

Regulation of parental effort in a long-lived seabird: an experimental manipulation of the cost of reproduction in the antarctic petrel, *Thalassoica antarctica**

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Summary. The fitness of a parent in an altricial bird species is likely to be a function of the proportion of resources allocated to offspring production in relation to the amount spent on its own survival. Here we report an experiment on the Antarctic petrel in which we manipulated the costs of rearing an offspring by placing small lead loads on the legs of one parent. The bird could then either decrease its own body reserves or reduce the food load to the chick. The manipulated birds decreased their food load and increased the feeding interval, compared with unmanipulated birds. Consequently, the rate of chick loss increased. No significant difference was found between the body weights of experimental and control birds during the experiment.

Key words: Antarctic petrel – Cost of reproduction – Parental care – Antarctica

Introduction

Optimal life-history theories are based on the idea of a trade-off between the amount of resources invested in current offspring production and the amount that remains for parental survival and future reproductive investment (Williams 1966; Charlesworth 1980). At every point in the nesting cycle parents must decide how much they should invest in their offspring at the expense of a reduction in the probability for their own future survival and reproduction. Parents are expected to maximize the reproductive success from current and future broods by weighing the effect of continued investment in the current offspring against future reproductive success (Carlisle 1982; Sargent and Gross 1985; Clutton-Brock 1991). In long-lived species high investment in current offspring is rarely favoured because a small re-

duction in the probability of future survival for the parents will reduce the number of subsequent breeding attempts (Curio 1988; Pugesek 1990; Pugesek and Diem 1990). Here we show experimentally that the consequence of an artificial increase in the effort required for feeding the offspring of the Antarctic petrel (*Thalassoica antarctica*) is decreased investment in the offspring, without change in the body condition of the adults.

Methods

Study area. This study was conducted in January–February 1990 during the austral summer in Svarthamaren, Mühlig-Hofmannfjella in Dronning Maud Land (71° 53'S, 5° 10'E) in Antarctica. Here approximately 200 000 Antarctic petrel pairs breed (Mehlum et al. 1988). The colony is located more than 200 km from the nearest open sea. In order to provide food to their single chick the parents must fly at least 400 km.

The colony is situated along the north-east facing slope of a mountain, at an altitude of 1650 m. The temperature fluctuated between -1°C in the day and -25°C at night. During the nights there was a strong southerly katabatic wind from the Antarctic plateau. For further description of the topography and climate, see Mehlum et al. (1988).

In order to disturb the birds as little as possible, our experiments were conducted in the lower-lying part of the colony (see Sæther et al. 1990 for location of the plots).

Experimental procedure. Offspring hatch relatively synchronously (Haftorn et al. 1991), and in 1990 the mean hatching date was 14 January. The single chicks were brooded by one of the parents until thermal independence which was reached after 9–11 days (Bech et al. 1988). The chick was then left unattended. At this stage of the nesting cycle we captured the parents at an experimental group of 37 nests when they arrived to feed their nestling. One of the parents was given a 20-g ring of lead on each leg; these are henceforth termed *manipulated* birds. In this way the bird would carry an extra load of about 6% of the body weight of an average Antarctic petrel in the study area. Judging from the behaviour of the birds both in the air and on the ground, combined with observations of the foraging behaviour of the Antarctic petrel at sea, the extra weight was unlikely to interfere with their ability to forage. The other parent in the pair was ringed with a steel ring. These birds are henceforth referred to as *unmani-*

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pulated. Age and sex distribution of experimental birds was not known. However, studies of sexed birds in the same area (S.H. Lorentsen, unpubl.) have revealed a high degree of synchrony between the sexes in return periods. Consequently, catching of manipulated birds throughout a 1-week period, as in this study, would most likely secure an even sex distribution.

In order to weigh the chick immediately after feeding all nests were continuously watched during the whole experimental period. In addition all chicks were weighed every 4 h. The difference between the weight of the chick after being fed and the weight at the previous weighing was used to estimate the amount of food given to the offspring. Since the Antarctic petrels were very tame, we managed to capture and weigh several adults just after they had fed their offspring. In order to avoid unnecessary mortality of chicks in the manipulated group we made use of the fact that Antarctic petrel parents do not recognize their own young and moved the chicks of manipulated parents that showed signs of severe malnutrition to the nests of other birds whose chick had been recently predated. In none of these cases did the real parents return in time to have prevented the chick from dying if we had not moved it.

