 0.001$, $n = 83$ respectively). Correlations

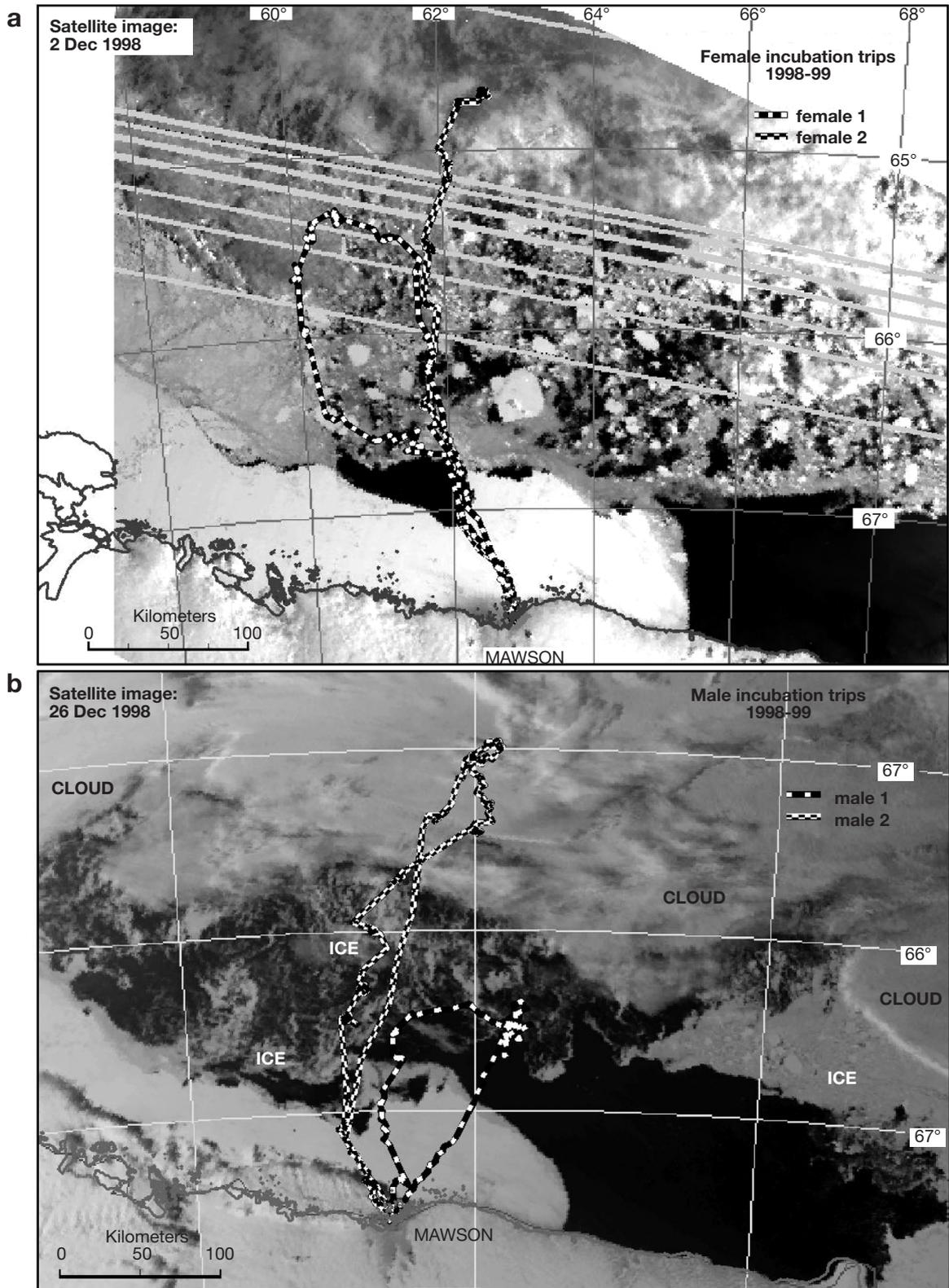


Fig. 3. *Pygoscelis adeliae*. Foraging trips of (a) females and (b) males during the incubation period of 1998–99. Tracks are superimposed upon AVHRR images of the sea ice during early and late December respectively. The polynya to the northwest of Mawson is a consistent feature in all seasons. Birds walked towards the polynya on their outward journey; their return routes were less consistent

