

Can a handicapped parent rely on its partner? An experimental study within Adélie penguin pairs

Michaël Beaulieu*, Thierry Raclot, Antoine Dervaux, Yvon Le Maho, Yan Ropert-Coudert, André Ancel

Institut Pluridisciplinaire Hubert Curien (IPHC), Département Ecologie, Physiologie et Ethologie (DEPE), UMR 7178 CNRS-UDS

ARTICLE INFO

Article history:

Received 16 March 2009
Initial acceptance 14 April 2009
Final acceptance 4 May 2009
Published online 27 June 2009
MS. number: 09-00179

Keywords:

Adélie penguin
begging
biparental care
breeding effort
chick
compensation
Pygoscelis adeliae

In biparental species, the response of parents when their mates are disadvantaged is highly variable. Moreover, experimental studies on parental effort have mainly focused on short-lived birds whose breeding constraints largely differ from those of long-lived species such as seabirds. We investigated the short- and long-term consequences of handicapping one parent within Adélie penguin, *Pygoscelis adeliae*, pairs. We also examined whether handicapped mates and offspring could convey cues informing the other parent of the need to increase breeding effort and whether this parent adjusted its behaviour accordingly. While handicapped penguins foraged for longer and lost more mass than controls, partners, fasting for longer at the nest, did not change their behaviour or lose more mass suggesting that they compensated at least for themselves. Information exchange was increased between mates after the return of handicapped females from foraging. However, partner males did not respond to this. Handicapped-pair chicks, which were smaller than control chicks, did not increase their solicitation rate for food. In the subsequent breeding season, compared to controls, 40% of previously handicapped females laid fewer eggs, the resight rate of previously handicapped males was lower and pair instability was higher. No additional cues seemed to be detected by Adélie penguins when their mates were handicapped and, for handicapped-pair offspring, the cost associated with a higher solicitation rate was probably too high for these small chicks to support. Consequently, we found no compensatory behaviour from partners in this long-lived species: handicapped individuals and offspring both supported the whole additional cost in both the short term and the long term.

© 2009 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

In species where both parents provide parental care, a conflict of interest may arise between partners which are both expected to minimize current reproductive effort but are none the less forced to cooperate to breed (Houston et al. 2005). Many experimental studies on parental effort, mainly carried out on passerines (Houston & Davies 1985), have shown that parents could respond to a reduction in care by their partners, by modifying their own effort. However, depending on the species, the partners' responses may show discrepancies and vary from a decreased effort (Sanz et al. 2000) or no response (Sanz et al. 2000; Schwagmeyer et al. 2002; Tajima & Nakamura 2003) to incomplete (Velando & Alonso-Alvarez 2003; Paredes et al. 2005; Navarro & González-Solís 2007) or complete compensatory responses (Wright & Cuthill 1990; Sanz et al. 2000) and these responses may be sex biased (Sanz et al. 2000; Tajima & Nakamura 2003; Velando & Alonso-Alvarez 2003).

These species and sex-specific differences may be determined by: (1) the availability of proximate cues that indicate the reduced effort of the mate (such as the feeding need of offspring, expressed through begging behaviour, or the mate's behaviour) and the individuals' capacity to detect them (Houston et al. 2005; Johnstone & Hinde 2006); (2) the individuals' capacity to sustain additional effort, implying that the individual had not been working at its maximum capacity before; and (3) the consequences of this additional cost for survival and future breeding attempts. Indeed, animals should balance the cost of their current reproductive investment against the potential negative effects of this current reproduction on future reproductive attempts (Williams 1966; Roff 1992; Stearns 1992). Short-lived individuals with low interannual survival are thus expected to vary the level of investment in their current reproduction, and thus to compensate for a reduction in care by their partner, at the expense of their own body condition and survival. In contrast, to maximize their lifetime reproductive success, long-lived animals with high interannual survival should minimize their current reproductive effort at a level that none the less allows them to breed. They are therefore expected to invest an optimal fixed amount in current reproduction, independent of the

* Correspondence: M. Beaulieu, IPHC, DEPE, UMR 7178 CNRS-UDS, 23 rue Becquerel, 67087 Strasbourg Cedex 2, France.

E-mail address: michael.beaulieu@c-strasbourg.fr (M. Beaulieu).

current reproductive constraints (Ricklefs 1987; Mauck & Grubb 1995). In that case, if the cost of breeding increases, offspring are expected to support the whole additional cost while parents put in a constant effort.

In the present study, we examined the consequences of an experimental increase in breeding constraints in a long-lived biparental species, the Adélie penguin, *Pygoscelis adeliae*. From the methods that have been used in the field (reviewed in Hinde 2006), we selected one that reduces the hydrodynamic properties of the animal. Externally fitted equipment affects diving behaviour if the cross-sectional area (CSA) of the equipment represents more than 1% of the animal's CSA (Culik & Wilson 1991). Among diving animals, penguins are particularly appropriate for manipulating breeding cost through an increase in their foraging cost while at sea as these birds are extremely streamlined. Their breeding behaviour has been well studied and effects of external handicaps are predictable (Ropert-Coudert et al. 2007). We investigated the responses of both the handicapped individual and its partner over short and long timescales. To explain why the partner would or would not compensate, we focused on the exchange of information between mates during nest relief and from the chicks to the adults. For this purpose, we first investigated the direct effects of a handicap on the time budget and changes in body mass in handicapped individuals and their partners. Second, we examined the indirect effects of a handicap on chicks, in terms of reproductive success, chick body mass and chick behaviour. Finally, to investigate the long-term consequences of previously increased breeding constraints, the same pairs were monitored during the subsequent breeding season.

METHODS

Study Species and Area

Adélie penguins breed during the austral summer. Females lay one or two eggs and generally leave the first incubation shift to the male while they feed at sea. About 12 days later, they take the second incubation shift for the same duration. Incubation lasts on average 34 days. After the eggs have hatched, both adults take turns to forage at sea and attend the chick at the nest. After returning from a foraging trip, during nest relief ceremonies, both birds stand and wave their necks back and forth while uttering a loud cackling call with open bill. This behaviour, called 'loud mutual display' (LMD), is related to the readiness to switch roles at the nest and the number of LMDs during the first 30 s indicates more information exchanges than during the remainder of the relief time (Müller-Schwarze & Müller-Schwarze 1980). After 3–4 weeks of the guarding stage, chicks become mobile and parents continue to feed their offspring irregularly for a few weeks until fledging (crèche stage).

In this study, we focused on the incubation and the guarding stages since it was impossible to monitor the birds regularly during the crèche stage. The study was conducted in Dumont d'Urville (66°40'S, 140°01'E), Adélie Land, Antarctica during the austral summers 2006–2007 and 2007–2008 and was approved by the ethic committee of the French Polar Institute (IPEV) and the Terres Australes et Antarctiques Françaises (TAAF).

