Petrel parents shunt all experimentally increased reproductive costs to their offspring

R. A. MAUCK & T. C. GRUBB, JR
Behavioral Ecology Group, Department of Zoology, The Ohio State University, Columbus, OH 43210, U.S.A.

(Received 7 December 1993; initial acceptance 2 March 1994; final acceptance 12 April 1994; MS. number: a6865)

Abstract. Investment in current reproduction should be balanced against future reproduction. Thus, the allocation of resources during a breeding season is a trade-off between the needs of the parent and the needs of the offspring. Life-history theory predicts the trade-off point to favor the parent in long-lived species and the offspring in short-lived species. To investigate parent-offspring conflict in a long-lived species, the cost of flight was manipulated (by reducing wing span) in Leach’s storm-petrel, Oceanodroma leucorhoa. The effect of the manipulation on adult nutritional condition was measured using ptilochronology and the effect on offspring nutritional condition was measured by tracking chick growth. No difference was found in nutritional condition between treatment and control parents. Treatment chicks gained mass more slowly and spent a greater proportion of nights without being fed by either parent. As predicted for a long-lived species, when faced with an increased cost of parental care, the storm-petrel parents apparently shunted that cost to their offspring. These results are compared with previous studies of long- and short-lived species in which parental costs were artificially increased.

Parental effort, as defined by Trivers (1972), is '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'. Parental effort that maximizes an individual adult's lifetime reproductive success may yield parental care that is less than that required by its offspring to maximize its own lifetime reproductive success. A balance is struck between these competing demands. While Trivers (1974) showed that the balance may be partially a function of parental age, one may also expect the nature of the balance to be influenced by the life history of the species, with bias towards offspring in short-lived species and towards parents in long-lived species (Linden & Møller 1989). Members of the avian order Procellariiformes are long-lived, pelagic seabirds that exhibit delayed maturity, single-egg clutches, and long periods of parental care. We manipulated the cost of flight in one of the smaller Procellariiforms, Leach's storm-petrel, Oceanodroma leucorhoa, to investigate parent-offspring conflict in a long-lived species.

During the period of parental care, Procellariiforms often forage far from the colony. Satellite tracking of wandering albatrosses, Diomeda exulans, has recorded foraging trips lasting up to 33 days and covering 15 200 km (Jouventin & Weimerskirch 1990). Such detailed study of the foraging flights of Leach’s storm-petrels has not been possible because of the small size of the animals. However, the pelagic nature of their food sources necessitates long journeys to ephemeral feeding patches. Leach’s storm-petrels are surface feeders, preying on euphausids and other zooplankton that are concentrated in areas of upwelling and local current clines (Haney 1985; Brown 1988a; Pittman & Ballance 1990) often unpredictable in space and time (Brown 1980, 1988b; Duffy 1989).

Adult petrels provisioning chicks return to the colony once every 2-3 nights (Ricklefs et al. 1985), arriving after dark and leaving before dawn. While the normal amount of time spent airborne during the chick-provisioning period is unknown, one adult was known to spend 42·7 of 142·5 h (approximately 30%) in flight (P. Sieverts, unpublished data). Certainly, the cost of flight is a major energetic requirement for chick-provisioning Leach’s storm-petrels (Ricklefs et al. 1986). Any increase in the cost of flight should affect the
ability of petrels to provision their young, and thus, affect the balance between the nutritional condition of parent and offspring.

Pennycuick (1989) calculated the energetic cost of both flapping and soaring flight of birds. He estimated that storm-petrels split their flight time equally between these two modes. The primary variables in his calculations were (1) the mass of the bird and its payload, (2) wing span (for flapping flight) and (3) wing area (for soaring flight). Increasing the first variable or decreasing the second and/or third increases the energetic cost of flight.