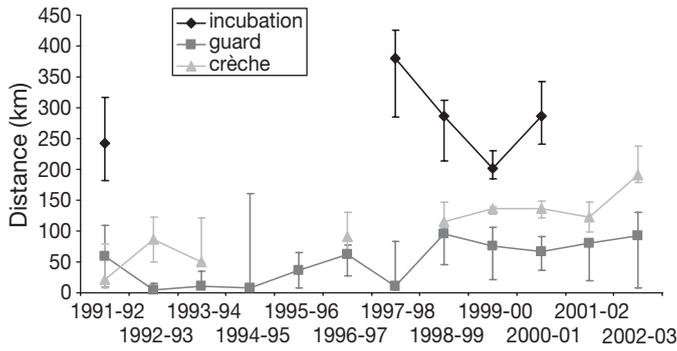


Fig. 4. *Pygoscelis adeliae*. Median foraging ranges for each season and stage of breeding. Bird means were used as sampling units. Error bars indicate upper and lower quartile values. The pre-moult stage was omitted because for most birds only partial journeys were recorded

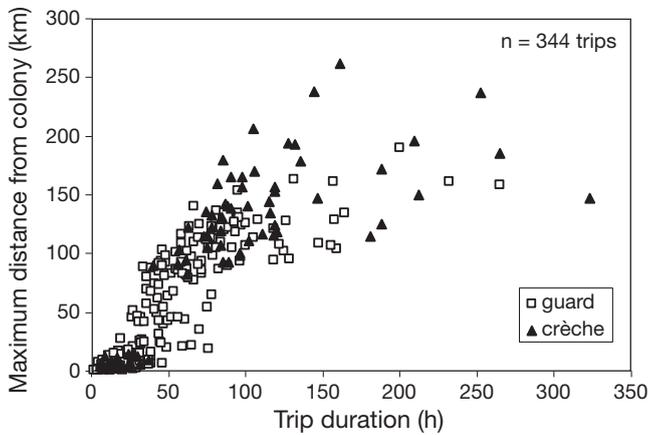


Fig. 5. *Pygoscelis adeliae*. Scatter plot of foraging trip duration versus maximum distance from the colony for 344 trips carried out by satellite tracked birds during the chick rearing period (guard and crèche) of all seasons combined

remained significant when seasons were analysed separately (r_s ranging from 0.646 to 0.953, $p < 0.001$ to 0.022, $n = 10$ to 82). The consistently significant nature of this relationship provided confidence in the use of foraging trip duration as a surrogate for foraging distance. Apparent also in Fig. 5 is the bimodal distribution of foraging distances during the crèche stage. Penguins performed either short trips on which they remained within 30 km of the colony or long trips of distances 80 to 200 km from the coast (see also Fig. 2c). A similar bimodality in trip durations has been observed in APMS data (Clarke et al. 1998).

Foraging trips generally lengthened in proportion to a decrease in penguin body weight (Fig. 6, Table 3a). Within any year both sexes showed the same proportional rate of increase in foraging trip duration with decreasing departure weight. Females spent an estimated 31% (95% CI: 24 to 38%) longer foraging in the guard stage and 7% (95% CI: 1 to 14%) longer in the crèche stage than males. Seasonal variations were significant, but the pattern of change was the same for both sexes. For the guard stage the rate of increase in time spent foraging per 100 g of body weight lost varied from -0.6 to 5.2% and in the crèche stage from 0.3 to 7.7% (Table 4a). These rates were significantly different from zero in all years except 1993–94, 1996–97 and 2001–02 in the guard stage and 1997–98 and 2001–02 in the crèche stage. The years in which foraging duration did not change as a function of body weight in the guard stage were the 3 seasons of highest breeding success recorded over the 12 yr of the study (J. Clarke unpubl. data). No data were available for the crèche stage in 1994–95 because all chicks

