

Chick feeding in the diving petrels *Pelecanoides georgicus* and *P. urinatrix exsul*

DANIEL D. ROBY

Cooperative Wildlife Research Laboratory and Department of Zoology, Southern Illinois University, Carbondale, Illinois 62901, USA

Abstract: Chick feeding in common diving petrels (*Pelecanoides urinatrix exsul*) and South Georgia diving petrels (*P. georgicus*) was studied on Bird Island, South Georgia. Complete chick meals removed from the proventriculus of adults averaged 25.5 g (n = 32) for common diving petrels (17.6% of adult mass) and 23.3 g (n = 24) for South Georgia diving petrels (20.2% of adult mass); neither contained stomach oils. The sum of the positive mass increments during overnight weighings (SUM) averaged 48.6 g for common diving petrel chicks (n = 78 chick nights) and 41.6 g for South Georgia diving petrel chicks (n = 78 chick nights). Average adult feeding frequencies were 0.95 meals day⁻¹ and 0.92 meals day⁻¹, respectively. Relative meal size in diving petrels was similar to that of other procellariiforms, but SUM averaged about twice that of other petrels. The lower conversion efficiency of meals to body mass in diving petrel chicks reflects the absence of stomach oils in the diet. Higher chick feeding frequency and lower variance in SUM are consistent with the hypothesis that diving petrels forage nearshore on reliable food supply compared with other procellariiforms.

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Introduction

The diving petrels (Pelecanoididae) are a monogeneric family of small petrels (Procellariiformes) restricted to the Southern Hemisphere. Their morphology and foraging behaviour are distinctly different from other procellariiforms and very similar to the small auks (Charadriiformes: Alcidae) of the Northern Hemisphere (Murphy & Harper 1921, Kuroda 1967, Warham 1977a). Similarities in breeding biology between diving petrels and alcids have been attributed to selection pressures upon species occupying similar ecological niches (Lack 1968, Thoresen 1969, Warham 1977a, Payne & Prince 1979, Roby & Ricklefs 1983).

Both diving petrels and alcids use their wings to propel themselves underwater in pursuit of prey. The high wing loading of pursuit-diving seabirds dramatically increases energy costs of flight and lowers energy return from long-distance foraging (Roby & Ricklefs 1986). From observations at sea and the frequency of meals delivered to nestlings, it appears that alcids foraging closer to the breeding colony than most pelagic seabirds, including petrels (Hunt *et al.* 1978, Roby & Brink 1986). One would predict that diving petrels, like their ecological counterparts the alcids, feed their young smaller less variable meals at a higher frequency than other petrels.

Few data are available on the feeding of diving petrel nestlings. Payne & Prince (1979) weighed five South Georgia diving petrel (*Pelecanoides georgicus* Murphy & Harper) chicks twice daily from 15 days old until fledging and concluded that nestlings are normally fed each night. By

weighing 11 chicks at three-hour intervals over a 24-hour period, they inferred that both parents often visit the nest in one night. This paper reports on both the size and frequency of meals for the nestlings of common diving petrels (*P. urinatrix exsul* Salvin) and South Georgia diving petrels breeding at Bird Island, South Georgia.

Methods

Work was conducted on Bird Island (54°00'S, 38°02'W), located at the western end of South Georgia, during January and February 1982. Nest burrows of common diving petrels were located on Goldcrest Point in the north-western part of Bird Island (Hunter *et al.* 1982). Nest burrows of South Georgia diving petrels were located in North Valley (Croxall & Hunter 1982). Payne & Prince (1979) describe in detail the nesting habitats and burrows of the two species of diving petrel.

Most common diving petrel eggs had hatched prior to initiation of field work on Bird Island, so the age of nestlings was estimated using data on age-specific wing length collected by Payne & Prince (1979). The straightened wing chord (bend of wrist to tip of longest primary) was measured to the nearest 1 mm with a flexible plastic ruler. Estimated ages derived from a sample of 161 wing length measurements taken from known-age South Georgia diving petrel chicks (aged 7–21 days) were 97% accurate to within three days of actual age.

Daily food intake of chicks was estimated by weighing chicks at three-hour intervals during the night. Nestling

mass was measured to the nearest 1 g with Pesola spring scales (100 to 300 g capacity). Chicks were weighed and their wing length measured at 23:00 GMT (local time), prior to the arrival of adults with chick meals. Chicks were weighed again at 02:00, 05:00 and again at 23:00 the following evening to determine the net weight gain (NET) as a result of the previous night's feeding. The sum of the positive mass increments overnight (SUM) was used as an estimate of the amount of food delivered by the parents. Overnight weighings were conducted with 15–22 of the most accessible nests on four different nights for each species, for a total of 78 chick nights for each species of diving petrel. Nestlings were eliminated from overnight weighings if their growth rates were abnormally low, indicating possible death or abandonment by one of the parents.

