

# Effects of variability in prey abundance on reproduction and foraging in chinstrap penguins (*Pygoscelis antarctica*)

D. A. Croll<sup>1</sup>, D. A. Demer<sup>2</sup>, R. P. Hewitt<sup>2</sup>, J. K. Jansen<sup>3</sup>, M. E. Goebel<sup>2</sup> & B. R. Tershy<sup>1</sup>

<sup>1</sup> Ecology and Evolutionary Biology Department, University of California, Santa Cruz, CA, USA

<sup>2</sup> Southwest Fisheries Science Center, National Marine Fisheries Service, La Jolla, CA, USA

<sup>3</sup> National Marine Mammal Laboratory, National Marine Fisheries Service, Seattle, WA, USA

## Keywords

penguin; foraging; Antarctica; krill; seabird.

## Correspondence

Donald A. Croll, Ecology and Evolutionary Biology Department, 100 Shaffer Road, University of California, Santa Cruz, CA 95060, USA.

Email: croll@biology.ucsc.edu

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## Abstract

Life-history theory predicts that adults of long-lived species such as seabirds should optimally balance investment in current and future offspring. However, when trying to optimize investment in offspring provisioning, the most energetically costly component of seabird parental care, adults need to contend with large interannual fluctuations in prey availability and hence the cost of chick provisioning. Adults faced with this uncertainty can mechanistically balance parental care by adopting a strategy somewhere along the continuum between maintaining constant investment in foraging effort between years and letting chick provisioning fluctuate or holding chick provisioning constant and varying investment in foraging effort. Using ship-based hydroacoustic assessment of prey, time-depth recorders attached to penguins and land-based observations at the breeding colony, we examined how foraging and reproductive effort in breeding chinstrap penguins *Pygoscelis antarctica* responded to interannual variation in the abundance of Antarctic krill *Euphausia superba* in the vicinity of Seal Island, South Shetland Islands, 1990–1992. Regional measures of krill density varied by a factor of 2.5 (47.0, 23.8 and 61.2 g m<sup>-2</sup> in 1990, 1991 and 1992, respectively) and was correlated with annual measures of breeding adult body weight and reproductive performance (breeding population size, duration of chick rearing, chick growth, breeding success and fledgling weight). In contrast, measures of penguin foraging effort (dive depth, dive duration, number of trips day<sup>-1</sup>, trip duration, number of dives trip<sup>-1</sup> and dive rate) did not differ between years. We conclude that chinstrap penguins reduce reproductive success rather than increase foraging effort in response to decreases in prey abundance in a manner consistent with predictions of life-history strategies for long-lived seabirds.

## Introduction

Food availability is an important factor regulating animal population dynamics through its constraints on life-history traits such as growth, reproductive success and survival (Martin, 1987; Stearns, 1992). Compared with terrestrial birds, seabird life histories are characterized by high adult survival, low fecundity and deferred maturity (Lack, 1968). In general, seabird populations are relatively stable (Furness & Monaghan, 1987), with catastrophic mortality of adults being rare (Cairns, 1987). Lack (1954) suggested that seabird populations are regulated by decreases in the production of offspring in response to decreased food availability rather than adult mortality, as breeding adults trade off current versus future reproductive success (Stearns, 1992). This predicts that adult seabirds faced with large interannual fluctuations in prey availability should hold chick provisioning foraging effort relatively constant and let annual reproductive success fluctuate between years.

Although numerous studies have shown that seabird reproduction is linked to large-scale oceanographic events (Kitaysky & Golubova, 2000; Croxall, Trathan & Murphy, 2002), few studies have simultaneously measured reproductive success, foraging behavior and offshore prey abundance. Thus, it is unclear whether seabirds respond to interannual changes in prey abundance by trading off investment in foraging for chicks against future reproductive success (Croxall, Reid & Prince, 1999).

The ability to conduct such studies has been limited by an inability to manipulate offshore prey abundance, potential prey switching by the seabirds, limited ability to measure foraging effort in seabirds or inability to measure prey abundance and seabird behavioral and reproductive response simultaneously. Most studies that have examined this question have compared measures of the reproductive success or foraging effort of seabirds with indirect indicators of offshore prey availability (e.g. Bergman, 1978; Lid, 1980; Anderson, Gress & Mais, 1982; Monaghan *et al.*, 1994;

Uttley *et al.*, 1994). Other studies have examined how seabird foraging behavior and reproductive effort responded to manipulations of the seabird's ability to forage (Saether, Andersen & Pedersen, 1993; Weimerskirch, Chastel & Ackermann, 1995).

Jansen, Russell & Meyer (2002) found that chinstrap penguins *Pygoscelis antarctica* increased the number of foraging trips they made in response to chick growth, and Meyer *et al.* (1997) found that chinstrap penguins increase foraging effort to meet the demands of larger broods. Both studies attributed observed increases in foraging effort to increased chick demand rather than changes in offshore krill resources. Meyer *et al.* (1997) also found that foraging effort as measured through foraging trip frequency and duration was different in only 1 year out of 4. In that year, anecdotal observations indicated that large quantities of prey were located close to the colony. Thus, although variability in reproductive performance in penguins has been attributed to variability in krill abundance (Ainley, O'Connor & Boekelheide, 1984; Williams & Rothery, 1990; Loeb *et al.*, 1997; Lynnes, Reid & Croxall, 2004), it is not clear whether adults adjust foraging effort in response to interannual variability in krill abundance.