Summer 2006–2007

We followed 46 pairs: 16 pairs were assigned to the control group and 30 to the treated group in which one member of the pair was handicapped (further referred to as handicapped bird) while the other remained untreated (further referred to as partner bird). Such a design meant that three pair groups were used (control

pairs, handicapped-female pairs and handicapped-male pairs); each pair group comprised males and females, resulting in six bird groups (Table 1).

At the end of the courtship period, birds were captured on their nest and weighed with an electronic balance (Ohaus, ± 2 g). Body mass changes thereafter were calculated considering this first weighing as the reference (100%). The left flipper (from the humeral head to the tip of the outstretched flipper) was measured with a ruler (± 1 mm). Birds were identified with a Nyanzol-D mark painted on the breast feathers and with a subcutaneous passive transponder (31.2 \times 3.8 mm, 0.8 g, Texas Instruments TIRIS, Dallas, TX, U.S.A.). To insert the transponders, we followed the procedure described by Renner & Davis (2000): the sterile transponder was injected with a needle cleaned with iodine solution before each injection. In addition, to avoid the transponder migrating into the penguin's body, it was injected in the lower part of the bird (i.e. in the loose skin between the tail and the left thigh). The procedure took only a few minutes and did not require sedating the birds. No complications have been related to the insertion of the transponder. This procedure is known to be safe and reliable (Renner & Davis 2000); it can be used for the lifetime of the bird and therefore in long-term studies (Dugger et al. 2006). For these reasons, the transponders were not removed at the end of the experiment, so we could monitor identified birds year after year.

To handicap penguins, we used dummy Plexiglas devices. They were attached with mastic, cyanoacrylate glue, Tesa tape and cable ties to the middle-back feathers. Our devices were parallelepiped (2.5 \times 3.5 \times 6.0 cm) and weighed 60 g; this size was chosen not to be too deleterious for birds and was comparable to the size of devices known to have negative effects on Adélie penguins (e.g. longer foraging trips, increased mass loss, decreased provisioning rate and lower breeding success; Wilson et al. 1989; Culik & Wilson 1991, 1992; Watanuki et al. 1992; Miller & Davis 1993). Handicapped birds were then released close to their nest. Two days later (to minimize disturbance from consecutive captures on the same nest), the partner underwent a similar treatment except for the attachment of the device. Penguins were captured and weighed only once more during the guarding stage, 40–45 days after laying.

The 46 nests were observed from a distance for periods ranging from 10 min to 2 h to monitor copulation behaviours, laying, foraging trip duration and reproductive success. Laying date was considered as the laying date of the first egg. Provisioning rate was defined from the chick's perspective and was calculated as the number of parental returns (male + female) from the sea. The final reproductive success was approximated by the number of chicks surviving until the crèche stage since, at this stage, chick mortality is very rare (Davis & McCaffrey 1986; Clarke et al. 2002). Penguins were sexed by a combination of parameters including cloacal inspection before egg laying, copulatory position and incubation routine (Taylor 1962; Kerry et al. 1993).

During the guarding stage, we filmed 39 returns from a foraging trip from a distance to examine LMD, solicitations and chick feeding in each group. Observations were limited to the first 1.5 h since, in penguins, most chick feeding occurs soon after the return of a parent from the sea, over a relatively short period, usually of less than 1 h (Taylor 1962; Williams 1982). Over the duration of the video record, we counted both chick solicitations and feeding events. Solicitations were considered successful if they resulted in a feeding bout and unsuccessful if not. In the case of successful solicitations, we checked that parents regurgitated with characteristic heaves of their body. Feeding was analysed by the number of feeding events and the total time that adults spent feeding (Van Heezik & Seddon 1996) since this duration includes both the number and the duration of feeding events and should approximate the amount of food given better than the two parameters

Table 1
Breeding parameters in the season when the handicap was used (Year N)

	Control males (N=16)	Control females (N=16)	Partner males (N=13)	Handicapped females (N=13)	Handicapped males (N=17)	Partner females (N=17)
Wing length (mm)	198±2	191±2	197±2	189.15±1.78	193.06±1.56	191.18±1.56
Courtship body mass (kg)	5.33±0.10	4.58±0.10	5.16±0.10	4.69±0.10	5.06±0.12	4.55±0.12
% CSA	—	—	—	4.22±0.06	3.88±0.05	—
Laying date	—	17 Nov±0.58 days	—	18 Nov±0.88 days	—	18 Nov±0.66 days
First foraging trip duration (days)	11.90±0.46	11.52±0.46	10.09±0.51	13.63±0.51	14.82±0.47	10.91±0.44
Foraging trip duration (guarding, days)	0.97±0.03	1.02±0.03	1.02±0.05	1.83±0.05	1.62±0.16	1.05±0.04
Time together on the nest (days)	5.67±0.36	—	2.71±0.39	—	4.06±0.49	—
No. of eggs per pair	1.87±0.08	—	1.85±0.10	—	1.75±0.11	—
No. of chicks per pair*	1.19±0.13	—	1.08±0.13	—	0.59±0.12	—
Chick age (days)*	25.87±0.87	—	23.92±0.93	—	22.50±1.07	—
Brood mass (kg)*	3.09±0.15	—	1.93±0.16	—	1.38±0.18	—
No. of provisionings*	22.27±1.22	—	15.25±1.13	—	15.75±1.40	—
Total no. of solicitations†	72.37±18.89	—	76.92±12.50	—	30.81±9.76	—
Duration of solicitations (s)†, ‡	7.23±0.48	—	6.46±0.40	—	9.61±1.44	—
Duration of feeding events (s)†	3.42±0.22	4.41±0.35	3.49±0.24	3.79±0.28	4.37±0.16	4.92±0.22
No. of feeding events†	21.53±6.28	12.96±4.79	21.26±10.36	23.86±4.19	16.57±6.60	8.14±0.74
No. of feeding events†, §	19.04±2.24	16.36±6.00	16.74±3.70	19.85±2.69	20.43±4.66	17.89±2.93
No. of feeding events†	19.06±4.61	—	22.51±4.65	—	12.26±3.85	—
No. of feeding events†, §	18.37±2.88	—	18.34±2.36	—	19.49±3.16	—
Total feeding duration (s)†	68.18±28.93	53.69±30.12	91.06±31.07	98.98±26.93	70.13±39.45	35.42±39.36
Total feeding duration (s)†, §	64.54±20.77	49.40±21.84	86.84±21.80	82.81±18.74	87.89±21.80	67.64±29.39
Total feeding duration (s)†	61.79±19.71	—	95.37±19.76	—	52.77±25.67	—
Total feeding duration (s)†, §	57.77±14.72	—	83.69±18.67	—	78.43±19.83	—

Results are expressed as means ± SE. % CSA = cross-sectional area of the handicap/cross-sectional area of the bird. Numbers in bold indicate a significantly different result ($P < 0.05$) between the group considered and its respective control.

* Data obtained at end of the guarding stage.

† Data obtained in first 1.5 h after return of parent.

‡ Only successful solicitations were taken into account.