The ratio of NET:SUM was used as a measure of conversion efficiency of food to biomass (Ricklefs 1984). The ratio of NET:SUM would be expected, *a priori*, to vary with stage of development (i.e., chicks that are half grown would be expected to deposit more body mass from a meal of a given size than a full-grown chick). Interspecific comparisons of chick conversion efficiencies requires SUM and NET data from comparable stages of development. Consequently, only data from chicks that had reached their asymptotic phase of growth (i.e., no daily change in body mass, on average) were used in regressing NET against SUM. The asymptotic phase begins at about 27 days post-hatching in common diving petrels and about 25 days in South Georgia diving petrels (Roby 1986).

Chick meals were collected by capturing adults in mist nets as they returned to feed chicks in parts of the colony removed from nests used in overnight weighings. Common diving petrel adults with chick meals were captured on five nights, including the four nights when overnight weighings were conducted. South Georgia diving petrel adults were captured on four nights, including three of the four nights when overnight weighings were conducted. Diving petrels transport chick meals in a distensible proventriculus and it is very difficult to obtain complete chick meals from live birds. Consequently, captured adults were humanely killed, placed in plastic bags, and frozen for later dissection and removal of the meal. In the laboratory, the proventriculus was dissected and the contents weighed to the nearest 0.01 g on a Sartorius 2463 electronic top-loading balance. Each adult, together with empty proventriculus, was weighed to the nearest 0.01 g.

Chick feeding frequency was estimated from the SUM and the mass of chick meals collected from adults. Due to excretion and respiration between feeding and weighing, the value of SUM is always somewhat less than the actual mass of food fed to the chick. To compensate for this bias, it was assumed that chicks were fed on average one and a half hours (half the period between weighings) before they were weighed. Mass loss during this period was estimated by halving the mass loss during the subsequent three-hour period (02:00–

05:00). This amount was added to the value of SUM to obtain an estimate of the actual mass of food fed to each chick. If the estimate of meal mass exceeded the largest meal removed from adults, then it was assumed that the chick had been fed by both parents.

Results

The average masses of chick meals from adults are shown in Table I. For common diving petrels, the largest meal collected from adults was 37.2 g, similar to twice the mass of the smallest meal (18.5 g). Similarly, for South Georgia diving petrels the mass of the largest meal was 30.6 g, close to twice the mass of the smallest meal (15.8 g).

One-way analysis of variance revealed that, within species, there was no significant between-night difference in meal mass ($F_{(4,27)} = 0.48, P > 0.05$ for common diving petrel meals; $F_{(3,20)} = 1.35, P > 0.05$ for South Georgia diving petrel meals). The average body mass of common diving petrel adults (145.0 g, $sd = 6.85, n = 32$) was significantly greater than that of South Georgia diving petrel adults (115.3 g, $sd = 6.99, n = 24$) collected during the chick-rearing period. The average mass of common diving petrel meals (25.5 g) was also significantly greater ($t = 1.95, P < 0.05$) than that of South Georgia diving petrel meals (23.3 g). However, meal mass as a percentage of adult body mass was significantly less for common diving petrels (17.6%, $sd = 3.03, range = 11.6–24.7, n = 32$) than for South Georgia diving petrels (20.2%, $sd = 3.37, range = 14.2–26.2%, n = 24, t = 3.03, P < 0.005$). Meal mass and adult body mass were not significantly correlated in either common or South Georgia diving petrels ($r = 0.193, df = 30, P > 0.05$ and $r = 0.152, df = 2, P > 0.05$, respectively).

Table I. Mass of diving petrel chick meals¹ from Bird Island, South Georgia during the 1982 breeding season.