Here, we examine whether chinstrap penguins adjust foraging effort or reproduction in response to variability in prey availability. We use data gathered between 1990 and 1992 by the US Antarctic Marine Living Resources Program on the abundance of krill, penguin reproductive performance and penguin foraging effort in the vicinity of Seal Island, South Shetland Islands. This system is unique because (1) krill abundance was directly measured by the US-AMLR survey efforts, (2) detailed studies of the foraging effort and reproduction of breeding chinstrap penguins were simultaneously conducted on Seal Island and (3) chinstrap penguins in this region have been shown to feed almost exclusively upon krill (Volkman, Presler & Trivelpiece,

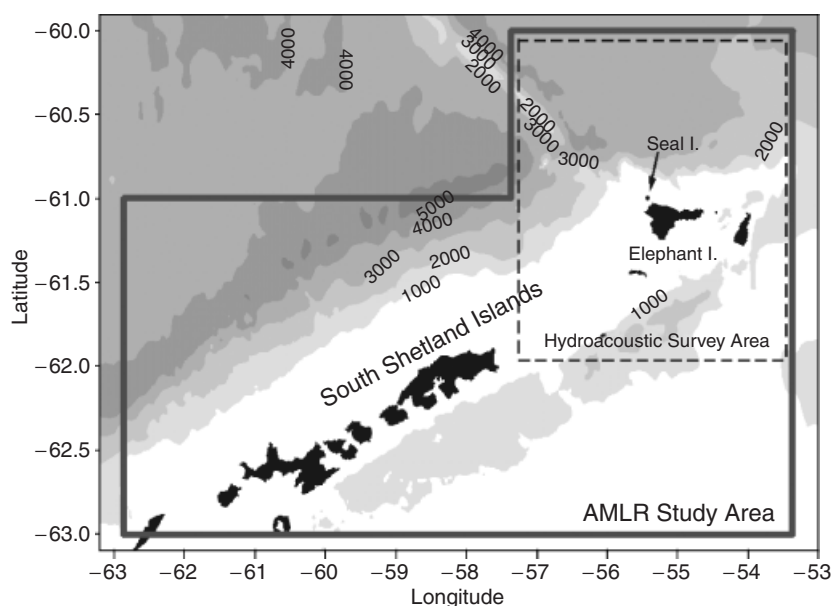
1980; Lishman, 1985; Jansen, Boveng & Bengtson, 1998). Because prey availability and penguin data were gathered concurrently, they provide the unique opportunity to examine directly whether seabirds respond to variability in offshore prey abundance by adjusting investment in foraging for their chicks, investment in reproduction or both.

## Methods

We examined the reproductive and foraging behavior of chinstrap penguins breeding on Seal Island, South Shetland Islands (60°59'S, 55°23' W) (Fig. 1) between 1990 and 1992. To examine how these parameters varied in response to offshore prey abundance, we concurrently conducted hydroacoustic surveys of krill abundance in the vicinity of Seal Island (Fig. 1, Table 1). Specifically, we examined the reproductive and foraging responses of penguins to interannual changes in krill abundance measured in three surveys conducted within 200 km of Seal Island during January 1990, 1991 and 1992.

## Study system

Studies that simultaneously measure natural variation in reproduction, foraging effort and prey abundance provide the opportunity to examine how seabirds adjust investment in foraging and reproduction in response to variability in food availability (Weimerskirch *et al.*, 1995). The Southern Ocean is an ideal, simplified, trophic system in which to conduct such a study due to the reliance of high-level predators on a single prey species, Antarctic krill *Euphausia superba* (Murphy *et al.*, 1988). Several Antarctic seabirds, including the chinstrap penguin *P. antarctica*, feed almost exclusively on krill (Volkman *et al.*, 1980; Lishman, 1985). The chinstrap penguin is the most abundant penguin species that breeds on the Antarctic Peninsula and islands of the Scotia Sea



**Figure 1** US AMLR study area (depth in meters).

**Table 1** Acoustic estimates of krill biomass in the Elephant Island area

Date	Survey area (km <sup>2</sup> )	Biomass (10 <sup>3</sup> ton)	CV (%)	Krill density (g m <sup>-2</sup> )
21–26 January 1990	36 271	1702	32.1	47.0
21–31 January 1991	43 380	1036	29.9	23.8
19 January–2 February 1992	36 271	2220	15.8	61.2

The large-area surveys were centered on Elephant Island and measured krill abundance within 200 km of penguins breeding on Seal Island. Survey details in Macaulay & Mathisen (1991) and Hewitt & Demer (1991, 1993, 1994).