§ Data calculated with total number of solicitations as a covariate.

separately. The duration of each feeding bout was defined as the time elapsed between the chick's bill insertion into the parent's mouth until withdrawal.

At the end of the guarding stage, the chicks were quickly and lightly sprinkled with paint (Raidex, Raidex GmbH, Dettingen/Erms, Germany) for individual recognition when left unguarded for the first time. This nontoxic paint remained only a few days on the down of chicks and had no obvious effect on the chicks' or the adults' behaviour. At the same time they were weighed with a spring balance (Salter, ±20 g).

To avoid the stress of additional capture of adult penguins, dummy devices were left on the birds until the moult, at the end of the austral summer, when the device fell off with the feathers to which it was attached.

Summer 2007–2008

At the end of the courtship period the following summer, we checked with a manual antenna all the nests that had been occupied by experimental pairs in 2006–2007 to search for penguins identified with a transponder. In addition, all the nests in the subcolony and in adjacent subcolonies ($N \approx 330$ nests) were checked twice more during the male and female incubation shifts. Previously manipulated birds as well as their new partner (if they formed a new pair) were identified and weighed with the same procedure as that in 2006–2007. For the rest of the breeding cycle, the procedure was the same as described in 2006–2007 with the difference that no bird was handicapped.

Data Analysis

Direct and indirect effects of the handicap were analysed in 2006–2007 and in 2007–2008. As foraging trip durations during incubation and the guarding stage are not comparable in Adélie penguins, comparisons between groups were carried out

independently for the first foraging trip during incubation and for all foraging trips during the guarding stage. For video analyses we used The Observer Video Pro (Noldus Information Technology, Wageningen, The Netherlands). Solicitations were compared between the three pair groups to examine the overall chick need. In contrast, feeding parameters were compared both between the three pair groups and between the six bird groups (sex*status interaction). In 2007–2008, only stable pairs that had raised at least one chick successfully in 2006–2007 were included in the comparisons. Resight and divorce rates (and, thus, pair stability) were calculated. A divorce occurred when both members of a pair were resighted but were not breeding together. A pair was considered as not stable if one member did not return to the colony or divorced.

To compare groups (first foraging trip duration, body mass, body mass changes, wing length, laying date, time spent together by partners at the nest, age and masses of chicks and feeding duration), we used general linear models (GLM) and general linear mixed models (GLMM, in the case of repeated measures) which allow pseudoreplication to be taken into account by including a random and a repeated factor. Normality of residuals was assessed using a Shapiro–Wilk test. If this latter condition was not fulfilled, generalized estimating equations (GEE) were used, with a gamma distribution (foraging trip duration during the guarding stage, duration of solicitations). Generalized linear models (GzLM) or GEE (in the case of repeated measures) with a Poisson distribution were also used for count data (provisioning rate, number of LMDs, solicitations, feeding events and reproductive success). Multiple comparisons were undertaken using the post hoc Bonferroni test. Chi-square and Fisher's exact tests were used to compare return and divorce rates and pair stability. The same tests were used to compare the proportion of females that reduced their clutch size between the two breeding seasons. Spearman correlations were used to test the relationship between the number of LMDs and the time elapsed between the arrival of one parent and

the departure of the other parent, and between the number of chick solicitations and feeding (number of feeding events and total duration of feeding).

All analyses were conducted using SPSS 16.02 (SPSS Inc., Chicago, IL, U.S.A.). Results are expressed as means \pm SE and the significance level was set at $\alpha = 0.05$.

RESULTS

Sex of Experimental Birds

In 2006–2007, the sex of the 92 individuals initially determined by cloacal inspection and copulation behaviour was first confirmed by examination of the incubation routine and afterwards in the subsequent season (2007–2008) even when identified individuals changed mate. In 2006–2007, 13 females and 17 males were handicapped in the treatment group (Table 1).

Effects of Handicap During Breeding Season

Intergroup differences

Male and female wing length and body mass were significantly different (GLM: $F_{1,86} = 18.40$, $P < 0.001$; $F_{1,83} = 52.65$, $P < 0.001$, respectively). The device's CSA as a proportion of the handicapped birds' CSA was significantly less important in males than in females (GLM: $F_{1,28} = 20.20$, $P < 0.001$). Importantly, within male and female groups, wing length (GLM: $F_{2,86} = 0.80$, $P = 0.45$), body mass (GLM: $F_{2,83} = 0.55$, $P = 0.58$) and laying date (GLM: $F_{2,40} = 0.392$, $P = 0.39$) did not differ between control, handicapped and partner birds (Table 1), so these groups were considered to be comparable for the following analyses.

Time budget

The experiment affected the time budget of the handicapped birds: the duration of the first foraging trip during incubation was affected by the status (GLM: $F_{1,84} = 33.51$, $P < 0.001$), with handicapped penguins performing longer foraging trips (14.22 ± 0.35 days) than controls (11.21 ± 0.32 days; $P < 0.001$) and partners (10.50 ± 0.34 days; $P < 0.001$). The same trend was observed during the guarding stage (GEE: Wald $\chi^2_2 = 70.13$, $N = 733$, $P < 0.001$), with handicapped penguins performing longer foraging trips (1.73 ± 0.08 days) than controls (1.00 ± 0.02 days; $P < 0.001$) and partners (1.03 ± 0.03 days; $P < 0.001$; Table 1).

Over the study period, control mates remained together for longer on the nest (GLM: $F_{2,33} = 15.77$, $P < 0.001$) than mates in handicapped-female pairs ($P < 0.001$) and mates in handicapped-male pairs ($P = 0.04$; Table 1). During nest reliefs, the information exchange was also affected by the experimental procedure: the number of LMDs during the first 30 s was negatively correlated with the time elapsed between the return to the nest of males and the departure of females (Spearman correlation: $r_s = -0.50$, $N = 19$, $P = 0.03$) but this was not observed after female returns ($r_s = -0.09$, $N = 20$, $P = 0.71$; Fig. 1a). The interaction between sex and status had an influence on the occurrence of LMDs during the first 30 s after returning (GzLM: Wald $\chi^2_2 = 17.80$, $N = 39$, $P < 0.001$) with more LMDs observed after the return of handicapped females than after the return of control ($P = 0.02$) and partner females ($P < 0.001$). In contrast, the return of any male (control, partner or handicapped) was followed by the same number of LMDs (all $P = 1.00$; Fig. 1b).

