

Reproductive effort in biparental care: an experimental study in long-lived Cape gannets

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Life-history theory predicts a trade-off between current and future reproduction, such that long-lived species should not increase their reproductive effort (RE) at a cost to their own survival. In species with long-term pair bonds and biparental care, each parent must balance its reproductive investment against that of its partner. Although the effects of “handicapping” studies on the focal individual are sometimes difficult to interpret, they are a powerful approach for investigating compensatory responses of the partner. In the present experiment, we manipulated flying ability of one parent in long-lived Cape gannets (*Morus capensis*), thereby indirectly increasing the demands on RE of the unmanipulated partner. Handicapped birds doubled their foraging trip duration and reduced nest attendance. Their partners showed behavioral compensation via increased nest attendance for chicks younger than 30 days and increased foraging trip frequency for older chicks. The behavioral responses of partners did not fully compensate for the reduced care of handicapped adults. For manipulated nests, overall foraging trip frequency was 21% lower, chicks were left unattended at 5 days younger, and their growth and survival was reduced compared with control nests. Handicapped adults lost 10% of their body mass during the experiment, but their partners showed no decrease in body mass. Our results show that long-lived Cape gannets can increase current RE when needed, without negative effects on body condition or survival. The reduced care of one parent was partly compensated for by its partner, and remaining costs were borne by the chick. *Key words:* chick provisioning, foraging behavior, life-history trade-off, long-lived seabird, parental conflict, reproductive investment. [*Behav Ecol* 20:736–744 (2009)]

Two concepts central to life-history theory are that natural selection acts to maximize individual fitness and that fitness trait combinations are constrained by trade-offs (Fisher 1930; Roff 2002). A key example is the trade-off between reproduction and adult survival. Increased reproductive effort (RE) can enhance reproductive success through improved chick growth and survival (Roff 2002) but at the same time may compromise adult survival (Dijkstra et al. 1990; Hanssen et al. 2005). In species with biparental care, an individual must balance its own effort against that of its partner (Trivers 1972; Drent and Daan 1980). If one parent decreases its care, its partner should compensate in order for the offspring to survive (Houston and Davies 1985), but may thereby risk decreasing its own survival prospects (e.g., Dijkstra et al. 1990). For long-lived species, which have many breeding opportunities, lifetime reproductive success is marginally affected by the success of individual breeding attempts. Long-lived species should therefore exercise restraint in increasing current RE at the cost of survival and future reproduction (Williams 1966; Goodman 1974; Drent and Daan 1980).

Consequences of the trade-off between reproduction and adult survival can be studied experimentally by increasing reproductive costs to parents by means of “handicapping” (e.g., Linden and Møller 1989; Wright and Cuthill 1989; Markman et al. 1995; Sanz et al. 2000). Table 1 gives an overview of

handicapping studies in which flight costs were increased in long-lived seabird species. Several of these studies have confirmed the theoretical prediction that parents should prioritize themselves over their chicks: handicapped parents maintained their body condition, whereas their offspring showed reduced growth, body condition, and/or survival. However, increases in RE without negative effects on offspring growth and survival have also been reported (Table 1). Several studies have interpreted a reduction in body condition of handicapped birds as the result of increased RE (Weimerskirch et al. 1995, 2000; Velando 2002; Nisbet et al. 2004; Paredes et al. 2005). Changes in body mass may, however, reflect functional adjustments of wing loading rather than deleterious effects (Norberg 1981; Lind and Jakobsson 2001), and in such cases, RE may remain constant or even decrease. Because body mass can be subject to such mitigating factors, it is important to measure RE directly, via behavioral responses. Moreover, to avoid measuring effects of confounding factors resulting directly from the manipulation, handicapping one parent is preferred over handicapping both. The decreased parental care of handicapped birds indirectly increases the demand on RE of the unmanipulated partner, allowing for firm conclusions based on the unmanipulated partner's body mass changes and behavior.

We know of 2 studies in which one parent was handicapped, and changes in body condition and behavior were recorded for its partner. Antarctic petrels (*Thalassoica antarctica*) did not compensate or lose body mass when their partners were handicapped, resulting in increased chick mortality (Saether et al. 1993). Thick-billed murrelets (*Uria lomvia*) whose partners were handicapped showed behavioral compensation, resulting in equal chick fledging success compared with controls and no reduction in resighting rate in the following breeding season (Paredes et al. 2005). Conclusions on the trade-off between

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Table 1
Overview of handicapping studies that manipulated flight ability in long-lived seabirds