Researchers studying flight have manipulated the first and third variables. Videler et al. (1988a,b) weighted European kestrels, Falco tinnunculus, during flight tests in wind tunnels and demonstrated an increase in wing-beat frequency and change in angle of attack in response to the handicap. To investigate parental effort in European starlings, Sturnus vulgaris, Wright & Cuthill (1989) added mass to one member of a breeding pair, thereby handicapping its ability to provision young. Saether et al. (1993) followed this procedure in their study of parental effort in the Antarctic petrel, Thalassia antarctica. Harris (1971) and Verbeek & Morgan (1980) reduced wing area in gulls to investigate molt dynamics and parental behaviour. Slagsvold & Lifjeld (1988, 1990) employed a similar technique to assess the impact of a handicap on clutch size in the pied flycatcher, Ficedula hypoleuca, and in blue tits, Parus caeruleus, and coal tits, P. ater. In their study of sexual selection in bobolinks, Dolichonyx oryzivorus, Mather & Robertson (1993) reduced wing span to increase variation in flight display durations among males.

Adding mass to a free-ranging bird may not be desirable for two reasons. It is difficult to add mass to a bird without significantly affecting its centre of gravity, stability and drag. If the bird is not recaptured or if the mass is not removed by some other mechanism, the bird remains permanently handicapped. Reducing wing span or wing area by clipping feathers can have a less dramatic effect on the mechanics of flight and the handicap will disappear soon after the experiment due to the normal post-breeding moult. Such phenotypic manipulation enables one to design an experiment that minimizes disruption and limits its persistence (see Cuthill 1991), yet still elicits a measurable response.

We adjusted the wing span of Leach’s storm-petrels during the period of chick provisioning in order to investigate an adult's allocation of resources during parental care in the face of higher energetic demand. We examined the allocation of resources delivered to chicks by tracking chick growth and the cost of parental care to the parent using ptilochronology (Grubb 1989, in press).

Ptilochronology uses growth rates of feathers to index the nutritional condition of birds (e.g. Cimprich & Grubb 1990; Waite 1990; Yosef & Grubb 1992). The method involves pulling a bird’s rectrix (tail feather), thereby inducing the growth of a replacement. When the bird is re-captured several weeks later and the induced feather pulled, the growth characteristics of the induced rectrix provide an index of the bird’s nutritional status during the intervening period. A bird in good nutritional condition will grow its induced feather at a faster rate than will a bird in poor nutritional condition. We used feather growth as a direct measure of the nutritional status of a bird engaged in parenting.

If parental care were to become unnaturally costly due to a handicap, a petrel might reduce its own nutritional condition, the nutritional condition of its chick, or both. Such reductions could be manifested in a number of ways. A parent could maintain its own nutritional condition and allocate fewer resources to the chick, a strategy predicted for long-lived species. If this hypothesis were true, then during the chick-provisioning period, handicapped petrels should regenerate a rectrix as rapidly as controls, but their chick should grow more slowly. We predicted that the chicks of handicapped petrels would remain unfed for more days, would receive less food when fed, and would show reduced growth rates of mass and wing length than would chicks of control parents.

Alternatively, a handicapped parent could provision its chick with normal amounts of food at normal intervals and degrade its own nutritional condition. If this hypothesis were true, induced feather growth should proceed more slowly for handicapped adults than for controls, but chick feeding rate and growth should not vary.

A third hypothetical response to handicapping would involve the parent reducing both its own and its chick’s nutritional condition. If this were true, then growth rate of the parent’s induced
rectrix and rate of chick growth should both be reduced.

Finally, if parental care in Procellariiformes has such a low energetic demand that slightly handicapped flight (see Methods) has no appreciable effect, there should be no significant differences between experimental and control groups.

**METHODS**

During the summers of 1991 and 1993, we identified and banded 20 breeding pairs of Leach’s storm-petrels at the Bowdoin College Scientific Station on Kent Island, New Brunswick, Canada (66°45’W, 44°35’N). The birds’ burrows, dug in the floor of the mixed spruce/hardwood forest, were monitored for hatch date of the eggs. On hatch day, the brooding adult present was removed from the burrow long enough to pull its outer right rectrix (OR6) and to perform the treatment or control procedures described below. We continued to monitor each burrow daily until the second member of the pair had been caught and treated. In all cases, the second member of the pair was captured within 2 days. To control for possible variation in responses due to hatch date, assignment to treatment or control group was decided by coin toss within successive pairs of burrows based on hatch date.