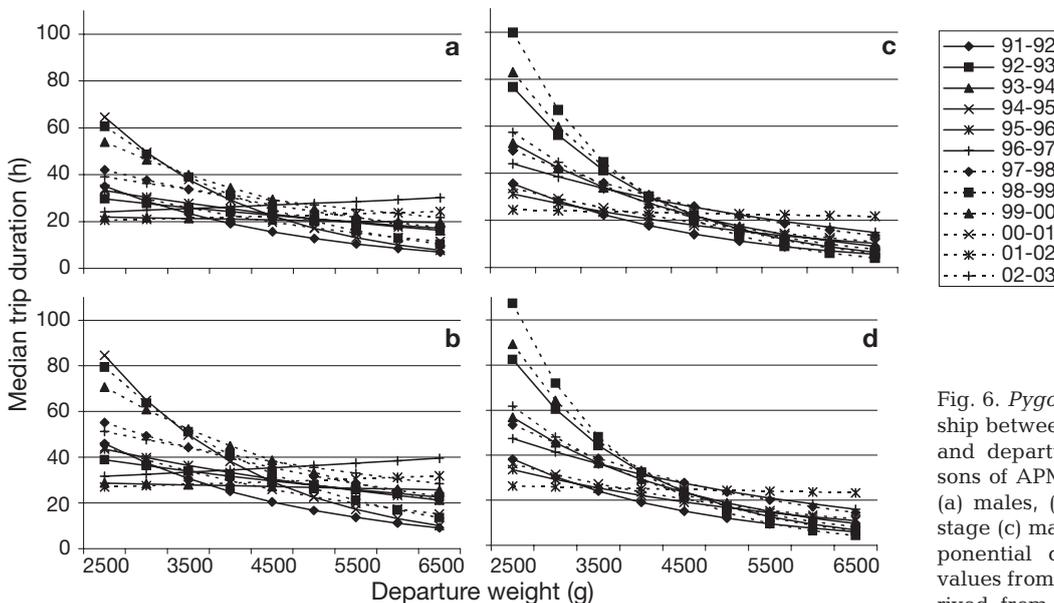


Fig. 6. *Pygoscelis adeliae*. Relationship between foraging trip duration and departure weight for 12 seasons of APMS data for guard stage (a) males, (b) females, and crèche stage (c) males and (d) females. Exponential curves represent fitted values from the minimal models derived from the statistical analyses

Table 3. ANOVA for fixed effects in the minimal models that fitted the data: (a) foraging trip duration during chick rearing as a function of departure weight, season and sex; (b) departure weight during chick rearing as a function of chronological date, season and sex; and (c) foraging trip duration during chick rearing as a function of chronological date, season and sex

Source	df	F	p-value
(a) Foraging trip duration			
Guard stage			
Departure weight	1, 5178	146.03	<0.0001
Season	11, 1673	16.88	<0.0001
Sex	1, 1673	113.8	<0.0001
Departure weight × Season	11, 5178	6.05	<0.0001
Crèche stage			
Departure weight	1, 8591	132.27	<0.0001
Season	10, 1542	15.16	<0.0001
Sex	1, 1542	11.69	0.001
Departure weight × Season	10, 8591	5.78	<0.0001
(b) Departure weight			
Guard stage			
Chronological date	1, 5177	2286.8	<0.0001
Season	11, 1673	29.1	<0.0001
Sex	1, 1673	517.6	<0.0001
Chronological date × Season	11, 5177	23.9	<0.0001
Chronological date × Sex	1, 5177	187	<0.0001
Crèche stage			
Source			
Chronological date	1, 8591	256.3	<0.0001
Season	10, 1542	15.4	<0.0001
Sex	1, 1542	365.8	<0.0001
Chronological date × Season	10, 8591	12	<0.0001
(c) Foraging trip duration			
Guard stage			
Chronological date	1, 6690	8.2	0.004
Season	11, 1899	22.3	<0.0001
Sex	1, 1899	282	<0.0001
Chronological date × Season	11, 6690	10	<0.0001
Crèche stage			
Source			
Chronological date	1, 11751	552.62	<0.0001
Season	10, 1611	17.11	<0.0001
Sex	1, 1611	49.03	<0.0001
Chronological date × Season	10, 11751	26.54	<0.0001

starved to death during the guard period that season (Kerry et al. 1995a).