Reference	Species	Manipulation		Response in condition			Response in behavior	
		Method	Subject	Handicapped bird	Partner	Chick	Handicapped bird	Partner
Saether et al. (1993)	Antarctic petrel <i>Thalassoica antarctica</i>	Extra weight	1	Body mass (\approx)	Body mass (\approx)	Mortality (+)	Feeding interval (-) Food load (-)	Foraging load (\approx)
Paredes et al. (2005)	Thick-billed murres <i>Uria lomvia</i>	Extra weight (logger)	1	Body mass (-) Resighting (-)	Resighting (\approx)	Fledging success (\approx)	Trip duration (+) Trip frequency (-) Nest attendance (-)	Trip frequency (+) Nest attendance (+) Mate fidelity (-)
Mauck and Grubb (1995)	Leach's storm-petrel <i>Oceanodroma leucorhoa</i>	Feather clipping	2	Feather growth (\approx)		Growth (-)	Trip frequency (-)	
Weimerskirch et al. (1995)	Thin-billed prion <i>Pachyptila belcheri</i>	Feather clipping	2	Body mass (-)		Body mass (\approx)	Trip frequency (\approx)	
Duriez et al. (2000)	Thin-billed prion <i>P. belcheri</i>	Extra weight	1	Body mass (\approx) Resighting (\approx)		Body mass (\approx) Mortality (\approx)	Trip duration (+) Food load (\approx)	
Weimerskirch et al. (2000)	Yellow-nosed albatross <i>Diomedea chlororhynchos</i>	Extra weight	2	Body mass (-) Resighting (\approx)		Body mass (-) Growth (-) Mortality (\approx)	Trip duration (+) Nest attendance (\approx) Food load (-)	
Navarro and González-Solís (2007)	Cory's shearwater <i>Calonectris diomedea</i>	Feather clipping	1	Body mass (\approx) Resighting (\approx)		Growth (-)	Trip duration (+) Foraging efficiency (\approx) Incubation (-)	
Tveraa et al. (1997)	Antarctic petrel (females) <i>T. antarctica</i>	Extra weight	1	Body condition (-)			Trip duration (+) Nest desertion (+)	
Weimerskirch et al. (1999)	Antarctic prion <i>Pachyptila desolata</i>	Extra weight	1	Body mass (\approx)			Trip duration (+) Food load (\approx) Nest desertion (+)	
Velando and Alonso-Alvarez (2003)	Blue-footed boobie <i>Sula nebouxii</i>	Feather clipping	1	Body mass (\approx)	Body mass (-)	Body mass (-)		
Velando (2002)	Blue-footed boobie <i>S. nebouxii</i>	Feather clipping	1	Body mass (-)		Body mass (-) Growth (-)		
Nisbet et al. (2004)	Common tern <i>Sterna hirundo</i>	Feather clipping	1	Feather growth (-) Resighting (\approx)		Growth (+) Fledging success (+)		

The column "subject" indicates whether one or both parents in a couple were handicapped. In the studies of Velando (2002) and Velando and Alonso-Alvarez (2003), only female blue-footed boobies were used.

adult survival and reproduction based on these studies remain equivocal for several reasons. Saether et al. (1993) investigated foraging load as compensatory behavior without recording behaviors such as feeding frequency. Furthermore, because petrels had to fly at least 200 km to their feeding site, the unmanipulated partners of handicapped birds were limited in their ability to “effectively” compensate by increasing provisioning rates. Paredes et al. (2005) handicapped birds for 1–4 days. During such a short period, it may have been possible for unmanipulated partners to increase RE without detrimental effects on their survival; a different outcome might have resulted from a longer manipulation. Furthermore, over such a short handicapping period, negative effects on chick fledging success were unlikely to be apparent, and changes in chick mass would have been a more appropriate measure. Thus, there is need for further behavioral data on whether long-lived species are willing to increase RE, at a potential cost to their own survival, or instead shunt increased reproductive costs onto their chicks.

In this study, we sought to understand the aforementioned trade-off by means of a handicapping experiment on Cape gannets (*Morus capensis*). The Cape gannet is a pelagic seabird species with postponed sexual maturity, biparental care, a modal clutch size of one egg, slow chick development, and high adult survival rates (Nelson 1978). By handicapping one parent, we increased the demands on its partner's RE without artificially restricting its foraging or flight abilities. We recorded both adult's provisioning behavior and nest attendance throughout a 31-day period, as well as chick growth and survival. We predicted that handicapped Cape gannets would show reduced parental care and that their partners would show restraint in the degree to which they compensated by increasing RE. In this long-lived species, the increased reproductive costs would be transferred to chick growth and survival rather than adult body condition and survival.

MATERIALS AND METHODS

The study was conducted at Ichaboe Island (Namibia 26°29'S, 14°94'E) between 14 December 2005 and 20 January 2006. The breeding colony consisted of approximately 8700 Cape gannet pairs (Crawford et al. 2007).

At the periphery of the colony, we randomly selected 75 nests containing chicks of various ages (range 1–52 days). We captured the adult present on the nest and marked its back feathers yellow with picric acid to facilitate observations. Adults were banded with a steel ring on the right tarsus. The lengths of the bill, head, and tarsus were measured to the nearest 0.1 mm, the length of the flattened wing chord to the nearest millimeters, and body mass was recorded to the nearest 25 g. Marked adults from 26 nests were handicapped by taping together the 2 outer primary feathers on both wings at 2 positions with Tesa tape (Tesa, Beiersdorf AG, Hamburg, Germany), thereby increasing wing loading and decreasing flight efficiency (Pennycuik 1989). All unmanipulated nests (49) were used as controls. After capturing and marking the first adults, we captured all partners within 3 days and measured their structural sizes and body mass. These birds were also ringed on the right tarsus and were fitted with a plastic color ring at the left tarsus for identification purposes. Birds were captured and measured at fixed times per day to avoid overestimating adult body mass (from 9 AM to 11 AM and 4 PM to 6 PM). The average chick age at the start of the experiment, which was 17 days in the control group (standard deviation [SD] ± 10.5 , $n = 49$, range = 1–42) and 20 days in the experimental group (SD ± 13.7 , $n = 26$, range = 2–52), did not differ between treatment groups (1-way analysis of variance [ANOVA]: $F_{1,73} = 1.35$, $P = 0.25$).

