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Sex-specific parental strategies according to the sex of offspring in the Adélie penguin

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In sexually dimorphic species, the sex of the offspring may induce different constraints for parents. At the same time, within pairs, males and females may have conflicting optimal reproductive strategies. As a result, they may adjust their level of parental investment differently according to the sex of the young. In this study, we examined whether Adélie penguin (*Pygoscelis adeliae*) chicks were sexually dimorphic and whether parents adjusted their parental investment accordingly. Male chicks were on average approximately 10% heavier than female chicks but not larger. Despite the presumed additional cost associated with male chick growth, no fitness cost differences were observed between parents rearing 1 chick whatever its sex: Adult body mass changes and resight rates during the subsequent breeding season were similar. However, the sex of offspring affected the duration of foraging trips during the early guard stage: At this stage, female adults rearing a female chick performed longer foraging trips than female adults rearing a male chick and males rearing either a male or a female chick. We propose that, because female adults present a lower survival rate after a breeding attempt, they are more prone to modify their level of parental investment than male adults. Moreover, the modulation of the foraging behavior by female adults according to the sex of the chick is likely to reduce intraspecific competition at a time when resource availability at sea is not optimal and when food requirement for female chicks may be lower than for male chicks. *Key words:* biparental care, foraging strategies, sex-related breeding effort. *[Behav Ecol]*

Life history theory predicts that animals should balance the cost of their current reproduction against its potential negative effects on future reproductive attempts (Williams 1966). Parents are therefore expected to adjust their current investment according to resource availability, their own body condition, and their offspring need and value (Erikstad et al. 1997). In sexual size dimorphic species, when sexual dimorphism already exists in offspring, rearing a male or a female young may induce different breeding costs for parents (Cameron-MacMillan et al. 2007): Offspring of the larger sex may require more resources and therefore may incur additional reproductive costs. Moreover, if male and female offspring differ in their fitness value, parents should tolerate greater risks for offspring which is the most likely to survive and reproduce.

When both parents provide care to the young, males and females may have conflicting optimal reproductive strategies. In such a situation, who, from the male or the female, would take charge of this additional breeding cost? Different answers are conceivable: 1) both parents bear the additional cost (Weimerskirch and Lys 2000; Weimerskirch et al. 2000; Cameron-MacMillan et al. 2007), 2) male and female parental investment remains the same whatever the sex of the young (Lessels et al. 1998), and 3) only 1 parent modulates its investment according to the sex of the young. In this last case, the additional cost triggered by the larger offspring sex may generate sex-specific consequences on parents' body condition and survival: If consequences are too deleterious for 1 parent, it seems likely that this parent will not sustain the additional cost related to the larger young and will transfer this cost to its mate. Alternatively, interannual survival probability may differ between male and female parents: To maximize their lifetime reproductive success, individuals with high interannual survival should minimize their current reproductive effort at an optimal fixed level (Ricklefs 1987; Mauck and Grubb 1995). In contrast, individuals with a low interannual survival are expected to adjust the level of investment in their current reproduction at the expense of their own body condition.

Parents can modify their breeding effort by regulating provisioning rate toward offspring. For this purpose, they can adjust the duration of their foraging trips by alternating long and short foraging trips. It has been suggested that long foraging trips serve to enhance adult body condition at the expense of the offspring, whereas short trips enable the parents to provision the young at a high rate at the expense of the adult body condition (Weimerskirch 1998).

In this context, seabirds constitute a good model to examine sex-specific parental investment according to the sex of the young, as both parents provide care to the young (Gowaty 1996), they usually exhibit sexual dimorphism (Serrano-Meneses and Szekely 2006) and many species alternate short and long foraging trips (see Ropert-Coudert et al. 2004). Within seabirds, Adélie penguins (*Pygoscelis adeliae*) match these features: Males are larger than females (Ainley and Emison 1972) and during chick rearing, adults exhibit a bimodal distribution of foraging trip durations with short (15–25 h) and long (45–65 h) trips (Clarke et al. 1998; Clarke 2001). In addition, the interannual survival after a breeding attempt is higher in males than in females (Ainley and DeMaster 1980; Dugger et al. 2006): Consequently, female adults are expected to be more likely to modify their parental investment than male adults.