The handicapping treatment was applied to both members of the 10 treatment pairs. After extending a petrel’s wings across a flat surface, dorsal surface up, we used a felt-tipped marker to draw lines across the wing perpendicular to the long axis of the wing and 1.5 cm from each tip. We cut the primary remiges along that line with a pair of scissors. According to Pennycuick’s equations (Pennycuick 1989), this reduction of wing span by 3 cm increased the cost of flight by approximately 9%, given the average mass (45 g) and wing span (48 cm) of Leach’s storm-petrel (Gross 1935; Ricklefs 1987; R.A.M., unpublished data). The 20 birds in the 10 control pairs were handled in an identical manner with the exception that we merely touched the scissors to the wing along the line marked on each wing. After the manipulations had been completed, we returned each bird to its burrow.

Chick growth was monitored daily between days 7 and 44 post-hatch. This span covered the period of greatest daily mass gain in Leach’s storm-petrel chicks (Gross 1935; Ricklefs et al. 1980b; R.A.M., unpublished data). Flattened wing chord was measured to the nearest millimetre, and mass was taken to the nearest 0.1 g with an OHAUS Model 66 balance. Day 44 post-hatch is the latest date used in our analysis since we began trapping parents to retrieve the induced rectrix on day 45, an intervention that is likely to have disrupted their provisioning routine.

We recaptured adult petrels as they returned to feed the chick by placing one-way traps in burrows. We checked the traps at about 0400 hours each night and when we found an adult, we removed it from the burrow, pulled its induced outer right (IR6) rectrix, and then released it.

The daily mass gain and daily wing growth for each chick were modelled by simple linear regression. The values for the slopes of the regression lines were used to compare parental input by treatment and control adults. A previous analysis had shown that the slopes of growth curves from 100 unmanipulated burrows were normally distributed (R. A. Mauck & C. E. Huntington, unpublished data), so we used two-factor ANOVA to test daily mass gain and daily wing growth against year and treatment group.

We used Ricklefs et al.’s (1985) criteria relating daily mass gain in Leach’s storm-petrel chicks to parental feeding visits to determine the number of nights during the study period in which a chick was not fed by either parent, or by at least one parent. For those nights during which at least one parent fed a chick, we used these criteria to calculate mean change in chick mass per parental visit as an index of load size carried by one adult. We used the Mann–Whitney U-test to compare days spent fasting and mean mass change when fed of control and treatment chicks.

We measured the length of original and induced rectrices of adults to the nearest 0.01 mm using electronic calipers. To obtain an index of growth rate for the induced feather, we divided induced feather length by original feather length, divided by the number of days between pulling the original and induced feathers (including the original feather length within the index standardized for body size). To ensure statistical independence of data, we used the burrow, rather than the parent bird, as the primary sampling unit when employing Mann–Whitney U-tests to assess the treatment effect on feather growth. Thus, when induced
feathers from both parents were available, we used the mean value.

**RESULTS**

Daily mean (± SD) mass gain was significantly greater for control chicks (1.39 ± 0.18 g/day) than for treatment chicks (1.12 ± 0.31 g/day; Table I). Year effect (P = 0.68) and treatment*year interaction (P = 0.58) were not significant (Table II). Daily mean (± SD) growth of the wing was greater for control chicks (2.39 ± 0.42 mm/day) than for treatment chicks (2.27 ± 0.30 mm/day), although the difference was not statistically significant (Table III).

Treatment chicks went unfed on a significantly greater proportion of nights (Table I). On nights when chicks were fed, no statistical difference was found in the mean chick mass change per parental visit between control and treatment groups (Table I). However, treatment adults did deliver somewhat larger loads (3.72 ± 0.92 g) than control adults (3.48 ± 0.54 g).

Twenty-nine of the 40 adults in the study were recaptured and their induced feathers collected. No difference was found in the index of feather growth between treatment and control groups (Table I).

**DISCUSSION**

The results best fit the hypothesis that adult Leach’s storm-petrels maintain their own nutritional condition and allocate fewer resources to the chick when faced with increasing energetic demands. A dult nutritional condition, as indexed by feather growth, was not statistically different between treatment and control birds (Table I),...
but treatment chicks grew at a slower rate than control chicks (Table I).

Owing to the difference in chick growth rate, the peak mass attained by control chicks (79.0 ± 11.2 g) exceeded that of treatment chicks (69.3 ± 10.1 g). Chick body mass declines sharply in the final 7–10 days prior to fledging and at fledging is approximately 121% the mass of an adult (Ricklefs et al. 1985). The relationship between peak mass and chick survivorship is not clear. However, chicks with higher peak masses are also heavier at fledging (R. A. Mauck & C. E. Huntington, unpublished data), a condition thought to increase the probability of post-fledging survivorship in other Procellariiforms (Perrins et al. 1973).

