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Original Article

Everybody needs somebody: unequal parental effort in little penguins

Claire Saraux,[a,b,c] **André Chiaradia,**[d] **Yvon Le Maho,**[a,b] **and Yan Ropert-Coudert**[a,b]
[a]Université de Strasbourg, Institut Pluridisciplinaire Hubert Curien, 23 rue Becquerel, 67087 Strasbourg, France, [b]Centre National de la Recherche Scientifique, Unité Mixte de Recherche 7178, 23 rue Becquerel, 67087 Strasbourg, France, [c]AgroParisTech ENGREF, 19 avenue du Maine, F 75732 Paris, France, and [d]Research Department, Phillip Island Nature Park, PO Box 97, Cowes, VIC 3922, Australia

According to life-history theory, individuals optimize their decisions in order to maximize their fitness. This raises a conflict between parents, which need to cooperate to ensure the propagation of their genes but at the same time need to minimize the associated costs. Trading-off between benefits and costs of a reproduction is one of the major forces driving demographic trends and has shaped several different parental care strategies. Using little penguins (*Eudyptula minor*) as a model, we investigated whether individuals of a pair provide equal parental effort when raising offspring and whether their behavior was consistent over 8 years of contrasting resource availability. Using an automated identification system, we found that 72% of little penguin pairs exhibited unforced (i.e., that did not result from desertion of 1 parent) unequal partnership through the postguard stage. This proportion was lower in favorable years. Although being an equal pair appeared to be a better strategy, it was nonetheless the least often observed. Individuals that contributed less than their partner were not less experienced (measured by age), and gender did not explain differences between partners. Furthermore, birds that contributed little or that contributed a lot tended to be consistent in their level of contribution across years. We suggest that unequal effort during breeding may reflect differences in individual quality, and we encourage future studies on parental care to consider this consistent low and high contributor behavior when investigating differences in pair investment into its offspring. *Key words:* attendance patterns, individual quality, meal size, parental care, reproductive costs, seabirds. *[Behav Ecol 22:837–845 (2011)]*

INTRODUCTION

Maximizing individual fitness has driven evolution to shape mating systems and their strategies of parental care throughout the animal kingdom. From monoparental to biparental care or communal breeding (where several adults of a group take care of all the offspring), a diversity of partnerships can be found amongst animals. Birds are unique among vertebrates in that biparental care is the norm with more than 90% of the species (Lack 1968). In long-lived species that exhibit biparental care, there is a potential conflict between partners where both try to minimize cost of reproduction but must cooperate to breed at the same time (Trivers 1972; Maynard Smith 1977a; Houston et al. 2005). This conflict occurs because each parent will increase its fitness by investing in its offspring but may also risk its own survival at the same time and decrease its chance of breeding in the future (Clutton-Brock 1991). Each parent will thus benefit if the other does more of the work involved in raising the offspring. Life-history theory suggests that in order to maximize its fitness, an individual will invest a specific amount of parental care resulting from the trade-off between benefits and costs associated with raising chicks (Stearns 1989). The solution of this conflict depends on the interactions between parents, the behavior of other animals in the population, and individual differences within sex (Webb et al. 1999; Barta et al. 2002).

Parental investment is defined as "any investment by the parent in an individual offspring that increases the offspring's chance of surviving at the cost of the parent's ability to invest in other offspring" (Trivers 1972), and in the case of birds for instance, includes nest building, incubating eggs, chick rearing, and nest defense. But for many bird species, the chick provisioning phase, that is, the period when chicks cannot feed by themselves and during which the parents deliver meals, is an energetically costly period when crucial decisions between costs and benefits have to be made (Drent and Daan 1980). Most studies on parental care have thus focussed their investigation to this crucial phase of the life cycle.

Parameters such as the age or sex of each partner in a pair could potentially affect parental investment share between parents. Age-related differences in foraging efficiency (e.g., Daunt et al. 2007) could result in parental care differences and consequently in breeding success differences (Lack 1968). Many studies have indeed documented such a lower reproductive success for young birds (reviewed in Saether 1990; Clutton-Brock 1991, see also Komdeur 1996).

However, in most of the studies in which parental investment has been investigated, the division of that investment has been regarded as a "battle of the sexes" (Andersson 1994; Guerra and Drummond 1995; Aho et al. 1997; Weimerskirch et al. 2000; Barlow and Croxall 2002; Lewis et al. 2002, 2005; Velando and Alonso-Alvarez 2003; Markman et al. 2004; Quillfeldt et al. 2004; Hamer et al. 2006). Parental differences in offspring provisioning have been recorded in a number of sexually size-dimorphic species (Aho et al. 1997; Weimerskirch et al. 2000; Velando and Alonso-Alvarez 2003; Lewis et al. 2005) and are usually attributed to the influence of parents' body size on foraging efficiency and competitive ability (Andersson 1994;

Address correspondence to A. Chiaradia. E-mail: achiaradia@penguins.org.au.