**Table 2** Summary foraging dive data for chinstrap penguins *Pygoscelis antarctica* breeding on Seal Island, South Shetland Islands

Year	Number of birds	Dive duration (s)		Depth (m)		Trips day <sup>-1</sup>	Trip duration (h)	Dives trip <sup>-1</sup>	Dive rate (m min <sup>-1</sup> )
		Day	Night	Day	Night				
January 1990	5	90.5	61.3	37.6	18.2	0.8	11.4	275	23.4
		(7.8)	(7.3)	(10.2)	(6.9)				
January 1991	8	78.3	64.5	32.3	23.3	1.0	11.2	273	23.9
		(5.2)	(25.7)	(5.5)	(12.8)				
January 1992	5	82.0	70.1	36.5	27.4	1.0	12.5	205	25.4
		(8.4)	(22.1)	(5.4)	(9.0)				

Values in parentheses are standard deviations. All differences were not significant using one-way ANOVA.

(Woehler & Croxall, 1997), and several studies have shown that krill abundance in the South Shetland Islands region of the Scotia Sea undergoes considerable interannual variability (Hewitt & Demer, 1993, 1994; Siegel & Loeb, 1995; Loeb *et al.*, 1997).

### Krill distribution and abundance

Interannual patterns in the abundance and dispersion of krill were described from 120 kHz acoustic backscatter data collected during AMLR surveys in the vicinity of Seal Island during late January 1990–1992 [Fig. 1, Table 2; see Macaulay & Mathisen (1991) for a description of survey design and instrumentation used in the 1990 and 1991 surveys and Hewitt & Demer (1993) for a description of survey design and instrumentation used in the 1992 surveys]. Measurements of volume backscattering strength were filtered with a threshold at  $-81$  dB re 1 W (equivalent to *c.* 1 krill m<sup>-3</sup>). Bottom return, system noise and reflections from non-krill backscatter were removed and the remaining volume backscattering strengths were integrated from 10 to 250 m depth (or to 1 m above the bottom where shallower than 250 m) and averaged over 1 nautical mile (1852 m). Integrated volume backscattering strength was scaled to estimates of krill biomass density by applying a factor equal to the quotient of the weight of an individual krill and its backscattering cross-sectional area, summed over the sampled krill body length frequency distribution for each survey. Average biomass densities and associated variances for the 1990 and 1991 surveys were estimated by pooling the data into rectangles, 30 min of latitude by 1° of longitude (*c.* 900 square nautical miles at 60°S), and then applying cluster sampling procedures (Macaulay, English & Mathisen, 1984; Macaulay & Mathisen, 1991). Reported biomass

density values for 1990 and 1991 (Table 1) were subsequently increased by a factor of 1.503 to account for a change in the definition of krill target strength (Everson *et al.*, 1990; Foote *et al.*, 1990; Greene *et al.*, 1991; Hewitt & Demer, 1991, 1994). Average biomass densities and associated variances for the 1992 surveys were estimated (Table 1) by considering the mean biomass density on each of the parallel transects as an independent estimate of the overall mean density following the procedures outlined by Jolly & Hampton (1990). For comparison, the 1992 surveys were also processed in a manner similar to the 1990 and 1991 surveys; differences in the estimates of mean and variance were less than 3% and the originally reported values are used here. See Simmonds *et al.* (1991) for a thorough discussion of spatial averaging techniques used in the analysis of acoustic data.

The combined random measurement and sampling error for acoustic estimates of krill abundance is closely approximated by the sampling error (Demer, 2004), because of the large number of measurements averaged to derive the ultimate biomass estimate. However, some potential sources of bias [e.g. stemming from uncertainties in the target strength model (see Demer & Conti, 2005), the krill length-to-weight model, the species classification method, bubble attenuation, signal thresholding and survey area definition] may be more appreciable components of measurement uncertainty. To permit an analysis of the interannual krill abundance, the survey and analysis methods were consistent and the systematic error was considered to be constant.

### Penguin foraging behavior

To measure penguin foraging behavior, we attached Wildlife Computers Mk 4 time and depth recorders (TDRs) (103 g), using methods similar to those described by

Bengtson, Croll & Goebel (1993), to adult chinstrap penguins breeding on Seal Island. For all TDR deployments, we captured adults as they prepared to depart the colony for foraging trips. The TDRs were programmed to measure depth every 5 s with a minimum depth resolution of  $\pm 1$  m. We attached TDRs to the feathers of the middle of the back using a quick-setting adhesive (Devcon 5 min epoxy) and two plastic cable ties. After *c.* 5–10 days, the recorders were recovered from the birds and the data were downloaded to a laptop computer. The attachment of TDRs was found to affect the behavior and energy requirements of diving seabirds (Wilson, Grant & Duffy, 1986; Croll, Osmek & Bengtson, 1991). Consequently, the instruments we applied may have increased the energetic cost of foraging for the penguins through an increase in drag and package discomfort. However, instruments and attachment methods were identical during each deployment period. Thus, comparisons among instrumented birds should be valid. Because chinstrap penguins tend to porpoise when leaving and returning to the colony (Trivelpiece *et al.*, 1986), we followed the convention of Bengtson *et al.* (1993) and defined foraging dives for chinstrap penguins as dives of at least 5 m in depth or at least 20 s in duration.

