Chick provisioning by the Yellow-nosed Albatross *Diomedea chlororhynchos*: response of foraging effort to experimentally increased costs and demands

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We examined the provisioning strategy of a long-lived seabird to test the prediction from life-history theory that adults should preferentially allocate resources towards their own needs rather than towards their offspring, and to test the abilities of adults to regulate provisioning according to the chick needs. The individual provisioning behaviour of Yellow-nosed Albatrosses *Diomedea chlororhynchos* was studied, costs of flight being increased by adding a weight handicap to foraging parents, and needs of the chicks being increased by induced regurgitation (underfed chicks) or decreased by food supplementation (overfed chicks). Control birds were found to regulate provisioning in relation to the nutritional status of the chick and to the mass of the adult. As a result of increased foraging costs, and possibly of reduced foraging ability, handicapped adults spent more time foraging and delivered smaller meals. Unlike control birds, they were unable to regulate provisioning and lost slightly more mass than control birds, but they had similar survival to the next breeding season. The behaviour of parents rearing underfed chicks was similar to that of control birds, but adults rearing overfed chicks delivered smaller meals, at the same frequency as control birds. Thus, although parent Yellow-nosed Albatrosses can perceive the nutritional status of the chick and regulate provisioning accordingly, they are unable to increase the provisioning rate significantly. They primarily keep resources for themselves, their own body condition determining the level of investment in the chick. Most albatrosses and petrels behave so that primarily adult body condition is protected often at the expense of chick provisioning. Regulation abilities differ between species probably according to several factors such as foraging strategies, distance to feeding zones or body size.

Integration of the study of foraging behaviour with the study of life-history strategies (Stearns 1976, 1992) permits a better understanding of the evolution of reproductive behaviour (Trivers 1972, Nur 1987). When foraging to provision an offspring, the two constraints on predators searching from a central place are time and energy (Ydenberg *et al.* 1992). The energy gathered during foraging bouts has to be allocated between present and future reproduction so as to maximize inclusive fitness (Williams 1966).

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Thus, at any time during the period of provisioning, parents have to evaluate how much energy they should invest in their offspring at the risk of a reduction in their ability to breed again. The amount of reserves stored by the animal is likely to play an important role in these foraging and allocation decisions (Drent & Daan 1980, MacNamara & Houston 1996).

Seabirds such as petrels and albatrosses (Procellariiformes) are typical central place foragers that provision their offspring irregularly, supposedly because food resources are distant or unpredictable (Lack 1968, Ashmole 1971). Because they are long-lived, life-history theory predicts that they should limit the risk taken during a breeding event (Goodman

1974), and several studies have recently shown that they do so by monitoring their body reserves (Chaurand & Weimerskirch 1994, Chastel *et al.* 1995, Tveera *et al.* 1997). Their foraging decision to search in one or another environment is also primarily regulated by adult body condition (Weimerskirch *et al.* 1997a, Weimerskirch 1998). Provisioning and foraging decisions are also likely to depend on the needs of the chicks. It is well known that, in general, the rate of provisioning is regulated by interactions between the energy needs of the chick, its begging behaviour and the response of the adult (Hussell 1991, Kilner & Johnstone 1997). However, in Procellariiformes there is much debate as to whether parents are able to regulate food supply according to the needs of the chick. Although several studies have suggested that chick provisioning is not regulated according to the needs of the chick but, rather, is maximized through an intrinsic rhythm (Ricklefs 1987, 1992, Hamer & Hill 1993, Saether *et al.* 1993, Ricklefs & Schew 1994), others indicate that parents could respond to chick needs (Bolton 1995, Weimerskirch *et al.* 1995, 1997b, Hamer & Thompson 1997). These inconsistencies may arise from different causes. First they could result from differences between species that may exploit close or distant resources, therefore using different provisioning strategies (Weimerskirch *et al.* 1997b). Secondly, most studies have used individual nest rather than individual parent as the unit of analysis because it is difficult to study the individual behaviour of seabird parents, which provision their chick infrequently. The few studies that have worked at the level of the individual parent have shown the existence of specific provisioning strategies in several species (e.g. Weimerskirch *et al.* 1994). Thirdly, the few studies that have investigated the role of adult body condition on provisioning behaviour have indicated that body condition can play a striking role in allocation decisions (Chaurand & Weimerskirch 1994, Weimerskirch *et al.* 1995, Lorentsen 1996, Weimerskirch *et al.* 1997a, Weimerskirch 1998) similar to that found in non-seabird species (e.g. Martins & Wright 1992, Witter & Cuthill 1993). Fourthly, for experimental studies it is important to employ comparable types of manipulation to compare the parental ability to respond to chick demands, but this has rarely been done (Bertram *et al.* 1996).