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Markman et al. 2004). However, differences between males and females in provisioning behavior may also occur in the absence of sexual size dimorphism (in northern gannets, *Sula bassanus*, Lewis et al. 2002; in Manx shearwaters, *Puffinus puffinus*, Quillfeldt et al. 2004; Hamer et al. 2006). Additionally, whereas males may provide more parental care in some species (e.g., the wandering albatrosses, *Diomedea exulans*, Weimerskirch et al. 2000; or the lesser spotted woodpecker, *Picoides minor*, Witkander et al. 2000), females may be the ones to invest more into offspring in others (such as the willie wagtail, *Rhipidura leucophrys*, Goodey and Lill 1993; the blue-footed booby, *S. nebouxii*, Guerra and Drummond 1995; or the macaroni penguin, *Eudyptes chrysolophus*, Barlow and Croxall 2002).

However, differences in parental care might not solely be explained by a sexual bias, and some species have been shown to equally share parental duties between sexes (sandwich tern, *Thalasseus sandvicensis*, Fasola and Saino 1995). Equal sharing at the species level does not necessarily mean that both parents equally share in each pair but rather that depending on the pairs, it may be either the male or the female that compensate for its partner. Yet, to date, few studies have considered alternatives to sexual bias in order to explain differences in investment into parental care. Because breeding costs are probably not the same nor have the same impact on survival or further breeding attempts in different birds, parental care may be dependent of individual quality. In house sparrows, *Passer domesticus*, for instance, Schwagmeyer and Mock (2003) showed that good parents exhibit consistency in provisioning behavior across breeding events. These authors suggested that variation in parental care could be attributed to differences in individual quality (the so-called "parental quality differences" hypothesis, Schwagmeyer and Mock 2003).

A substantial number of studies on parental care have been experimental, that is, where 1 partner was handicapped, and the performances of the 2 members of the pair were evaluated (cf. Beaulieu et al. 2009 and references therein). Furthermore, most of these studies were conducted on a yearly time basis, and very few studies have been carried out on multiple breeding seasons (only 4 studies on the 16 previously cited). Except for Schwagmeyer and Mock (2003), none of them investigated how parental care might change over years. Yet, such information is necessary to understand how the environment may influence parental decisions, as well as to test for the parental quality differences' hypothesis. Environmental variability and seasonal fluctuations might lead to different breeding costs endured by the parents and thus to different parental care strategies depending on the breeding season.

In this study, we investigated parental investment (parental effort and costs of this effort) through differences between partners (without limiting our study to a sex effect) in little penguins, *Eudyptula minor*, over multiple breeding seasons and in natural conditions. Little penguins are long-lived seabirds, showing small sexual size dimorphism (Arnould et al. 2004). Their foraging ability is probably more constrained during the breeding season than most other seabirds, as they have one of the shortest foraging ranges (<20 km during chick rearing, Collins et al. 1999), and forage in an environment with very unpredictable food supply (Gales and Pemberton 1990; Chiaradia et al. 2010). These features make them a useful model to study differences in individual quality at critical times when they are raising their offspring. During the postguard phase, chicks are left unattended by their parents, and both parents are foraging at sea. Parents attendance and investment thus become independent of each other (Daniel et al. 2007), unlike their attendance pattern at other stages (Chiaradia and Kerry 1999). Therefore, foraging differences should be more apparent at individual level.

Here, parental effort was investigated during postguard by examining if individual contribution in parental care was more, less, or equal to its partner. We measured both the frequency of visits and meal size brought back to the chicks. Using long-term continuous data, we further examined whether this behavior was consistent over 8 years of contrasting environmental conditions, that is, whether there is any intrinsic individual quality associated with differential parental investment. We also investigated at the population level how parental strategies were determined by resource availability (i.e., in different years, as inferred by breeding success, Chiaradia and Nisbet 2006) and the success of previous breeding stages. We finally examined benefits of the different parental strategies through the reproductive outcomes (fledging success and chick growth) and their costs (impacts on return rates and local survival).

MATERIALS AND METHODS

Monitoring and field protocol

Little penguins were studied at the Summerland Peninsula on the western end of Phillip Island, Victoria, Australia (lat 38°15′S, long 143°30′E), where about 14 000 pairs of little penguins nest (Cullen et al. 2009). This study was conducted during 8 breeding seasons from 2001 to 2008, where 2001 refers, for instance, to the breeding season 2001–2002. The study site (see details in Chiaradia and Kerry 1999) is a part of a colony containing 100 artificial burrows (wooden nest boxes) of which 50–86 boxes were occupied in each year (see Table 1). All adults nesting in these burrows for more than 2 years were included in the study. They had been previously marked with electronic transponder tags (Allflex Australia Pty Ltd, Capalaba, Queensland, Australia), subcutaneously implanted between the scapulae, mostly as chicks, and sexed by bill measurements in subsequent years, when first found in the colony as adults. The bill-size discriminant has been calibrated for birds of Phillip Island with an accuracy of 91% (see Arnould et al. 2004). Furthermore, as we investigated pairs, sex ID was double checked by male–female association, meaning that any chance of error would occur at a probability of less than 1%. About 35 % of individuals were marked as adults and had their age estimated by adding 3 years at the marking date (Daniel et al. 2007), based on the average age of first breeding of 2–3 year olds (Nisbet and Dann 2009). Because little penguins show a high site fidelity (Bull 2000), this adult age correction should not have underestimated their ages as nesting site was checked for unmarked birds at regular intervals since 1978 (Dann and Cullen 1990). To make sure this method did not introduce a bias, whenever we investigated for an eventual effect of age, we ran our models over 2 datasets including either all birds or only those marked as chicks. Our analyses yielded similar results and only those on all birds are presented below.