Until now, very few studies dealing with parental investment have taken into consideration simultaneously the sex of the parents and the sex of the young (Lessels et al. 1998; Weimerskirch and Lys 2000; Weimerskirch et al. 2000;

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Cameron-MacMillan et al. 2007). In this study, we checked whether sexual dimorphism was already present at the chick stage in Adélie penguins, then we tested the hypothesis that the level of parental investment depends on the sex of the parent and the sex of the chick. For this purpose, we analyzed parental provisioning decisions (foraging trip duration and feeding events) toward male and female offspring along the breeding cycle and investigated the consequences of the sex of the young on adult condition and survival.

MATERIALS AND METHODS

Study area and species

The study was conducted during 2 consecutive breeding seasons in Dumont d'Urville (66°40′S; 140°00′E), Adélie Land, Antarctica, during austral summers 2007–2008 and 2008–2009. In mid-November, female Adélie penguins lay 1 or 2 eggs. After hatching, males and females alternate foraging at sea and chick attendance at nest. This guard stage lasts from mid-December until mid-January. After 3–4 weeks, chicks get mobile and parents continue to feed their offspring sporadically for a few weeks until fledging (crèche stage, Figure 1). Adélie penguins feed mainly on krill (*Euphausia superba*, Ridoux and Offredo 1989) whose abundance, energy density, and distribution depend on the season (Clarke 1980; Nicol 2006).

Study protocol

We limited our fieldwork to pairs with only 1 chick from hatching till fledging so that the effects of offspring number and offspring sex are not confounded and the influence of sibling competition is excluded.

In 2007–2008, 32 pairs with only 1 chick were randomly selected within 1 colony to assess chick sexual dimorphism. Among these, 18 pairs were monitored more precisely to examine parental behavior: At the end of the courtship period, birds were captured on their nest and weighed with an electronic balance (Ohaus, ±2 g) and 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 (Renner and Davis 2000). From the end of the courtship period until the end of the guard stage, these nests were observed from a distance every 2 h at worst and continuously at best to monitor copulation behaviors, laying, and foraging trip duration. Adult sex determination was carried out by a combination of parameters including cloacal inspection and copulation behavior and confirmed by examination of the incubation routine (Taylor 1962; Kerry et al. 1993). Adults were weighed a second time 40–45 days after laying when chicks were 7–10 days, while leaving the colony for a foraging trip.

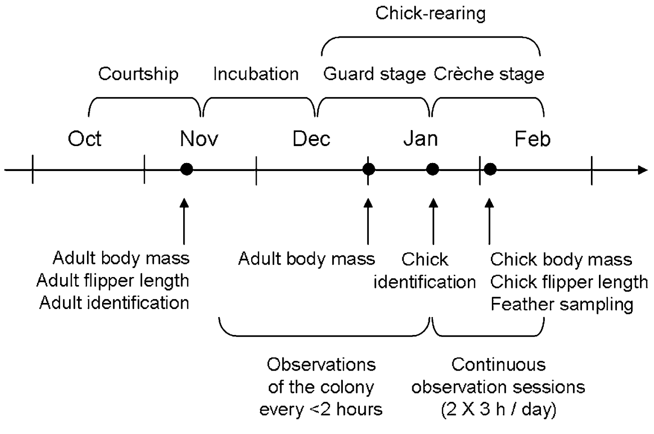

Figure 1
Breeding cycle of Adélie penguins (*Pygoscelis adeliae*) at Dumont d'Urville and study protocol.

During the crèche stage, it was impossible to obtain foraging trip durations by checking visually the presence of parents because they returned sporadically to the colony. To overcome this problem, the chicks were individually identified at the end of the guard stage with colored fish tags (FloyTag, Seattle, WA.) subcutaneously anchored in the neck. Each fish tag had a unique color code easily distinguishable from a distance. The colony was observed ad libitum, continuously with 8 × 20 binoculars from a blind overhanging the subcolony, about 20 m apart, and every parental feeding was noted. Observation sessions lasted 3 h every morning (0800–1100 h) and 3 h every afternoon (1500–1800 h) all along the crèche stage.

The 32 chicks were weighed on the colony with a spring balance (Salter, ±20 g) and their left flipper measured with a ruler (±1 mm) when they reached their maximum weight at 43–45 days (Ainley and Schlatter 1972). At the same time, 2 or 3 feathers were collected and stored at −20 °C for subsequent genetic sex determination (Figure 1).

In 2008–2009, the presence on the colony of formerly studied parents was checked with a manual antenna able to detect the subcutaneous transponder, during the courtship and the incubation periods.