Analyses of departure weight as a function of chronological date showed a difference between the guard and crèche stages of chick rearing. In the guard stage departure weight declined as time progressed and the rate of decline varied with both season and sex (Fig. 7a,b). Penguins were generally at their lightest weight at the beginning of the crèche stage and then showed an increase in weight over time (Fig. 7c,d). Males and females showed the same rate of change in the crèche stage. Analysis of variance results for the

Table 4. (a) Estimated percentage increase in foraging trip duration for each 100 g reduction in departure weight. (b) Estimated percentage change in foraging trip duration for each week into the stage of breeding. Numbers of foraging trips are provided in brackets. Asterisks indicate significant differences from 0, where *0.01 < p < 0.05, **p < 0.01

	Guard	Crèche
(a) Foraging trip duration and departure weight		
1991–92	4.0 (551)**	4.5 (669)**
1992–93	1.4 (514)*	6.0 (843)**
1993–94 ^a	0.3 (276)	4.4 (1249)**
1994–95 ^b	5.2 (142)**	No chicks alive
1995–96 ^b	1.8 (358)*	2.8 (422)*
1996–97 ^a	-0.6 (660)	2.7 (1111)**
1997–98	2.2 (328)**	3.2 (343)
1998–99 ^b	4.3 (215)**	7.7 (324)**
1999–00	3.0 (527)**	6.4 (644)**
2000–01	2.7 (858)**	2.8 (1724)**
2001–02 ^a	-0.4 (1453)	0.3 (1657)
2002–03	1.5 (994)**	4.9 (1170)**
(b) Foraging trip duration and stage of breeding		
1991–92	0.0 (735)	-13.0 (906)**
1992–93	-5.0 (690)	-22.0 (1098)**
1993–94 ^a	2.0 (464)	-12.0 (2507)**
1994–95 ^b	48.0 (384)**	No chicks alive
1995–96 ^b	12.0 (591)**	-20.0 (591)**
1996–97 ^a	-6.0 (745)	-1.0 (1479)
1997–98	7.0 (539)*	-27.0 (454)**
1998–99 ^b	26.0 (338)**	-41.0 (463)**
1999–00	-1.0 (592)	-21.0 (730)**
2000–01	3.0 (951)	-19.0 (1954)**
2001–02 ^a	-2.0 (1506)	-4.0 (1931)
2002–03	0.0 (1079)	-27.0 (1272)**
^a Seasons in which breeding success was >0.9 chicks crèched per nest		
^b Seasons in which breeding success was <0.4 chicks crèched per nest		

minimal models for guard and crèche are provided in Table 3b. During the guard stage females lost body weight at average rates ranging from 57 to 309 g wk⁻¹ across seasons. Males lost weight at an average of 119 g wk⁻¹ more than females, varying from 176 to 428 g wk⁻¹ across years (Table 5). These rates were significantly different from zero in all years at the 0.01 level. Rates of weight gain during crèche were lower than the rates of loss in the guard period, ranging from 0 to 103 g wk⁻¹ with no sex differences and significance at the 0.05 level in all seasons except 2000–01 (Table 5).

Foraging trip durations remained stable or increased over the guard stage and generally decreased during the crèche stage after peaking early in the latter period (Fig. 8, Table 3c). Rates of increase during the guard stage were significantly different from zero in 1994–95, 1995–96 and 1998–99 (Table

Table 5. Estimated change in departure weight (g) for each week into the stage of breeding

	Male	Female	Crèche
1991–92	-176 (257)**	-57 (294)**	42 (669)**
1992–93	-288 (253)**	-169 (261)**	84 (843)**
1993–94 ^a	-327 (135)**	-207 (141)**	51 (1249)**
1994–95 ^b	-398 (68)**	-279 (74)**	No chicks alive
1995–96 ^b	-428 (181)**	-309 (177)**	98 (422)**
1996–97 ^a	-216 (328)**	-97 (332)**	100 (1111)**
1997–98	-326 (177)**	-206 (151)**	36 (343)*
1998–99 ^b	-360 (122)**	-241 (93)**	103 (324)**
1999–00	-330 (273)**	-211 (254)**	85 (644)**
2000–01	-361 (438)**	-242 (420)**	0 (1724)
2001–02 ^a	-213 (720)**	-94 (733)**	43 (1657)**
2002–03	-304 (486)**	-185 (508)**	19 (1170)*

^aSeasons in which breeding success was >0.9 chicks crèched per nest
^bSeasons in which breeding success was <0.4 chicks crèched per nest

4b), all seasons of poor breeding success (Irvine et al. 2000). Rates of decline in foraging trip duration during the crèche stage varied among years. Long trips early in the crèche stage (Fig. 8) were consistent with results from the tracking study, although short trips were less commonly carried out by tracked penguins later in the crèche period compared to non-instrumented birds recorded by the APMS. This may be indicative of an instrument effect that was not statistically significant when equal numbers of trips of instrumented and control birds were compared (see next section).