Table 1

Summary of annual data on breeding success and mean body mass of little penguins from 2001 to 2008 at Phillip Island

	Numder of pairs observed	Mean fledgling number per pair	Male body mass (g)	Female body mass (g)
2001	58	0.52 ± 0.07	1085 ± 7	969 ± 6
2002	50	1.58 ± 0.07	1119 ± 5	1034 ± 4
2003	50	1.18 ± 0.08	1149 ± 4	1050 ± 4
2004	66	0.71 ± 0.06	1094 ± 5	993 ± 5
2005	75	1.03 ± 0.07	1146 ± 6	1028 ± 5
2006	63	0.82 ± 0.08	1125 ± 7	1012 ± 7
2007	52	1.23 ± 0.09	1127 ± 6	1026 ± 5
2008	86	0.52 ± 0.06	1137 ± 5	999 ± 4

Individual attendance was recorded continuously using an automatic penguin monitoring system (APMS) designed by the Australian Antarctic Division (Kerry et al. 1993). Penguins marked with a transponder, that is all penguins in the study site, were detected when they crossed the APMS platform on their way in and out the colony. The APMS automatically recorded the transponder number, body mass (to the nearest gram), date, time, and direction of each arriving and departing penguin (see details in Robinson et al. 2005).

Nests were checked 3 times a week using a purpose-built transponder reader. This allowed us to determine the exact breeding timing (laying, hatching, and fledging dates as well as end of chick guard stage). Chicks were weighted 3 times a week to the nearest 1 g (in a bucket on a digital weighing scale) during postguard stage, when both parents were foraging during the day and therefore absent from the nest. Body mass was used to examine chick growth using peak growth mass and fledging mass as variables (Chiaradia and Nisbet 2006).

Breeding success

Overall, breeding success was measured as the number of chicks fledged (chicks which were fully feathered—ages $>$ 45 days—when last encountered were considered fledged) per female, hatching success as the number of eggs hatched per eggs laid, guard success as the number of chicks reaching postguard stage per eggs hatched, and postguard success as the number of fledged chicks per chicks beginning postguard. We also used an index of success before postguard, as a combination of hatching and guard success: Number of chicks reaching postguard on number of eggs laid, hereafter referred to as hatching/guard success index. Both postguard success and hatching/guard success index were divided into 3 categories: low (success < 0.6), average ($0.6 \leq$ success $<$ 0.8), and high success (success ≥ 0.8).

Adult body mass and meal size

We concentrated our analyses of body masses on the first 40 days of postguard (the mean duration of postguard was 43 days) because the number of mass records dropped thereafter by almost 50% as the birds reduced progressively their returning to the colony.

Meal size in this study is defined as the amount of food (in grams) brought ashore by an adult to its chicks. We used the body mass difference between a bird entering and leaving the colony to calculate meal size. As parents always arrive after sunset and depart before sunrise, staying only a few hours at night in the colony to feed the chicks during postguard (Daniel et al. 2007), mass difference was a reasonable proxy of the amount of food brought to chicks. In fact, meal sizes found in this study (mean 258 g) were consistent with previous findings measured by directly weighing chicks before and after meals (see Figure 4 in Chiaradia and Nisbet 2006).

Number of foraging trips in the pairs

Arrival and departure data from the APMS were also used to calculate the number and duration (in days) of foraging trips during the postguard stage. The number of foraging trips was used as a proxy of parental effort. We calculated the number of foraging trips during the postguard for each breeding individual from 2001 to 2008. For each pair, we defined 2 types of partnerships: 1) equal pairs, that is, pairs that made equal number of trips during postguard. 2) unequal pairs, that is, parents that made unequal number of trips, that is, 1 parent made 3 or more trips than its partner (a difference of 3 trips representing on average 14% more trips by 1 partner). This 3-trip cutoff has been selected as a result of the distribution of the difference in number of trips. In each unequal pair, we then examined which parent made more or fewer trips than its partner. To simplify, we refer to them here as high and low contributors, respectively. To investigate if an unequal partnership was due to desertion of either one of the partners at one stage of postguard, we tested whether the difference in the number of trips achieved by the 2 partners was constant over postguard. Therefore, we divided postguard into 10-days period and computed a mixed model with period as explanatory variable.

It is important to note as well that we could not study whether differences between partners resulted from an individual contributing a lot or from its partner contributing much less. Environmental conditions vary both from year to year and within a season. Thus, the absolute number of trips a bird performed could neither be compared from 1 year to another nor with the number of trips of other birds. Only partners would endure similar conditions and be comparable.

Statistics

All statistics were computed using R 2.8.0 statistical program (R Development Core Team 2008). Data were longitudinal because individual penguins were recorded over multiple breeding seasons. Data were modeled using a maximum of likelihood mixed model approach (lme4 package, Bates and Maechler 2009). Generalized linear mixed models were computed with the individual or the pair, that is, the individual and the partner (when looking at data originating from the pair and not the individual, such as breeding success) as random effects, enabling us to account for repeated measures, because birds were tracked over multiple breeding seasons. Whenever no effect of the years was investigated, year was added as a random effect. Fitted models were generalized linear ones with either Poisson distribution for body mass and chick growth analyses or binomial distribution for breeding success.