We compared the foraging effort of breeding penguins to simultaneously measured changes in krill abundance from the 1990–1992 breeding seasons. For diving parameters (depth, duration), data from daytime (03:00–21:00 h) and nighttime (21:00–03:00 h) dives were analyzed separately. Birds interspersed foraging trips to sea with visits on land. We defined a foraging trip as ending with the termination of the last dive of a series where no further dives occurred during the following 3 h and the instrument salt water switch indicated the bird was out of the water during the interval. We calculated the number of foraging trips per day, foraging trip duration, number of dives per foraging trip and dive rate (total vertical distance traveled per total time spent diving; Boyd *et al.*, 1994). To avoid sample bias due to birds that performed many short-duration dives less than 20 s in duration, we averaged each foraging parameter across the mean values for individuals (*i.e.* individual birds, not dives were considered a sample). Deployment of TDRs was timed to correspond to large-area surveys conducted offshore of Seal Island (Table 1).

## Penguin reproduction

We measured chick fledging mass, breeding population size, timing of breeding, chick growth and creche success (defined as survival to the point at which chicks are no longer guarded by adults) as indicators of reproductive effort for each year. In addition, we measured adult body mass at hatching as an index of adult condition during the breeding season each year.

### Breeding adult body mass and chick mass at fledging

We weighed adult penguins that were guarding recently hatched chicks (late December to early January) as a measure

of breeding adult body condition (48, 60 and 58 individuals in 1990, 1991 and 1992, respectively). In the analysis, we excluded birds that had recently arrived at their nests with full stomachs.

Chinstrap penguin chicks move from the nesting areas to beaches as they prepare to depart to sea. To estimate fledging condition, we weighed samples of fledglings preparing to depart from the beach from the date fledglings first appeared near the water until the first week in March. A total of 141, 251 and 264 fledglings were weighed in 1990, 1991 and 1992, respectively.

### Nesting population census

Each year we recorded the number of breeding pairs of chinstraps in all accessible penguin nesting areas on the island *c.* 2 weeks after the completion of egg laying. All birds in the incubation posture were assumed to be occupying a nest site and were counted. Large nesting areas were photographed and breeding pairs were counted from the photograph. Smaller nesting areas were counted by eye from *c.* 20 m using a hand counter.

### Reproductive success and timing of reproduction

To estimate breeding success and timing of reproduction, we observed plots of nests from blinds at two nesting areas (north cove and parking lot: a total of 200, 237 and 237 nests in the two areas in 1990, 1991 and 1992, respectively). We monitored the presence of attending adults, eggs and chicks every other day from the completion of egg laying until the time dependent chicks began to aggregate in groups away from the nest sites in creches. For this paper, we defined breeding success as the mean number of chicks that creched from each nest that was active at the start of observations (completion of laying).

Peak hatching and fledging dates were estimated as the modal date from our observations at study plots. We estimated the duration of chick rearing from peak hatching to peak fledging dates.

### Chick growth

As chicks grow, they form large, mobile, creches making it difficult to follow individual chicks from hatching to fledging without creating considerable disturbance to the colony. Therefore, we weighed at least 50 chicks every 5 days between hatching and fledging at a nesting area of >2000 nests. This is the standard method for determining chick growth adopted by the Scientific Committee for the Conservation of Antarctic Marine Living Resources (CCAMLR, 1991). Chicks were weighed using Pesola scales in open mesh bags that reduced the wetting and matting of down. Before creching, we sampled at least 50 chicks from at least 30 haphazardly selected nests. After creching, we weighed 75 chicks during each sampling period, again

haphazardly selected. Weighed chicks were marked to avoid resampling.

## Results

### Krill abundance

There was marked interannual variability in the January krill abundances in the Seal Island vicinity estimated from regional surveys. Krill abundance was high in 1990 and 1992, and relatively low in 1991 (Table 1).

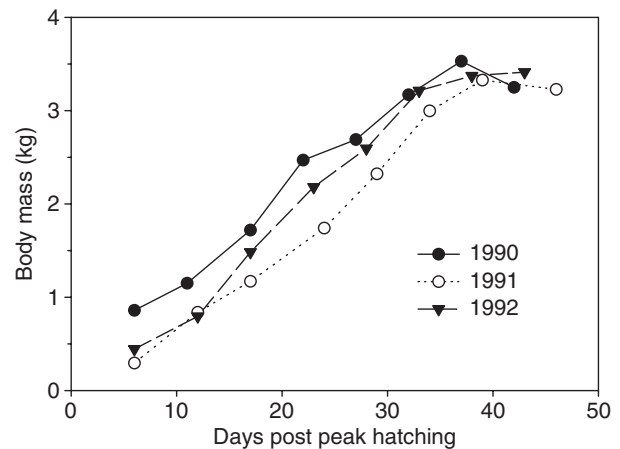
### Penguin foraging behavior

A total of 27 347 foraging dives was recorded for 18 penguins (five, eight and five individuals in January 1990, 1991 and 1992, respectively; Table 2). A two-way ANOVA using time of day and year as factors indicated that dive depths were significantly greater during the day (overall mean  $34.9 \pm 7.1$  SD) than at night (overall mean  $22.7 \pm 10.2$  SD), depth did not differ across years, and there was no interaction between year and time of day on dive depth (time of day  $F_{1,32} = 16.56$ ,  $P < 0.001$ ; year  $F_{2,32} = 0.75$ ,  $P = 0.48$ ; time of day and year  $F_{2,32} = 1.26$ ,  $P = 0.30$ ). Similarly, a two-way ANOVA using time of day and year as factors indicated that dive durations were longer during the day (overall mean  $84.7 \pm 9.1$  SD) than at night (overall mean  $65.2 \pm 12.0$  SD), durations did not differ across years, and there was no significant interaction between year and time of day on dive duration (time of day  $F_{1,32} = 30.65$ ,  $P < 0.001$ ; year  $F_{2,32} = 1.72$ ,  $P = 0.20$ ; time of day and year  $F_{2,32} = 2.27$ ,  $P = 0.12$ ).

