

Working less to gain more: when breeding quality relates to foraging efficiency

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Abstract. In animal populations, a minority of individuals consistently achieves the highest breeding success and therefore contributes the most recruits to future generations. On average, foraging performance is important in determining breeding success at the population level, but evidence is scarce to show that more successful breeders (better breeders) forage differently than less successful ones (poorer breeders). To test this hypothesis, we used a 10-year, three-colony, individual-based longitudinal data set on breeding success and foraging parameters of a long-lived bird, the Adélie Penguin, *Pygoscelis adeliae*. Better breeders foraged more efficiently than poorer breeders under harsh environmental conditions and when offspring needs were higher, therefore gaining higher net energy profit to be allocated to reproduction and survival. These results imply that adverse “extrinsic” conditions might select breeding individuals on the basis of their foraging ability. Adélie Penguins show sufficient phenotypic plasticity that at least a portion of the population is capable of surviving and successfully reproducing despite extreme variability in their physical and biological environment, variability that is likely to be associated with climate change and, ultimately, with the species’ evolution. This study is the first to demonstrate the importance of “extrinsic” conditions (in terms of environmental conditions and offspring needs) on the relationship between foraging behavior and individual quality.

Key words: Adélie Penguin (*Pygoscelis adeliae*); breeding success; colony size; competition; environmental change; foraging behavior; individual quality; phenotypic plasticity; satellite transmitter; seabirds; time–depth recorder; weighbridge.

INTRODUCTION

In animal populations, a minority of individuals consistently achieves higher breeding success than others and therefore contributes the most descendants to the next generation (Clutton-Brock 1988, Newton 1989, Annett and Pierotti 1999). Difference in relative fitness forms the basis for natural selection (Darwin 1859). Understanding how “high-quality” breeders (i.e., individuals that reproduce more successfully than others from the same population at the same time) outperform others is therefore of great interest for evolutionary ecologists.

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A number of factors contribute to breeding success. First, at the scale of the breeding season, early breeders, at least in birds, generally have the highest breeding success (e.g., Lewis et al. 2006; but see Ezard et al. 2007). Second, body size, mass, and condition have been related to breeding success (Jensen et al. 2004, Robinson et al. 2005, Murphy 2007), but more often have been identified in relation to survival (e.g., Blums et al. 2005). Third, physiological parameters have also been investigated as potential predictors of breeding success. For example, Blackmer et al. (2005) showed that basal metabolic rate (BMR) could influence aspects of individual quality such as hatching date and chick growth rate in male storm-petrels, but BMR did not influence lifetime hatching success. No relationship was found between individual quality and corticosterone or prolactin levels among experienced breeding Black-browed Albatrosses (Angelier et al. 2007b). However, the probability of successfully fledging a chick was negatively correlated with corticosterone levels, which could be explained by interindividual differences in

foraging behavior and success (Angelier et al. 2007a). Finally, behavior can also be an important determinant of breeding success. Mate guarding (e.g., Setchell et al. 2005), mate choice, and fidelity (e.g., Lewis et al. 2006), or the ability to find and secure high-quality habitat (e.g., Krüger and Lindström 2001) can significantly influence an individual's breeding output.

Most of these hypotheses are nonexclusive. Interestingly, interindividual differences in energy acquisition can affect both breeding output and survival rates (Annett and Pierotti 1999) and differences in foraging behavior can influence several of the parameters just listed. Best foragers may be able to improve condition more rapidly and return earlier from migration to initiate breeding activities. Alternatively, individuals that attain higher foraging success might have lower corticosterone levels and would therefore be less prone to abandon reproduction. The use of alternative foraging behaviors such as kleptoparasitism (Shealer et al. 2005) or the reliance on "junk" vs. "natural" food sources (Annett and Pierotti 1999, Grémillet et al. 2008) has also been demonstrated to impact breeding success. More subtle adjustment of foraging parameters such as trip duration (Lewis et al. 2006), offspring feeding rates (Lewis et al. 2006, O'Dwyer et al. 2007), and foraging effort (Cam et al. 2003, MacColl and Hatchwell 2003) can also explain interindividual or interpair differences in breeding success and offspring quality. Yet, although evidence exists that foraging performance is an important determinant of breeding success, evidence is scarce from longitudinal studies to show that higher quality breeders have different foraging ability than lower quality individuals (including average and below-average individuals).

To test this hypothesis, we used a 10-year, three-colony, individual-based longitudinal data set on breeding success and foraging parameters (foraging trip duration and number, food load) of a long-lived bird, the Adélie Penguin *Pygoscelis adeliae*. This species exhibits heterogeneity in breeding quality with impacts to adult survival (Lescreôl et al. 2009), and its breeding cycle is constrained by the short duration of the Antarctic summer (Ainley 2002). We also assessed diving ability of birds of known breeding quality by fitting them with time-depth recorders. We made the following predictions: (1) better breeders exert a lower overall foraging effort but a more intense diving activity than do poorer breeders; (2) better breeders forage more successfully, both at the level of the trip and at the level of the dive, than do poorer breeders; (3) better breeders dive deeper than do poorer breeders, therefore gaining access to a larger potential foraging volume, and have shorter postdive recovery intervals for any given depth (hereafter PDI); and (4) better breeders forage more efficiently and feed their chicks more often than do poorer breeders.

If differences in foraging tactics are linked to differences in individual fitness, and given that foraging

behavior can be heritable (MacColl and Hatchwell 2003, Missoweit et al. 2007), we may wonder why the "high-quality" phenotype does not spread throughout the population. We hypothesize that the strength of the relationships between foraging behavior and breeding performance is modulated by the conditions under which individuals live and forage. Under favorable conditions, most phenotypes raise offspring successfully, and only under demanding conditions do the interphenotype differences become apparent. Adverse conditions could include harsh climate, strong competition, or the increased food demand of older offspring. We therefore further predicted that the strength of the relationships between breeding performance and foraging ability is greater: (5) under harsh environmental conditions; (6) when competition levels are higher; and (7) when offspring needs are increased.

METHODS

Species and study sites

The Adélie Penguin is a sea-ice-obligate bird that spends only 10% of its life on land, where it forms breeding colonies distributed around the Antarctic coast and on high-latitude offshore islands (Ainley 2002). Data were collected at the three Adélie Penguin colonies on Ross Island, southwestern Ross Sea (for a map of study sites, see Ainley et al. 2004): Cape Crozier (77°27' S, 169°12' E; 164 000 pairs), Cape Bird (77°13' S, 166°26' E; 43 000 pairs), and Cape Royds (78°33' S, 166°10' E; 2 600 pairs). These colonies span the entire breadth of colony size in this species (cf. Woehler 1993). Intraspecific competition, as a function of colony size, has been shown to be a factor that can extend trip distances and durations, and can increase energy expenditure (Ainley et al. 2004, 2006, Ballance et al. 2009). Breeders arrive in late October; the females usually lay two eggs by mid-November; chicks are fed from mid-December to early February. During the guard stage, one parent remains with the chick(s) while the other forages at sea. Nest reliefs occur every 1–3 days and chicks are fed relatively small meals by the attending parent. During crèche, chick demands are too great for one parent to provide, so chicks are left on their own while both parents forage simultaneously. Adélie Penguins forage by diving, mostly at depths \leq 50 m but to a maximum of \sim 140 m. In the southern Ross Sea, they feed almost exclusively on crystal krill (*Euphausia crystallophias*) and Antarctic silverfish (*Pleuragramma antarcticum*; Ainley et al. 1998, 2003, Ainley 2002).