To study whether Yellow-nosed Albatrosses *Diomedea chlororhynchos* can regulate their provisioning behaviour in relation to the needs of the chick and to ascertain the role of parental body condition, we experimentally increased the flight costs of a group

of adults, and increased or decreased the nutritional status of the chicks in two other groups. We compare the provisioning behaviour of these groups to a control group of parents to test (1) whether adults are able to perceive the nutritional status of the chick and to modify their behaviour accordingly, (2) whether adults are able to compensate for increased foraging costs, (3) how adults allocate resources between their own body condition and their chick, and (4) whether increased foraging costs can lead to increased adult mortality. We compare the results with other studies of Procellariiformes, confining the discussion to this group because of the uniformity in clutch size and variety of foraging strategies.

METHODS

The study was carried out at Pointe d'Entrecasteaux, Amsterdam Island (37°50′S, 77°30′E) between December 1995 and March 1996. In early December, during the brooding period when adults were attending young chicks in 72 nests, adults were ringed with a metal and a plastic ring and, to facilitate identification at a distance, one adult of each pair was marked on the breast with a patch of picric acid. A numbered peg identified each nest. At the end of the brooding period, between 20–22 December, for each nest at least one adult attending the chick was weighed with a spring balance accurate to 1%. Between 5–18 January 1996, the 72 study nests were observed from a vantage point continuously by one or two observers with binoculars from dawn (05:15 h) to dusk (19:30 h) to monitor the visits of the individual parent birds to their chick. At the beginning of the study period all chicks, aged on average 33 days, were alone on their nests. They were in their phase of rapid growth and had not yet reached peak mass at the end of the study (Jouventin *et al.* 1983, unpubl. data). At this time, adults feed their chicks regularly with a mixture of fresh food, mainly fish, and of water and oil. The exact times of arrival and departure of the adult, and its behaviour, were noted continuously.

The data collected allowed us to calculate the duration of individual foraging trips, the time of arrival and the time spent with the chick. During the last five days of the continuous observation period, adults were weighed after they had delivered a meal. All the chicks were weighed with a spring balance accurate to 1% at 05:00 h and 19:00 h. Whenever feeding was observed, the chick was also weighed either immediately or within 3 h after the departure of the parent. As chicks lose mass on the nest from respiration and defaecation,

the difference in mass between the morning weighing and mass after a feed is not exactly the mass of the feed (Ricklefs *et al.* 1985). We therefore calculated the average mass loss at 1 h, 2 h, 3 h etc. after meals of 0–300 g, of 301–600 g and heavier than 600 g. This value of expected mass loss before the meal was delivered was added to the observed mass gain to estimate the net mass of the meal. Only the chick masses recorded immediately after or within 1 h after the departure of the parent were used to calculate meal mass. To estimate chick condition and individual chick growth rate, the mass of the chick was regressed upon date. The condition of the chick was estimated as the residuals from this regression, for each chick separately. The estimated values from the regression on the first and last day of the study period were used to estimate the overall daily mass gain.

Between 20–22 December 1995 at 12 nests, chosen randomly among the 72 study nests, in addition to being weighed, both adults of each nest were fitted with a 70-g band of lead on each tibiotarsus representing in total 6.4% of the average body mass of adults (2.2 kg) at this period of the breeding cycle. These birds are referred to as handicapped birds. The lead rings were retrieved from the birds at the end of the study. In September to October 1996, during the incubation period, the study colony and neighbouring colonies were searched for birds banded in December 1995 to estimate their return rate the following breeding season.