Body mass changes

Body mass changes between the courtship and the guarding stage did not differ between sexes (GLM: $F_{1,64} = 0.45$, $P = 0.50$) but were significantly different between the three statuses (GLM:

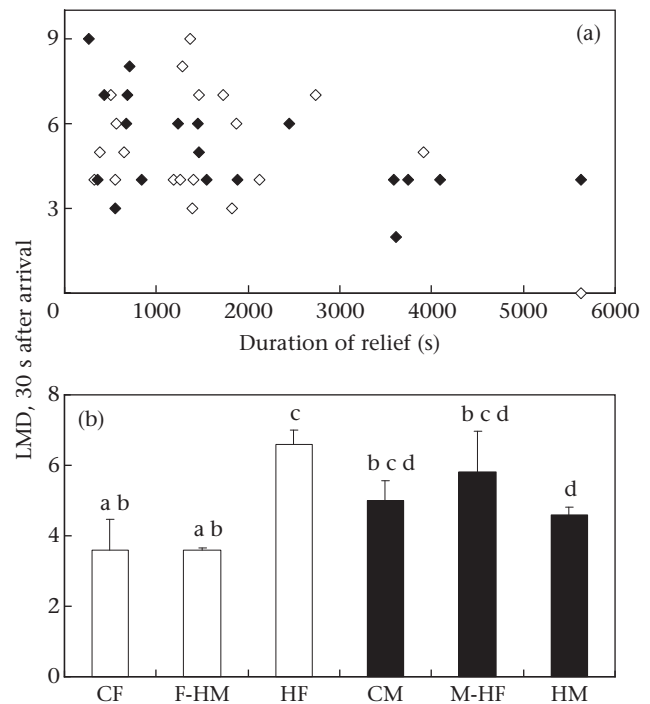


Figure 1. (a) Relationship between the number of loud mutual displays (LMDs) during the first 30 s of a nest relief and the duration of nest relief after a male returned (black diamonds) and after a female returned (white diamonds). (b) Number of LMDs after the return of control females (CF), handicapped-male females (F-HM = partner females), handicapped females (HF), control males (CM), handicapped-female males (M-HF = partner males) and handicapped males (HM). Different letters indicate significant differences between groups ($P < 0.05$).

$F_{1,64} = 10.06$, $P < 0.001$) with control and partner penguins weighing $91.3 \pm 1.0\%$ and $91.2 \pm 1.1\%$ of their initial body mass, respectively, while handicapped birds weighed $85.3 \pm 1.1\%$ of their initial body mass ($P < 0.001$ and $P = 0.001$, respectively; Fig. 2). The sex*status interaction was not significant (GLM: $F_{1,64} = 0.10$, $P = 0.91$).

Reproductive success and chick body mass

Reproductive success was significantly different between groups (GzLM: Wald $\chi^2_2 = 7.56$, $N = 46$, $P = 0.02$) and was highly affected by the handicap: while the number of eggs laid was the same in each group (all $P > 1.00$), the number of chicks differed at the end of the guarding stage with fewer chicks produced in handicapped-male pairs ($P = 0.01$; Table 1).

At the end of the guarding stage, even though handicapped-pair chicks were left alone for the first time by their parents earlier than control chicks, this difference was not significant (GLM: $F_{2,35} = 3.08$, $P = 0.06$). Brood mass differed between groups (GLM: $F_{2,35} = 29.86$, $P < 0.001$): control broods weighed significantly more than handicapped-male broods ($P < 0.001$) and handicapped-female broods ($P < 0.001$; Table 1). The lower body mass of handicapped chicks was associated with a lower provisioning rate during the guarding stage. Total provisioning differed between pair groups (GzLM: Wald $\chi^2_2 = 20.69$, $N = 35$, $P < 0.001$) with handicapped-male and handicapped-female pairs provisioning at lower rates than control pairs ($P < 0.001$ and $P = 0.001$, respectively; Table 1).

Since one chick may die during the guarding stage, the same comparisons were performed for pairs that had only one chick during the entire guarding stage. Chicks from handicapped-male pairs were left by parents at a younger age at the end of the guarding stage (GLM: $F_{2,17} = 6.45$, $P = 0.008$): they were 22.4 ± 0.9

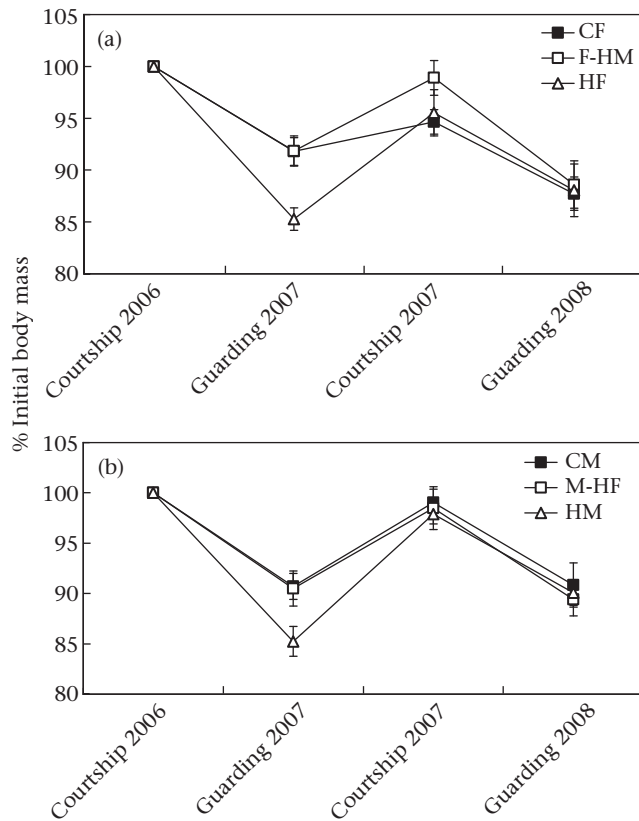


Figure 2. Body mass changes (%) along the study period in (a) females and (b) males. CF: control females; F-HM: handicapped-male females (=partner females); HF: handicapped females; CM: control males; M-HF: handicapped-female males (=partner males); HM: handicapped males.

days old while control chicks were 27.3 ± 1.1 days old ($P = 0.008$) and handicapped-female chicks were 25.5 ± 1.1 days old ($P = 0.12$). Control chicks were significantly heavier (GLM: $F_{2,17} = 25.14$, $P < 0.001$) than handicapped-male chicks ($P < 0.001$) and handicapped-female chicks ($P = 0.007$; Fig. 3a). Moreover, handicapped-male chicks were significantly lighter than handicapped-female chicks ($P = 0.01$). When we controlled for provisioning rate and chick age, the status still had an influence on chick body mass (GLM: $F_{2,13} = 8.46$, $P = 0.004$) but the difference was only found between handicapped-male chicks and control chicks ($P = 0.008$) and between handicapped-male chicks and handicapped-female chicks ($P = 0.02$; Fig. 3b).