Models were used for 2 different purposes:

1. To investigate the influence of different parameters (e.g., age, sex) on a variable, such as the number of trips or the meal size. Fitted models were thus selected through a stepwise procedure by using Akaike's Information Criterion (AIC). The explained deviance of the model (in relation to the null model, that is, the relative variability explained by the model compared with the entire variability in the dataset) and P values were then used to conclude as to the effect of the parameters.
2. In order to assess differences between groups (e.g., equal pairs vs. unequal pairs or high vs. low contributors). Mixed models were then computed, and P values alone were used to conclude if there were significant differences between groups.

For cross-sectional data (1 data per bird, comparison in between seasons or comparisons of means over all years studied), independence of the data was not violated and so nonparametric tests could be used. When homoscedasticity between groups was ascertained (but not normality), Wilcoxon's rank summed test was used. Variables were considered significant for $P < 0.05$, and Bonferroni's correction was applied whenever multiple comparisons were tested (differences were thus considered significant for $P < \frac{0.05}{n}$ with n the number of comparisons done).

RESULTS

Equal versus unequal number of foraging trips between partners

We grouped 8 years of foraging trips to examine whether there were differences in the number of trips completed

Table 2

Parameters used to measure differences between equal and unequal pairs of little penguins over 8 years

	Equal pairs	Unequal pairs	df	Z values	P values
Proportions	28% (169)	72% (433)	—	—	—
Total number of postguard trips	44 ± 2 (170)	45 ± 1 (432)	202	0.7	0.51
Postguard duration	**41 ± 1(134)**	**45 ± 1 (194)**	25	−4.1	<0.001
Age	8.3 ± 0.3 (169)	8.5 ± 0.2 (424)	395	−1.3	0.20
Breeding success	1.18 ± 0.07 (169)	1.27 ± 0.03 (432)	98	−0.6	0.32
Chick peak mass	**1141 ± 12 (96)**	**1093 ± 9 (265)**	359	12.2	<0.001
Chick fledging mass	**986 ± 19 (94)**	**942 ± 10 (265)**	357	12.1	<0.001

Values are mean ± standard error. Sample size into brackets. df stands for degree of freedom of the mixed model. Significant results are in bold.

between partners during postguard stage in relation to sex, age, and pair bond. Overall, 72 % of pairs exhibited an unequal partnership, and we found that 1 parent made on average 7 more trips than its partner (standard error = 0.2, $n = 570$ pairs × years), that is, as much as around 30% trips more. These percentage and mean number of trips were not affected by brood size at the beginning of postguard (mean difference in number of trips between partners, 6.4 ± 0.3 vs. 6.5 ± 0.6 for 1 and 2 chicks, respectively). Unequal number of trips was not related to sex (22 ± 1 trips in average for females and 23 ± 1 for males, $n = 340$ for each group, mixed model: degrees of freedom [df] = 466, $n = 680$ trips for 212 individuals, $Z = -0.14$, $P = 0.89$). Importantly, there was no difference in the total number of trips between equal and unequal pairs ($P = 0.51$, Table 2), but postguard stage lasted longer (4 days on average) for unequal pairs than it did for equal pairs ($P < 0.001$, Table 2).

Between years, the proportion of unequal pairs was highly variable (ranging from 54% in 2002 to 88% in 2006; Table 3), as was the mean difference in number of trips (ranging from 4.8 to 8.8). The mean difference in number of trips and the proportion of unequal pairs were highly correlated ($P = 0.003$, rho = 0.90), and we thus only present results on proportion. We separated years into 3 categories of low (prop ≤ 0.6), average (0.6 < prop ≤ 0.7), and high (prop > 0.7) proportions of unequal pairs. These proportions were correlated to what happened both before postguard (hatching/guard success index) and during postguard (postguard success): The proportion of unequal pairs was low when both measurements of success (postguard and hatching/guard success index) were high (year 2002, Table 3), whereas high levels of unequal pairs appeared when either postguard or hatching/guard success indexes were low, except in 2008 (Table 3). We thus investigated how the minimum of these 2 measures of success affected the proportion of equal and unequal pairs, so that a low level from one of the successes would be taken into account. This minimum explained partly the proportion of equal and unequal pairs (linear regression: adjusted $R^2 = 0.39$, df = 7, $t = -2.3$, $P = 0.05$). The year 2008 presented a much higher Cook's distance (more than twice the following one) and was thus considered as an outlier. The same regression was thus computed excluding 2008, and the minimum explained 79% of the variation in the proportion (adjusted $R^2 = 0.79$, df = 6, $t = -4.9$, $P = 0.004$).

In addition, the difference in the number of trips achieved by partners was constant over the whole postguard. The model with period as explanatory variable was not better than the null model (ΔAIC < 2 and less than 1% of the deviance was explained). Finally, there was no age difference between individuals of equal and unequal pairs (mean of 8 years for both groups, $P = 0.20$, Table 2).