Between 5 and 10 January 1996, an experiment was conducted on two groups of six chicks among the 72 study nests, but separate from the nests with handicapped adults. In the first group, termed 'underfed', the food fed to the chick was collected by induced regurgitation each time an adult fed the chick. Inverting the chick over a large plastic funnel and pressing its belly induced regurgitation. In a second group of six chicks, termed 'overfed', the food taken from the underfed chicks was given to these chicks. To study the effect of the manipulation on the behaviour of the adult, we used the information on the mass of feeds delivered between 5 and 10 January and on the duration of foraging trips that started between 5 and 10 January.

To study the relationship between the mass of the adults, the duration of foraging trip and the mass of meals, we used data from a study of provisioning carried out in January 1992 in the same colony using the same methodology as in 1996.

Information on weather conditions (wind speed, wind direction and rainfall) was provided by the meteorological station 8 km north of the study colony. Values are presented as mean ± 1 sd. Hours are given in local time (GMT + 5 h). Statistical analysis was performed using SYSTAT 7.0 (Wilkinson 1996). To avoid duplicate data for the same individual for the same categorical variables in ANOVA and Student *t*-tests we used average values.

RESULTS

The numbers of parents visiting their chicks in the study colony varied significantly from one day to the next (χ^2_{13} = 67.4, P < 0.0001) being higher during three days (46–53% of parents visiting their chick) and lower for the other days, varying between 23 and 30%. There was no significant correlation between the number of parents visiting chicks each day, average and maximum wind speed, wind direction or rainfall (P > 0.1 in all cases). Chicks received between three and 14 meals during the study period (8.9 ± 2.8) and had daily mass gains ranging between –31.5 and 87.1 g/day (n = 55). The rate of mass gain was related to the number of meals delivered (r = 0.62, P < 0.0001) but not to the average size of the meals delivered (r = 0.03, P = 0.83). Birds spent between 0.6 and 12 days at sea (Fig. 1) and delivered meals weighing between 50 and 800 g (Fig. 2). There was no change over time in the size of the meals delivered (r = 0.0797, n = 196, P = 0.267).

Comparison between control and handicapped birds

Handicapped birds spent a similar amount of time with their chick to control birds (t = 0.67, df = 118, P = 0.51) but spent longer periods foraging at sea than control birds (Fig. 1; t = 7.5, df = 116, P < 0.0001). Meals delivered by control birds were significantly heavier than those delivered by handicapped birds (Fig. 2; t = 2.53, df = 109, P = 0.013), being on average 67 g heavier. As a result of the lower provisioning rate, chicks of control adults gained on average 38.4 ± 21.4 ·g/day (n = 38) whereas chicks of handicapped birds gained only 18.9 ± 30.3 g/day (n = 12) (t = 2.32, P = 0.026). Although the estimated mass at the end of the continuous observation period was higher for chicks of control birds compared with those of handicapped parents (2041.3 ± 334.4 g and 1303.8 ± 462.7 respectively, t = 5.68, P < 0.0001), the mass of chicks in March before fledging did not differ significantly between the two groups (2988.0 ± 412.6, n = 35 and 2677.3 ± 668.2, n = 11 respectively, t = 1.71,
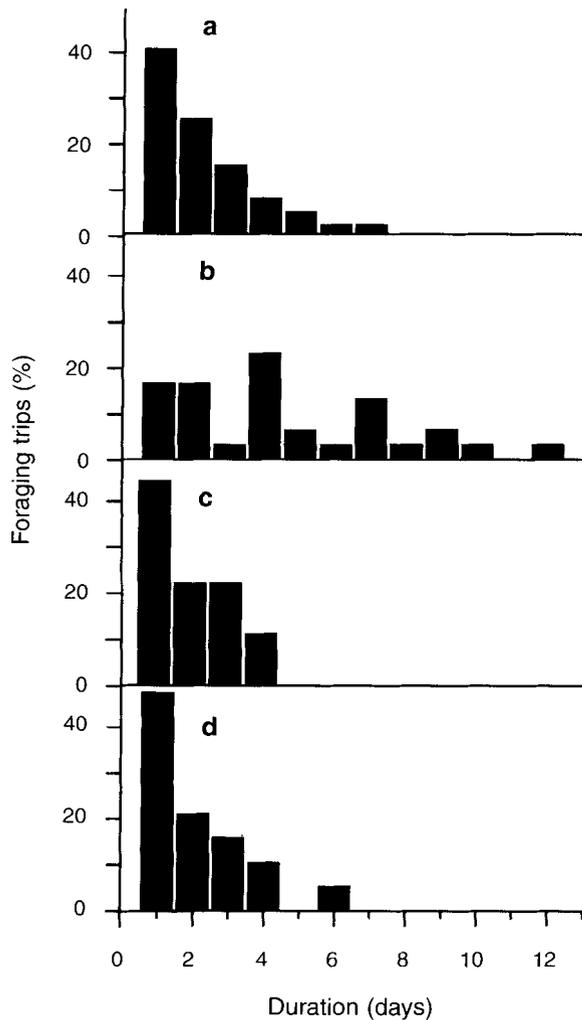
Figure 1. Frequency distribution of the duration of foraging trips in the different groups. (a) Control n = 293; (b) handicapped n = 30; (c) parents of overfed chicks n = 9; (d) parents of underfed chicks n = 19.