Our study period included most of chick-rearing, i.e., all of the guard stage and three-fifths of the crèche stage, mid-December to mid-January, for 10 austral summers, 1997–1998 to 2006–2007. Hereafter, we refer to austral summers as seasons, using the initial year (e.g., 1997 refers to the breeding season that began in October 1997 and ended in February 1998).

Assessment of foraging behavior

Instrumentation: weighbridge and SPLASH tags.—In all three colonies and all seasons (1997–2006), a subcolony ranging from 90 to 259 pairs (varying by year and by colony) was surrounded by a plastic fence, leaving only one access point, which was filled with a weighbridge, as described in Ballard et al. (2001). The weighbridge consisted of an electronic scale, direction indicator, and radio frequency identification (RFID) reader connected to a data logger (following Kerry et al. 1993; see also Beigel et al. 2004), and was installed between 10 December and 15 December, at about peak hatching in 1997–2000, and beginning 15 November thereafter. In the weighbridge subcolony, adult individuals (hereafter “WB birds”) were implanted with unique RFID tags and banded on the left flipper (Dugger et al. 2006) and were followed each season (25–59 individuals at Cape Crozier, 3–93 individuals at Cape Bird, and 16–74 individuals at Cape Royds, depending on season). Data were not available for Cape Bird in 1997, due to technical difficulties with the weighbridge. Bird identification, date and time, direction, and body mass were recorded automatically as the RFID-implanted birds crossed the weighbridge. We used only crossings from birds that had at least one chick when they left the subcolony for foraging.

At Cape Crozier, we also equipped 24 adult birds (hereafter “SPLASH birds”: five females, seven males in 2005; seven females, five males in 2006) from a subcolony adjacent to the weighbridge subcolony with SPLASH tags (Wildlife Computers, Redmond, Washington, USA) as well as small, streamlined cylindrical radio transmitters (46 mm long, 14 mm diameter, 8 g; model A2630, Advanced Telemetry Systems, Isanti, Minnesota, USA). SPLASH tags recorded depth, light, and temperature every second; they weighed 62 g (1.6% of a 4-kg Adélie Penguin) and had a cross-sectional area of $3.2 \times 10^{-4} \text{ m}^2$ (1.0–1.6% of a bird’s cross-sectional area). All birds (both weighbridge and SPLASH) were banded and had a known breeding history (but not a known age). One to four consecutive trips were recorded for each equipped individual (48 trips and 42 932 dives in total). Radio transmitters helped to locate the birds immediately when they returned to the colony. For details on attachment procedures, please refer to Ballard et al. (2001). Diving data were processed using the program divesum (v.7.5.5; G. Ballard, unpublished software). This program corrected the record baseline and computed several individual dive parameters such as maximum dive depth, PDI and number of undulations (number of changes in underwater swimming direction from ascent to descent $>1 \text{ m}$). Divesum also classified dives into three types: foraging, exploratory, and other (Chappell et al. 1993, Schreer et al. 2001). See Appendix A for more details on dive-data processing and analysis.

Foraging effort.—Total energy expended during a foraging trip by chick-rearing Adélie Penguins increases with trip duration (Ballance et al. 2009). Therefore, trip

duration was a proxy for foraging effort in the test of our predictions. Trip durations were determined from weighbridge data and were based on the time elapsed between the departure from and the return to the colony. Trips $< 6 \text{ h}$ or $> 8 \text{ days}$ were discarded (Ballard et al. 2001).

Daily vertical (diving) distance measured in km,

$$\sum_{i=1}^n \frac{\text{Maxdepth} \times 2}{\text{Tripdur}} \times 0.001$$

(where n is number of dives during a foraging trip, Maxdepth is maximum depth of a foraging dive in meters, and Tripdur is trip duration expressed in days), calculated from SPLASH data, was used as an index of diving activity (Boyd et al. 1994).

Foraging success.—Foraging success was assessed at both trip and dive levels. At the trip level, we used food load as an index of foraging success. Food load was calculated from weighbridge data as the difference between individual parent’s out-mass (departing) and their most recent in-mass (returning from sea), i.e., the body mass of an individual parent weighed when entering the nesting area after a trip at sea minus its mass when it left the nesting area again for a new foraging trip. This is a measure of how much food a parent brought back to the colony and includes both the food to be delivered to chicks and the food to be digested by the parent while attending the nest. Mass was calculated using a highly accurate, year- and colony-specific algorithm because each weighbridge installation varied slightly in physical characteristics. In all cases, the scales were calibrated against known standard weights, they measured mass 12.5 times/s, and the bird had to be on the scale for at least 0.8 s for a valid estimate to be recorded. The scales tared themselves automatically to adjust for any mass of gravel or snow blown onto them. For analysis, we only included food loads $< 1300 \text{ g}$ (Ainley et al. 2004).

At the dive level, the number of undulations per foraging dive provided an index of prey catch (Ropert-Coudert et al. 2001, Bost et al. 2007).

Foraging efficiency and feeding frequency.—We calculated a catch per unit effort (CPUE) from weighbridge data by dividing food load (in grams; see *Foraging success*) by trip duration (in minutes). This mass of food gathered per minute was used as an index of foraging efficiency.

The individual feeding frequency was defined by the number of foraging trips performed by a parent divided by the time (days) during which it had at least one chick.

Assessment of breeding quality

We calculated a breeding quality index (BQI) for each individual based on previous breeding success (Lescroël et al. 2009; see Appendix B for details on BQI calculation). The BQI is the mean per individual of the difference between the actual breeding success (0 for

unsuccessful or deferred breeders, 1 for successful breeders) and the predicted breeding success (a numeric value between 0 and 1) for every year, a unique value per individual. The BQI reflects the relative breeding performance of an individual compared to others of similar characteristics (i.e., breeding in the same subcolony, banded in the same year, and seen for the same number of years) over the same time span.

Foraging conditions

Demanding environmental conditions occurred when two giant icebergs calved from the Ross Ice Shelf. These bergs eventually settled against Ross Island, near Cape Crozier, in January 2001 (Ainley et al. 2004) and remained until July 2006. During their presence these icebergs restricted the normal drift of pack ice, resulting in (1) higher spring–summer ice cover (ice per unit area) that induced a regional 40% reduction in primary productivity (Arrigo et al. 2002), and (2) significantly less open water, thus reducing access, requiring more walking, for penguins on foraging trips (as reviewed in general by Ainley 2002). Massom et al. (2006) found that short-term, anomalously heavy pack ice negatively affected Adélie Penguin colony access and breeding success at a colony on the west coast of the Antarctic Peninsula. We evaluated the effect of the interaction between BQI and a binary variable corresponding to the presence–absence of the giant icebergs (iceberg-free seasons, 1996–2000 and 2006, vs. iceberg seasons, 2001–2005) on foraging parameters.

Previous studies showed that interference or exploitative competition affects foraging effort most dramatically at the largest of the study colonies (Ainley et al. 2004, 2006). We postulated that three orders of magnitude in colony size corresponded to increasing levels of intraspecific competition. Here, we evaluated the effect of the interaction between BQI and study colony (size in descending order: Cape Crozier, Cape Bird, Cape Royds) on foraging parameters.

Because Adélie Penguins are highly synchronous breeders (Ainley 2002), offspring needs increase consistently among all individuals as the breeding season progresses. Thus, as a proxy for offspring needs we used “study day” (a continuous variable with 0 = 20 December) and evaluated the effect of the interaction between BQI and study day on foraging parameters.