Molecular sexing

Sex determination was carried out from an adapted protocol described by Kahn et al. (1998) and Ellegren (1996). DNA was extracted from feathers according to the method used by Sambrook et al. (1989). Polymerase chain reaction–based sexing was performed using the 1237L/1272H primer pair (Kahn et al. 1998).

Data analysis

We used flipper length as a body size indicator (De Leon et al. 1998; Minguez et al. 1998). A dimorphism index (DI; Storer 1966) was calculated for adults and chicks as: DI = (mean of females − mean of males)/[(mean of females + mean of males)/2] in which a negative result indicates that males are larger. As body mass was linearly related to wing length in adults (courtship: $F = 16.74$, $P < 0.001$; guard stage: $F = 28.05$, $P < 0.001$) and in chicks ($F = 9.77$, $P = 0.004$), we derived a body condition index from the residuals of a linear regression between the body mass and the flipper length (Green 2001; Benson et al. 2003; Schulte-Hostedde et al. 2005).

In adult penguins, flipper does not vary with time (Minguez et al. 1998) so that we were able to compare flipper length between chicks and adults and between males and females simultaneously. For this, we used a general linear model with the sex of the individual, the age class (chick or adult), and their interaction as fixed factors. In contrast, penguin body mass is highly variable according to the breeding stage (Vleck et al. 1999). For this reason, body mass analyses were compared in chicks and in adults independently. In chicks, sexual dimorphism for body mass was analyzed with a Student's *t*-test, whereas in adults, we used a general linear model with the sex of the adult, the sex of the chick, and their interaction as fixed factors (the same test was also used for adult flipper length). Changes in adult body mass were analyzed with a general linear mixed model with the number of the weighing (courtship and guard stage) as the repeated factor. A generalized linear model with a gamma distribution was used to compare foraging trip duration between groups. Because each individual did not perform the same number of foraging trips, we

Table 1

Sexual dimorphism for body mass and flipper length in Adélie penguin adults ($n = 18$) and chicks ($n = 32$)

		Male	Female	DI
Body mass (kg)	Adult	5.15 ± 0.11	4.49 ± 0.12	−13.71
	Chick	4.28 ± 0.14	3.89 ± 0.11	−9.55
Flipper length (mm)	Adult	198 ± 2	189 ± 2	−4.65
	Chick	190 ± 2	189 ± 2	−0.53

Results are presented as means ± standard error. DI = (mean of females − mean of males)/[(mean of females + mean of males)/2]. A negative result indicates that males are larger.

divided the guard stage into 3 substages (early, middle, and late), each of which comprising a third of the total number of foraging trips performed by an individual. A generalized linear model with a Poisson distribution was also used in the case of count data (number of feeding events during the crèche stage). Finally, resight rates were compared between groups using Fisher's exact tests. When necessary, multiple comparisons were undertaken using the post hoc Bonferroni test.

All analyses were conducted using SPSS 16.02 (SPSS Inc., Chicago, IL). Results are expressed as means ± standard error and significance level was set at $\alpha = 0.05$.

RESULTS

Sexual dimorphism in adults and chicks

Among the 32 pairs which reared only 1 chick between hatching and fledging, 14 had a male chick and 18 had a female chick.

Male adults were 0.7 kg heavier than female adults during the courtship period ($F = 16.84$, $P < 0.001$), and male chicks were 0.4 kg heavier than female chicks ($t_{27} = 2.16$, $P = 0.04$; Table 1). The age class and the sex of the individual affected flipper length ($F = 4.17$, $P = 0.04$): The flipper was 9 mm longer in male adults than in female adults ($P < 0.001$), but the flipper of male chicks was as long as the flipper of female chicks ($P = 0.56$). The flipper of female adults and that of female chicks were the same size ($P = 0.88$), whereas the flipper of male chicks was significantly smaller than the flipper of male adults ($P = 0.008$). Sexual dimorphism was more pronounced in adults: The chick DI for body mass represented 75% of the adult DI, and the chick DI for wing length represented 23% of the adult DI (Table 1).

During the crèche stage, male chicks were in a better condition than female chicks (body mass/flipper length residuals: 195.7 ± 4.5 g and −152.2 ± 4.6 g, respectively; $t_{28} = 2.15$, $P = 0.04$).