relationships in handicapped birds (r = –0.01, P = 1, n = 40 and r = –0.19, P = 0.26, n = 37 respectively). Control birds tended to spend more time at sea after they had delivered a meal to a chick in good condition (r = 0.214, P = 0.003, n = 196) whereas there was no such relationship for handicapped birds (r = 0.09, P = 0.68, n = 30).

Overall, adult birds were heavier between 20–22 December than at the end of the study period in mid-January (2.41 ± 0.30, n = 51 and 2.16 ± 0.20, n = 34 respectively, t = 4.16, P < 0.0001). In December, control and handicapped birds were of similar mass (2.42 ± 0.30, n = 38 and 2.37 ± 0.30, n = 13; t = 0.53, P = 0.597) and both group lost mass during the study period (paired samples t-test for control birds t = 3.7,

P = 0.096). However, chicks of control birds had significantly longer wings in March than those of handicapped birds (452.6 ± 17.6 mm, n = 25 and 431.4 ± 30.7, n = 11; t = 2.6, P = 0.013). Survival of chicks from the end of the study to fledging was similar for the two groups (Yates corrected χ^2_1 = 0.0, P = 1.00).

The size of the meals was unrelated to the time spent foraging in both control and handicapped birds (r = 0.07, P = 0.37, n = 161 and r = 0.08, P = 0.72, n = 25). In control birds, the size of the meal was related to the time elapsed since the previous meal was received by the chick (r = 0.273, P = 0.014, n = 184) and inversely related to the body condition of the chick (r = –0.160, P = 0.036, n = 171). There was no such
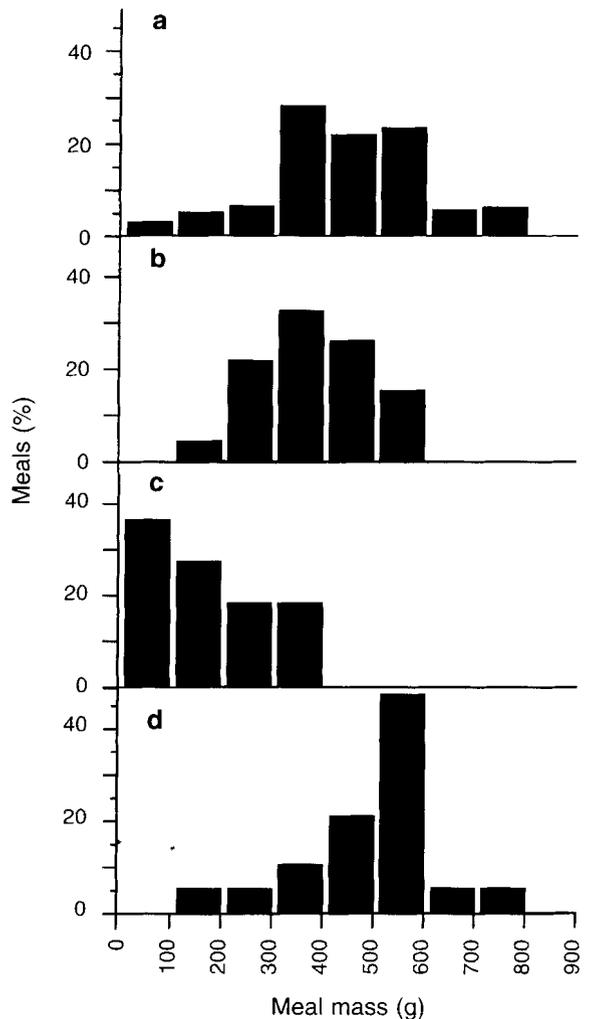