Re-formulation of predictions

With the variables of interest defined, predictions can be re-formulated as follows. Better breeders: (1a) exhibit shorter trips but (1b) greater daily vertical distance than poorer breeders; (2a) exhibit larger food loads and (2b) a higher foraging success (undulations) per dive than poorer breeders; (3a) dive deeper than poorer breeders, (3b) without exhibiting longer postdive recovery phases; and (4a) exhibit higher CPUE and (4b) a higher chick feeding frequency than poorer breeders. Moreover, the strength of these relationships is greater: (5) when the

giant icebergs are present; (6) at Cape Crozier than at Cape Bird and at Cape Bird than at Cape Royds; and (7) as the season progresses.

Means \pm SE are given unless indicated otherwise. Linear mixed models allowed us to take into account the heterogeneity of our data set regarding colonies, years, identity of the birds, and number of trips per bird without discarding data (i.e., without having to randomly select the same number of observations for each grouping level). Details of statistical techniques are provided in Appendix C.

RESULTS

Results are summarized by prediction in Table 1 and described here in more detail.

Foraging effort and diving activity

As the season progressed, foraging trips became longer for all birds, but especially for poorer breeders (Fig. 1a, b, Table 2: model 4a). At the beginning of the season, there was no difference in trip durations between better breeders and poorer breeders, but later in the season better breeders performed trips that were progressively shorter relative to poorer breeders (Table 1: prediction 1a). Across all colonies, females performed longer trips than males (1.27 ± 0.10 days vs. 1.12 ± 0.10 days, respectively; Table 2: model 1a). Foraging trip duration varied as a function of colony size: longer at the largest colony (Cape Crozier; females: 1.59 ± 0.05 days, males: 1.41 ± 0.05 days), than at the medium-sized colony (Cape Bird; females: 1.39 ± 0.05 days, males: 1.22 ± 0.05 days), and longer at Cape Bird than at the smallest colony (Cape Royds; females: 0.93 ± 0.05 days, males: 0.80 ± 0.05 days; Table 2: model 3a). However, no significant effect on trip duration was apparent in the interaction between BQI and colony size. Foraging trips tended to be shorter in iceberg-free years (95% highest posterior density interval [HPDI] for the iceberg term: -0.51 – 0.03) but the interaction between BQI and presence–absence of the icebergs had no significant effect on trip duration.

We did not find any significant effect of BQI, the interaction between BQI and presence–absence of icebergs, or the interaction between BQI and the season progression on daily vertical distance (Table 1: prediction 1b). Daily vertical distance was significantly higher during the iceberg-free seasons (Table 2: model 2b), a function of there being more dives per day when icebergs were not present (598 ± 133 vs. 462 ± 123 dives when icebergs were present).

Foraging success

At the trip level, foraging success (i.e., food load) was much higher for better breeders than for poorer breeders when the giant icebergs were present (Fig. 2a, Table 1: prediction 2a, Table 2: model 2c). Food load also increased for all birds as the season progressed (Table 2: model 4c) and was not affected by the interaction

TABLE 1. Summary of predictions and respective outcomes (T, true; F, false) for foraging parameters comparing better breeders with poorer breeders in Adélie Penguins (*Pygoscelis adeliae*).

Prediction: Better breeders...	Outcome	Interaction with:		
		Iceberg? (pred. 5)	Colony size? (pred. 6)	Chick needs? (pred. 7)
1a) have shorter duration foraging trips	T	F	F	T
1b) travel greater daily vertical distance	F	F	F	F
2a) return with larger food loads	T	T	F	F
2b) have higher foraging success per dive	T	F	NA	T
3a) dive deeper	T	F	NA	T
3b) have shorter postdive recovery periods	F	NA	NA	NA
4a) have higher catch per unit effort	T	T	F	F
4b) have higher chick feeding frequency	F	F	F	F

Notes: Predictions (pred.) that were not explicitly evaluated are marked "NA." We hypothesize that the strength of the relationships between foraging behavior and breeding performance is modulated by the conditions under which individuals live and forage. We predicted that the strength of the relationships between breeding performance and foraging ability is greater: under harsh environmental conditions (i.e., when giant icebergs are present; pred. 5); when competition levels are higher (i.e., when the colony is bigger; pred. 6); and when offspring needs are increased (i.e., as the season progresses; pred. 7).

between BQI and season progression. Food load was not significantly different between sexes or among colonies. We did not find any significant effect of the interaction between BQI and colony on food load.

At the dive level, foraging success (i.e., number of undulations per dive) increased as the season progressed. It was slightly higher for poorer breeders than for better breeders at the beginning of the season, but later became much higher for better breeders (Fig. 3, Table 1: prediction 2b, Table 2: model 4d). Number of undulations per dive did not differ between sexes or according to the presence-absence of giant icebergs. We did not find any significant effect on foraging success of the interaction between BQI and presence-absence of icebergs.

Diving parameters

Penguins dived deeper as the season progressed, and although there was no difference in diving depth between better breeders and poorer breeders initially, better breeders dived deeper than poorer breeders at the end of the season (Fig. 1c, Table 1: prediction 3a, Table 2: model 4e). Males dived deeper than females (46.9 ± 4.2 m and 37.6 ± 2.4 m, respectively; Table 2: model 1e). Maximum dive depth did not differ according to the presence-absence of giant icebergs, nor was it influenced by the interaction between BQI and presence-absence of icebergs.

Predictably, penguins spent more time recovering at the surface (longer PDIs) after diving deeper (Fig. 4, Table 2: model 5; see Schreer et al. 2001). More interestingly, better breeders tended to exhibit shorter PDIs than poorer breeders for shallower dives, but this difference weakened with deeper dives (95% HPDI for the BQI \times Maxdepth interaction term: $-0.0004 - 0.13$; Table 1: prediction 3b, Fig. 4). Despite the sex

differences in diving depth, there was no significant difference in PDI between sexes.

Foraging efficiency and feeding frequency

Better breeders foraged more efficiently than poorer breeders (Table 1: prediction 4a, Table 2: model 2f) and the difference between them was much stronger when the giant icebergs were present (Fig. 2b, c). Males were more efficient than females (0.45 ± 0.05 g/min vs. 0.38 ± 0.05 g/min, respectively; Table 2: model 1f). Adélie Penguins at the smallest colony, Cape Royds, gathered more food per unit of time (males, 0.58 ± 0.03 g/min; females, 0.50 ± 0.03 g/min) than birds from medium-sized Cape Bird (males, 0.42 ± 0.03 g/min; females, 0.35 ± 0.02 g/min); in turn the latter were more efficient foragers than birds from the largest colony, Cape Crozier (males, 0.36 ± 0.03 g/min; females, 0.29 ± 0.03 g/min; Table 2: model 3f). For all birds, foraging efficiency increased slightly as the season progressed (0.002 ± 0.0005 g \cdot min $^{-1}\cdot$ d $^{-1}$; Table 2: model 4f). We did not find any significant effect of the interaction between BQI and colony, or between BQI and season progression on foraging efficiency.

Feeding frequency was not influenced by BQI, by the interaction between BQI and presence-absence of icebergs, or by the interaction between BQI and colony (Table 1: prediction 4b). Chicks were fed less often when the giant icebergs were present (0.42 ± 0.03 feeds/day vs. 0.49 ± 0.04 feeds/day; Table 2: model 2g). A parent fed its chicks more often at Cape Royds (0.52 ± 0.03 feeds/day), the smallest colony, than at Cape Bird (0.46 ± 0.02 feeds/day), the medium-sized colony, and more often at Cape Bird than at Cape Crozier (0.41 ± 0.02 feeds/day), the largest colony (Table 2: model 3g). Despite sex differences in trip duration, feeding frequency was similar for males and females, probably because males spent more time in the colony than females.