We thus obtained data on the feeding frequency and the amount of food given by individual adults, and the weight change of parents during the nesting period. These figures were compared with data from a group of 32 nests with *control* birds. The experiment was terminated on 14 February, approximately 14 days before fledging. The loads of all birds were then removed.

Both theoretical analyses (Houston and Davies 1985; Winkler 1987) and empirical data (Wright and Cuthill 1989) suggest that in monogamous species the amount of resources invested by an individual in its offspring is also influenced by the effort invested by the mate. The feeding rate of the mates of the manipulated individuals was therefore also compared with the feeding rate of the individuals in the control nests.

The choice. In this experimental set-up the Antarctic petrel has two options. If it decreases the amount of food given to the offspring, the chick, especially in the hostile Antarctic environment, will have a higher probability of dying or of sustaining a slower growth rate, which may in turn reduce its probability of survival in the post-fledging period (Brooke 1986). Furthermore, there is only a short period when open water outside the ice shelf is available. This is probably why the Antarctic petrel has evolved a very rapid juvenile growth rate compared to other Procellariiformes (Mehlum et al. 1987) since the survival expectancy of slow-growing nestlings will be extremely low. The other option, of carrying the normal amount of food at least 200 km, represents a high energetic burden to the adult bird (Pennycuik 1989), which is likely to influence its own body condition. Since there is no open water at a closer distance, the manipulated birds have little opportunity to respond to this extra cost of reproduction by changing their foraging behaviour, for instance, as in many other species, by accepting larger predation risks (Magnhagen 1991).

Results

The manipulated birds reduced both the rate and amount of food provisioning to the chick. The mean weight of the food given by a manipulated parent to the chick was significantly lower than the amount given by its unmanipulated mate (Fig. 1; $F=4.47$, $P<0.05$, df 1, 84). In addition, the interval between the visits was significantly longer for loaded than for unmanipulated birds ($\bar{x}=5.2$ days, $n=40$ and $\bar{x}=3.9$ days, $n=86$, respectively; $F=11.13$, $P<0.001$, df 1, 124). Thus, the manipulation of one of the parents reduced the food provisioning rate to the chick.

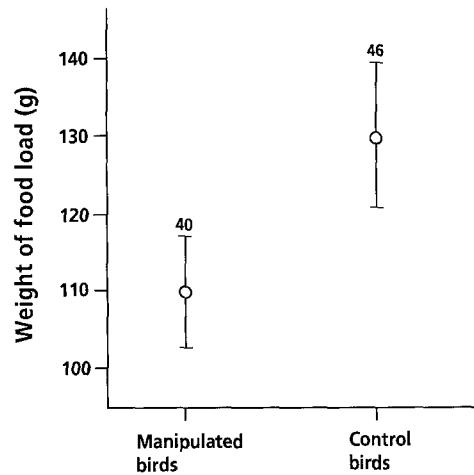


Fig. 1. The mean weight (\pm SD) of the food loads (g wet weight) provisioned to the Antarctic petrel chick in experimental nests by parents carrying an extra weight (*manipulated*) and by unmanipulated parents (*control*). The figures denote sample size

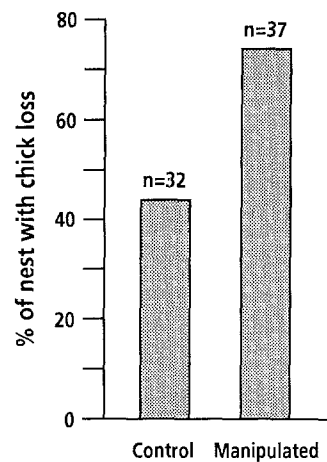


Fig. 2. The proportion of the nests where the chick "died" during the experimental period in pairs where one of the parents was carrying an extra load (*manipulated*) and in *control* pairs (pairs where none of the birds was manipulated). n = number of nests

The mean amount of food provided by the parents in the control nests ($\bar{x}=126.4$ g) did not differ significantly from the feeding load of the unmanipulated individuals in the experimental group ($t=0.22$, $P>0.1$, df 59). Thus, the unmanipulated bird did not compensate for the reduced feeding efficiency of its partner.