Figure 2. Frequency distribution of the mass of meals delivered to chicks in the different groups. (a) Control n = 196; (b) handicapped n = 48; (c) parents of overfed chicks n = 11; (d) parents of underfed chicks n = 22.

P = 0.003, n = 14 pairs; for handicapped birds t = 2.74, P = 0.025, n = 9 pairs). Handicapped birds were on average 127 g lighter than control birds in January (t = 1.92, df = 32, P = 0.058).

The rate of return the next season was similar for control and for handicapped adults (χ^2_1 = 2.26, P = 0.133).

Comparison between control birds and the parents of underfed and overfed chicks

Control adults spent a similar time with their chick to adults rearing overfed or underfed chicks ($F_{2,111}$ = 0.103, P = 0.902). The duration of foraging trips did not differ between the three groups (Fig. 1; $F_{2,110}$ = 0.360, P = 0.698). The mass of meals delivered to control, underfed and overfed chicks differed (Fig. 2; $F_{2,102}$ = 10.39, P = 0.0001), with control chicks receiving larger meals than overfed chicks (Tukey post-hoc test, P = 0.0004) but similar meal size to underfed chicks (P = 0.146).

Relation between adult body mass and foraging parameters

In January 1992, adult birds were of similar mass (2.19 ± 0.20 kg, n = 49) to those in January 1996 (t = 0.67, P = 0.50). The change in mass of adults from one trip to the next was not related to the duration of the foraging (r = 0.02, n = 36, P = 0.89) or to the mass of the meal delivered (r = 0.026, n = 35, P = 0.89). The mass of the adult was related to the duration of the next foraging trip (r = –0.35, n = 42, P = 0.02) indicating that birds with a high mass after having delivered a meal tended to do shorter trips than birds with a lower mass.

DISCUSSION

Regulation of provisioning

Seabirds can adjust their provisioning behaviour by modifying the time spent foraging, the amount of food delivered, or both. The regulation of provisioning is likely to occur when food availability varies, or when the needs of the chick vary, either naturally or experimentally. Adult Yellow-nosed Albatrosses are able to regulate provisioning in relation to the nutritional status of the chick. They reduce feeding frequency when the chick is in good condition. They also tend to deliver smaller meals to chicks in good condition. However, underfed chicks are not fed more frequently

or with significantly heavier meals. This result does not contradict the observational evidence that adults regulate provisioning. It indicates that the ability of adults to increase chick provisioning is limited. Similar results have been obtained using the same methodology on Black-browed Albatrosses *Diomeda melanophrys* (Weimerskirch *et al.* 1997b) and with other manipulations in Leach's Storm Petrels *Oceanodroma leucorhoa* (Ricklefs 1987, 1992).