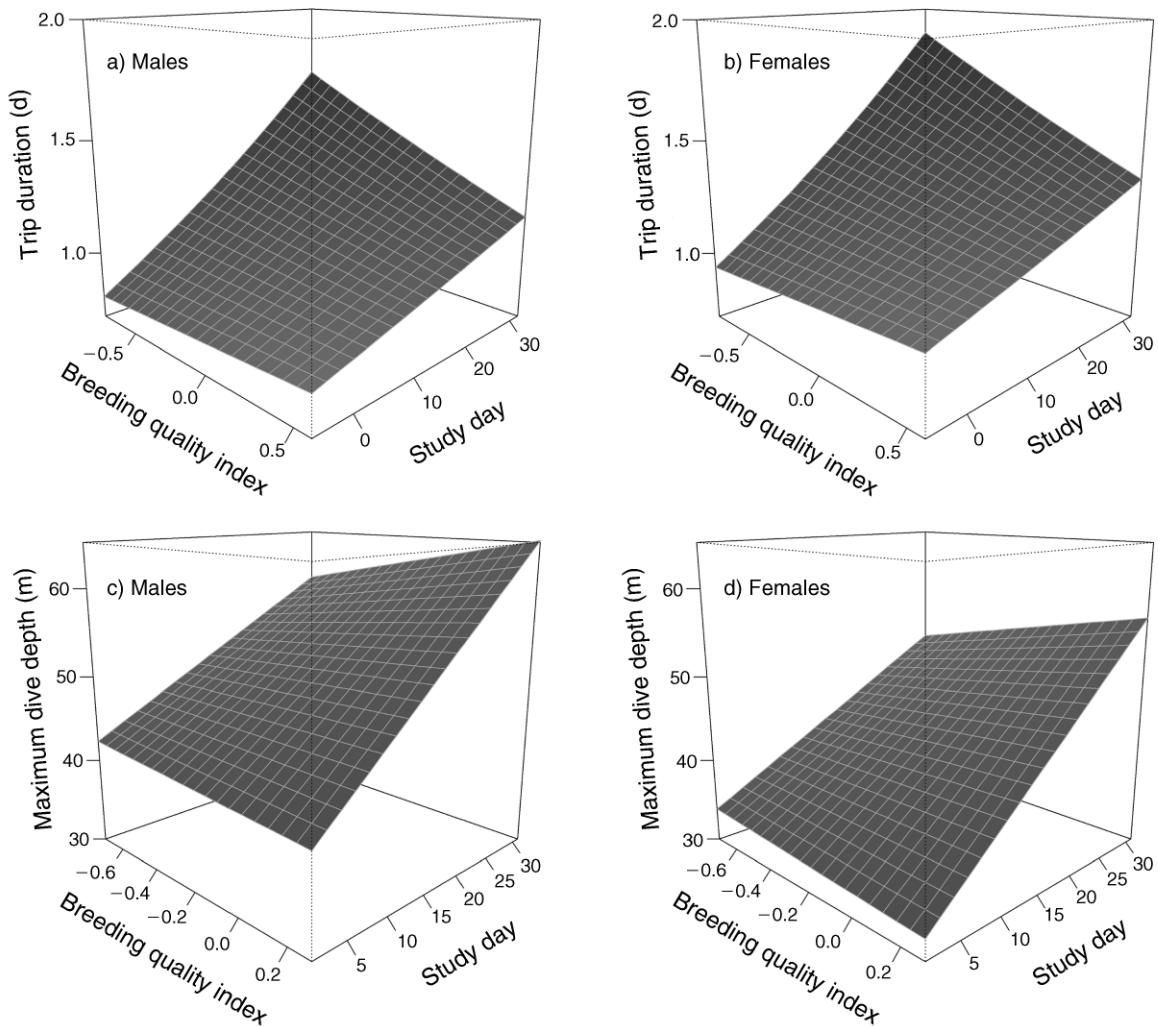


FIG. 1. Predicted effects of breeding quality index (BQI) and season progression on the foraging trip duration (upper panels) and on the maximum dive depth (lower panels) of (a, c) male and (b, d) female Adélie Penguins (*Pygoscelis adeliae*). Study day is a proxy for offspring needs, where study day 0 = 20 December. BQI is the mean per individual of the difference between the actual breeding success (0 for unsuccessful or deferred breeders, 1 for successful breeders) and the predicted breeding success (a numeric value between 0 and 1) for every year. Predictions were calculated from Table 2 models: (4a) $\log(\text{trip duration} + 1) = 0.72 + 0.01 \times \text{study day} - 0.01 \times \text{BQI} \times \text{study day} - 0.07 \times \text{sex}$ (male); (4e) $\text{maximum depth} = 37.17 + 0.27 \times \text{study day} + 1.72 \times \text{BQI} \times \text{study day} + 8.46 \times \text{sex}$ (male).

DISCUSSION

Our results show that, when confronting adversity, better breeders gather food more efficiently and bring back more food to the colony than poorer breeders, therefore making higher net energy profit to be allocated to reproduction and survival. To our knowledge, this study is the first to demonstrate the importance of “extrinsic” conditions on the relationship between foraging behavior and individual quality.

Limitations of the study

Because we were not working with birds of known age, there is a possibility that our quality measure was partially confounded by age or experience (see further discussion on BQI in Lescroël et al. 2009). However,

individuals of different BQI that were followed from 1998 to 2006 exhibited relative differences in foraging efficiency that were maintained over time (Appendix D: Fig. D1).

External devices, and in particular devices fitted with an antenna, are known to affect penguins’ at-sea energetics (for a review, see Wilson and McMahon 2006). Device size has a significant effect on diving behavior (Robert-Coudert et al. 2007). In this study, SPLASH tags had an antenna, which could have significantly increased the drag produced by the device, but the tags were also relatively small (1.0–1.6% of a bird’s cross-sectional area) and we did not detect any effect on foraging trip duration (i.e., on foraging effort; see Appendix A). Furthermore, any effect of the tags

TABLE 2. Estimates and 95% highest posterior density intervals (HPDI) for significant fixed effects in REML models fitted to foraging behavior response variables for all individual Adélie Penguins followed.