The above analyses showed that in most seasons, except those of highest breeding success, penguins (particularly males) lost body condition during the guard stage whilst feeding their chicks frequently and alternating duties with their partners. Penguins generally regained some weight during the crèche stage once freed from the constraints of the nest. Foraging trip durations and distances travelled from the colony peaked early in the crèche stage and birds maintained their own body condition at both stages of chick rearing by increasing their foraging durations (and thus distances travelled from the colony) whenever their body mass was low.

Instrument effects

No significant differences in trip duration between PTT carriers and non-instrumented birds were found in any season except 1998–99 and 2000–01 when trips of instrumented birds were longer than those of controls (medians of 98.1 and 60.2 h respectively in 1998–99, Mann-Whitney rank sum test: $t = 520$, $n = 20$, $p = 0.003$; medians of 41.9 and 26.6 h respectively in 2000–01, $t = 7465$, $n = 82$, $p = 0.021$). Further analysis showed that the difference during the latter season was restricted to the crèche stage, whilst in 1998–99 differences were present in both guard and crèche stages of breeding. The overall ratio of short (<40 h) to long (>40 h) trips (as defined in Clarke et al. 1998) carried out by tracked birds was 1:2, whilst in the APMS data set as a whole this ratio is approximately 2:1 (J. Clarke unpubl. data).

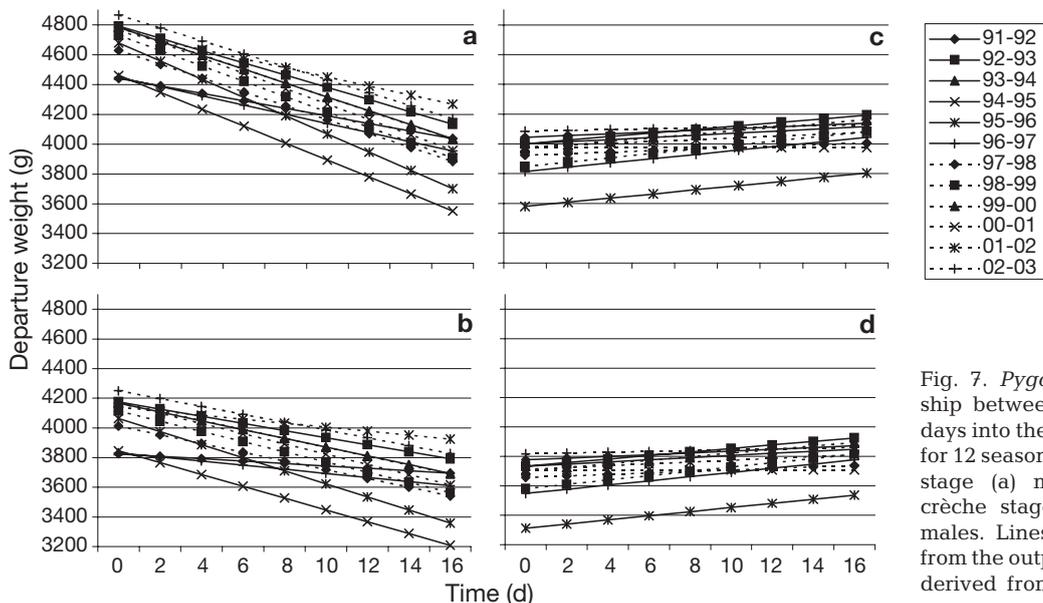


Fig. 7. *Pygoscelis adeliae*. Relationship between departure weight and days into the guard and crèche stages for 12 seasons of APMS data for guard stage (a) males, (b) females, and crèche stage (c) males and (d) females. Lines represent fitted values from the output of the minimal models derived from the statistical analyses