No change occurred in the weight of either the control or the manipulated birds during the experimental period (Pearson product moment correlation coefficient between weight and date, $r=0.13$, $P>0.1$, $n=33$ and $r=0.08$, $n=33$, $P>0.1$ for unmanipulated and manipulated individuals, respectively). Thus, the manipulated birds did not lose more weight than the control birds. In addition, the maximum weight change was computed for each individual which was weighed at least twice during the experimental period. No significant difference was found between the group of birds ($\bar{x}=90.2$ g, $n=28$ and $\bar{x}=80.5$ g, $n=18$ for unmanipulated and manipulated birds, respectively, $F=0.28$, $P>0.1$, df 1, 44).

The reduced rate of food provisioning resulted in a high rate of "loss" (see Methods) of chicks from the experimental nests. A significantly higher proportion of the chicks from the experimental group died compared with the chicks in the control nests (Fig. 2, $\chi^2=6.49$, $P<0.05$, $df\ 1$).

Discussion

These results demonstrate that adding a small extra load to the parents decreased their feeding efficiency, and that this reduction in the food provision rate reduced their nesting success. Currently, we are not able to state whether this reduced feeding efficiency is due to a reduction in foraging ability or an increased flight cost. However, the lead weight was small and did not seem to interfere with the birds' ability to move. On the other hand, according to the computations of Pennycuik (1989), carrying such an extra load at least 400 km would generate a substantial extra energetic cost to the bird. However, this extra cost did not affect the body mass of the manipulated birds. The similarity of the reduction in mean food load (Fig. 1) and the load weight may support the flight-cost hypothesis. This suggests that maintenance of body condition may be an important determinant of reproductive success in the Antarctic petrel. Hence, an understanding of the factors influencing adult body condition may give information about the environmental factors that determine variation in breeding success in long-lived seabirds.

We found no compensation by the unmanipulated birds for the reduced feeding performance of their manipulated partners. This contrasts with the results from a similar experiment with starlings (*Sturnus vulgaris*) where the unmanipulated individual partly compensated for the decreased foraging efficiency of its manipulated mate (Wright and Cuthill 1989). This suggests that a different strategy of parental care has evolved in seabirds. Whereas poor nutrition of the offspring in smaller altricial birds stimulates increased parental effort (Kacelnik and Cuthill 1990), both our results and previous results by Ricklefs (1987, 1992) indicate that no such response seems to have evolved in petrels. This lack of increase in parental effort may be due to an increased mortality cost of reproduction (cf. Pugsek and Diem 1990) resulting in a large reduction in future lifetime reproductive success (e.g. Wooller et al. 1989). Parental investment is assumed to be strongly influenced by the reproductive value of the parents (Trivers 1974; Sargent and Gross 1985; Kacelnik and Cuthill 1990). In California gulls (*Larus californicus*) Pugsek (1990) demonstrated variation in offspring investment with age; older parents withhold food for shorter periods than younger parents. Whereas California gulls lose significant amounts of body mass during the breeding season (Pugsek and Diem 1990), no such trend was found in this study, indicating an even more extreme parent-offspring conflict in the longer-lived petrels. Consequently, increased feeding effort as a response to higher energetic requirements of the offspring is unlikely to evolve.

Recent long-term studies of seabirds have shown several cases of large variation in survival and breeding success (see reviews in Croxall and Rothery 1991; Wooller et al. 1992). In addition, in several species there are large differences between individuals in their reproductive performance (e.g. Ollason and Dunnet 1988; Wooller et al. 1989). This study suggests that an understanding of the factors influencing the ability of the parents to provide food to their offspring may be important in explaining such variation. Similarly, Croxall and Briggs (1991) have tried to explain interspecific differences in reproductive performance by differences between the species in their efficiency in providing food to their offspring.

Low reproductive investment in seabirds has been assumed to have evolved because such long-lived individuals are not expected to jeopardize their own survival chances (Goodman 1974; Charlesworth 1980). As predicted, the manipulated Antarctic petrels reduced investment in their own offspring, even though this increased chick "mortality" (Fig. 2). An implication of this reluctance by the parents to decrease their body weight is that a trade-off between reproductive investment and adult survival rate may operate through a common correlation with body weight. Thus, in long-lived seabirds there may exist a threshold for the possible reduction in body weight of the parents during the breeding season. Below this threshold the survival probability will be reduced, and further reproductive investment should be avoided.

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