Unequal parental care: a consistent behavior at the individual level

Unequal pairs were when one individual (the high contributor) made more foraging trips during postguard than its partner (the low contributor). The age difference between the 2 partners did not explain the high or low contributor status of the birds: high contributing birds could be either younger or older than their low contributing partner (mixed model: df= 350, $n = 542$ for 192 birds, $Z = -1.24$, $P = 0.21$). Furthermore, high and low contributors exhibited similar return rates after 1 year (i.e., resighted in the following season, 0.81 ± 0.03 vs. 0.79 ± 0.02 for high and low contributors, respectively; mixed model: df = 281, $n = 462$ for 180 birds, $Z = 0.47$, $P = 0.64$) and similar local survival (which is the probability that a particular individual occupying a site during one breeding season survives and settles in the same site during one of the next breeding seasons, i.e., resighted in any season after, 0.87 ± 0.02 vs. 0.84 ± 0.02 for high and low contributors, respectively; mixed model: df = 281, $n = 462$ for 180 birds, $Z = 0.83$, $P = 0.41$).

A total of 69% of little penguins (135 of 197 birds) in unequal partnership group were consistently high and low contributors over the years, either always making more trips than their partners or always making fewer trips than their partners (Figure 1). The remaining 31% (62 birds) alternated between being high and low contributing partners over the years. Within the alternating parent group, a total of 21 of 62 were recorded with an equal number of years as high and low contributor. Altogether these 62 birds changed 108 times from being low to high contributors, or vice versa, and in approximately 50% of these changes (53 cases of 108), they stayed with the same partner. When examining whether penguins divorced or reunited with previous partners, there was no difference in pair bond between alternating birds and

Table 3

Proportion of unequal pairs in little penguins depending on Hatching/guard success index and postguard success

	Hatching/guard success index	Postguard success	Proportion of unequal pairs
2001	High (0.84)	Low (0.42)	High (0.80)
2002	High (1)	High (0.86)	Low (0.54)
2003	High (0.90)	Average (0.73)	Average (0.67)
2004	Average (0.77)	Low (0.53)	High (0.71)
2005	Low (0.57)	High (0.93)	High (0.76)
2006	Low (0.46)	High (1)	High (0.88)
2007	High (0.98)	Average (0.68)	High (0.71)
2008	Average (0.69)	Low (0.38)	Average (0.67)

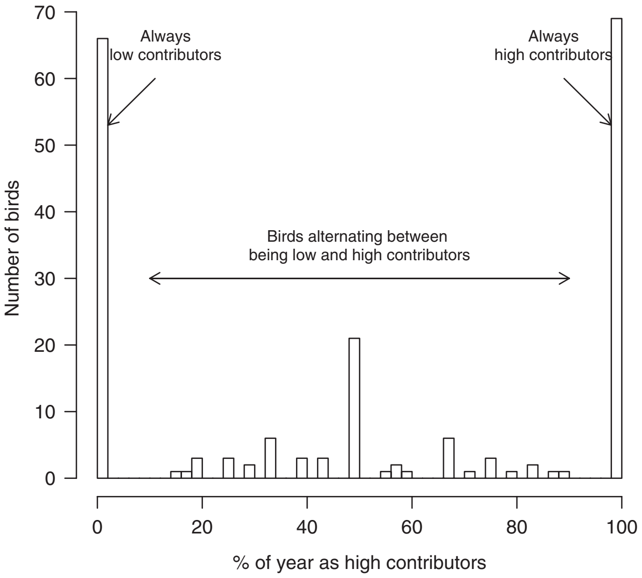

Figure 1
Number of little penguins displaying low or high contribution to their partnership.

consistent ones (Wilcoxon test $P = 0.92$, Table 4). There were also no differences of breeding success between penguins that alternated between being low and high contributor and consistent penguins (one chick fledged per pair in average, $P = 0.37$, Table 4). However, when alternating birds were analyzed separately, they exhibited a much higher breeding success during a year when they changed from high to low or vice versa, than when they kept the same pattern over 2 or more consecutive years (1.33 after a change vs. 0.97 after no change, mixed model: df = 282, $n = 345$ for 62 birds, $Z = 2.95$, $P = 0.003$). Finally, alternating and consistent birds exhibited similar mean differences in the number of trips between partners (6.6 vs. 6.3 trips for consistent and alternating birds, respectively; mixed model: df = 401, $n = 599$ for 197 birds, $Z = 0.57$, $P = 0.56$).

Meal size

Overall, females brought 9% less food to the chicks than males (meal size = 250 ± 2 g vs. 276 ± 3 g, mixed model: df = 6622, $n = 6784$ for 161 individuals, $Z = 2.71$, $P = 0.007$; Figure 2A). However, regardless of sex, high contributors brought back 4% more food than low contributors (meal size = 264 ± 2 g vs. 253 ± 3 g, mixed model: df = 5349, $n = 5496$ for 146 individuals, $Z = 14.8$, $P < 0.001$; Figure 2B). There were no significant differences in the meal size between high contributing females and their low contributing partners (255 ± 3 g for high contributing females and 267 ± 4 g for low contributing males, mixed model: df = 2603, $n = 2701$ for 97 individuals, $Z = 1.53$, $P = 0.13$, Figure 2C). But high contributing males brought 15% more food than their partner (meal size = 284 ± 3 g vs. 242 ± 3 g, mixed model: df = 2690, $n = 2795$ for 104 individuals, $Z = 4.4$, $P < 0.001$, Figure 2D). Finally, meal size was affected by brood size (192.7 ± 8.1 g vs. 219.6 ± 3.4 g, for 1 and 2 chicks, respectively, $P < 0.001$).