In Leach’s storm-petrel chicks, wing growth is less sensitive to rate of food delivery than is change in body mass (Ricklefs et al. 1980b, 1987; Ricklefs 1992), a result confirmed by our results which revealed no statistical difference in wing growth between control and treatment groups (Table I). Wing growth proceeds in a monotonic curve that is sufficiently buffered from short-term variations in rate of food delivery that it can be used as a reliable indicator of chick age (Ricklefs et al. 1987; R. A. M., unpublished data). In one experiment, chicks partially deprived of food for 15 days had normal rates of wing growth even though they were underweight (Ricklefs 1992). In an investigation of dietary quality and growth rate, petrel chicks did not accelerate wing growth if given supplemented diets (Ricklefs et al. 1987). Thus, while wing growth may be an index of whether some minimum food requirement is met, gain in body mass more accurately tracks the amount of food delivered by parents, and is, therefore, a more sensitive measure of parental input.

While we were not able to monitor directly the number of parental visits, the calculated proportions of nights spent fasting by the chick suggest that the primary method employed by the treatment parents to reduce the cost of the handicap to themselves was to make fewer visits. Treatment chicks spent a significantly greater proportion of nights fasting than did control chicks (P = 0.03), suggesting that food delivery was more consistent for control than for treatment chicks.

Periodic fasting is common in petrel chicks and the rapid lipid accumulation also characteristic of petrel chicks may be a hedge against the risks associated with unpredictable food sources. While fat stores in O. leucorhoa chicks exceed the demands of the normal 1–3-day fasts (Ricklefs et al. 1980a), a foraging model developed by Ricklefs & Schew (in press) demonstrated that high levels of fat storage may serve to ensure chick survival through rare periods of extensive fasting. In our study, no fasting bout exceeded 3 days. Thus, the increased fasting by treatment chicks may simply have reflected the mechanism by which parents cope with any sort of reduction in net energy accumulation at sea.

The apparent decrease in visitation rate may have been misleading. An alternative interpretation might be that treatment parents compensated for the reduced wing length by carrying smaller loads. Such a strategy would inflate our estimation of nights spent fasting, if some feeding visits were not tallied at all. If so, we would also expect a smaller percentage of calculated double-feed nights in the treatment chicks due to a failure of two small loads to attain the threshold value for the two-feed classification. This was not the case. If we use Ricklefs’ criteria of chick mass gain to define double-feed nights, we see no difference in the proportion of double-feed nights between controls (0.21) and treatments (0.21) and a slight decrease in proportion of single-feed nights from control (0.51) to treatment (0.45). There is no evidence, therefore, that handicapped adults adjusted load size downward to compensate for the increased cost of flight. Lowered visitation rates, alone, may be sufficient to explain the difference in chick growth.

Feeding frequency reflects the balance struck between satisfying offspring and parental needs (Nur 1984). Ricklefs et al. (1985) suggested that chick reserves allow Leach’s storm-petrel adults to bring large loads less often, thus increasing foraging efficiency. While not statistically significant, the difference between groups in mean chick mass change per parental visit (Table I) suggests that handicapped parents may have further shifted balance towards even fewer, heavier loads to compensate for the cost of the handicap.

Handicapped parents may have shifted to a more risk-prone foraging strategy in response to the added cost of flight, venturing to less reliable patches that held opportunities for higher payoffs. This strategy would produce the observed pattern of fewer nights fed, yet more mass gained by the chick per parental feeding visit. Risk-prone
parents should produce a temporal pattern of feedings marked by high variance; therefore, we would predict that the variance in the duration of fasting bouts in treatment chicks would be greater than in controls. However, the trend ran counter to the prediction. Control mean (± sd) variance (0.38 ± 0.18) exceeded treatment mean variance (0.32 ± 0.16), a trend not significantly different from random (Mann–Whitney U-test: U* = 62.5, P = 0.25). Thus, we have no evidence to suggest that handicapped parents shifted to a more risk-prone strategy.