Response	Model	Fixed term	Estimate \pm SE	95% HPDI	<i>n</i>
log(trip duration + 1)	1a	sex (male)	-0.07 \pm 0.02	-0.10, -0.04	5541
	3a	sex (male)	-0.07 \pm 0.02	-0.10, -0.04	5541
Daily vertical distance	4a	colony (CROZ)	0.08 \pm 0.02	0.04, 0.12	5541
		colony (ROYD)	-0.21 \pm 0.02	-0.25, -0.18	
	sex (male)	-0.07 \pm 0.02	-0.10, -0.05		
	study day	0.01 \pm 0.00	0.01, 0.01		
Food load	2b	BQI \times study day	-0.01 \pm 0.00	-0.01, -0.002	48
	2c	iceberg (no)	10.47 \pm 3.36	4.71, 16.79	3320
Number of undulations	4c	BQI	0.26 \pm 0.08	0.12, 0.40	3320
	4d	BQI \times iceberg	-0.26 \pm 0.08	-0.41, -0.11	3320
Maximum depth	1e	study day	0.01 \pm 0.00	0.005, 0.008	18 248
	4e	study day	0.05 \pm 0.01	0.02, 0.07	18 248
PDI	5	BQI \times study day	0.25 \pm 0.08	0.08, 0.40	18 248
		sex (male)	9.31 \pm 3.39	3.59, 14.71	
log(CPUE + 1)	2f	sex (male)	8.46 \pm 2.96	3.38, 13.69	3320
		study day	0.27 \pm 0.08	0.13, 0.43	
Feeding frequency	3f	BQI \times study day	1.72 \pm 0.51	0.81, 2.71	3320
		sex (male)	0.34 \pm 0.01	0.33, 0.35	
Feeding frequency	3g	sex (male)	0.05 \pm 0.01	0.02, 0.07	650
		BQI	0.15 \pm 0.06	0.04, 0.25	
Feeding frequency	4f	BQI \times iceberg	-0.13 \pm 0.06	-0.23, -0.01	3320
		sex (male)	0.05 \pm 0.01	0.02, 0.07	
Feeding frequency	3g	colony (CROZ)	-0.04 \pm 0.02	-0.08, -0.01	650
		colony (ROYD)	0.11 \pm 0.02	0.07, 0.14	
Feeding frequency	3g	sex (male)	0.05 \pm 0.01	0.02, 0.07	650
		study day	0.002 \pm 0.0005	0.0005, 0.002	
Feeding frequency	3g	iceberg (no)	0.07 \pm 0.02	0.02, 0.11	650
		colony (CROZ)	-0.04 \pm 0.02	-0.07, -0.01	
Feeding frequency	3g	colony (ROYD)	0.07 \pm 0.02	0.03, 0.10	650

Notes: Penguins were followed using weighbridge technology ($n_{wb} = 360$ individuals) and SPLASH tags ($n_{splash} = 24$ individuals). Trip duration and CPUE data were log-transformed in order to meet assumptions of the statistical tests; n = number of observations. Study day is a continuous variable used as a proxy for offspring needs, where study day 0 = 20 December. The fixed term iceberg (no) indicates absence of the giant icebergs. Abbreviations: REML is residual maximum likelihood estimation, PDI is postdiving recovery interval, CPUE is catch per unit effort, CROZ and ROYD are Cape Crozier and Cape Royds, and BQI is breeding quality index.

that was potentially compounded by the amount of time the tags were worn would have been controlled for in our mixed modeling (i.e., trip number was included as a random effect). Still, SPLASH tags could have had effects on foraging efficiency that we were not able to detect. Most of our conclusions, and particularly those regarding foraging efficiency, come from non-instrumented birds (i.e., WB birds). Also, all birds in our study were banded, which could have affected foraging behavior (Dugger et al. 2006), but we believe that our conclusions regarding the links between breeding performance and foraging strategy are valid. If anything, bands and SPLASH tags might have exaggerated differences between better breeders and poorer breeders (i.e., mimicking demanding conditions). Bands were removed from all individuals that were no longer being studied in ongoing work.

In species with biparental care, offspring survival and condition are the result of the work and coordination of both parents, not of a single individual (Lewis et al. 2006). Chick-feeding rate, in particular, would be more meaningful if both parents were taken into account. However, examining the behavioral determinants of quality at the level of the pair can only be done on a

multiyear basis in the case of species exhibiting high mate fidelity. Due to the shortness of the breeding season and the importance of arrival and breeding synchrony, mate fidelity is low in high-latitude Adélie Penguins (Ainley 2002), and we were not able to follow banded pairs through time.

Better breeders are more efficient foragers

In terms of energetics, CPUE is a key parameter, as it will ultimately determine the amount of energy that could be invested in other components of life history. Better breeders were more efficient foragers than poorer breeders, especially when conditions were challenging. Better breeders attained higher efficiency by being able to find sufficient food during shorter trips than poorer breeders toward the end of the season, when food need was increasing and when food was also becoming scarce. Indeed, both trip duration and foraging depth increased as the season progressed, therefore adding to evidence that depletion (or an alteration of availability) was occurring in the vicinity of the colonies during the breeding season (Ainley et al. 2004, Ballance et al. 2009). If food was becoming scarce, how did better breeders find sufficient food without having to stay at sea as long

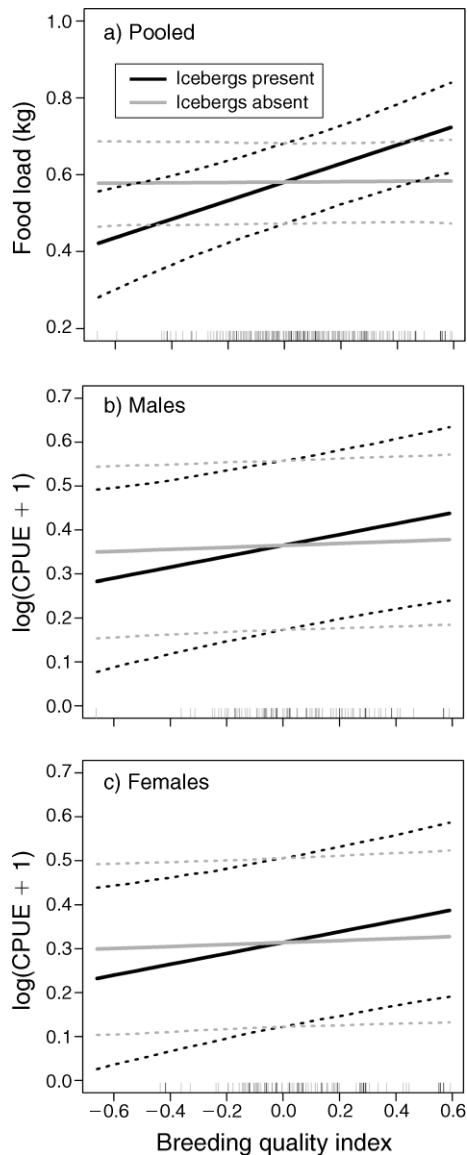


FIG. 2. Relationship between Adélie Penguin breeding performance and (a) food load (for males and females pooled because there were no significant gender differences) or (b, c) log-transformed foraging efficiency (measured as catch per unit effort in g/min), $\log(\text{CPUE} + 1)$, depending on the presence or absence of giant icebergs. Predictions were calculated from Table 2 models: (2c) food load = $0.57 + 0.26 \times \text{BQI} - 0.26 \times \text{BQI} \times \text{iceberg (no)}$; and (2f) $\log(\text{CPUE} + 1) = 0.28 + 0.15 \times \text{BQI} - 0.13 \times \text{BQI} \times \text{iceberg (no)} + 0.05 \times \text{sex (male)}$. The prediction for the years when giant icebergs were present is depicted as a solid black line (with 95% HPDI [highest posterior density intervals] as dotted black lines). The prediction for the years when giant icebergs were absent is depicted as a solid gray line (with 95% HPDI as dotted gray lines).

as poorer breeders? Probably they solved this problem by diving deeper and therefore exploiting a larger foraging area (i.e., a larger volume of ocean), given that the two most common prey species captured by Adélie in our study area (diet summarized by Ainley et al. 2003)

are available at depths attained by penguin individuals studied, and both of these prey species exhibit diel vertical migrations: crystal krill are abundant between 100 and 400–500 m (Pakhomov and Perissinotto 1996, Taki et al. 2008); silverfish are found around 100 m but are more abundant between 200 and 350 m, at least where their air-breathing predators are abundant (Fui-man et al. 2002). This might have enabled better breeders to make shorter trips by reaching resources made unavailable at shallow depths by repeated pursuit by air-breathing predators. On a daily basis, birds of different BQI traveled similar vertical distances, meaning that better breeders performed fewer deep foraging dives while poorer breeders performed more numerous shallow dives. In contrast to female Common Guillemots *Uria aalge* (Lewis et al. 2006), Adélie Penguin better breeders did not take advantage of their higher foraging efficiency to increase chick-feeding rates. Rather, they spent more time attending the nest, potentially dedicating extra time to strengthening the pair bond and defending territory and offspring (Zador and Piatt 1999, Lewis et al. 2006).