Equal versus unequal parents

Equal and unequal pairs had similar postguard success ($P = 0.32$, mixed model with year as a random factor to take into account the fact that the number of equal pairs increased in favorable years, Table 2), and the difference in number of trips between partners had no effect on their success (mixed model: df = 69, $n = 270$ for 105 birds and 95 partners, $Z = 0.084$, $P = 0.93$). However, equal pairs fledged heavier chicks than unequal pairs (45 g difference at fledging and 50 g, i.e., about 5% of their total body mass at peak growth, both $P < 0.001$, Table 2). Furthermore, equal and unequal pairs exhibited similar return rates (resighted in the following year, 0.76 vs. 0.78, respectively, $P = 0.66$) and similar local survivals (resighted in any year, 0.82 vs. 0.85, $P = 0.71$).

In unequal partnerships, there were no differences of postguard success in high contributing male pairs versus low contributing male pairs (mixed model: df = 80, $n = 280$ for 103 birds and 96 partners, $P = 0.95$). However, pairs with high contributing males fledged chicks on average 10 g heavier than pairs with high contributing females (model: df = 334, $n = 336$, $Z = -2.71$, $P = 0.007$).

DISCUSSION

Understanding parental investment is fundamental for discussion on sexual selection and the evolution of mating systems. Here, we examined one important aspect of parental effort, that is, unequal parental care in chick provisioning in a typical biparental care species, the little penguin. Most pairs (72% throughout the whole study) exhibited unequal parental effort, meaning that one individual of the pair contributed more than the other one (7 more trips on average) and that independently of brood size. Such unequal parental care in the chick provisioning period could result either from differences in provisioning effort all along the period or from desertions of one of the 2 partners. According to the parental investment theory, female desertions are not frequent in species where success varies only with postcopulatory investment, a typical situation in birds (Wade and Shuster 2002). Desertions in males occur when the fitness gain, which might accrue to a male from his caring for existing young and incrementing their viability, is much smaller than that obtained from additional mating (Maynard Smith 1977b). Nest desertion nest desertion in little penguins can occur at incubation and during chick guarding, but usually results in early

Table 4
Summary of the breeding activities between little penguins that were displaying consistent and alternating behavior at high or low parental investment (see text for definition)

	Consistent birds	Alternating birds	df	Test statistics	P values
Proportions	69% (135)	31% (62)	—	—	—
Divorce rate	0.38 ± 0.04 (99)	0.35 ± 0.04 (61)	—	$W = 2992.5$*	0.92
Breeding success	0.94 ± 0.04 (135)	1.00 ± 0.05 (62)	195	$T = 0.90$**	0.37

*Wilcoxon test. **Student t-test. Values are means ± standard error. Sample size into brackets. df is the degree of freedom from mixed models.