It is possible that the age structure of our samples influenced results. Williams (1966) suggested that animals of long-lived species have been selected to show reproductive restraint during early breeding attempts, and then to increase their effort as they age (see also Beauchamp & Kacelnick 1990; Clark & Ydenberg 1990). Annual survival of Leach’s storm-petrel is known to increase after the first two breeding seasons, to stabilize between years 3 and 17, and to decline slowly after the 17th year (Huntington 1990). Age-specific reproductive investment is one possible cause of the gradual decline in survival during the later years. Had the proportion of old individuals in the control group been significantly greater than in the treatment group, the observed difference in chick provisioning may be explained by Williams’ effort hypothesis. Conversely, the increased annual survival after the second breeding year may be a function of breeding experience. If breeding experience increases parental ability as well as the probability of survival, a preponderance of first- and second-year breeders in the treatment group could explain the observed difference in chick mass gain between experimental groups.

The individuals in this experiment were a random sample of unknown age. However, we assessed the probability of an inter-group age imbalance by examining the age structure of a nearby colony. During the 1993 breeding season, birds in their first and second breeding seasons accounted for approximately 30% of that population, while individuals with more than 17 breeding seasons accounted for approximately 5% (C. E. Huntington, unpublished data). We calculated the probabilities that the treatment group had one or more first- or second-year breeders than predicted by chance (cumulative binomial P = 0.42). The overall probability of such an imbalance is the product (P = 0.16) of the individual binomial probabilities. Increasing the magnitude of the imbalance quickly decreases the probability of its occurrence. For example, increasing the disparity by one more first- or second-year breeder per group yields an overall probability of less than 0.03. Similar calculations for a between-group imbalance among old individuals (>17 breeding seasons) yield similar overall probabilities (P = 0.09 and P < 0.03). Any intra-pair age asymmetries would have required an even greater inter-group imbalance to significantly affect the results at the burrow level. Therefore, it appears highly unlikely that our results were biased by age-specific parental investment or experience.

Saether et al. (1993) found results similar to ours in a manipulation of another Procellariiform, the Antarctic petrel. In their experiment, one member of a breeding pair was handicapped by adding leg weights (6% of body weight). A dult Antarctic petrels, like Leach’s storm-petrel, transferred the cost of the handicap to the chick by making fewer feeding visits. Unlike Leach’s storm-petrel, handicapped T. antarctica delivered smaller loads. While chick growth rates were not reported, the authors reported a greater proportion of moribund chicks among pairs with one handicapped parent than among control pairs.

The double adjustment by manipulated T. antarctica, decrease in both rate and size of food deliveries, may have resulted from the nature of the handicap. According to Pennycuick’s equations, the increased cost of flight was similar in T. antarctica and O. leucorhoa (approximately 9%, assuming mass = 666 g and wing span = 1.05 m for T. antarctica; Marchant & Higgins 1990). However, it is difficult to add mass to a bird without substantially affecting its centre of gravity, stability, and flight. Adjusting wing span may have had a less dramatic effect on the mechanics of flight in O. leucorhoa than did adding mass to T. antarctica.

It is also possible that Antarctic petrels are more severely constrained than are Leach’s storm-petrels by large travel costs between food sources and nest site. The Antarctic petrel colony studied was located 200 km inland, ensuring a round-trip commute of at least 400 km. Leach’s storm-petrels
Table IV. Handicapping studies in which the effect on both parent and offspring nutritional condition was monitored