Date	Average mass (g)	n	sd	se	cv	Range
Common diving petrel						
10 January	23.5	7	4.01	1.52	17.0	17.2–29.9
13 January	25.5	6	2.74	1.12	10.8	21.5–29.0
22 January	25.4	6	4.45	1.82	17.5	18.5–30.2
31 January	27.0	7	6.04	2.28	22.4	19.1–37.2
5 February	25.9	6	5.39	2.20	20.8	19.2–33.8
All	25.5	32	4.54	0.80	17.8	17.2–37.2
South Georgia diving petrel						
10 February	21.5	6	1.35	0.55	6.3	19.4–23.0
14 February	22.7	6	4.56	1.86	20.1	17.7–29.2
20 February	23.0	6	4.83	1.97	21.0	15.8–29.0
24 February	25.8	6	3.58	1.46	13.9	22.5–30.6
All	23.3	24	3.92	0.80	16.8	17.7–30.6

¹ complete contents of the proventriculus of adults returning to the nest site to feed chicks

Although some chick meals were partially digested, in no case were stomach oils found in the proventriculus of an adult diving petrel. This supports the hypothesis that diving petrels are the only procellariiforms that do not feed stomach oils to their young (Warham 1977b).

With the exception of one common diving petrel chick, all nestlings were fed by at least one parent between 23:00 and 02:00 on those nights when overnight weighings were conducted ($n = 156$ chick nights). In three of 78 cases, common diving petrel chicks also gained mass between the 02:00 and 05:00 weighings. In 14 of 78 cases South Georgia diving petrel chicks also gained mass between the 02:00 and 05:00 weighings.

The distribution of values of SUM for the two species are shown in Fig. 1. The average SUM for common diving petrel chicks (48.6 g) was close to twice the average mass of chick meals dissected from adults (25.5 g). This indicates that most nestlings were fed by both parents during the four nights when overnight weighings were conducted. The average SUM for South Georgia diving petrel chicks (41.6 g) was also similar to twice the average mass of meals carried by adults (23.3 g). The average SUM for common diving petrel chicks was significantly greater than that of South Georgia diving petrel chicks ($t = 3.62$, $P < 0.001$; Table II). The average values of SUM as a percentage of average adult body mass were 33.5% and 36.1% for common and South Georgia diving petrels, respectively.

The value of SUM for some chicks was close to or less than the average mass of chick meals removed from adults (Fig. 1), indicating that these chicks were fed by only one parent. Thus for common diving petrels, it was estimated that chicks were fed by neither parent on one of 78 chick nights (1.3%) and by one parent on six of 78 chick nights (7.7%), or an

average feeding frequency of 1.90 meals chick⁻¹ day⁻¹. This is equivalent to an average adult feeding frequency of 0.95 day⁻¹. For South Georgia diving petrels, single meals were received on 13 of 78 chick nights (16.7%), an average feeding frequency of 1.83 meals chick⁻¹ day⁻¹ and an average adult feeding frequency of 0.92 day⁻¹. The estimated average mass of food consumed daily ([average feeding frequency] × [average meal mass]) was 48.5 g for common diving petrel chicks and 42.6 g for South Georgia diving petrel chicks. These estimates are in close agreement with the average value of SUM for the two species (48.6 and 41.6 g, respectively).

If parents feed their chicks independently of each other, then the proportion of chicks that were fed zero, one and two meals would be expected to be close to q^2 , $2pq$, and p^2 , where p is the average adult feeding frequency and $q = 1 - p$. For common diving petrel chicks, these expected frequencies are 0.003, 0.095, and 0.903, close to the observed frequencies. For South Georgia diving petrel chicks, expected frequencies were 0.006, 0.147 and 0.846, also similar to observed frequencies.

Although the data from overnight weighings indicate nestlings were usually fed by both parents each night and parents fed chicks independently of each other, observations indicated that this was not always the case. For example, on 26 February 40% of the South Georgia diving petrel chicks that were weighed overnight were fed by only one parent, considerably more than the expected frequency of 14.7%. Nevertheless, using the $R \times C$ test of independence (G-test; Sokal & Rohlf 1981, Box 17.8) there was no significant heterogeneity among sample nights in the frequencies of single and double meal deliveries ($G_{adj} = 7.618$, $P = 0.25$). However, on 12 February at 23.00, 12 South Georgia diving petrel chicks were weighed 24 hours after they had been weighed on 11 February as part of the overnight weighings.