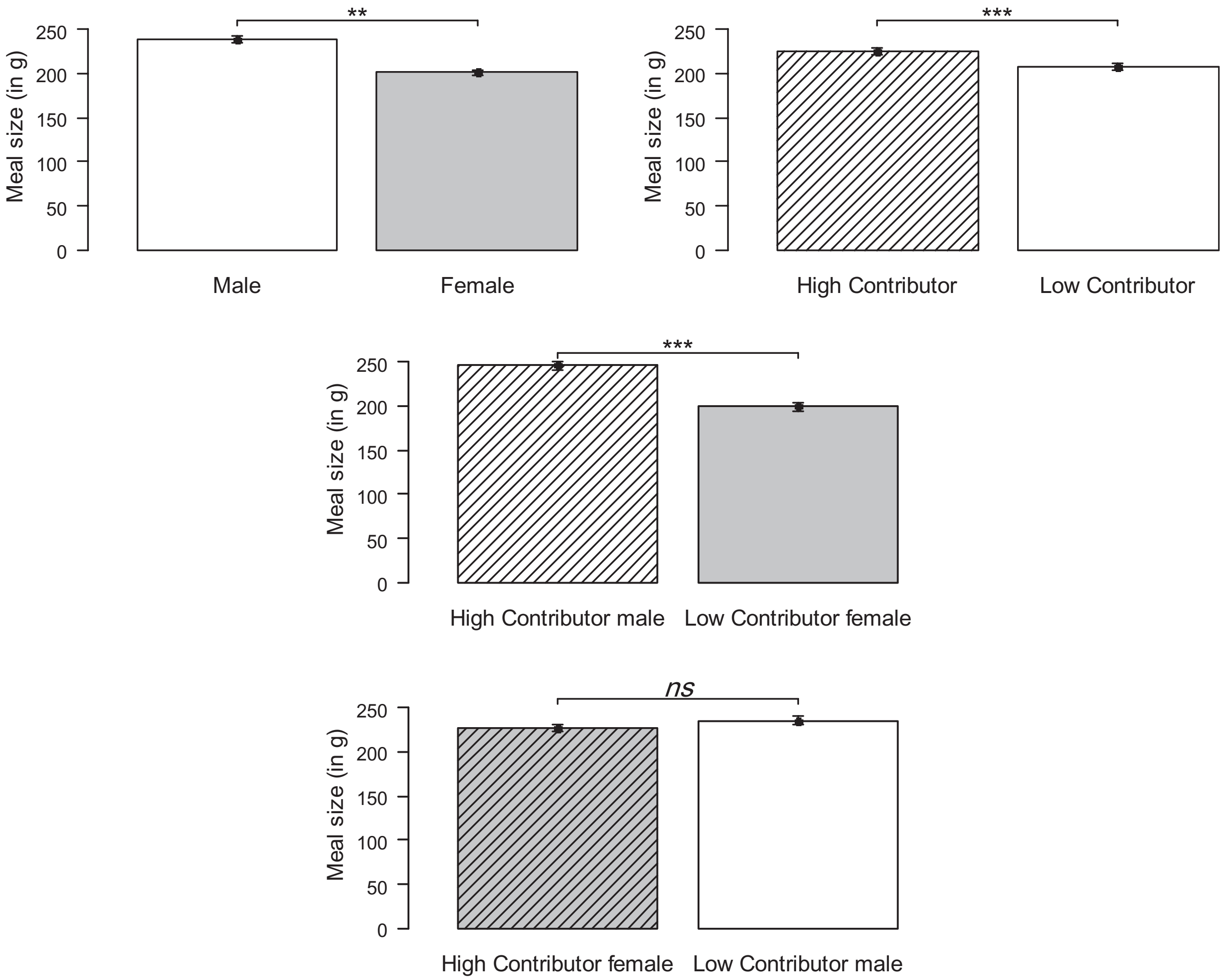

Figure 2
Meal size delivered to chicks inferred from the adult body mass difference between arrival (in) and departure (out) to and from the little penguin–breeding colony during the postguard stage.

breeding failure, as sharing parental care is necessary until the end of the postguard stage (parents alternate during these periods; Chiaradia and Kerry 1999; Numata et al. 2000). Successful parents thus cannot desert their chicks too early in the reproduction. For this reason, we only examined parents with chicks during the postguard stage. A desertion during postguard would usually not allow enough time to additional mating, which very rarely occurs this late in the breeding cycle (Saraux C, Chiaradia A, Ropert-Coudert Y, personal observations) as it would not result into fitness gain. Therefore, desertions were not expected in that stage unless the survival of one parent was at risk. This was confirmed by our data, as no desertions were observed during postguard along our 8 years of study.

Furthermore, meal size is another sensitive parameter to measure parental effort along with the frequency of feeding. Thus, we controlled for this parameter to confirm that penguins which appeared to be high contributors (i.e., higher frequency of visits than its partner) were not doing so at the expense of meal size and indeed contributed more to chick rearing. In general, males fed larger meals to the chicks than females during our 8 years of study. Sex-biased meal size may result from differences in diving behavior as males are able to dive deeper and longer than females (Bethge et al. 1997; Yorke et al. 2004). To avoid the confounding effect of sex and high/low contributor status, we analyzed separately pairs with mothers as the high contributors and pairs with fathers as the high contributors. Pairs with high contributing fathers exhibited a much greater difference between the 2 partners than the basal difference between males and females alone. High contributing males fed meals, which were 15% heavier than their partners, whereas pairs with high contributing females did not exhibit any differences in meal size within the pair. This shows that not only did high contributing males provision their chicks more frequently but also carried more food than did their partners. High contributing females fed their chicks a similar meal size as their mate but did come ashore to feed the chicks more frequently.

Differences in provisioning of offspring are usually attributed to sex dimorphism, foraging efficiency, and intraspecific competition (Andersson 1994; Markman et al. 2004). In little penguins, males are larger than females (Arnould et al. 2004) and breeding and foraging successes change with experience and age (Nisbet and Dann 2009; Zimmer et al. 2011). In this study, however, these patterns did not emerge in relation to unequal care, which was not related to sex as either the male or the female could be the high contributor in the pair (i.e., the parent feeding the chicks more frequently than its partner). Unequal care was not related to age either. Furthermore, not only did individuals show unequal parental effort within a season but further maintained this behavior consistently during subsequent seasons. Because our data encompassed 8 years, parents thus retained their behavior over at least half of their life (Sidhu et al. 2007), suggesting that one individual, regardless of its sex, always tended to make substantially greater effort than its partner toward raising its offspring.

High contributor behavior was not related to an increase in age and breeding experience, rather from an individual-specific characteristic, which does not change over the years. This supports the hypothesis of parental quality differences of Schwagmeyer and Mock (2003), which states that variation in parental care could be attributed to quality differences among individuals. It should be noted that there were exceptions when birds were not consistent on their parental investment over time. Some birds were observed to alternate between being a high and a low contributor across years. These birds did not exhibit a higher divorce rate than consistent birds, which suggests that changes in their investment status were not due to finding of a better partnership. Furthermore, in half of the cases of alternating investment status, birds shifted from high to low contributors without changing partners. These birds could be individuals of similar quality, for which parental care strategies could result from a punctual decision, possibly due to actual body condition at any time during the breeding season (such as in king penguins, Gauthier-Clerc et al. 2001).