Cape gannets are sexually monomorphic, and sex was determined by isolating DNA from breast feathers taken from the first caught adult (for detailed methods, see Fridolfsson and Ellegren 1999). The overall sex ratio (males/females) of marked individuals was 0.48 (39 females and 36 males), specifically 0.55 in the control group (22 females and 27 males) and 0.35 in the handicapped group (17 females and 9 males). These sex ratios were different neither from 0.50 (chi-square tests: marked birds $\chi^2 = 0.12$, $P = 0.726$; control $\chi^2 = 0.51$, $P = 0.475$; handicap $\chi^2 = 2.46$, $P = 0.117$) nor from each other (multinomial regression: $\chi^2 = 6.03$, $P = 0.110$).

We recorded nest attendance at each study nest once every hour from sunrise to sunset (5 AM to 7 PM) for 31 days. Cape gannets in this colony make foraging trips of about 36 h on average (Lewis et al. 2006) during which the partner stays at the nest when the chick needs guarding. Gannets are visual hunters and do not forage at night (Ropert-Coudert et al. 2004). Therefore, if a difference in nest attendance was observed between sunset and sunrise, we assumed that the change in occupation had occurred soon after sunset. From the observational data on nest attendance, we calculated 6 response variables: 1) time between leaving the nest and returning (trip duration, hours), 2) time between arriving at and leaving the nest (attendance bout, hours), 3) average number of times per day an adult left the nest (trip frequency), 4) fraction of time each adult was at the nest (nest attendance), 5) time between either parent returning to the nest (feeding interval, hours), and 6) fraction of total time the chick was unattended at the nest (nonattendance). To quantify the extent to which compensation occurred, we also analyzed the sum of nest attendance and trip frequency of both parents per nest. During the study period, we obtained data on 2244 foraging trips and 2177 attendance bouts from which we calculated all foraging and nesting behaviors. We calculated a measure of relative RE by correcting trip frequency for chick age (controlling for differences in onset of breeding) and experimental group (residual RE; generalized linear model [GLM], $r^2 = 0.54$, $F_{7,132} = 22.5$, $P < 0.01$).

Once per week, we measured chick bill and head length to the nearest 0.1 mm and flattened wing chord length to the nearest millimeters. Body mass less than 1000 g was measured to the nearest 5 g and more than 1000 g to the nearest 25 g. We started measurements at the same time of day and measured chicks in the same sequence each measurement day. Chick age (in days) was estimated with bill and wing length at the first measurement (see Navarro 1991). Chick growth was analyzed using a nonparametric analysis in which growth was scaled to represent the number of SDs above or below average growth rate (Mullers and Tinbergen 2009).

At completion of the experiment, we caught as many adults as possible (110 birds), removed the handicap and plastic color rings, and recorded final body mass. The change in body mass over the experimental period was averaged per day (mass increment per day, MID in grams). In the following breeding season (between 17 December 2006 and 5 March 2007), we retrapped as many experimental birds as possible and calculated resighting probabilities. Cape gannets are faithful to their breeding site, so resighting probability approximates local survival (Klages 1994).

Ethical considerations

After considering several experimental handicapping methods (e.g., extra weight and clipping flight feathers), we decided on the novel procedure of taping together the outermost 2 flight feathers of each wing. This method has the advantage of being immediately reversible because the tape could be removed without damage to the feathers. Furthermore, it is

nonpermanent, whereas applying extra weight will remain a handicap if the individual is not recaptured and clipping the flight feathers is irreversible until the feathers molt. Two birds that were not recaptured were monitored by the staff on the island, and we observed that the tape wore off by itself. The chicks of adults from whom the handicap was removed were all resighted 1 month after the experiment, as were the chicks from the adults of which the handicap wore off by itself. This suggests that once the handicap was removed, the parents could resume normal behavior and successfully rear their chicks. Research on Ichaboe Island was conducted under permission from the Namibian Ministry of Fisheries and Marine Resources.

Analyses

Normality of residuals was judged by visual inspection (Miller 1986). To normalize residuals, the response variables were either ln transformed or arcsine square-root transformed in case of fractions. To obtain a representative and accurate quantification of behaviors, we omitted nests if both parents did not make at least 2 foraging trips while their chick was alive ($n = 5$). For analyses of chick mortality and adult resighting probability, all nests were included ($n = 75$). Response variables were analyzed in a multilevel hierarchical modeling procedure in MLwiN 2.02 with nest ($n = 70$), individual parent ($n = 140$), and observation as levels. Multilevel models were used in order to control for repeated observations of individuals within nests. Even with a multilevel analysis, dependency between parents within a control nest might exist: we therefore additionally analyzed the data for one randomly selected parent from each control nest. The outcomes from these analyses were similar to the outcome when using both parents of control nests. We present the results from models

including both parents. The explanatory variables in the models were sex and treatment (control, handicapped, or partner) as factors and chick age as covariate. Included interactions were: treatment \times chick age, treatment \times sex, and sex \times chick age. We used stepwise backward deletion to remove non-significant variables and interactions. In these models, female controls equaled the intercept, and predictors can be derived by adding the coefficients of the explanatory variables of interest (see Supplementary material). Significance levels were calculated with restricted iterative generalized least squares. Response variables of the summed parental behaviors were tested in a model with treatment (control or manipulated) as a factor, mean chick age per growth interval as a covariate, and their interaction. Chick mortality and adult resighting probability were analyzed using a GLM with a binomial distribution and a logit-link function.