Thus, working harder by making longer foraging trips (and therefore expending more energy; Ballance et al. 2009) does not improve reproductive output. Takahashi et al. (2003) proposed two hypotheses to explain this in Adélie Penguins: large interindividual variation in (1) foraging efficiency (also suggested by Lewis et al. 2006) and/or (2) allocation of food between parents and offspring. Our results strongly support the first hypothesis while not ruling out the second. If Adélie Penguin better breeders are more efficient foragers, they might also have better body condition at the beginning of the

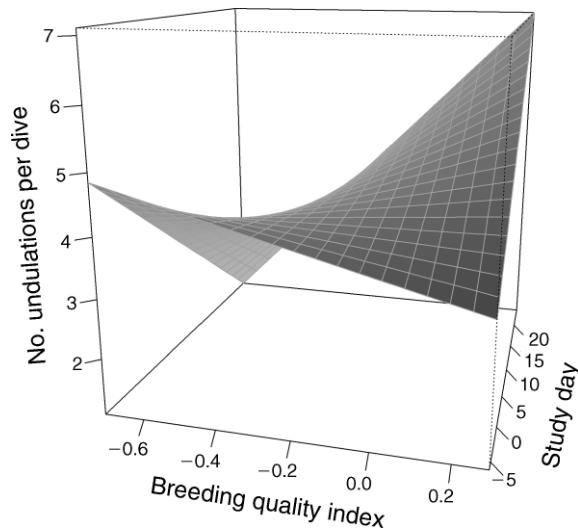


FIG. 3. Predicted effects of breeding performance and season progression (study day 0 = 20 December) on the number of undulations per dive of Adélie Penguins. Predictions were calculated from model 4d (Table 2): number of undulations = $4.09 + 0.05 \times \text{study day} + 0.25 \times \text{BQI} \times \text{study day}$.

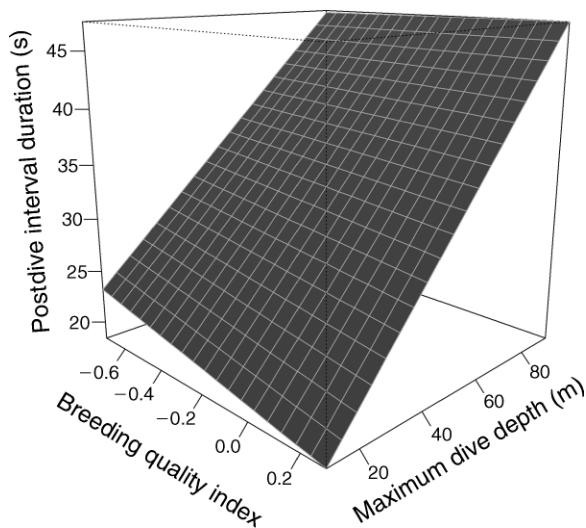


FIG. 4. Predicted effects of breeding performance and maximum dive depth on the postdive interval (PDI) duration of Adélie Penguins. Predictions were calculated from model 5 (Table 2): $PDI = 16.20 + 0.34 \times \text{Maximum depth} + 0.06 \times BQI \times \text{Maximum depth}$.

breeding season and therefore may be able to afford losing mass and allocating more food to their offspring without risking their own survival (Takahashi et al. 2003; Ballard et al., *in press*).

We also highlighted sex differences in foraging efficiency. Sex-related variation in foraging efficiency has been little studied in seabirds (but see Gonzalez-Solis et al. 2000), especially in species with little size dimorphism such as Adélie Penguins. In our study, females dived more shallowly than males during longer trips and came back with a similar food load, therefore exhibiting lower foraging efficiency. In Adélie Penguins, longer trips by females are widely documented (e.g., Chappell et al. 1993, Clarke et al. 1998, 2006, Ballard et al. 2001), but apparently this has little effect on food load (see also Clarke et al. 1998).

When comparing CPUE among individuals, we assumed that they were feeding on the same prey, or at least on prey of similar energetic content. In the southern Ross Sea, Adélie Penguins feed on a mix of crystal krill (4.6 ± 0.1 kcal/g [$=19.3 \pm 0.4$ kJ/g]) and silverfish (5.2 ± 0.2 kcal/g [$=21.8 \pm 0.8$ kJ/g]), with diet being similar among colonies (Ainley et al. 2003). However, fish and krill proportions in the diet could differ among individuals, as a function of foraging depth. The potential links between diet and individual quality remain to be assessed.

Quality matters more under difficult conditions

The relationship between BQI and foraging strategy was only, or mostly, apparent under harsh environmental conditions when giant icebergs restricted access to foraging areas, but also when offspring needs were

higher later in the season. If foraging behavior is heritable (MacColl and Hatchwell 2003, Missoweit et al. 2007) and a given foraging strategy is associated with higher breeding performance, then a differential in selective value among individuals only appears under particular space- and time-delimited circumstances (i.e., similar to the punctuated equilibrium hypothesis: “relatively brief episodes of rapid change that punctuate much longer periods of stasis” [Gould and Eldredge 1993]) (see also Grant and Grant 1993). Even a marginal benefit derived from a given foraging capability can result in the individuals possessing this capability doing better in the end, in terms of fitness, than those that do not (Grant and Grant 1993). This highlights that some relationships or patterns require a sufficiently long timescale or heterogeneous extrinsic conditions to be detected. Given the relatively rapid changes in the physical environment now projected by climate models (see Ainley et al. 2010), the ability of Adélie Penguins to adapt is likely to be tested repeatedly in the coming decades. Because a proportion of the population is capable of successful reproduction during the most demanding environmental conditions yet witnessed by humans, we predict that higher foraging capabilities will become relatively more prevalent in the overall population. The consistently more competitive conditions at the largest colonies (Ainley et al. 2004, 2006, Ballance et al. 2009) could already serve as a facultative mechanism, encouraging a wider prevalence of higher foraging performance in these populations.

Intraspecific competition (based on colony size) did not affect or reveal any relationship between BQI and foraging strategy. When considering foraging parameters only, however, colony size did matter; foraging efficiency decreased with increasing colony size and feeding frequency was lower at the largest colony. It would have been ideal to use actual colony size rather than static categories (Cape Royds, Cape Bird, or Cape Crozier) for this analysis, but the data are not yet available for the time period of our study. Using actual colony size and its variations over time, the effect of the BQI \times colony size interaction may still prove to be important. Our results show that it is probably more difficult to achieve good reproductive performance and/or to maintain good body condition in large colonies than in small ones, all other things being equal (i.e., assuming similar levels of food abundance, although empirical data are lacking). This also stresses the need to be careful when generalizing results obtained from one colony over a given time frame to the whole species.