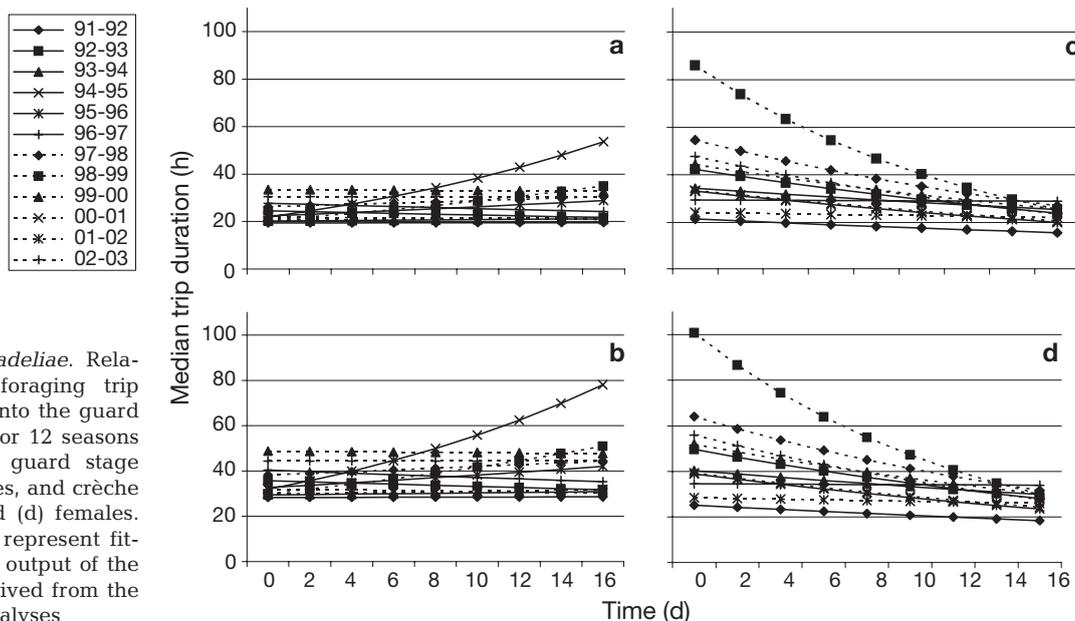


Fig. 8. *Pygoscelis adeliae*. Relationship between foraging trip duration and days into the guard and crèche stages for 12 seasons of APMS data for guard stage (a) males, (b) females, and crèche stage (c) males and (d) females. Exponential curves represent fitted values from the output of the minimal models derived from the statistical analyses

DISCUSSION

Instrument effects

It is unlikely that the consistent increase in foraging range between guard and crèche phases documented in this study was due to instrument effects because the crèche stage was influenced differently than the guard stage only in 2000–01. Results were consistent with previous work at this location (Clarke & Kerry 1994) and with that of Ballard et al. (2001), both of which found that individual variation in foraging duration during chick rearing precluded detection of significant instrument effects on a within season basis. However, the greater tendency of instrument carriers to make trips in excess of 40 h raises the possibility that birds encumbered by satellite trackers may need to carry out long trips more frequently to maintain body condition than do birds not carrying instruments. This corresponds with the findings of Watanuki et al. (1992), Hull (1997) and Bost et al. (2004), who observed that instrument effects were most pronounced at times of year when foraging penguins are most energetically stressed.

Foraging ranges during breeding and environmental constraints

The distribution of foraging penguins during the breeding season can be expected to correlate with the distribution of their prey within constraints imposed by physical barriers such as sea ice and the need to return

regularly to the colony to provision offspring. Adélie penguin foraging distances vary widely depending on colony location and stage of breeding. For example, penguins provisioning chicks at Hukuro Cove (69° 00' S, 39° 39' E) limit their foraging to a 5 km radius throughout chick rearing (Kato et al. 2003), whilst those at Signy Island (60° 43' S, 45° 34' W) range up to 177 km in the crèche stage (Lynnes et al. 2002). In this study the foraging ranges of Adélie penguins at Béchervaise Island changed as the breeding season progressed in all years examined. Penguins travelled long distances during incubation and shorter distances during chick rearing. Adult foraging ranges typically expanded in both distance and area as chicks progressed from guard to crèche stages, and were greater still during the period when birds accumulate fat reserves prior to carrying out their annual moult.