Differences in individual quality have been used to explain variation among individuals in different traits (Vaupel et al. 1979; Cam and Monnat 2000). Despite of the widespread interest in this heterogeneity between individuals; “individual quality remains a somewhat elusive concept within ecology” according to Wilson and Nussey (2010) likely due to the complexity of measuring it. Fitness is often perceived as a proxy to individual quality and confusion between the 2 terms frequently occurs. Here, because low contributors are always paired with high contributors and the outcome of a reproduction is the same for both partners of a pair, breeding success of high and low contributors will be the same. Fitness would thus only differ through differences in longevity, which was beyond the scope of this study. However, we showed that there were no differences in return rates and local survival between high and low contributors. If as we suggest here, high contributors are of better quality, we would expect them to be able to sustain higher reproductive costs without affecting their survival and return rates. Thus, our findings suggest that the amount of parental effort is a reflection of parent quality and the amount of energy it could allocate to reproduction without jeopardizing its future breeding prospective. Further, in the context of parental investment theory, birds investing more energy in reproduction should endure higher associated costs and exhibit lower return rates. Here, we found no differences in costs associated to higher parental effort and suggest that the unequal parental care observed results from a difference in parental effort (by-product of individual quality) but not from a difference in parental investment. Yet, consequences of this disproportional investment on parents’ longevity require further investigations. Indeed, costs of one single reproduction could well be not visible immediately on survival but significantly affect longevity when added on multiple reproductive years. In order to test whether unequal parental care is a by-product of individual quality, individual quality should not be measured by fitness directly but as a result of differences in phenotype (Wilson and Nussey 2010). Further studies may for instance consider investigating individual quality through other parameters which can provide a better index of quality which does not rely on life-history traits. For instance, the initial length and shortening rate of telomeres have been shown to affect some of the fitness components in different species (Monaghan and Haussmann 2006; Bize et al. 2009).

Strategies of chick provisioning result from the balance between benefits of raising chicks and associated costs (Stearns 1989). We therefore investigated how different strategies between equal and unequal pairs would impact breeding success and ultimately individual fitness. Equal and unequal pairs made the same total number of trips, when both partners were analyzed together. Postguard success was neither affected by the behavior of the pairs (i.e., equal or unequal) nor by the difference in the number of trips achieved by parents, which is similar to findings of Takahashi et al. (2003) on Adélie penguins *Pygoscelis adeliae*. However, breeding success is not the only important parameter to be considered. About 75% of the variance in the number of recruits in breeding bird populations is not accounted for by differences in number of fledglings and results from the period between fledging and sexual maturity (median $r^2 = 0.25$ for studies reviewed in Newton 1989). Environmental pressures experienced during the growth period may affect individual phenotypes and future survival expectancies (especially first-year survival). Some fledging traits such as body size or condition have indeed been found to be correlated with postfledging survival (Korpimäki and Lagerström 1988; Owen and Black 1989; Harris et al. 1991; Schmutz 1993). Although breeding success is a composite of several confounding factors such as incubation failure and predation, chick growth and fledging quality could thus be a finer measurement of parental care differences. In little penguins, fledging body mass has been shown to be an important factor of survival of fledglings during their first year after leaving the colony (Dann 1988). In our study, equal pairs fledged heavier chicks than unequal pairs. Chicks from equal pairs would have a more regular food intake, which could positively affect their growth. Although equal parental care seems a better strategy in terms of benefits in raising chicks, it was the least observed amongst little penguins. As long lived species, seabirds are expected to favor their survival at the expense of the current breeding attempt (Stearns 1989; Mauck and Grubb 1995, “the prudent parent” Drent and Daan 1980). They will thus choose the best strategy in terms of reproduction only when associated costs are not too high, that is, when their survival is not at stake. In years of good conditions, such as 2002, the costs associated with breeding were probably lower, and both partners could maintain the same level of parental investment resulting in a larger number of equal pairs. Conversely, in years of unfavorable breeding conditions, individuals may try to minimize reproductive costs, in particularly in long-lived species (e.g., Weimerskirch et al. 1997), leading to more apparent within pair differences. This long-term strategy to reduce breeding costs within the partnership seems relevant as unequal pairs exhibited similar return rate and local survival to those of equal pairs. Besides, higher reproductive costs could be the result of unfavorable environmental conditions occurring during only one part of the breeding season, for example, a short-term decrease in resource availability that would take place either before or during postguard. We detected that by comparing the number of foraging trips. The proportion of unequal pairs and average difference in number of trips was negatively correlated with an index summarizing the hatching and guard success, and with the postguard success. Years of poor hatching or guard success would result in high expected costs and as adults base offspring allocation decisions on expected levels of resource availability (Lalonde 1991), in a high level of unequal investment. However, years with high hatching/guard success could also become poor years, when postguard conditions turned up to be unfavorable (2001, 2004, and 2007). Thus, parental investment strategies do not seem to be set at the beginning of the breeding season but can change dynamically depending on environmental changes during postguard itself.

Our findings suggest that differences in parental care were related to differences in individual quality regardless of age and gender. Such a result may shift the focus of parental investment studies from looking at differences between males and females to considering the inherent individual quality, elusive as it may be (Bergeron et al. 2010; Wilson and Nussey 2010), which can play a crucial role in parental investment in biparental system.

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