Proximate mechanisms

In Adélie Penguins, better breeders are more efficient foragers. What are the particular dynamic or permanent characteristics allowing some individuals to forage more efficiently than others? First, these individuals could be older and/or more experienced (dynamic characteristics;

Pyle et al. 1991, Desrochers 1992a). However, these differences are more likely to be found between juveniles and adults than among breeders (Desrochers 1992b). Accordingly, Woo et al. (2008) did not find any relationship between age and foraging behavior in adult Brünnich's Guillemots (*Uria lomvia*). Although our results also suggest that interindividual differences in foraging efficiency persist over time, the relationship between age and foraging efficiency, while controlling for individual quality, needs investigation. Second, as for permanent characteristics, better breeders could have superior, genetically determined physiological ability enabling them to reach deeper depths repeatedly at a lower cost. This hypothesis is partially supported by our results: better breeders tended to have shorter recovery periods at the surface than poorer breeders, but this was only true for relatively shallow dives (Fig. 4). Furthermore, a few poorer breeders dived deeper than better breeders, and the relationship between PDI, BQI, and maximum dive depth was mainly driven by one or two data points. Thus, the potentially higher physiological ability of better breeders, which could also relate to genetically affected hormone levels, needs to be tested by measuring the oxygen carrying capacity of birds of varying quality. Morphology, and body size in particular, is also an important characteristic in diving birds or mammals: larger divers can make longer and deeper dives (Schreer and Kovacs 1997) due to larger capacity for O₂ storage and lower rate of O₂ consumption (Kooyman 1989). At the interface of dynamic and permanent characteristics is cognitive ability, which is likely to be different among individuals and to improve with age and experience. Little is known about cognitive ability of seabirds in relation to foraging (but see Kitaysky et al. 2006); testing whether better breeders have higher cognitive abilities than poorer breeders would require carefully controlled experiments, which is challenging in the wild. In the field of human cognition, one hypothesis for explaining the positive correlation between early-life cognitive ability and longevity is that cognitive ability is an indicator of a "well-put-together system" (Deary 2008). In seabirds, better breeders, which can also be best survivors (Cam et al. 2002, Lescroël et al. 2009) and most efficient foragers (this study), might have the "best-wired" organism. From this perspective, it would be very interesting to investigate interindividual differences in locomotion ability and reaction speeds.

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LITERATURE CITED

- Ainley, D. G. 2002. The Adélie Penguin: bellwether of climate change. Columbia University Press, New York, New York, USA.
- Ainley, D. G., G. Ballard, K. J. Barton, B. J. Karl, G. H. Rau, C. A. Ribic, and P. R. Wilson. 2003. Spatial and temporal variation of diet within a presumed metapopulation of Adélie Penguins. *Condor* 105:95–106.
- Ainley, D. G., G. Ballard, and K. M. Dugger. 2006. Competition among penguins and cetaceans reveals trophic cascades in the Western Ross Sea, Antarctica. *Ecology* 87: 2080–2093.
- Ainley, D. G., C. A. Ribic, G. Ballard, S. Heath, I. Gaffney, B. J. Karl, P. R. Wilson, and S. Webb. 2004. Geographic structure of Adélie Penguin populations: overlap in colony-specific foraging areas. *Ecological Monographs* 74:159–178.
- Ainley, D. G., J. Russell, S. Jenouvrier, E. Woehler, P. O'B. Lyver, W. R. Fraser, and G. L. Kooyman. 2010. Antarctic penguin response to habitat change as Earth's troposphere reaches 2°C above preindustrial levels. *Ecological Monographs* 80:49–66.
- Ainley, D. G., P. R. Wilson, K. J. Barton, G. Ballard, N. Nur, and B. J. Karl. 1998. Diet and foraging effort of Adélie Penguins in relation to pack-ice conditions in the southern Ross Sea. *Polar Biology* 20:311–319.
- Angelier, F., S. Shaffer, H. Weimerskirch, C. Trouvé, and O. Chastel. 2007a. Corticosterone and foraging behavior in a pelagic seabird. *Physiological and Biochemical Zoology* 80: 283–292.
- Angelier, F., H. Weimerskirch, S. Dano, and O. Chastel. 2007b. Age, experience and reproductive performance in a long-lived bird: a hormonal perspective. *Behavioural Ecology and Sociobiology* 61:611–621.
- Annett, C. A., and R. Pierotti. 1999. Long-term reproductive output in Western Gulls: consequences of alternate tactics in diet choice. *Ecology* 80:288–297.
- Arrigo, K. R., G. L. van Dijken, D. G. Ainley, M. A. Fahnestock, and T. Markus. 2002. Ecological impact of a large Antarctic iceberg. *Geophysical Research Letters* 29: 1104.
- Ballance, L. T., D. G. Ainley, G. Ballard, and K. J. Barton. 2009. Colony size and foraging effort in seabirds: is there an energetic correlate? *Journal of Avian Biology* 40:279–288.
- Ballard, G., D. G. Ainley, C. A. Ribic, and K. J. Barton. 2001. Effect of instrument attachment and other factors on foraging trip duration and nesting success of Adélie Penguins. *Condor* 103:481–490.
- Ballard, G., K. M. Dugger, N. Nur, and D. G. Ainley. *In press*. Foraging strategies of Adélie Penguins: adjusting body condition to cope with environmental variability. *Marine Ecology Progress Series*.
- Beigel, M., S. Marcus, and G. Ballard. 2004. Exception management for RFID systems. *Smart Labels Analyst* 36: 1–8.
- Blackmer, A., R. Mauck, J. Ackerman, C. Huntington, G. Nevitt, and J. Williams. 2005. Exploring individual quality: basal metabolic rate and reproductive performance in storm-petrels. *Behavioral Ecology* 16:906–913.