The sex of the chick was not related to the adult initial body mass ($F = 0.92$, $P = 0.35$), the adult flipper length ($F = 0.73$, $P = 0.40$; Table 2), and the adult initial body condition ($F = 0.32$, $P = 0.58$).

Breeding decisions from adults

In total, we analyzed 394 foraging trips: 199 performed by male adults and 195 performed by female adults. Foraging trip duration was 0.12 days (9%) shorter in males than in females (Wald's $\chi^2 = 15.02$, degrees of freedom (df) = 1, $P < 0.001$; Figure 2a). The sex of the chick also modulated the duration of the foraging trips performed by parents (Wald's $\chi^2 = 5.78$, df = 1, $P = 0.02$): Female adults rearing a female chick performed 0.15 days (11%) longer foraging trips than female adults rearing a male chick ($P = 0.02$). Female adults with a female chick also performed longer foraging trips than males, whatever the sex of the chick (all $P < 0.01$, Figure 2b).

The substages of the guard stage also influenced foraging trip duration (Wald's $\chi^2 = 29.13$, df = 6, $P < 0.001$). In the early substage, foraging trips performed by females rearing a female chick were 0.38 days (24%) longer than those performed by female adults rearing a male chick ($P < 0.01$) and longer than those performed by male adults (female chick: $P < 0.001$; male chick: $P = 0.01$). The duration of the foraging trips performed by female adults rearing a female chick decreased from 1.60 ± 0.10 days to 1.06 ± 0.04 days between the early and the late substages ($P < 0.01$). Females rearing a male chick performed foraging trips as long in the early substage (1.21 ± 0.04 days) as in the middle substage (1.36 ± 0.04 days, $P = 0.8$) but the foraging trip duration decreased in the late substage (1.09 ± 0.06 days, $P = 0.03$). Foraging trip duration performed by males rearing a male chick was constant along the guard stage (~1.2 days, all $P > 0.05$) and foraging trips performed by males rearing a female chick decreased only between the middle (1.33 ± 0.06 days) and the late (1.13 ± 0.06 days) substages ($P = 0.04$; Figure 2c).

During the crèche stage, male adults fed their chicks more than female adults although not significantly (5.25 ± 0.58 and 3.83 ± 0.49 feeding events, respectively; Wald's $\chi^2 = 3.50$, df = 1, $P = 0.06$), and the sex of the chick did not influence the number of feeding events by male and female adults (Wald's $\chi^2 = 0.11$, df = 1, $P = 0.74$; Table 2).

Adult body mass, body condition, and resight rate

Between the courtship period and the guard stage, body mass decreased similarly in parents (males or females) rearing a male chick and parents rearing a female chick ($F_{3,\ 27} = 1.14$, $P = 0.35$). In terms of percentage, male and female adults lost the same amount of body mass (10.21 ± 1.71%

Table 2

Characteristics of Adélie penguin parents classified according to the sex of the adults and the sex of the chicks

	Male adult ($n = 18$)		Female adult ($n = 18$)	
	Male chick	Female chick	Male chick	Female chick
Flipper length (mm)	197 ± 2	197 ± 3	191 ± 2	187 ± 3
Body mass during courtship (kg)	5.10 ± 0.17	5.21 ± 0.14	4.59 ± 0.19	4.39 ± 0.14
Body mass during the guard stage (kg)	4.61 ± 0.16	4.63 ± 0.11	4.33 ± 0.16	4.04 ± 0.11
Body mass loss (%)	9.44 ± 2.65	10.98 ± 2.16	5.42 ± 2.90	8.98 ± 2.45
Foraging trip duration in the guard stage (days)	1.21 ± 0.03	1.15 ± 0.04	1.23 ± 0.03	1.38 ± 0.05
Number of feeding events during the crèche stage	5.50 ± 0.96	5.00 ± 0.65	3.83 ± 0.80	3.83 ± 0.57
Resight rate in the next breeding season (%)	100	100	100	92

Results are presented as means ± standard error.