RESULTS

RE: individual parents

Handicapped birds doubled their foraging trip duration compared with control birds, but their partners did not alter their average trip duration (Figure 1a). With increasing chick age, trip duration decreased in each treatment group equally. Female gannets made longer foraging trips than males (control birds: females 26.3 h, standard error [SE] +1.35, -1.28; males 20.6 h, SE +1.06, -1.01), but there was no sex difference in age-related changes in trip duration (multilevel model: treatment $\chi^2 = 86.1$, $P < 0.001$; sex $\chi^2 = 24.6$, $P < 0.001$; chick age $\chi^2 = 52.4$, $P < 0.001$; treatment \times chick age $\chi^2 = 0.20$, $P = 0.906$; sex \times chick age $\chi^2 = 0.25$, $P = 0.881$; Figure 1a).

Trip frequency was reduced for handicapped birds (0.31 trips per day, SE ± 0.03) compared with controls (0.44 trips per day, SE ± 0.04). In all 3 treatment groups, parents made

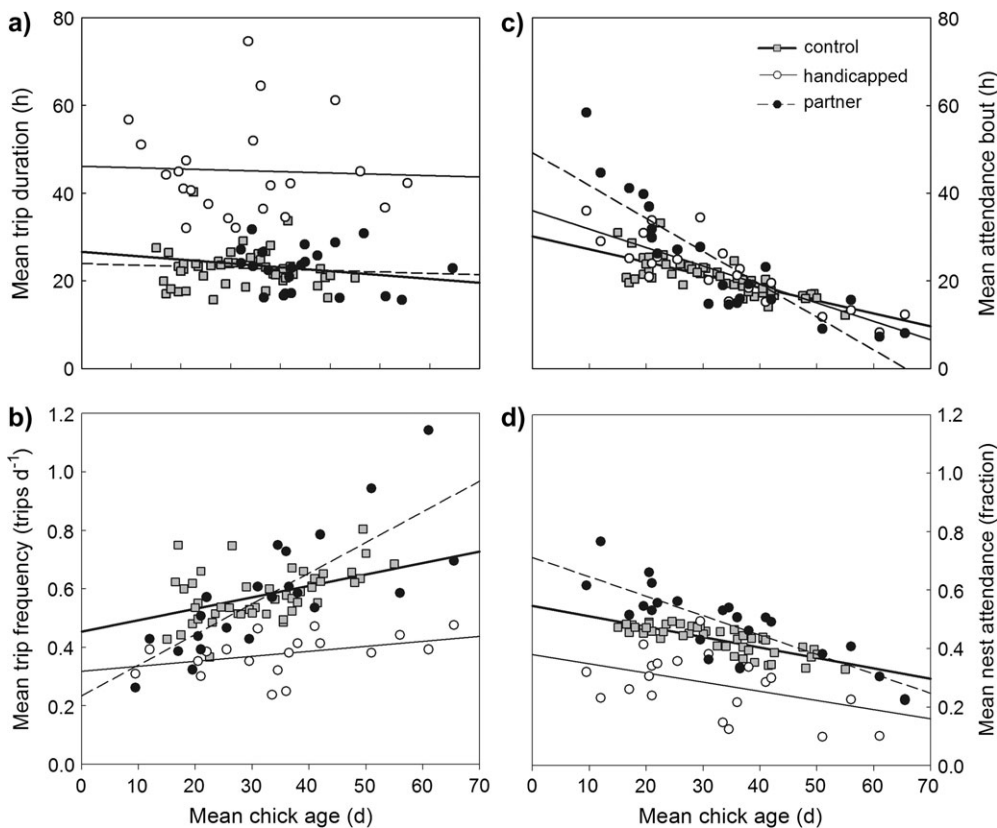


Figure 1

Parental behaviors at an individual level. Four behaviors are presented: (a) trip duration (hours), (b) trip frequency (per day), (c) attendance bout (hours), and (d) nest attendance (fraction of time). Parental behaviors were related to chick age (in days) for control (thick line), handicapped (thin line), and partners of handicapped adults (dashed line). For representation purposes, all behaviors and chick ages were averaged over the total experimental period.

more trips per day when chicks got older, but partners of handicapped birds increased their trip frequency at a faster rate than control birds (Figure 1b). Male trip frequency was higher than that of females (control birds: females 0.44 trips per day, SE ± 0.01 ; males 0.50 trips per day, SE ± 0.02 , -0.01), but changes with chick age did not differ between the sexes (Multilevel model: treatment $\chi^2 = 24.9$, $P < 0.001$; sex $\chi^2 = 20.0$, $P < 0.001$; chick age $\chi^2 = 21.0$, $P < 0.001$; treatment \times chick age $\chi^2 = 22.5$, $P < 0.001$; sex \times chick age $\chi^2 = 1.4$, $P = 0.232$; Figure 1b).