Adult Yellow-nosed Albatrosses feeding overfed chicks deliver less food than control birds but do not modify the duration of their next foraging trips accordingly, whereas British Storm Petrels *Hydrobates pelagicus* and Black-browed Albatrosses similarly reduced feed mass but also spent more time foraging when provisioning overfed chicks (Bolton 1995, Weimerskirch *et al.* 1997b). Reducing the amount of food delivered should be considered as passive from the point of view of the adult since it is likely to be the result of the reduced swallowing capacities of the chick: the chick could not swallow more food, and the adult is unable to deliver more food. On the other hand, spending more time foraging suggests an active response to overfeeding that seems not to occur in Yellow-nosed Albatrosses. More surprisingly, Leach's Storm Petrels and Cory's Shearwaters *Calonectris diomeda* with overfed chicks did not modified their provisioning rate accordingly (Ricklefs 1992, Hamer & Hill 1994). However different levels of overfeeding may explain the differences since albatross chicks were fed with large amounts of food until they were satiated whereas in the two latter cases chicks were fed with fixed quantities of food. This emphasizes how difficult it is to compare manipulations when differences existed in procedure (Bertram *et al.* 1996). Also the comparison between species in the response of adults is made difficult by the scarcity of data on individual behaviour that is essential, for example, for an indication of the duration of foraging trips.

Thus, in contrast to several studies suggesting that seabirds regulate their feeding effort according to a fixed schedule independent of the needs of the chicks (Ricklefs 1987, 1992, Hamer & Hill 1993, Saether *et al.* 1993, Ricklefs & Schew 1994) it appears that certain species, including the Yellow-nosed Albatrosses, can regulate provisioning in relation to the nutritional status of the chick (see also Bolton 1995, Weimerskirch *et al.* 1997b). However, when chick needs are experimentally increased almost all species, including Yellow-nosed Albatrosses, are unable to increase the provisioning rate significantly. This indicates that birds can perceive the nutritional status

of the chick (probably through the chick begging intensity, Kilner & Johnstone 1997) and modify their behaviour accordingly. However they are probably unable to increase their foraging effort, probably because food availability is limited.

Effects of increase in foraging costs

Yellow-nosed Albatrosses fitted with a load handicap are unable to provision their chick at the same rate as control birds. They delivered slightly lighter (–15%) feeds, but spent much more time foraging (+125%). Adding weight increases wing loading and therefore presumably energy requirements (Pennycuick 1989), thus reducing foraging efficiency. However, it should be noted that additional loads represent only 6% of the adult body mass whereas average food loads carried by control birds represent 20% and maximum food loads 36%. In view of the marked response to the addition of loads it appears that foraging ability may be reduced. Indeed, adding loads not only adds mass to the bird but also may change the bird's centre of gravity (Mauck & Grubb 1995) and may therefore impose compensatory energy requirements (Wright & Cuthill 1989). The additional cost or difficulty of foraging is apparently expressed as additional time spent foraging, suggesting that handicapped birds tend to maximize the size of meals at the expense of their frequency. The handicap also reduced the ability of birds to regulate the size of the meal or the duration of the foraging trip in relation to the nutritional status of the chick.

The lower provisioning rate of handicapped birds results in a much lower growth rate of their chicks, but not in a lower fledging success. Since the effects of additional loads only lasted for about a fifth of the overall fledging period, it had a limited effect on chick growth. Yet the delays in growth of the chick were not negligible since, at fledging, chicks of handicapped birds had shorter wings and were slightly lighter than those of control birds.

Two other studies have used load handicaps (with a similar relative mass) to increase the foraging costs of adult Procellariiformes provisioning chicks, one on 650 g Antarctic Petrels *Thalassoica antarctica* (Saether *et al.* 1993), the other on 150 g Antarctic Prions *Pachyptila desolata* (Weimerskirch *et al.* in press). In both species, handicapped adults reduced the rate of provisioning the chick, a significant proportion of handicapped birds deserted the nest and breeding success was reduced compared with control birds. The same manipulation had a greater impact on the fitness of the adults of the two smaller species than we have

observed in Yellow-nosed Albatrosses. Antarctic Petrels reduced provisioning through feeding chicks less frequently and delivering smaller feeds, whereas the Antarctic Prion delivered similar food loads to controls but less frequently by spending more time foraging on long pelagic foraging trips. Yellow-nosed Albatrosses are similar to these species in that they also spend more time foraging to compensate for additional costs, again suggesting that in all three species compensation operates more at the level of feeding frequency through variable foraging time rather than at the level of meal mass.