No significant interannual differences were found in number of trips  $\text{day}^{-1}$  (one-way ANOVA:  $F_{2,17} = 2.26$ ,  $P = 0.14$ ), trip duration (one-way ANOVA:  $F_{2,14} = 0.24$ ,  $P = 0.79$ ), number of dives  $\text{trip}^{-1}$  (one-way ANOVA:  $F_{2,15} = 1.01$ ,  $P = 0.39$ ) or dive rate (vertical distance  $\text{min}^{-1}$ ) (one-way ANOVA:  $F_{2,17} = 0.59$ ,  $P = 0.57$ ). Although we found no significant differences across years in our measures of foraging effort, the logistics and expense in attaching recording devices limited sample size. For all parameters measured (Table 2), the estimated power was less than 0.6.

### Penguin reproduction

Adult penguin body mass and reproductive success varied with regional krill abundance estimates (Table 2). Adult body mass during early chick brooding (January) was significantly lower in 1991 than in 1990 and 1992 (one-way ANOVA:  $F_{2,63} = 5.21$ ,  $P < 0.001$ ; Tukey multiple comparisons: 1991 vs. 1990,  $q = 4.86$ ,  $P < 0.05$ ; 1991 vs. 1992,  $q = 4.21$ ,  $P < 0.05$ ). The size of the breeding population on Seal Island was lowest in 1991 (31 416 individuals) and highest in 1992 (45 362 individuals) (Table 2). The number of chicks raised to creche/nest was significantly higher in 1992 than in 1990 and 1991 (Kruskal–Wallis:  $H_2 = 8.74$ ,  $P < 0.001$ ; Dunn's test multiple comparisons: 1992 vs. 1990,  $Q = 7.47$ ,  $P < 0.05$ ; 1992 vs. 1991,  $Q = 6.71$ ,  $P < 0.05$ ). The



**Figure 2** Chick growth of chinstrap penguins *Pygoscelis antarctica* on Seal Island, South Shetland Islands, 1990–1992.

duration of the chick-rearing period (peak hatching to peak fledging) was longest in 1991 (64 days) and shortest in 1992 (55 days). Chick growth rate was slower in 1991 than in 1990 and 1992 (Fig. 2), and chick fledgling weights were significantly lower in 1991 than in 1990 and 1992 (Kruskal–Wallis:  $H_2 = 63.91$ ,  $P < 0.001$ ; Dunn's test multiple comparisons: 1991 vs. 1990,  $Q = 57.94$ ,  $P < 0.05$ ; 1991 vs. 1992,  $Q = 133.03$ ,  $P < 0.05$ ).

## Discussion

Chinstrap penguins nesting on Seal Island have been radio tracked 7.4–28 km offshore (Bengtson *et al.*, 1993), and have been estimated to range from 3.3 to 26.4 km offshore of the colony (Bengtson *et al.*, 1993). Trivelpiece *et al.* (1986) estimated that foraging chinstrap penguins breeding on King George Island, South Shetland Islands, range 27–33 km offshore. Thus, the distance that chinstrap penguins forage from shore is contained within the range of our krill survey region (from nearshore out to 200 km offshore of Seal Island). Because krill are advected into the immediate vicinity of Seal Island from outside the penguin foraging range (Siegel, 1991), the larger scales of the krill surveys are appropriate to penguins foraging from Seal Island.

Krill density in the Seal Island region varied by a factor of 2.5 between 1990 and 1992 (47.0, 23.8 and  $61.2 \text{ gm}^{-2}$  in 1990, 1991 and 1992, respectively; Table 1). Such changes in krill abundance have been attributed to large-scale processes such as annual patterns in primary productivity (Loeb *et al.*, 1997), seasonal advection of krill through the Seal Island area by currents (Siegel, 1991) and annual patterns in krill recruitment (Loeb *et al.*, 1997). In spite of this interannual variability in krill density, we found no differences in penguin foraging effort between 1990 and 1992 (Table 2). These results contrast with those of several studies that were based upon indirect measures of prey abundance where they hypothesized that seabirds increase foraging effort to compensate for decreases in prey availability (Burger & Piatt,

1990; Cairns, 1992; Monaghan *et al.*, 1994; Boyd & Croxall, 1996; Fraser & Trivelpiece, 1996; Monaghan, 1996).