Handicapped birds did not differ from control birds in average duration of attendance bouts, but their partners stayed longer at the nest (Figure 1c). In each treatment group, the duration of attendance bouts decreased as chicks got older. Partners of handicapped birds stayed longer at the nest when chicks were young (≤ 30 days old) and showed a steeper decrease in attendance bouts with increasing chick age than control birds (Figure 1c). No differences in attendance bouts, or their rate of decrease with chick age, were detected between the sexes (multilevel model: treatment $\chi^2 = 17.2$, $P < 0.001$; sex $\chi^2 = 1.1$, $P = 0.295$; chick age $\chi^2 = 76.6$, $P < 0.001$; treatment \times chick age $\chi^2 = 13.8$, $P < 0.001$; sex \times chick age $\chi^2 = 0.04$, $P = 0.838$; Figure 1c).

As a consequence of the increased trip durations of handicapped birds and the increased attendance bouts of their partners, nest attendance was lower for handicapped birds and higher for their partners compared with control birds (Figure 1d). Nest attendance decreased with chick age for all treatment groups at the same rate for handicapped and controls but steeper for partners of handicapped birds (Figure 1d). Male gannets showed greater nest attendance than females (control birds: females 0.56 fraction of total time, SE ± 0.02 ; males 0.67, SE ± 0.02), and a significant treatment \times sex interaction revealed that handicapped males' nest attendance was higher than attendance of handicapped females (multilevel model: treatment $\chi^2 = 78.6$, $P < 0.001$; sex $\chi^2 = 26.9$, $P < 0.001$; chick age $\chi^2 = 39.0$, $P < 0.001$; treatment \times chick age $\chi^2 = 13.8$, $P < 0.001$; sex \times chick age $\chi^2 = 0.06$, $P = 0.807$; treatment \times sex $\chi^2 = 7.8$, $P = 0.020$; Figure 1d). For detailed statistical results, please see Table 1 of the Supplementary material.

RE: parents combined

Trip frequency was reduced for manipulated nests compared with control nests (control 0.86 trips per day, SE ± 0.03 ; manipulated 0.68 trips per day, SE ± 0.03 , -0.02) but increased with chick age at the same rate as control nests (multilevel model: treatment $\chi^2 = 40.6$, $P < 0.001$; chick age $\chi^2 = 43.1$, $P < 0.001$; treatment \times chick age $\chi^2 = 1.5$, $P = 0.225$; Figure 2a). Consequently, chicks from manipulated nests spent a longer time in between feedings than chicks from control nests (control 27.3 h, SE ± 2.81 , -2.55 ; manipulated 40.5 h, SE ± 4.17 , -3.78). Feeding intervals decreased similarly with chick age for both treatment groups (multilevel model: treatment $\chi^2 = 16.1$, $P < 0.001$; chick age $\chi^2 = 47.9$, $P < 0.001$; treatment \times chick age $\chi^2 = 2.8$, $P = 0.096$; Figure 2b). The fraction of nonattendance was larger in manipulated compared with control nests (control 0.80, SE ± 0.02 ; manipulated 0.92, SE ± 0.02), and nonattendance increased equally for both treatment groups when chicks got older (multilevel model: treatment $\chi^2 = 38.7$, $P < 0.001$; chick age $\chi^2 = 237.9$, $P < 0.001$; treatment \times chick age $\chi^2 = 0.05$, $P = 0.825$; Figure 2c). Chicks from manipulated nests were left unattended for the first time at an average age of 5.3 days younger than control nests (control 32.6 days, SD ± 6.8 ; manipulated 27.3 days, SD ± 4.0 ; 1-way ANOVA: $F_{1,49} = 6.6$, $P = 0.02$). Additionally, control birds were more often at the nest together (control 0.06 fraction