Role of adult mass in regulation ability

As in other species of petrels and albatrosses (Weimerskirch *et al.* 1997a, Tveraa *et al.* 1997, Weimerskirch 1998) adult body mass plays an important role in the foraging decision since the mass of the adult after it has delivered a meal influences the duration of the next foraging trip, suggesting that extra energy reserves allow birds to spend less time foraging. The ability of adults to regulate provisioning according to their own body condition and to the nutritional status of the chick contradicts the idea that adults have a fixed level of provisioning (e.g. Ricklefs & Schew 1994).

Adult birds lost only slightly more mass than control birds but the major mass loss between the beginning and end of the study was not due to the addition of loads. Indeed, both control and handicapped adults lost mass from the end of brooding, indicating that the major cause for mass loss at this time of the year could be a fixed process, perhaps induced by the energetic stress of the brooding period (see Ricklefs 1983) or as an adaptation to either reduce the costs of foraging (Norberg 1981) or to increase food transporting capacity. Alternatively, such mass loss could be due either to greater energy stores being needed during long periods on the nest or lower optimum adult body mass during sustained periods of foraging and provisioning young in the nest or both.

In the two smaller species, handicapped adults do not deteriorate in body condition (Saether *et al.* 1993, Weimerskirch *et al.* 1999) and Yellow-nosed Albatrosses reduce their mass, but only slightly. In another species of small petrel (Leach's Storm Petrel) where foraging has been impeded by increased flight costs through reduction of wing span, the adults did not lose body condition but reduced provisioning (Mauck & Grubb 1995). This indicates that when foraging costs are increased or foraging made more difficult, the first

priority for the birds is to keep their body mass at a high level, at the expense of provisioning. If they are not able to achieve this, birds desert, as is common in two small species (Saether *et al.* 1993, Weimerskirch *et al.* 1999). When they rear their chick, small petrel species have been shown to work with almost no 'safety margin', i.e. the difference between the working mass and the mass at desertion (Chaurand & Weimerskirch 1994) whereas larger species have a much larger safety margin (Weimerskirch 1999). The absence of desertion and the slight decrease in body mass of Yellow-nosed Albatrosses indicates that in this larger species birds are working with a margin that allows them to buffer, to a limited extent, the effects of increased foraging costs. Indeed, the mass at desertion is on average 1750 g in Yellow-nosed Albatrosses (Weimerskirch 1999), i.e. 350 g lower than the mass of handicapped birds at the end of the experiment. As could be expected for a long-lived species, the increased costs incurred by handicapped birds had no effect on their survival.

The reduced ability to increase provisioning in response to increased chick needs or foraging costs results either from the bird's inability to increase provisioning because of resource limitation (constraint hypothesis, Curio 1983), or birds restraining their effort. The latter is expected to be important in species such as long-lived seabirds that should balance current investment in the offspring against future reproduction (Williams 1966, Goodman 1974). As expected (Drent & Daan 1980) when faced with an increased cost of foraging or increased chick needs, parents first favour the maintenance of their body condition over that of their chick. Several studies have indeed shown that adult body condition plays a central role in foraging decisions as well as in breeding decisions (e.g. Chastel *et al.* 1995, MacNamara & Houston 1996, Weimerskirch 1998). Constraint on food availability is also likely to limit the ability of seabirds to regulate the provisioning of their chicks. Situations where resource availability naturally varies indicate that, in cases of food shortage, provisioning parameters are affected negatively (e.g. Monaghan *et al.* 1989, Weimerskirch *et al.* 1997b). It is highly likely that provisioning strategies have evolved in the context of naturally variable food availability. Increasing levels of food stress would be expected to lead to an inability to regulate provisioning, to reduced provisioning (Weimerskirch *et al.* 1997b), desertion or for birds to refrain from breeding (Chastel *et al.* 1995). When conditions are favourable (good season) reproduction may make a high proportional contribution to fitness (Erikstadt

et al. 1998). In this context, interpretation of the ability to regulate may vary according to the food availability during a particular season, and the ideal experimental procedure would be to carry out studies over several seasons with variable food availability.

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