Although we did not observe interannual differences in foraging effort, we did find positive correlations between large-area prey abundance measurements and indices of annual reproductive success. Compared with years with relatively high regional krill abundance (1990 and 1992), fewer adults bred in 1991 – a year of lower krill abundance (Table 1). Adult penguins had lower body mass, took longer to raise their chicks, raised fewer chicks, and these chicks fledged at lower body mass in 1991 compared with 1990 and 1992 (Table 3). Chicks also grew at a lower rate in 1991 (Fig. 2). These reproductive parameters integrate over larger spatial/temporal scales than parameters associated with foraging behavior; hence they should reflect regional processes affecting krill availability. For example, indices of chick growth and survival integrate over the entire provisioning period. The size of the breeding population and adult body condition early in brooding should similarly reflect regional prey availability before and at the beginning of breeding. This is particularly true if chinstrap penguins range more widely before brooding as suggested by extended trips during incubation (Lishman, 1985).

These results support predictions, derived from Lack (1954), that adult seabirds faced with large interannual fluctuations in prey availability should hold chick provisioning foraging effort relatively constant and let annual reproductive success fluctuate between years. There are at least three alternative hypotheses that could also explain our results. First, it is possible that krill in the vicinity of the colony were amply abundant and penguins did not need to adjust foraging effort to meet energy needs each year. This hypothesis is not consistent with our observations of variability in reproductive success and prey abundance. If prey resources were sufficiently abundant, we would predict a lack of variability in reproductive measurements as well as foraging effort.

A second hypothesis is that it is the distance between prey patches in the vicinity of the colony that determines foraging effort, whereas the density of prey patches determines reproductive success. In this scenario, the number and distribution – both horizontal and vertical – of prey

patches remain constant, whereas the density of krill within the patches varies. However, this is not consistent with the detailed observations of krill patch distribution from annual hydroacoustic surveys (US AMLR program, unpubl. rep.).

More troubling is the possibility that foraging effort is adjusted in response to changes in offshore prey abundance, but our power to detect such adjustments is low (less than 0.6 across all foraging effort parameters measured, Table 2). There is a great deal of individual variability that may reflect differences in quality or experience of individuals to find prey. This, combined with the generally low sample sizes inherent in TDR data sets, may render the ability to detect differences in foraging effort related to interannual variability in prey abundance low. This may limit the utility of such instruments in measuring the response of top predators to prey abundance. Alternatively, for management purposes it may be worthwhile to select  $\alpha$  levels greater than 0.05, reducing the issue of power for instrumentation.

With these caveats in mind, we feel that these data present the most comprehensive test of the hypothesis that seabirds hold foraging effort relatively constant despite interannual variability in prey availability, and allow annual reproductive success to vary in response to prey availability. Two seabird studies that manipulated adult foraging ability demonstrated a similar limitation of chick provisioning effort in the face of deteriorating body condition (Saether *et al.*, 1993; Weimerskirch *et al.*, 1995). With chinstrap penguins, Croll *et al.* (1996) increased the foraging costs of breeding adults and found that encumbered birds had decreased reproductive success, but did not significantly increase foraging trip duration.

One cost to adult penguins of increasing chick provisioning effort may be the consequences for the post-breeding molt. Adult chinstrap penguins return to the breeding colony to undergo a complete body molt within 2–3 weeks of chick fledging (D. A. Croll & J. K. Jansen, pers. obs.). During the intervening 2–3 weeks, adults increase their body mass by *c.* 25% in preparation for fasting during the molt (the mean adult body mass in 1990 was 4.09 kg  $\pm$  0.41 SD, 5.07 kg  $\pm$  0.42 and 2.83 kg  $\pm$  0.38 during the breeding, pre-molt and post-molt periods, respectively; D. A. Croll &

**Table 3** Summary reproductive data for chinstrap penguins *Pygoscelis antarctica* breeding on Seal Island, South Shetland Islands

Year	Breeding population size (number of nesting pairs)	Duration chick rearing (days) hatch to fledge	Mean number of chicks creched/nest	Mean fledgling weight (kg)	Mean adult weight (kg)
1990	38 116	60	1.10 (0.84)	2.97 (0.38)	4.04 (0.36)
1991	31 416	64	1.05 (0.78)	2.88 (0.31)	3.82 (0.44)
1992	45 632	55	1.26 (0.78)	3.13 (0.365)	4.00 (0.41)
Difference			$P < 0.05$ $H = 8.74$	$P < 0.0001$ $H = 63.91$	$P < 0.05$ $F = 5.21$

Values in parentheses are standard deviations.

S. D. Osmek, Seal Island, unpubl. data). If body condition during breeding declined sufficiently to compromise the high-energy requirements of molting while fasting, adult survival could decrease substantially.

Our study demonstrates that chinstrap penguins adjust reproductive and foraging effort differently in response to fluctuations in prey abundance at different temporal scales. Specifically, our data indicate that (1) foraging effort between years is not adjusted in response to interannual variability in regional prey abundance and (2) unlike foraging effort, annual patterns in adult body mass and reproduction, which integrate over larger spatio-temporal scales, are linked to regional measures of krill abundance. These observations are consistent with predictions of life-history strategies for a long-lived seabird.