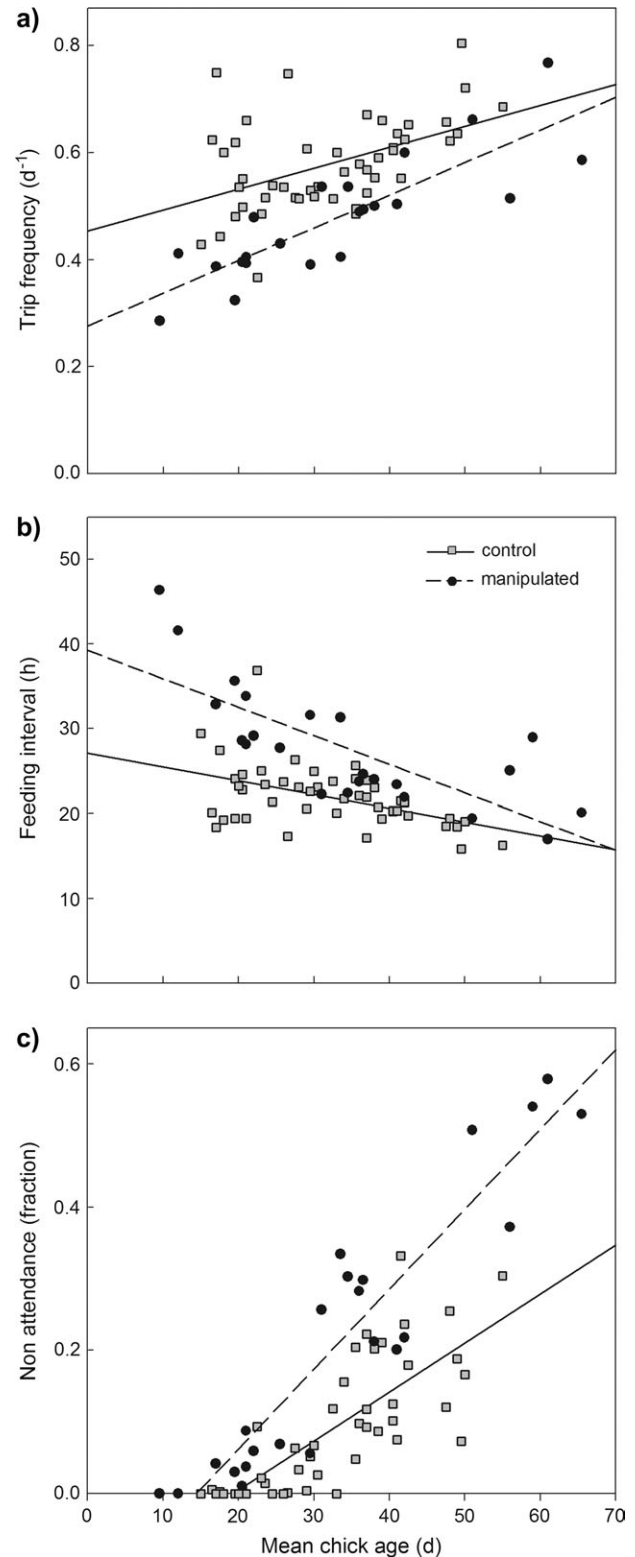


Figure 2 Parental behaviors at the nest level. Different panels represent: (a) mean trip frequency (per day), (b) feeding interval (hours), and (c) nonattendance (fraction of time). All behaviors are related to chick age (in days) for control nests (solid line) and manipulated nests (dashed line).

of total time, SD ± 0.03 ; manipulated 0.03, SD ± 0.02 ; 1-way ANOVA: $F_{1,68} = 17.1$, $P < 0.001$). For detailed statistical results, please see Table 2 of the Supplementary material.

Chick growth and survival

Chick growth was slower in manipulated nests compared with control nests (control 0.12 deviations from standardized growth, SD ± 0.88 ; manipulated -0.35 , SD ± 1.02 ; $t = 3.83$, $P < 0.001$). Growth was positively related to trip frequency (per day), which could therefore be used as an estimate for chick feeding frequency (mixed effect model: intercept -0.58 , coefficient 0.60, $t = 2.4$, $r^2 = 0.03$, $P = 0.02$). Chick mortality was higher in manipulated nests compared with control nests (control 6.1%; manipulated 26.9%; GLM: $W_{1,73} = 5.5$, $P = 0.02$). The chicks that died were all between 6 and 31 days old (average of 22 days). All but one of the dead chicks were found at the nest, suggesting starvation or dehydration as opposed to predation as a cause of death.

Adult body condition and survival

Adult body mass did not differ between treatment groups at the beginning of the experiment, and female gannets were on average 94 g heavier than males (females 2620 g, SD ± 211 ; males 2526 g, SD ± 276 ; GLM: treatment $F_{1,138} = 1.0$, $P = 0.354$; sex $F_{1,138} = 3.8$, $P = 0.052$). Over the experimental period, handicapped birds lost about 10% of their body mass (9.14 g d^{-1}), whereas control birds and partners of handicapped birds did not lose body mass (Table 2). Adults that lost their chicks were on average 144 g lighter at the beginning of the experiment than parents that had not lost their chick (successful parents 2591 g, SD ± 255 ; unsuccessful parents 2447 g, SD ± 175 ; 1-way ANOVA: $F_{1,140} = 5.6$, $P = 0.019$). Moreover, an adult's change in body mass (MID, grams per day) was negatively related to residual RE (GLM for controls: $r^2 = 0.06$, $F_{1,108} = 7.3$, $P = 0.008$; Figure 3a). The regression is given by $\text{MID} = -1.752 - 18.54 \times \text{residual RE}$. Mean chick growth over the experimental period was positively related to residual RE averaged between control parents (GLM: $r^2 = 0.15$, $F_{1,44} = 8.0$, $P = 0.007$). After removing one outlier (0.33, -0.24), the regression is given by $\text{chick growth} = 0.12 + 2.43 \times \text{residual RE}$ (GLM: $r^2 = 0.33$, $F_{1,43} = 20.9$, $P < 0.001$; Figure 3b).

Resighting probabilities in the following breeding season were 0.69 for control birds, 0.50 for handicapped birds, and 0.62 for their partners. Resighting probability did not differ significantly between treatment groups or sexes, and neither residual RE nor MID was significantly associated with resighting probabilities (Table 3).

Table 2

Body mass change over the experimental period for control, handicapped, and partners of handicapped adults

	Control	Handicap	Partner
Mass 1 (SD)	2588 (246)	2748 (328)	2528 (251)
Mass 2 (SD)	2548 (188)	2446 (137)	2525 (239)
MID (SD)	-1.27 (7.8)	-9.14 (9.9)	-0.05 (8.0)
N	82	12	16
T	1.44	3.19	0.05
P	0.154	0.009**	0.961

Averages and SDs of adult mass at the beginning of the experiment (mass 1), end of the experiment (mass 2), and adult MID over the total experimental period (MID in grams per day). The t statistics and P values (** states significance at 0.01 level) are from paired sample t -tests comparing mass 1 and mass 2.