Adélie penguins are considered ice-obligate over winter (Fraser & Trivelpiece 1996, Ainley 2002) and are closely associated with sea ice in summer (Trivelpiece & Fraser 1996, Ainley 2002). During incubation this species commonly forages 200 km or more from its breeding colonies (Davis & Miller 1992, Kerry et al. 1995a). Proximity of Adélie penguin colonies to polynyas provides crucial access to foraging grounds during spring as well as opportunities for faster travelling rates and wider distribution of foraging birds (Fraser & Trivelpiece 1996, Arrigo & van Dijken 2003, Ainley et al. 2004). Penguins tracked during incubation in this study walked directly to the nearest margin of the Taylor Glacier polynya before moving northwards into the pack ice, using the polynya as access to the pack ice zone rather than as a foraging locality per

se. Like Adélie penguins tracked from Inexpressible Island (74° 54' S, 163° 39' E) in the Ross Sea (S. Olmas-troni pers. comm.), the Béchervaise Island penguins foraged around the margin of the polynya, remaining in association with the ice rather than spending time in open water.

Large Adélie penguin breeding colonies are only found in regions where fast ice typically breaks out from the Antarctic coastline before or soon after chicks hatch (Trivelpiece & Fraser 1996, Ainley 2002). The presence of excessive fast ice or heavy pack ice during the chick rearing period restricts access to prey, resulting in reduced breeding success in years of extensive ice cover (Yeates 1968, Ainley & LeResche 1973, Spurr 1975, Whitehead et al. 1990, Irvine et al. 2000, Clarke et al. 2002). In the Mawson region, where a submarine canyon facilitates upwelling of warm water, pack ice is limited in extent by early January and the distance to the edge of the fast ice reduced in most years (Michael et al. 2003). Penguins return to the colony at 1 to 3 d intervals to feed their growing chicks and alternate guard duties with their mates. Their foraging range is constrained at this time by access to food and the requirement for regular provisioning of offspring.

The distribution and abundance of krill *Euphausia superba* and other zooplankton in the Mawson region is patchy and highly variable over short temporal and small spatial scales in summer (Hosie et al. 1988, Hosie et al. 1997, Pauly et al. 2000, S. Nicol unpubl. data). Although some local foraging took place, the penguins in this study concentrated much of their guard and crèche stage foraging activity along the continental shelf break where *E. superba* aggregate in greatest concentrations (Higginbottom et al. 1988, Hosie et al. 1988), and large krill predominate in summer (Lascara et al. 1999, Nicol et al. 2000, Salihoglu et al. 2001). Because the shelf break lies 100 to 110 km from the Mawson coast, penguins are required to travel this distance to reach reliable foraging grounds, necessitating trips of three or more days in duration.

Penguins from Béchervaise Island travel further to reach the productive foraging grounds at the shelf break than birds at other locations where the shelf break is closer (Lishman 1985), neritic species more abundant (Ainley et al. 1998, 2004), or *Euphausia superba* found closer to the coast (Watanuki et al. 1994). The range and distance travelled by penguins at each of these colonies is highly dependent on the environmental features of the particular area, and how these environmental features influence prey distribution and the penguins' access to prey. For example, the distribution of foraging penguins during the guard stage in this study was centred over a bathymetric canyon where zooplankton productivity is likely to be enhanced.

Adélie penguins are known to moult on large ice floes, ice bergs and sheltered areas of land (Ainley 2002), but how far they range from their breeding sites at this time of year is virtually unknown. Penguins foraging prior to moult are no longer provisioning offspring and are thus free to travel further from the colony to search for food. In this study birds foraged predominantly in waters over the continental shelf towards Enderby Land in the west, and north of Cape Darnley in the east. It is possible that by autumn, when sea ice is minimal, penguins are able to exploit krill patches associated with remnant ice and late summer phytoplankton blooms to the west of the Mawson region where fast ice persists until late summer (Michael et al. 2003). The region to the north of Cape Darnley, on the other hand, is known to be an area of high productivity (Quilty et al. 1985), even in seasons where krill is scarce elsewhere along the coast (S. Nicol unpubl. data). Concentration of penguin foraging activity in this locality is thus unsurprising, and there is also limited evidence that birds from Scullin & Murray Monoliths feed here on a regular basis (Kerry et al. 1997).