Chick solicitations and parental feeding

During the 39 video recordings of the first 90 min of visits, 2454 solicitations and 726 feeding events were observed. When we controlled for the number of chicks, handicapping a parent affected the number of chick solicitations (GzLM: Wald $\chi^2 = 10.58$, $P = 0.005$): handicapped-male chicks solicited half as many times as handicapped-female chicks ($P = 0.005$) and control chicks although this difference was not significant ($P = 0.11$; Table 1). Successful solicitations were on average 3 s (40%) longer than unsuccessful solicitations (GEE: Wald $\chi^2 = 49.87$, $P < 0.001$; Fig. 4a) but were not different between groups (GEE: Wald $\chi^2 = 5.22$, $P = 0.07$; Table 1). In contrast, the mean duration of feeding events differed between groups (GEE: Wald $\chi^2 = 14.43$, $P < 0.001$): feeding events from handicapped males were longer than those from control and partner males ($P = 0.001$ and $P = 0.05$, respectively; Table 1). Chick solicitations can be considered as the main initiator of parent feeding since the number of solicitations was positively

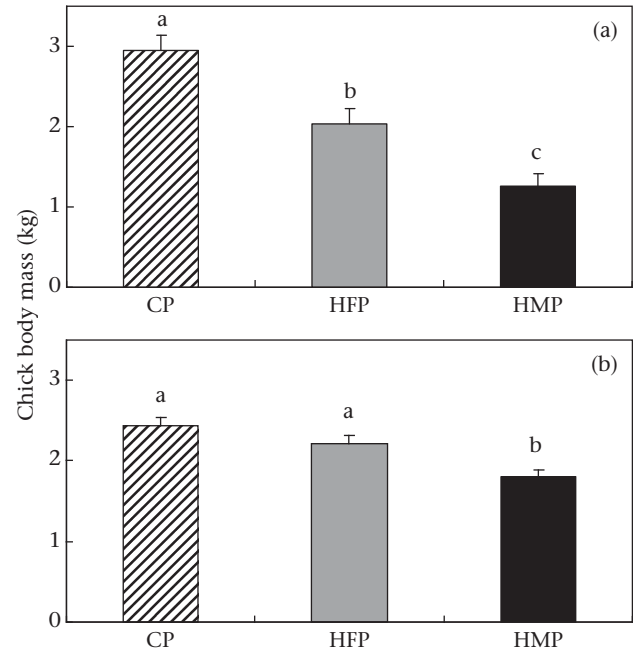


Figure 3. (a) Chick body mass and (b) chick body mass with provisioning rate and chick age as covariates in control pairs (CP), handicapped-female pairs (HFP) and handicapped-male pairs (HMP). Different letters indicate significant differences between groups ($P < 0.05$).

correlated with the number of feeding events (Spearman correlation: $r_s = 0.83$, $N = 39$, $P < 0.001$) and the total time spent feeding by adults ($r_s = 0.77$, $N = 39$, $P < 0.001$; Fig. 4b). However, the total number of feeding events and total feeding time were not significantly different between groups (GEE: Wald $\chi^2 = 2.83$, $P = 0.24$; GLMM: $F_{2,14} = 0.67$, $P = 0.53$, respectively; Table 1) even though handicapped males and partner females were feeding their offspring less. When we controlled for solicitation rate, this trend

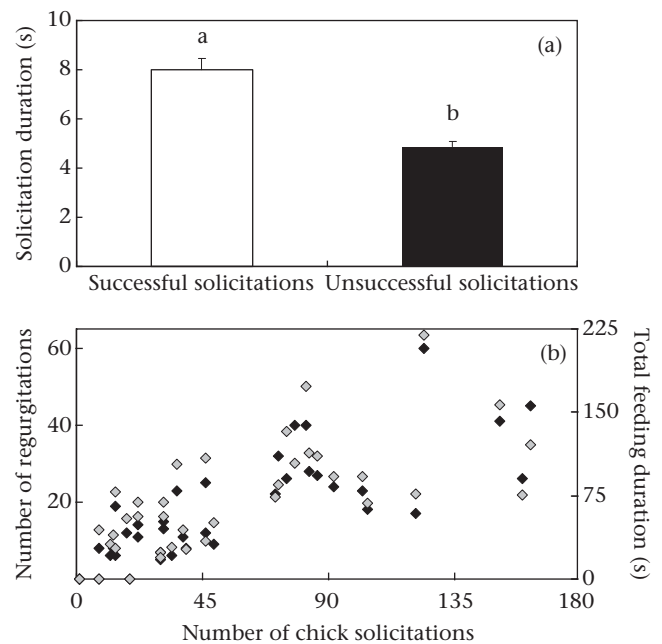


Figure 4. (a) Duration of successful and unsuccessful chick solicitations and (b) relationship between the number of solicitations and the number of feeding events (black diamonds) from parents and total duration of feeding (grey diamonds). Different letters indicate significant differences between groups ($P < 0.05$).

Table 2
Breeding parameters 1 year after the handicap was used (Year $N + 1$)

	Control males ($N=16$)	Control females ($N=14$)	Partner males ($N=12$)	Handicapped females ($N=12$)	Handicapped males ($N=12$)	Partner females ($N=12$)
Resighted individuals (%)	100.00	87.50	92.31	92.31	70.59	70.59
Divorce (%)	14.29		18.18		37.50	
Pair stability (%)	75.00		69.23		29.41	
Laying date	—	19 Nov \pm 1.05 days	—	19 Nov \pm 1.07 days	—	19 Nov \pm 0.04 days
No. of eggs per pair	2.00 \pm 0.40		1.58 \pm 0.36		1.87 \pm 0.48	
No. of chicks per pair*	1.20 \pm 0.34		1.11 \pm 0.35		1.25 \pm 0.56	
Chick age (days)*	28.78 \pm 2.07		28.37 \pm 2.20		29.00 \pm 2.78	
Brood mass (kg)*	3.02 \pm 0.34		2.69 \pm 0.36		2.76 \pm 0.46	
No. of provisionings*	20.78 \pm 1.52		20.88 \pm 1.62		20.20 \pm 2.01	

Results are expressed as means \pm SE. Numbers in bold indicate a significantly different result ($P < 0.05$) between the group considered and its respective control.

* Data obtained at end of guarding stage.

disappeared (number of feeding events: GEE: Wald $\chi^2_2 = 0.41$, $P = 0.81$; time spent feeding; GLMM: $F_{2,14} = 0.04$, $P = 0.96$; Table 1). We can thus conclude that after a parent returns, partners did not show compensatory feeding behaviour in response to the lower provisioning rate of their handicapped partner.

From the offspring's perspective, handicapped and control chicks were fed similarly after a parent returned (number of feeding events: GEE: Wald $\chi^2_2 = 2.83$, $P = 0.24$; total time spent being fed: GLMM: $F_{2,16} = 0.96$, $P = 0.40$) even though the feeding rate and feeding duration of handicapped-male chicks were the lowest of all groups. That trend was none the less suppressed after we controlled for the number of chick solicitations (number of feeding events: GEE: Wald $\chi^2_2 = 0.13$, $P = 0.94$; time spent being fed: GLMM: $F_{2,17} = 0.78$, $P = 0.47$; Table 1).