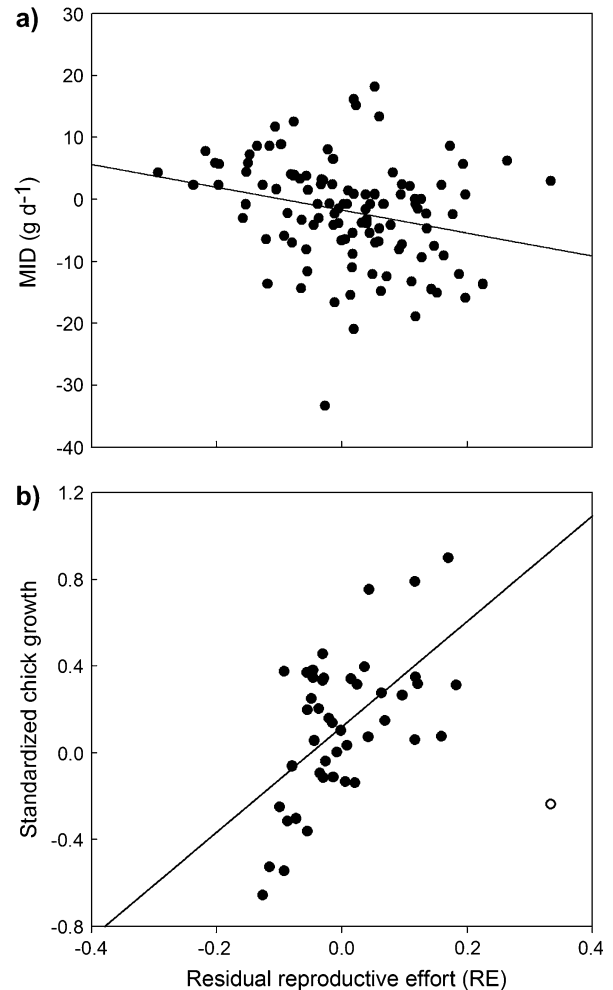


Figure 3

Estimation of the life-history trade-off between current and future reproduction. Standardized chick growth and adult MID over the experimental period (MID in grams per day) are used as estimates of current reproduction and adult survival, respectively. (a) MID is plotted against RE (see Materials and methods) and (b) chick growth is plotted against RE. The regression line in (b) is derived without the outlier (gray dot), as explained in Materials and methods.

DISCUSSION

Handicapping by altering flight ability caused long-lived Cape gannets to make longer foraging trips and reduce their trip frequencies. In response to this reduction in parental care, their unmanipulated partners increased nest attendance when they had young chicks. Partners increased their foraging trip frequency with increasing chick age, coinciding with increased chick energy requirements. Consistent with predictions from life-history theory, the behavioral compensation of unmanipulated partners did not result in decreased average body mass or lower resighting probability in the next breeding season. The observed compensatory behavior was not sufficient to maintain chick growth and survival; chicks of manipulated birds fared less well than those of controls. Together, these results suggest that long-lived Cape gannets can increase RE but do so without costs on body condition and survival, and additional costs of increased demands on RE are ultimately shunted onto the chicks.

Table 3
Results of multilevel binomial logit-link models with resighting as the dependent variable

		<i>B</i> (SE)	df	χ^2	<i>P</i>
a)	Intercept	0.92 (0.23)	1	16.3	<0.001
	Treatment ^a				
	<i>handicapped</i>	−0.92 (0.46)	2	4.3	0.119
	<i>partner</i>	−0.45 (0.47)			
b)	Intercept	0.63 (0.25)	1	6.7	0.01
	Sex ^b				
	<i>males</i>	0.06 (0.35)	1	<0.1	0.862
c)	Intercept	0.74 (0.19)	1	15.7	<0.001
	Reproductive effort	2.24 (1.43)	1	2.5	0.117
d)	Intercept	0.66 (0.20)	1	11.3	0.001
	MID	−0.02 (0.02)	1	1.0	0.306

Coefficient (*B*) indicates direction of effects, relative to the reference categories (intercept). Results are from 4 different models because samples sizes were too small to detect any effect in a full model. Differences in resighting probabilities were tested for (a) treatment (control, handicapped, and partners), (b) sex, (c) RE, Reproductive effort, and (d) MID. Abbreviations: df, degrees of freedom.

^a Reference category is control birds.

^b Reference category is females.

Effects on handicapped birds

Handicapped birds doubled their foraging trip durations, consequently reducing trip frequencies and nest attendance. These behavioral responses were consistent between the sexes, although handicapped males reduced nest attendance less dramatically than handicapped females. Handicapped gannets lost 10% of their body mass over the experimental period. We found no difference in the resighting probabilities between handicapped birds and control birds in the next year, suggesting that adult survival was unaffected. However, these results remain equivocal given the small sample sizes.

Results similar to ours have been reported in other handicapping studies on long-lived seabirds using different methods, for example, applying extra weight or clipping flight feathers (Table 1). Nevertheless, because of potential mitigating factors, the increased trip durations and reductions in body mass do not allow us to distinguish whether handicapped adults are working at their maximum capacity (i.e., priority to current reproduction) or at the maximum cost they are willing to pay (i.e., priority to adult survival). For example, on land, we observed that handicapped gannets needed longer runways and had more difficulties taking off with little or no wind. In pursuit of prey, gannets plunge dive on average 54 times per trip (Ropert-Coudert et al. 2004). Difficulties taking off from the water after each plunge dive would impact foraging costs, time, and efficiency, ultimately increasing trip durations. Moreover, a reduction in body mass could be an adaptation to increased wing loading, enabling handicapped birds to carry equal food loads to their chicks (Norberg 1981; Lind and Jakobsson 2001). Increased trip durations and reductions in body mass of handicapped individuals, therefore, do not necessarily convey information about the trade-off between reproduction and adult survival.