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## References

- Ainley, D.G., O'Connor, E.F. & Boekelheide, R.J. (1984). *The marine ecology of birds of the Ross Sea, Antarctica*. Washington, DC: American Ornithological Union.
- Anderson, D.W., Gress, F. & Mais, K.F. (1982). Brown pelicans: influence of food supply on reproduction. *Oikos* **39**, 23–31.
- Bengtson, J.L., Croll, D.A. & Goebel, M.E. (1993). Diving behaviour of chinstrap penguins at Seal Island. *Antarct. Sci.* **5**, 9–15.
- Bergman, G. (1978). Av näringsbrist förorsakade störningar i tefstens (tobisgrisslans) *Cephus grylle* häckning. *Mem. Soc. Fauna Flora Fenn.* **54**, 31–32.
- Boyd, I.L., Arnould, J.P.Y., Barton, T. & Croxall, J.P. (1994). Foraging behaviour of antarctic fur seals during periods of contrasting prey abundance. *J. Anim. Ecol.* **63**, 703–713.
- Boyd, I.L. & Croxall, J.P. (1996). Dive durations in pinnipeds and seabirds. *Can. J. Zool.* **74**, 1696–1705.
- Burger, A.E. & Piatt, J.F. (1990). Flexible time budgets in breeding common murres: buffers against variable prey abundance. *Stud. Av. Biol.* **14**, 71–83.
- Cairns, D.K. (1987). Seabirds as indicators of marine food supplies. *Biol. Oceanogr.* **5**, 261–272.
- Cairns, D.K. (1992). Diving behavior of black guillemots in northeastern Hudson Bay. *Col. Waterbirds* **15**, 245–248.
- CCAMLR. (1991). *CCAMLR ecosystem monitoring program: standard methods for monitoring studies*. CCAMLR: Hobart.
- Croll, D.A., Jansen, J.K., Goebel, M.F., Boveng, P.L. & Bengtson, J.L. (1996). Foraging behavior and reproductive success in chinstrap penguins: the effects of transmitter attachment. *J. Field Ornithol.* **67**, 1–9.
- Croll, D.A., Osmek, S.D. & Bengtson, J.L. (1991). An effect of instrument attachment on foraging trip duration in chinstrap penguins. *Condor* **93**, 777–779.
- Croxall, J.P., Reid, K. & Prince, P.A. (1999). Diet, provisioning and productivity responses of marine predators to differences in availability of Antarctic krill. *Mar. Ecol. Progr. Ser.* **177**, 115–131.
- Croxall, J.P., Trathan, P.N. & Murphy, E.J. (2002). Environmental change and Antarctic seabird populations. *Science (Washington, DC)* **297**, 1510–1514.
- Demer, D.A. (2004). An estimate of error for the CCAMLR. *Deep-Sea Res. II* **51**, 1237–1251.
- Demer, D.A. & Conti, S.G. (2005). New target-strength model indicates more krill in the Southern Ocean. *ICES J. Mar. Sci.* **62**, 25–32.
- Everson, I., Watkins, J.L., Bone, D.G. & Foote, K.G. (1990). Implications of a new acoustic target strength for abundance estimates of Antarctic krill. *Nature* **345**, 338–340.
- Foote, K.G., Everson, I., Watkins, J.L. & Bone, D.G. (1990). Target strengths of Antarctic krill (*Euphausia superba*) at 38 and 120 kHz. *J. Acoust. Soc. Am.* **87**, 16–24.
- Fraser, W. & Trivelpiece, W. (1996). Factors controlling the distribution of seabirds: winter–summer heterogeneity in the distribution of Adelie penguin populations. *Ant. Res. Ser.* **70**, 257–272.
- Furness, R.W. & Monaghan, P. (1987). *Seabird ecology*. Glasgow: Blackie and Son.
- Greene, C.H., Stanton, T.K., Wiebe, P.H. & McClatchie, S. (1991). Acoustic estimates of Antarctic krill. *Nature* **349**, 110.
- Hewitt, R.P. & Demer, D.A. (1991). Krill abundance. *Nature* **353**, 310.
- Hewitt, R.P. & Demer, D.A. (1993). Dispersion and abundance of Antarctic krill in the vicinity of Elephant Island in the 1992 austral summer. *Mar. Ecol. Progr. Ser.* **99**, 29–39.
- Hewitt, R.P. & Demer, D.A. (1994). Acoustic estimates of krill biomass in the Elephant Island area: 1981–1993. *CCALMR Sci.* **1**, 1–5.
- Jansen, J.K., Boveng, P.L. & Bengtson, J.L. (1998). Foraging modes of chinstrap penguins: contrasts between day and night. *Mar. Ecol. Progr. Ser.* **165**, 161–172.