Effects of Handicap in Subsequent Breeding Season

Return rate and pair stability

Handicapped-male pairs were significantly less stable than control pairs (Fisher's exact test: $P = 0.02$) but not handicapped-female pairs (Fisher's exact test: $P = 0.06$; Table 2). Resight rates for males and females did not differ (89.1% and 82.6%, respectively; chi-square test: $\chi^2_1 = 0.36$, $P = 0.77$) and resight rates between control, partner and handicapped birds in males and females were equivalent (Fisher's exact tests: $P > 0.05$) with the exception that handicapped males returned to the colony less than control males (Fisher's exact test: $P = 0.04$; Table 2). Although divorces occurred twice as often in handicapped-male pairs as in control pairs, divorce proportions were not significantly different between groups (Fisher's exact tests: all $P > 0.05$; Table 2).

Body mass changes

The handicap procedure had no long-term effects on body mass: relative to initial body mass measured during courtship in 2006–2007, penguin body mass during the courtship and the guarding stage in 2007–2008 did not differ between the sexes (GLMM: $F_{1,110} = 2.35$, $P = 0.13$) and the statuses (GLMM: $F_{1,110} = 0.17$, $P = 0.85$) and the sex*status interaction was not significant (GLMM: $F_{2,110} = 0.68$, $P = 0.51$; Fig. 2).

Reproductive success and chick body mass

All the female groups laid a similar number of eggs (GzLM: Wald $\chi^2_2 = 0.61$, $N = 32$, $P = 0.74$) on about the same date (GzLM: $F_{2,16} = 0.11$, $N = 32$, $P = 0.89$; Table 2). Nevertheless, compared to the laying in 2006, 41.7% of handicapped females laid fewer eggs while no control or partner females decreased their clutch size (Fisher's exact tests: $P = 0.04$ and $P = 0.11$, respectively). In contrast, 8.3% of handicapped females increased their clutch size while 16.7% of control females and 14.3% of partner females laid more eggs

(Fisher's exact tests: all $P < 0.001$; Fig. 5). Reproductive success was the same in each group (GzLM: Wald $\chi^2_2 = 0.06$, $N = 23$, $P = 0.97$), brood mass (GLM: $F_{2,19} = 0.25$, $P = 0.78$) and age at the end of the guarding stage (GLM: $F_{2,19} = 0.02$, $P = 0.98$) did not differ between groups and chicks were provisioned at similar rates (GzLM: Wald $\chi^2_2 = 0.08$, $N = 22$, $P = 0.96$; Table 2).

Effects of pair instability

From 2006 to 2007, 25 pairs were stable while 22 were newly established. No differences between the two groups were found. Their body masses were similar during courtship in 2007 in males and females (sex*stability interaction: GLM: $F_{1,82} = 0.001$, $P = 0.98$) and they lost mass at the same rate (sex*stability interaction: GLM: $F_{1,71} = 0.006$, $P = 0.94$). The number of chicks at the end of the guarding stage was lower than the number of eggs in both groups (GzLM: Wald $\chi^2_2 = 56.67$, $P < 0.001$) but the numbers of eggs (1.88 \pm 0.90 and 1.82 \pm 0.10, respectively) and chicks (1.12 \pm 0.12 and 0.96 \pm 0.13, respectively) were equivalent between the two groups (all $P > 0.05$). The brood mass was similar in stable and newly established pairs (2.84 \pm 0.20 kg and 2.68 \pm 0.22 kg, respectively; GLM: $F_{1,38} = 0.27$, $P = 0.61$). Chicks were provisioned at similar rates over the guarding stage (20.7 \pm 1.0 and 19.8 \pm 1.1 visits, respectively; GzLM: Wald $\chi^2_1 = 0.40$, $N = 40$, $P = 0.53$) and had similar ages at the end of this period (28.68 \pm 1.26 and 27.44 \pm 1.39 days, respectively, GLM: $F_{1,38} = 0.44$, $P = 0.51$).

DISCUSSION

Effects of Handicap During Breeding Season

Overall, the results of our study indicate that male and female Adélie penguins were affected by the handicap, and their chicks were smaller than control chicks especially in handicapped-male

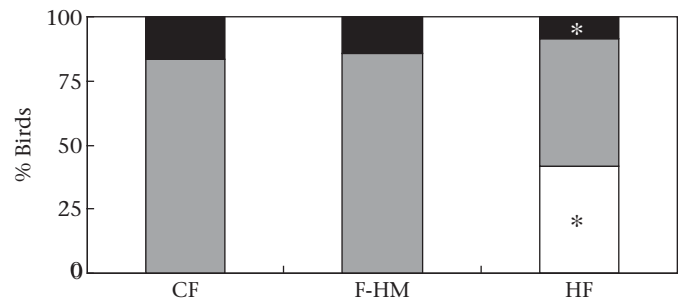


Figure 5. Percentage of birds for which clutch size increased (black), remained stable (grey) or decreased (white) between 2006 and 2007, in control females (CF), handicapped-male (=partner) females (F-HM) and handicapped females (HF). * $P < 0.05$.

pairs. In addition, no compensatory behaviour from the partners towards their offspring was seen.

Handicapped birds did not feed their offspring less than the controls after returning from a foraging trip. This suggests that handicapped parents returned to their breeding site when their stomach was full. However, because of a lower provisioning rate (at least), handicapped chicks, and especially handicapped-male chicks, were smaller than controls. When we controlled for provisioning rate, only handicapped-male chicks remained smaller than control chicks suggesting that the lower body mass of handicapped-female chicks was caused only by the lower provisioning rate. Handicapped-male chicks were the smallest, presumably because they were fed less after a parent returned (although not significantly). It is also likely that the quality of their food had changed and handicapped males may have been forced to select lower quality prey. Since males feed more extensively upon fish than females (Clarke et al. 1998), handicapped males may have been limited to prey upon krill which is less energetically valuable than fatty fish (Watanuki et al. 2002; Ainley et al. 2003) which promote growth in penguin chicks (Heath & Randall 1985). For this purpose, further qualitative analyses on the birds' diet would be worthwhile.

The increased foraging trip duration of handicapped birds obliged their partners to fast for longer than the controls. As a consequence, the partners had an additional energetic debt when returning to the sea to feed. Assuming that the rate of prey capture was similar in partners and controls, there are several possibilities for the partners to adapt to this additional cost: they could (1) stay longer at sea to increase the net energy gain, (2) return with a lower body mass or (3) feed their chicks less. In our study, partners did not modify their foraging trip duration, their body mass loss was equivalent to that of controls and their feeding behaviour towards chicks was not modified. In Adélie penguins, the time spent fasting before foraging does not affect foraging trip duration (Davis 1988; Miller & Davis 1993). In a previous study conducted on Adélie penguins, Watanuki et al. (1992) concluded that partners did not increase foraging effort in response to a decreased parental investment by their mates. Our conclusion is different: to keep body mass and feeding rate equivalent to controls without increasing foraging trip duration, partners had to increase the rate of prey capture and consequently their foraging effort. In other words, our results suggest that partners compensated for their mate's deficiency, at least for themselves. To support this hypothesis, it would be worth conducting studies examining their at-sea behaviour with the use of miniaturized data loggers such as time-depth recorders and GPS.