Compensatory behavior of unmanipulated partners

Because handicapping can have undesirable and unknown effects on behavior, we were especially interested in compensatory behavior of the unrestricted partners of handicapped birds. The main responses to the handicapped adults' reduced nest attendance and trip frequency were 2-fold: 1) increased nest attendance when chicks were young (≤ 30 days old) and 2) increased trip frequency with older chicks. Moreover, we observed a shift from full compensation in nest attendance with recently hatched chicks to partial compensation in trip fre-

quency with older chicks. Young chicks need constant guarding by their parents because they are vulnerable to predation and can only thermoregulate independently after about 30 days (Nelson 1978). In this study, all chick casualties occurred between the ages of 6 and 31 days, which illustrates their vulnerability at young ages. Parallel to the chicks' growing energy requirement, pairs from manipulated nests left their chicks unattended at an average age of 5 days younger than the chicks of control adults, thereby increasing trip frequency at an earlier age. Nonetheless, the chicks showed reduced growth.

Partial compensation of partners is an evolutionarily stable strategy for biparental care (Houston and Davies 1985), but if the risk of breeding failure is large, complete compensation can also be an evolutionarily stable strategy (Jones et al. 2002). The observed shift in our study from full compensation in nest attendance to partial compensation in trip frequency is in accordance with these models and with results from Paredes et al. (2005). Increased energetic demands of chicks coincide with a decreased risk of breeding failure; therefore, Cape gannet parents could afford to increase their feeding frequencies with older chicks. Additionally, as the chicks are closer to independence, the reproductive value is increased, favoring increased parental effort.

The compensatory behaviors of unrestricted partners did not result in reduced average body mass, contrary to Velando and Alonso-Alvarez (2003), nor was the resighting probability reduced, similar to Nisbet et al. (2004) and Paredes et al. (2005) (Table 1). However, differences in resighting rates require large sample sizes for discriminative statistical power. We found some costs of compensatory behavior, as residual RE was negatively related to changes in body mass. This suggests that only birds with sufficient energy reserves were able to increase their RE (Velando and Alonso-Alvarez 2003). Insufficient energy reserves would force a parent to invest in its own survival by foraging for itself at the expense of its offspring (Monaghan et al. 1992; Chaurand and Weimerskirch 1994; Olsson 1997). Indeed, we found that the initial body mass of Cape gannet parents whose chick died was lower than that of birds with surviving chicks (Tveraa et al. 1997).

Effects on the chicks

Chicks from manipulated nests experienced reduced growth and survival, due to reduced parental nest attendance, reduced trip frequency (21%), and increased feeding intervals (48%).

Other studies handicapping one member of a breeding pair also reported a reduction in reproductive parameters (Saether et al. 1993; Velando 2002; Velando and Alonso-Alvarez 2003; Navarro and González-Solís 2007), although some found no differences (Duriez et al. 2000; Paredes et al. 2005) or even reported increased reproductive success (Nisbet et al. 2004). Seabird chicks show protracted growth (Lack 1968; Goodman 1974), and to accurately study effects of manipulations on chick growth and particularly on fledging success, manipulations should last over a longer period of time (contra Paredes et al. 2005). Especially because reduced parental care should invariably manifest itself as reduced chick condition. Chicks of lower body condition would result in poorer quality fledglings that have lower survival chances (Jarvis 1974) and thus future fitness costs.

Ecological context and implications

In addition to methodological differences, inconsistencies in results between earlier parental handicapping studies on long-lived species could be due to differences in ecological conditions. Reduced parental care of manipulated birds is more easily compensated for by their partners if feeding conditions are profitable (Weimerskirch et al. 2001). In the Benguela ecosystem, the main prey species of Cape gannets are anchovies (*Engraulis encrasicolus*) and sardines (*Sardinops sagax*). These species have been extensively overfished in the Namibian waters, which is associated with a dramatic decrease in numbers of Cape gannets (Crawford et al. 2007). Cape gannets from Namibian colonies also showed increased foraging effort, reduced body condition, and lower energy gain compared with gannets breeding in South Africa (Lewis et al. 2006). Although Cape gannets may be able to compensate for the reduced availability of live prey by scavenging for fishery discards, this is not sufficient to meet both their own energy requirements and those of their chicks (Pichegru et al. 2007). In this study, we showed that Cape gannets can increase RE, but they do so only partially, probably to maintain a threshold body mass and secure future survival. If foraging conditions around the breeding colonies of this seabird species deteriorate further, chick rearing will require a population-level increase in adult RE. Without full compensation, successfully rearing offspring will be less likely, as was shown for the breeding season following our handicapping experiment (Mullers and Tinbergen 2009). This could have severe consequences for population numbers of Cape gannets, a species which is already qualified as “vulnerable” by IUCN (2008).

SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.beheco.oxfordjournals.org/>.

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