Partitioning of resources during chick rearing and life history constraints

Although a decrease in penguin foraging range between the incubation and chick rearing stages of breeding is well documented (Hull et al. 1997, Kerry et al. 1997, Barlow & Croxall 2002), variations in range post hatch are less consistent. Increasing foraging ranges as chick rearing progresses are reported for macaroni, royal and Adélie penguins at a number of locations (Hull et al. 1997, Watanuki et al. 1999, Wiencke et al. 2000, Barlow & Croxall 2002, Lynnes et al. 2002, Kato et al. 2003, Ainley et al. 2004), including Béchervaise Island (this study) but apparently not at others (Lishman 1985, Trivelpiece et al. 1987, Wiencke et al. 2000). Ainley et al. (2004) suggested that the foraging range expansion observed at Ross Island resulted from intraspecific competition and consequent effects on foraging effort. Alonzo et al.'s (2003) modelling study also predicted an increase in offshore foraging if prey were depleted close to the colony. Increasing energy demands as chick rearing progresses (Culik 1994) combined with local food depletion due to intraspecific competition might be expected to influence both foraging strategies and the distribution of foraging birds.

The Béchervaise Island colony is a small subcolony within the Mawson region where approximately 55 000 pairs breed along a 10 km stretch of coastline. With this number of penguins foraging in the area,

prey supplies could potentially be depleted within the vicinity of the colonies by the end of the guard stage. In addition, an estimated 66 000 pairs of Adélie penguins breed on the Rookery Islands (Woehler 1993, Woehler et al. 2001) situated less than 20 km west of Mawson. Competition between these two colonies for limited resources may exacerbate the challenge of meeting provisioning requirements as the breeding season progresses.

Many flying seabirds show a dual foraging strategy during chick rearing whereby they use a combination of long and short foraging trips as a means of partitioning energy resources, maximising use of distant food resources for self maintenance and thereby reducing intraspecific competition close to the colony (Chaurand & Weimerskirch 1994, Weimerskirch et al. 1994, Weimerskirch 1998). A single year study on Adélie penguins in the Mawson region (Clarke 2001) showed that breeding birds carried out short trips to provision chicks at the expense of stored body reserves and that these reserves gradually declined throughout the guard stage of chick rearing. Watanuki et al. (2002) found a similar relationship between departure mass and trip duration at 2 other locations in East Antarctica, and Culik (1994) observed declines in body weight during the guard period.

In this multi-year study we have shown that Adélie penguins typically carry out longer foraging trips when their weight is low compared to when they are in better body condition. Only in seasons of high breeding success does this relationship fail to hold, suggesting that plentiful food supplies close to the colony allow birds to maintain condition without lengthening their foraging trips. Adults lose weight during the guard stage, and foraging durations increase during years when feeding conditions are apparently poor (low chick survival). Trip durations generally peak in the early crèche period when adult body condition is lowest and chicks can be left unguarded whilst both parents forage. Freedom from the constraint of guard duty enables adults to forage simultaneously and regain some of their lost body condition without a reduction in overall chick feeding frequency.

In their modelling study, Alonzo et al. (2003) found that penguins adopting a time minimising strategy foraged close to the colony unless krill abundance was low, as tends to be the case in neritic waters close to Mawson during summer. More penguins were predicted to forage further offshore when penguins were food maximising. Although their model used the example of a simple penguin-krill system operating in waters between the coast and the edge of the continental shelf, it was based on a more general framework designed to examine interactions between species (Alonzo 2002). The behaviour of Adélie penguins

in the Mawson region is consistent with penguins adopting a time minimising foraging rule during chick rearing except when their body weight is low. The latter occurs most commonly during the early crèche stage when frequent provisioning rates are less critical and access to distant more productive foraging grounds advantageous for body condition maintenance. Our results provide empirical support for the proposition of Alonzo et al. (2003) that Adélie penguin distribution during chick rearing in regions where inshore resources are limiting is a result of foraging rules adopted by the birds under the constraints of competing demands for self maintenance and reproduction.

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