However, partners did not compensate by provisioning more frequently or by feeding their offspring more than control birds. This suggests that the cost imposed by potential compensatory behaviour would be too high for subsequent breeding attempts in this long-lived species. Another reason may be that partners lacked information from their mate and their offspring (Johnstone & Hinde 2006). The return of handicapped females produced more LMDs than that of control females, as if the exchange of information was increased between mates when females were handicapped. However, males were not responsive to the number of LMDs after the return of females. In contrast, females were responsive to the number of LMDs after the return of males, but the exchange of information was not increased between mates when males were handicapped. These discrepancies between the information transmitter and the information receiver did not seem to lead the partners to consider the disadvantage of handicapped birds. In addition, handicapped-pair chicks were expected to solicit their parents more as they had a lower body mass (Iacovides & Evans 1998; Kitaysky et al. 2000). As in other bird species (Kilner 1995;

Roulin et al. 2000), Adélie penguins respond positively to an increase in solicitations from their chicks and because of the strong correlations between the number of chick solicitations and adult feeding, chicks can be regarded as the main initiators of feeding. However, chicks from handicapped pairs did not solicit for food more often than control chicks and handicapped-male chicks solicited even less. Consequently handicapped-male chicks were fed less than other chicks (although not significantly). However, when we controlled for the number of chick solicitations, this trend disappeared. This suggests that if handicapped-male chicks were the smallest, it is also because they did not succeed in soliciting enough to obtain the necessary amount of food to grow normally. Handicapped chicks may not have been strong enough to sustain the cost of additional and/or longer solicitations for food. Indeed, begging is a costly activity for chicks (Verhulst & Wiersma 1997; Kilner 2001). In our study, the duration of chick solicitations importantly influenced the occurrence of consecutive feeding bouts, suggesting that successful solicitations are more costly to sustain than unsuccessful ones. To obtain food, chicks therefore have to be vigorous enough to 'persuade' their parents to give them food. In addition, handicapped-male chicks solicited less than handicapped-female chicks, suggesting that even though both groups had an increased need, handicapped-female chicks were still more vigorous than handicapped-male chicks.

Effects of Handicap in Subsequent Breeding Season

At the individual level, the handicap had deleterious consequences for females, with more than 40% of previously handicapped females decreasing their clutch size. This suggests that handicapped females put in more effort during the previous breeding season and almost half of them were not able to replenish their reserves fully during the winter. This may also be true for handicapped males whose resight rate on the colony was lower than that of control males because of an increase in mortality rate in winter, dispersion to other colonies or skipping of the breeding season. At the pair level, the main consequence was pair instability in previously handicapped-male pairs (Table 2). This pair instability was the result of both nonreturns and divorces. Divorces may also have affected pair stability since breeding failure was much higher in handicapped-male pairs than in other groups. Indeed, unsuccessful breeders often divorce their mates (Ens et al. 1996; Dubois & Cézilly 2002; Moody et al. 2005) and information on breeding performance can influence decisions for more than a year (Naves et al. 2006). Moreover, Lewis et al. (2006) demonstrated that, in species with biparental care, behavioural determinants of quality operated essentially on the time mates spent together at the nest site. In our study, pair bonds may have been weakened in handicapped pairs for which mates spent less time together and especially in handicapped-male pairs whose breeding success was strongly diminished during the year of the handicap experiment.

Finally, previously handicapped pairs behaved similarly to control pairs and had the same reproductive success as controls. Reproductive success was also equivalent between stable and newly established pairs so that the handicap experience in year N had no direct or indirect effects on the reproductive success in year $N + 1$ and the long-term cost may have been mainly transferred to chicks in year N .

CONCLUSION

In Adélie penguins, when one mate was handicapped, no compensatory care was observed from the partner. This was probably because (1) the cost of such a behaviour would have been too high for subsequent breeding attempts in this long-lived

species and (2) partners could not detect cues from their mate or their offspring, informing them of the need to put in more breeding effort. As a consequence, handicapped individuals and offspring both supported the whole additional breeding cost of the handicap. In this study, we investigated long-term consequences for adults and we showed that the handicap may affect the return rate of handicapped males, pair stability and clutch size during the subsequent season. However, the examination of long-term consequences for chicks, which also had to support the extra cost, would be of great interest; for instance, to what extent the early growth condition of the handicapped-pair chicks would affect their survival and breeding performance when adults remains to be investigated.

Acknowledgments

We are especially grateful to D. Lazin and A.-M. Thierry for their great help in the field and A. Jacobs for his help with The Observer software. We also thank A. Kato, F. Criscuolo and C. Hinde for constructive comments and Ilka Zimmer for improving the manuscript. The French Polar Institute Paul Emile Victor (IPEV) provided financial and logistical support in Dumont d'Urville.