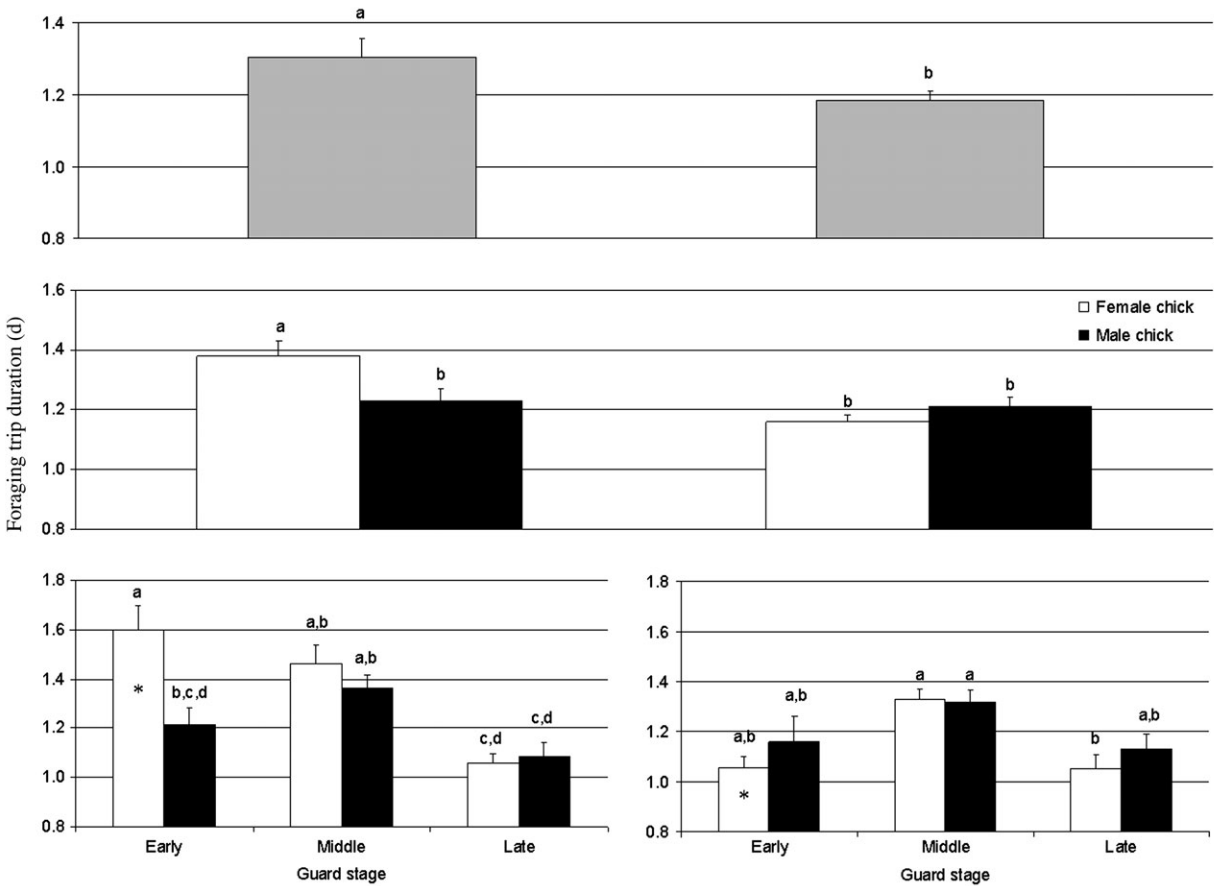

Figure 2

Foraging trip duration during (a) the guard stage in female and male adults; (b) according to the sex of the chick; (c) and in the early, the middle, and the late substages of the guard stage. Results are means ± standard error. Different letters indicate differences between substages and the chick sex for each parent. Asterisk indicates a significant difference between the male and female parents.

and 7.20 ± 1.90%, respectively; $F = 1.39$, $P = 0.25$) and this was not affected by the sex of the chick ($F = 1.55$, $P = 0.70$; Table 2). During the guard stage, the body condition of male and female adults was equivalent (body mass/flipper length residuals: 70.1 ± 79.4 g and −60.0 ± 78.2 g, respectively $F = 1.37$, $P = 0.25$) and the sex of the chick did not influence parental body condition neither in male adults nor in female adults ($F = 10.91$, $P = 0.35$).

Out of the 36 birds electronically identified in 2007–2008, 35 were resighted nesting in the colony during the subsequent breeding season. There were no differences in the resight rates of male or female parents rearing a male or a female chick 1 year before (Fisher's exact tests, all $P > 0.05$; Table 2).

DISCUSSION

In this study, sexual dimorphism has been described for the first time at the chick stage in penguins and we showed that parental foraging decisions were regulated by the sex of the young in female adults.