- Jansen, J.K., Russell, R.W. & Meyer, W.R. (2002). Seasonal shifts in the provisioning behavior of chinstrap penguins, *Pygoscelis antarctica*. *Oecologia* **131**, 306–318.
- Jolly, G.M. & Hampton, I. (1990). A stratified random transect design for acoustic surveys of fish stocks. *Can. J. Fish. Aquat. Sci.* **47**, 1282–1291.
- Kitaysky, A.S. & Golubova, E.G. (2000). Climate change causes contrasting trends in reproductive performance of planktivorous and piscivorous alcid. *J. Anim. Ecol.* **69**, 248–262.
- Lack, D. (1954). *The natural regulation of animal numbers*. Oxford: Oxford University Press.
- Lack, D. (1968). *Ecological adaptations for breeding in birds*. London: Methuen.
- Lid, G. (1980). Reproduction of the puffin on Rost in the Lofoten Islands in 1964–1980. *Fauna Norv. Ser. C Cinclus* **4**, 30–39.
- Lishman, G.S. (1985). The food and feeding ecology of Adelie penguins *Pygoscelis-Adeliae* and chinstrap penguins *Pygoscelis-Antarctica* at Signy Island South-Orkney Islands South Atlantic. *J. Zool. (Lond.)* **205**, 245–264.
- Loeb, V., Siegel, V., HolmHansen, O., Hewitt, R., Fraser, W., Trivelpiece, W. & Trivelpiece, S. (1997). Effects of sea-ice extent and krill or salp dominance on the Antarctic food web. *Nature* **387**, 897–900.
- Lynnes, A.S., Reid, K. & Croxall, J.P. (2004). Diet and reproductive success of Adelie and chinstrap penguins: linking response of predators to prey population dynamics. *Pol. Biol.* **27**, 544–554.
- Macaulay, M.C., English, T.S. & Mathisen, O.A. (1984). Acoustic characterization of swarms of Antarctic krill *Euphausia-superba* from Elephant Island and Bransfield Strait (special issue). *J. Crustacean Biol.* **4**, 16–44.
- Macaulay, M.C. & Mathisen, O.A. (1991). AMLR program: hydroacoustic observations of krill distribution and biomass near Elephant Island, austral summer 1991. *Ant. J. United States* **26**, 203–204.
- Martin, T.E. (1987). Food as a limit on breeding birds – a life-history perspective. In *Annual review of ecology and systematics*: 453–488. Johnston, R.F. (Ed.). Palo Alto: Annual Reviews, Inc.
- Meyer, W.R., Bengtson, J.L., Jansen, J.K. & Russell, R.W. (1997). Relationships between brood size and parental provisioning performance in chinstrap penguins during the chick guard phase. *Pol. Biol.* **17**, 228–234.
- Monaghan, P. (1996). Relevance of the behavior of seabirds to the conservation of marine environments. *Oikos* **77**, 227–237.
- Monaghan, P., Walton, P., Wanless, S., Uttley, J.D. & Burns, M.D. (1994). Effects of prey abundance on the foraging behaviour, diving efficiency and time allocation of breeding guillemots *Uria aalge*. *Ibis* **136**, 214–222.
- Murphy, E.J., Morris, D.J., Watkins, J.L. & Priddle, J. (1988). Scales of interaction between Antarctic krill and the environment. In *Antarctic Ocean and resource variability*: 120–130. Sahrhage, D. (Ed.). Berlin: Springer-Verlag.
- Saether, B.-E., Andersen, R. & Pedersen, H.C. (1993). Regulation of parental effort in a long-lived seabird: an experimental manipulation of the cost of reproduction in the Antarctic petrel, *Thalassioica antarctica*. *Behav. Ecol. Sociobiol.* **33**, 147–150.
- Siegel, V. (1991). Estimation of krill (*Euphausia superba*) mortality and production rate in the Antarctic Peninsula region. In *Selected scientific papers, 1991*: 145–155. CCAMLR (Ed.). Hobart: CCAMLR.
- Siegel, V. & Loeb, V. (1995). Recruitment of Antarctic krill *Euphausia-superba* and possible causes for its variability. *Mar. Ecol. Progr. Ser.* **123**, 45–56.
- Simmonds, E.J., Williamson, N.J., Gerlotto, F. & Aglen, A. (1991). Survey design and analysis procedures: a comprehensive review of good practice. *Comm. Meet. Int. Coun. Expl. Sea* **1991/B**, 54.
- Stearns, S.C. (1992). *The evolution of life histories*. Oxford, UK: Oxford University Press.
- Trivelpiece, W.Z., Bengtson, J.L., Trivelpiece, S.G. & Volkman, N.J. (1986). Foraging behavior of gentoo and chinstrap penguins as determined by new radiotelemetry techniques. *Auk* **103**, 777–781.
- Uttley, J.D., Walton, P., Monaghan, P. & Austin, G. (1994). The effects of food abundance on breeding performance and adult time budgets of guillemots *Uria aalge*. *Ibis* **136**, 205–213.
- Volkman, N.J., Presler, P. & Trivelpiece, W. (1980). Diets of Pygoscelid penguins at King-George Island Antarctica. *Condor* **82**, 373–378.
- Weimerskirch, H., Chastel, O. & Ackermann, L. (1995). Adjustment of parental effort to manipulated foraging ability in a pelagic seabird, the thin-billed prion *Pachyptila belcheri*. *Behav. Ecol. Sociobiol.* **36**, 11–16.
- Williams, T.D. & Rothery, P. (1990). Factors affecting variation in foraging and activity patterns of gentoo penguins *Pygoscelis-papua* during the breeding season at Bird Island South Georgia South Atlantic Ocean. *J. Appl. Ecol.* **27**, 1042–1054.
- Wilson, R.P., Grant, W.S. & Duffy, D.C. (1986). Recording devices on free-ranging marine animals – does measurement affect foraging performance. *Ecology* **67**, 1091–1093.
- Woehler, E.J. & Croxall, J.P. (1997). The status and trends of Antarctic and sub-Antarctic seabirds. *Mari. Ornithol.* **25**, 43–66.