References

- Ainley, D. G., Ballard, G., Barton, K. J., Karl, B. J., Rau, G. H., Ribic, C. A. & Wilson, P. R. 2003. Spatial and temporal variation of diet within a presumed metapopulation of Adélie penguins. *Condor*, **105**, 95–106.
- Clarke, J., Manly, B., Kerry, K., Gardner, H., Franchi, E., Corsolini, S. & Focardi, S. 1998. Sex differences in Adélie penguin foraging strategies. *Polar Biology*, **20**, 248–258.
- Clarke, J., Kerry, K., Irvine, L. & Phillips, B. 2002. Chick provisioning and breeding success of Adélie penguins at Bechervaise Island over eight successive seasons. *Polar Biology*, **25**, 21–30.
- Culik, B. M. & Wilson, R. P. 1991. Energetics of underwater swimming in Adélie penguins (*Pygoscelis adeliae*). *Journal of Comparative Physiology*, **161**, 285–291.
- Culik, B. M. & Wilson, R. P. 1992. Field metabolic rates of instrumented penguins using doubly-labelled water. *Journal of Comparative Physiology*, **162**, 567–573.
- Davis, L. S. 1988. Coordination of incubation routines and mate choice in Adélie penguins (*Pygoscelis adeliae*). *Auk*, **105**, 428–432.
- Davis, L. S. & McCaffrey, F. T. 1986. Survival analysis of eggs and chicks of Adélie penguins (*Pygoscelis adeliae*). *Auk*, **103**, 379–388.
- Dubois, F. & Cézilly, F. 2002. Breeding success and mate retention in birds: a meta-analysis. *Behavioral Ecology and Sociobiology*, **52**, 357–364.
- Dugger, K. M., Ballard, G., Ainley, D. G. & Barton, K. J. 2006. Effects of flipper bands on foraging behavior and survival of Adélie penguins (*Pygoscelis adeliae*). *Auk*, **123**, 858–869.
- Ens, B., Choudhury, S. & Black, J. M. 1996. *Mate Fidelity and Divorce in Monogamous Birds*. Oxford: Oxford University Press.
- Heath, R. G. M. & Randall, R. M. 1985. Growth of jackass penguin chicks (*Spheniscus demersus*) hand reared on different diets. *Journal of Zoology*, **205**, 91–105.
- Hinde, C. A. 2006. Negotiation over offspring care? A positive response to partner-provisioning rate in great tits. *Behavioral Ecology*, **17**, 6–12.
- Houston, A. I. & Davies, N. B. 1985. *Evolution of Cooperation in Dunnocks*, *Prunella modularis*. Oxford: Blackwell Scientific.
- Houston, A. I., Szekely, T. & McNamara, J. M. 2005. Conflict between parents over care. *Trends in Ecology & Evolution*, **20**, 33–38.
- Iacovides, S. & Evans, R. M. 1998. Begging as graded signals of need for food in young ring-billed gulls. *Animal Behaviour*, **56**, 79–85.
- Johnstone, R. A. & Hinde, C. A. 2006. Negotiation over offspring care: how should parents respond to each other's efforts? *Behavioral Ecology*, **17**, 818–827.
- Kerry, K. R., Clarke, J. R. & Else, G. D. 1993. Identification of sex of Adélie penguins from observations of incubating birds. *Wildlife Research*, **20**, 725–732.
- Kilner, R. 1995. When do canary parents respond to nestling signals of need? *Proceedings of the Royal Society B*, **260**, 343–348.
- Kilner, R. M. 2001. A growth cost of begging in captive canary chicks. *Proceedings of the National Academy of Sciences, U.S.A.*, **98**, 11394–11398.
- Kitaysky, A. C., Wingfield, J. C. & Piatt, J. F. 2000. Corticosterone facilitates begging and affects resource allocation in the black-legged kittiwake. *Behavioral Ecology*, **2**, 619–625.
- Lewis, S., Wanless, S., Elston, D. A., Schultz, M. D., Mackley, E., Du Toit, M., Underhill, J. G. & Harris, M. P. 2006. Determinants of quality in a long-lived colonial species. *Journal of Animal Ecology*, **75**, 1304–1312.
- Mauck, R. A. & Grubb Jr, T. C. 1995. Petrel parents shunt all experimentally increased reproductive costs to their offspring. *Animal Behaviour*, **49**, 999–1008.
- Miller, G. D. & Davis, L. S. 1993. Foraging flexibility of Adélie penguins *Pygoscelis adeliae*: consequences for an indicator species. *Biological Conservation*, **63**, 223–230.
- Moody, A. T., Wilhelm, S. I., Cameron-MacMillan, M. L., Walsh, C. J. & Storey, A. E. 2005. Divorce in common murre (*Uria aalge*): relationship to parental quality. *Behavioral Ecology and Sociobiology*, **57**, 224–230.
- Müller-Schwarze, D. & Müller-Schwarze, C. 1980. Display rate and speed of nest relief in antarctic pygoscelid penguins. *Auk*, **97**, 825–831.
- Navarro, J. & González-Solis, J. 2007. Experimental increase of flying costs in a pelagic seabird: effects on foraging strategies, nutritional state and chick condition. *Oecologia*, **151**, 150–160.
- Naves, L. C., Monnat, J. Y. & Cam, E. 2006. Breeding performance, mate fidelity, and nest site fidelity in a long-lived seabird: behaving against the current? *Oikos*, **115**, 263–276.
- Paredes, R., Jones, I. L. & Boness, D. J. 2005. Reduced parental care, compensatory behaviour and reproductive costs of thick-billed murre equipped with data loggers. *Animal Behaviour*, **69**, 197–208.
- Renner, M. & Davis, L. S. 2000. Marking penguins with implanted transponders. *Notornis*, **47**, 163–165.
- Ricklefs, R. E. 1987. Response of adult Leach's storm petrel to increased food demand at the nest. *Auk*, **104**, 750–756.
- Roff, D. A. 1992. *The Evolution of Life Histories: Theory and Analysis*. New York: Chapman & Hall.
- Ropert-Coudert, Y., Wilson, R. P., Yoda, K. & Kato, A. 2007. Assessing performance constraints in penguins with externally-attached devices. *Marine Ecology, Progress Series*, **333**, 281–289.
- Roulin, A., Kolliker, M. & Richner, H. 2000. Barn owl (*Tyto alba*) siblings vocally negotiate resources. *Proceedings of the Royal Society B*, **267**, 459–463.
- Sanz, J. J., Kranenborg, S. & Tinbergen, J. M. 2000. Differential response by males and females to manipulation of partner contribution in the great tit (*Parus major*). *Journal of Animal Ecology*, **69**, 74–84.
- Schwagmeyer, P. L., Mock, D. W. & Parker, G. A. 2002. Biparental care in house sparrows: negotiation or sealed bid? *Behavioral Ecology*, **13**, 713–721.
- Stearns, S. C. 1992. *The Evolution of Life Histories*. New York: Oxford University Press.
- Tajima, K. & Nakamura, N. 2003. Response to manipulation of partner contribution: a handicapping experiment in the barn swallow. *Ornithological Science*, **2**, 65–72.
- Taylor, R. H. 1962. The Adélie penguin *Pygoscelis adeliae* at Cape Royds. *Ibis*, **104**, 176–204.
- Van Heezik, Y. M. & Seddon, P. J. 1996. Scramble feeding in jackass penguins: within-brood food distribution and the maintenance of sibling asymmetries. *Animal Behaviour*, **51**, 1383–1390.
- Velando, A. & Alonso-Alvarez, C. 2003. Differential body condition regulation by males and females in response to experimental manipulations of brood size and parental effort in the blue-footed booby. *Journal of Animal Ecology*, **72**, 846–856.
- Verhulst, S. & Wiersma, P. 1997. Is begging cheap? *Auk*, **114**, 134.
- Watanuki, Y., Mori, Y. & Naito, Y. 1992. Adélie penguin parental activities and reproduction: effects of device size and timing of its attachment during chick rearing period. *Polar Biology*, **12**, 539–544.
- Watanuki, Y., Kato, A., Sato, K., Niizuma, Y., Bost, C. A., Le Maho, Y. & Naito, Y. 2002. Parental mass change and food provisioning in Adélie penguins rearing chicks in colonies with contrasting sea-ice conditions. *Polar Biology*, **25**, 672–681.
- Williams, A. J. 1982. Chick-feeding rates of Macaroni and rockhopper penguins at Marion Island. *Ostrich*, **53**, 129–134.
- Williams, G. C. 1966. *Adaptation and Natural Selection*. Princeton, New Jersey: Princeton University Press.
- Wilson, R. P., Coria, N. R., Spairani, H. J., Adelung, D. & Culik, B. M. 1989. Human-induced behavior in Adélie penguins *Pygoscelis adeliae*. *Polar Biology*, **10**, 77–80.
- Wright, J. & Cuthill, I. 1990. Biparental care: short-term manipulation of partner contribution and brood size in the starling, *Sturnus vulgaris*. *Behavioral Ecology*, **1**, 116–124.