In chicks, the flipper length of female and male chicks was similar and was the size of the flipper of female adults. This indicates that female chicks had finished their statural growth, whereas male chicks had not reached their full adult body size before fledging. This suggests that parents sustained the whole cost associated with the statural growth of female chicks, whereas male chicks will have to sustain by themselves the remaining cost while fledged. For this, male chicks may be helped by their better body condition (compared with female chicks) at the end of the crèche stage.

Chick sexual dimorphism for body mass was close to sexual dimorphism observed in adults. Culik (1994) reported that a chick with a 3500 g body mass needs about 28.8 kg of food during its first 45 days. In our study, male chicks were about 400 g heavier than female chicks suggesting that male chicks would require 3.3 kg (11%) of food more than female chicks. Parents did not deduct this additional cost from their own reserves because they did not lose mass at a higher rate when rearing a male chick. This suggests that parents rearing a male chick sustained a higher effort at sea by catching more prey than parents rearing a female chick. In the case of poor resource availability, it is therefore expected that male chicks would be more susceptible to die from starvation, which could potentially lead to a female-biased sex ratio at fledging (Stamps 1990).

As previously described (Clarke et al. 1998), female adults performed longer foraging trips than male adults during the guard stage. Our results showed that this sex-specific foraging strategy was due to a change in the foraging decisions by female adults rearing a female chick during the early guard stage. As expected by the lower interannual survival probability reported in female Adélie penguins (Ainley and DeMaster 1980; Dugger et al. 2006), female adults were more likely to vary their level of parental investment. However, the difference in the survival of male and female adults is not sufficient to explain why only females modulate their foraging effort according to the sex of the young. In the wandering albatross

(*Diomedea exulans*, Weimerskirch et al. 2000) and in the common murre (*Uria aalge*, Cameron-MacMillan et al. 2007), both parents modify their provisioning behavior according to the sex of the young, whereas in these species, annual survival rate follow the same trend than that observed in Adélie penguins (Sydeman 1993; Nel et al. 2003). Moreover, we expected female adults rearing a female chick to acquire benefits from this situation, such as a lower body mass loss resulting in a better condition than that of female adults rearing a male chick. Nevertheless, this was not observed as the sex of the chick did not affect body condition or interannual survival of female adults.

As suggested by Clarke et al. (1998), the most plausible benefit seems to be a reduction of intraspecific competition between male and female adults. In early summer, krill availability is low (Siegel 2000) and is mainly constituted by individuals of low energetic density (Clarke 1980; Nicol 2006). Krill energy density increases when individuals and especially females become sexually mature. In Dumont d'Urville Sea, krill reproductive cycle begins late in summer, in late December–January (Spiridonov 1995). This suggests that between hatching (mid-December) and the end of December, that is, the early guard stage, adults rely on limited, poor resources. Intersexual competition may thus be the highest at this time of the breeding cycle and females with enough flexibility (i.e., with a female chick) may have to modify their foraging behavior by increasing foraging trip duration.

The difference observed in the behavior of female adults according to the sex of the chick progressively disappeared during the guard stage and at the end of the breeding cycle (middle and late guard stage and crèche stage), female adults behaved similarly toward male and female chicks. Because resource availability became greater and energetically more valuable at the end of the breeding cycle (Clarke 1980; Nicol 2006), intraspecific competition is likely to be reduced between male and female adults. Concurrently, growing chicks require more food (Culik 1994) thus obliging the parents to perform shorter foraging trips. Though not observed in male adults rearing a male chick, this trend was found from the early to the late guard stage in female adults rearing a female chick and from the middle to the late guard stage in female adults rearing a male chick and in male adults rearing a female chick.

In the present study, we were able to provide new insights in the understanding of the regulation of parental investment in long-lived birds according to the sex of the young. However, our findings raise new questions, especially about the recognition of the sex of the young by parents. As already demonstrated in other bird species (Teather 1992; Von Engelhardt et al. 2006), male and female chicks may beg for food differently, and although this has not been yet demonstrated in Adélie penguins, female adults may respond to the level of chick solicitations by adjusting foraging trip duration. Because female adults can perform longer foraging trips at the beginning of the guard stage when rearing female chicks but not male chicks, this suggests that chick requirements differ at this stage between male and female chicks. To elucidate this, further studies examining the growth rates of male and female chicks and the diet of adults according to the sex of the offspring are required.

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