- Blums, P., J. Nichols, J. Hines, M. Lindberg, and A. Mednis. 2005. Individual quality, survival variation and patterns of phenotypic selection on body condition and timing of nesting in birds. *Oecologia* 143:365–376.
- Bost, C., Y. Handrich, P. Butler, A. Fahlman, L. Halsey, A. Woakes, and Y. Ropert-Coudert. 2007. Changes in dive profiles as an indicator of feeding success in King and Adélie penguins. *Deep-Sea Research II* 54:248–255.
- Cam, E., W. A. Link, E. G. Cooch, J. Monnat, and E. Danchin. 2002. Individual covariation in life-history traits: seeing the trees despite the forest. *American Naturalist* 159:96–105.
- Cam, E., J. Monnat, and J. Hines. 2003. Long-term fitness consequences of early conditions in the kittiwake. *Journal of Animal Ecology* 72:411–424.
- Chappell, M., D. Janes, V. Shoemaker, T. Bucher, and S. Maloney. 1993. Reproductive effort in Adélie penguins. *Behavioural Ecology and Sociobiology* 33:173–182.
- Clarke, J., L. Emmerson, and P. Otahal. 2006. Environmental conditions and life history constraints determine foraging range in breeding Adélie Penguins. *Marine Ecology Progress Series* 310:247–261.
- Clarke, J., B. Manly, K. Kerry, H. Gardner, E. Franchi, S. Corsolini, and S. Focardi. 1998. Sex differences in Adélie Penguin foraging strategies. *Polar Biology* 20:248–258.
- Clutton-Brock, T. 1988. Reproductive success. University of Chicago Press, Chicago, Illinois, USA.
- Deary, I. 2008. Why do intelligent people live longer? *Nature* 456:175–176.
- Desrochers, A. 1992a. Age-related differences in reproduction by European Blackbirds: Restraint or constraint? *Ecology* 73:1128–1131.
- Desrochers, A. 1992b. Age and foraging success in European Blackbirds: variation between and within individuals. *Animal Behaviour* 43:885–894.
- Dugger, K. M., G. Ballard, D. G. Ainley, and K. J. Barton. 2006. Effects of flipper bands on foraging behavior and survival of Adélie Penguins (*Pygoscelis adeliae*). *Auk* 123: 858–869.
- Ezard, T., P. Becker, and T. Coulson. 2007. Correlations between age, phenotype, and individual contributions to population growth in Common Terns. *Ecology* 88:2496–2504.
- Fuiman, L. A., R. W. Davis, and T. M. Williams. 2002. Behavior of midwater fishes under the Antarctic ice: observations by a predator. *Marine Biology* 140:815–822.
- Gonzalez-Solis, J., J. Croxall, and A. Wood. 2000. Sexual dimorphism and sexual segregation in foraging strategies of northern giant petrels, *Macronectes halli*, during incubation. *Oikos* 90:390–398.
- Gould, S., and N. Eldredge. 1993. Punctuated equilibrium comes of age. *Nature* 366:223–227.
- Grant, B. R., and P. R. Grant. 1993. Evolution of Darwin's finches caused by a rare climatic event. *Proceedings of the Royal Society of London B* 251:111–117.
- Grémillet, D., L. Pichegru, G. Kuntz, A. Woakes, S. Wilkinson, R. Crawford, and P. Ryan. 2008. A junk-food hypothesis for gannets feeding on fishery waste. *Proceedings of the Royal Society B* 275:1149–1156.
- Jensen, H., B. Sæther, T. Ringsby, J. Tufto, S. Griffith, and H. Ellegren. 2004. Lifetime reproductive success in relation to morphology in the house sparrow *Passer domesticus*. *Journal of Animal Ecology* 73:599–611.
- Kerry, K., J. Clarke, and G. Else. 1993. The use of an automated weighing and recording system for the study of the biology of Adélie Penguins (*Pygoscelis adeliae*). *Proceedings of the NIPR [National Institute for Polar Research] Symposium on Polar Biology* 6:62–75.
- Kitaysky, A., E. Kitaiskaia, J. Piatt, and J. Wingfield. 2006. A mechanistic link between chick diet and decline in seabirds? *Proceedings of the Royal Society B* 273:445–450.
- Kooyman, G. 1989. *Diverse divers*. Springer-Verlag, Berlin, Germany.
- Krüger, O., and J. Lindström. 2001. Lifetime reproductive success in common buzzard, *Buteo buteo*: from individual variation to population demography. *Oikos* 93:260–273.
- Lescroël, A., K. Dugger, G. Ballard, and D. Ainley. 2009. Effects of individual quality, reproductive success and environmental variability on survival of a long-lived seabird. *Journal of Animal Ecology* 78:798–806.
- Lewis, S., S. Wanless, D. Elston, M. Schultz, E. Mackley, M. Du Toit, J. Underhill, and M. Harris. 2006. Determinants of quality in a long-lived colonial species. *Journal of Animal Ecology* 75:1304–1312.
- MacColl, A., and B. Hatchwell. 2003. Heritability of parental effort in a passerine bird. *Evolution* 57:2191–2195.
- Massom, R. A., et al. 2006. Extreme anomalous atmospheric circulation in the West Antarctic Peninsula region in Austral spring and summer 2001/02, and its profound impact on sea ice and biota. *Journal of Climate* 19:3544–3571.
- Missoweit, M., S. Engels, and K. Sauer. 2007. Foraging ability in the scorpionfly *Panorpa vulgaris*: individual differences and heritability. *Behavioural Ecology and Sociobiology* 61:487–492.
- Murphy, M. 2007. Lifetime reproductive success of female Eastern Kingbirds (*Tyrannus tyrannus*): influence of lifespan, nest predation, and body size. *Auk* 124:1010–1022.
- Newton, I. 1989. *Lifetime reproduction in birds*. Academic Press, New York, New York, USA.
- O'Dwyer, T., W. Buttemer, and D. Priddel. 2007. Differential rates of offspring provisioning in Gould's petrels: are better feeders better breeders? *Australian Journal of Zoology* 55: 155–160.
- Pakhomov, E. A., and R. Perissinotto. 1996. Antarctic neritic krill *Euphausia crystallorophias*: spatio-temporal distribution, growth and grazing rates. *Deep-Sea Research I* 43:59–87.
- Pyle, P., L. B. Spear, W. J. Sydeman, and D. G. Ainley. 1991. The effects of experience and age on the breeding performance of western gulls. *Auk* 108:25–33.
- Robinson, S., A. Chiaradia, and M. Hindell. 2005. The effect of body condition on the timing and success of breeding in Little Penguins *Eudyptula minor*. *Ibis* 147:483–489.
- Ropert-Coudert, Y., A. Kato, J. Baudat, C. Bost, Y. Le Maho, and Y. Naito. 2001. Feeding strategies of free-ranging Adélie Penguins *Pygoscelis adeliae* analysed by multiple data recording. *Polar Biology* 24:460–466.
- Ropert-Coudert, Y., N. Knott, A. Chiaradia, and A. Kato. 2007. How do different data logger sizes and attachment positions affect the diving behaviour of little penguins? *Deep-Sea Research II* 54:415–423.
- Schreer, J. F., and K. M. Kovacs. 1997. Allometry of diving capacity in air-breathing vertebrates. *Canadian Journal of Zoology* 75:339–358.
- Schreer, J. F., K. M. Kovacs, and R. J. O. Hines. 2001. Comparative diving patterns of pinnipeds and seabirds. *Ecological Monographs* 71:137–162.
- Setchell, J., M. Charpentier, and E. Wickings. 2005. Mate guarding and paternity in mandrills: factors influencing alpha male monopoly. *Animal Behaviour* 70:1105–1120.
- Shealer, D., J. Spendlow, J. Hatfield, and I. Nisbet. 2005. The adaptive significance of stealing in a marine bird and its relationship to parental quality. *Behavioral Ecology* 16:371–376.
- Takahashi, A., Y. Watanuki, K. Sato, A. Kato, N. Arai, J. Nishikawa, and Y. Naito. 2003. Parental foraging effort and offspring growth in Adélie Penguins: Does working hard improve reproductive success? *Functional Ecology* 17:590–597.
- Taki, K., T. Yabuki, Y. Noiri, T. Hayashi, and M. Naganobu. 2008. Horizontal and vertical distribution and demography

- of euphausiids in the Ross Sea and its adjacent waters in 2004/2005. *Polar Biology* 31:1343–1356.
- Wilson, R., and C. McMahon. 2006. Measuring devices on wild animals: what constitutes acceptable practice? *Frontiers in Ecology and Environment* 4:147–154.
- Woehler, E. J. 1993. The distribution and abundance of Antarctic and sub-Antarctic penguins. Scientific Committee on Antarctic Research, Cambridge, UK.
- Woo, K., K. H. Elliott, M. Davidson, A. Gaston, and G. Davoren. 2008. Individual specialization in diet by a generalist marine predator reflects specialization in foraging behaviour. *Journal of Animal Ecology* 77:1082–1091.
- Zador, S. G., and J. F. Piatt. 1999. Time-budgets of Common Murres at a declining and increasing colony in Alaska. *Condor* 101:149–152.

APPENDIX A

BQI (breeding quality index) calculation method (*Ecological Archives* E091-141-A1).

APPENDIX B

Dive data analysis (*Ecological Archives* E091-141-A2).

APPENDIX C

Linear mixed-model statistics (*Ecological Archives* E091-141-A3).

APPENDIX D

Foraging efficiency over time (*Ecological Archives* E091-141-A4).