<table>
<thead>
<tr>
<th>Species</th>
<th>Annual adult survival</th>
<th>Handicap</th>
<th>Effect on nutritional condition of chick</th>
<th>Effect on nutritional condition of parent</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pied flycatcher, F. hypoleuca</td>
<td>30-70%</td>
<td>Feathers removed</td>
<td>Negative; lower feeding rates</td>
<td>Negative; re-nesting females had significantly reduced body condition</td>
<td>Berndt &amp; Sternberg (1963)*; Slagsvold &amp; Lifjeld (1988)†</td>
</tr>
<tr>
<td>Blue tit, P. caeruleus</td>
<td>35-50%</td>
<td>Feathers removed</td>
<td>Negative lower chick body mass at fledging</td>
<td>Negative when female handicapped, loss of body mass by both sexes</td>
<td>Perrins (1979)*; Slagsvold &amp; Lifjeld (1990)†</td>
</tr>
<tr>
<td>Coal tit, P. ater</td>
<td>33-66%</td>
<td>Weight added</td>
<td>Negative reduced chick growth rates, lower feeding rate</td>
<td>Negative; partner of handicapped mate increased feeding effort</td>
<td>Wright &amp; Cuthill (1989, 1990)**†</td>
</tr>
<tr>
<td>Starling, S. vulgaris</td>
<td>&gt;78%</td>
<td>Feathers shortened</td>
<td>Negative lower chick daily mass gain</td>
<td>None</td>
<td>Morse &amp; Buchheister (1979); Huntington (1990)*; this study†</td>
</tr>
<tr>
<td>Leach’s storm petrel, O. leucorhoa</td>
<td>&gt;80%</td>
<td>Weight added</td>
<td>Negative smaller loads delivered to chick, lowered feeding rate</td>
<td>None</td>
<td>Warham (1990)*; Saether et al. (1993)†</td>
</tr>
</tbody>
</table>

*Survivorship.  †Handicapping.
nest on islands, making possible much shorter round trip flights and, therefore, an avenue for compensation not available to the Antarctic petrels in Saether’s study.

Ricklefs (1987) manipulated demand at the nest in an attempt to increase the rate of food delivery by Leach’s storm-petrel. When presented with food-deprived, begging chicks on every visit to the nest, the adult petrels failed to increase their rates of food delivery. Ricklefs concluded that parents control the feeding frequency, even in the face of increased demand at the nest. Ricklefs (1992) suggested that feeding rate is set at a level sufficient to rear the chick successfully and the chick has little influence on that set rate. Our results conform with this interpretation in that adult storm-petrels apparently could not be induced to bear the nutritional cost of increased energetic demands.

Manipulations of parental effort in less long-lived avian species show a different pattern (Table IV). When adult flycatchers, starlings, and tits were handicapped, the nutrition of their nestlings was reduced, but the cost of the handicap was at least partially shared by the parents. Wright & Cuthill (1989, 1990) reported increased parental effort by starlings in response to lessened care by their handicapped partners. However, the compensation was not sufficient to prevent slower chick growth and lower chick body mass of fledging. In one year of Slagsvold & Lifjeld’s study (1988), handicapped female flycatchers showed significantly decreased nutritional condition, indexed as $10 \times$ body mass/tarsus length$^3$. In this species, males could not be induced in reduce their body mass. When Slagsvold & Lifjeld (1990) repeated their experiment with blue tits and coal tits they found that both sexes lost body mass while rearing offspring after the female member of the pair had been handicapped. While offsprings growth was adversely affected by the handicap in all three of the above studies of passerine birds, it seems that in these short-lived (relative to Procellariiforms) species, parents assumed some of the cost.

It is worth noting that mean clutch size in flycatchers, starlings and tits ranges from five to 11 eggs. Because of the low annual survival rates of adults in these species, each clutch accounts for a large proportion of a parent bird’s lifetime reproductive success. Selection, therefore, might favour parents that invest more highly in present reproduction rather than withholding effort for future attempts. Petrels, however, allocate their reproductive effort in smaller annual packets. For a long-lived species like Leach’s storm-petrel, in which the probability of adult survival is high (Table IV), the one chick reared each year represents a small portion of lifetime reproductive success. Any increase in current reproductive effort beyond a level promoting both current reproductive success and high probability of survival will be selected against (Williams 1966; Bell 1980). Thus, any nutritional cost due to phenomena such as reduced availability of prey, extended periods of heavy storm, or reduced flight efficiency, should be shunted to the chick rather than be borne by the parent.

ACKNOWLEDGMENTS

We thank Nancy Yorinks, Kerry Bacher and Holly Wagner for field assistance, as well as Nat Wheelwright and Chuck Huntington for arrangements and advice at the Bowdoin College Scientific Station, from which this paper is contribution no. 117. We thank R. Bruce MacWhirter and Patricia Parker for comments on an early draft. The suggestions of two anonymous referees and Dale F. Lott improved the manuscript. This experiment was performed during research periods supported by a Frank M. Chapman Award from the American Museum of Natural History and a Paul A. Stewart Award from the Cooper Ornithological Society.

REFERENCES