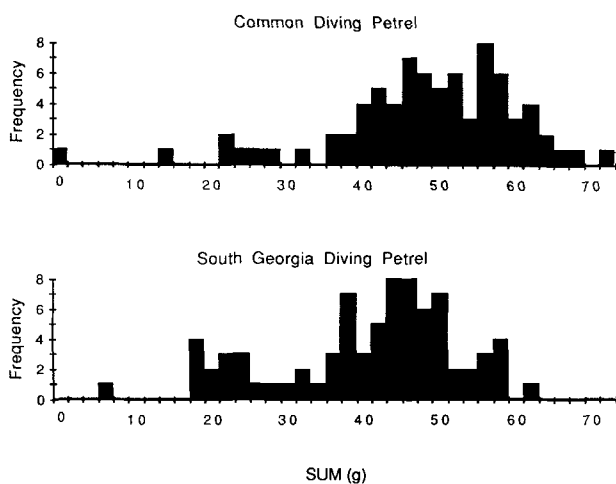


Fig. 1. Distribution of values of SUM (sum of the positive mass increments during overnight weighings) for common diving petrels and South Georgia diving petrels. Overnight weighings were conducted on four different nights for each species.

Table II. Values of SUM¹ for common and South Georgia diving petrel chicks on Bird Island, South Georgia during the 1982 breeding season.

Date	Average SUM (g)	n	sd	cv	% of chicks fed by both parents
Common diving petrel					
13 January	46.1	22	15.15	32.9	91
22 January	56.0	20	6.75	12.0	100
31 January	45.3	20	9.28	20.5	90
5 February	46.9	16	14.89	31.7	81
All	48.6	78	12.55	25.8	91
South Georgia diving petrel					
10 February	40.5	21	10.29	25.4	86
14 February	45.8	22	7.17	15.7	96
20 February	42.7	20	10.48	24.5	86
26 February	35.7	15	16.31	45.7	60
All	41.6	78	11.39	27.4	83

¹ SUM = the sum of the positive increments in chick mass from overnight weighings at three-hour intervals

Seven of these 12 chicks lost weight (average = 6.7 g, range = 3–11 g) over the 24-hour period and the remaining five chicks only gained 2–4 g. These data suggest that seven chicks (58%) were fed by only one parent and five chicks (42%) were not fed at all the previous night. If these data are included with data from overnight weighings, then the between-night heterogeneity is highly significant ($G_{\text{adj}} = 46.69$, $P < 0.001$). All day and most of the night of 11 February a strong north-east gale brought heavy rain to Bird Island, suggesting that weather may have played a role in the low feeding frequency of chicks.

Values of SUM are plotted against chick age in Fig. 2. For common diving petrels, values of SUM appear to increase up to about 35 days post-hatching and then decline until fledging. A fitted quadratic equation explained 26% of the variation in SUM (Fig. 2a). Thus it appears that the period of peak food delivery by parents coincided with peak energy requirements of nestlings. However, for South Georgia diving petrels no clear pattern in the values of SUM with respect to chick age was apparent (Fig. 2b).

In order to determine the conversion efficiency of food to biomass, mass changes over the 24-hour period (NET) were regressed against the amount of food ingested during the previous night (SUM). In this analysis, only data from chicks that had reached the asymptotic phase of growth were used (see Methods). The average values of NET for common and South Georgia diving petrels did not differ significantly from zero (-0.13 g, $se = 0.51$; 0.69 g, $se = 0.76$, respectively). For both species, the regression of NET against SUM (Fig. 3) was significant ($F_{(1,45)} = 42.6$, $P < 0.001$, $r^2 = 0.49$ for common diving petrel and $F_{(1,43)} = 43.0$, $P < 0.001$, $r^2 = 0.42$ for South Georgia diving petrel). The slopes were 0.220 g g^{-1} ($se = 0.034$) and 0.251 g g^{-1} ($se = 0.038$), respectively, and the intercepts were -11.10 ($se = 1.72$) and -9.34 ($se = 1.61$). The regression equations predicted that NET = 0 g when SUM = 50.6 g for common diving petrels and when SUM = 37.2 g for South Georgia diving petrels. The values for SUM used in these two regressions averaged 50.0 g ($sd = 11.22$, $n = 47$) for common diving petrels and 40.0 g ($sd = 13.19$, $n = 45$) South Georgia diving petrels, close to the respective predicted values for SUM when NET = 0. The average mass of these older chicks prior to feeding was 128.4 g for common diving petrels ($sd = 11.78$, $n = 47$, 88.6% of adult mass) and 133.0 g for South Georgia diving petrels ($sd = 16.47$, $n = 45$, 115.4% of adult mass), and the average values of SUM as a percentage of average chick mass were 38.9% and 30.1%, respectively.

Discussion

The close agreement between the average value of SUM and the product of average meal size and feeding frequency supports the use of periodic weighing to estimate food intake of seabird chicks. Several factors may have contributed to

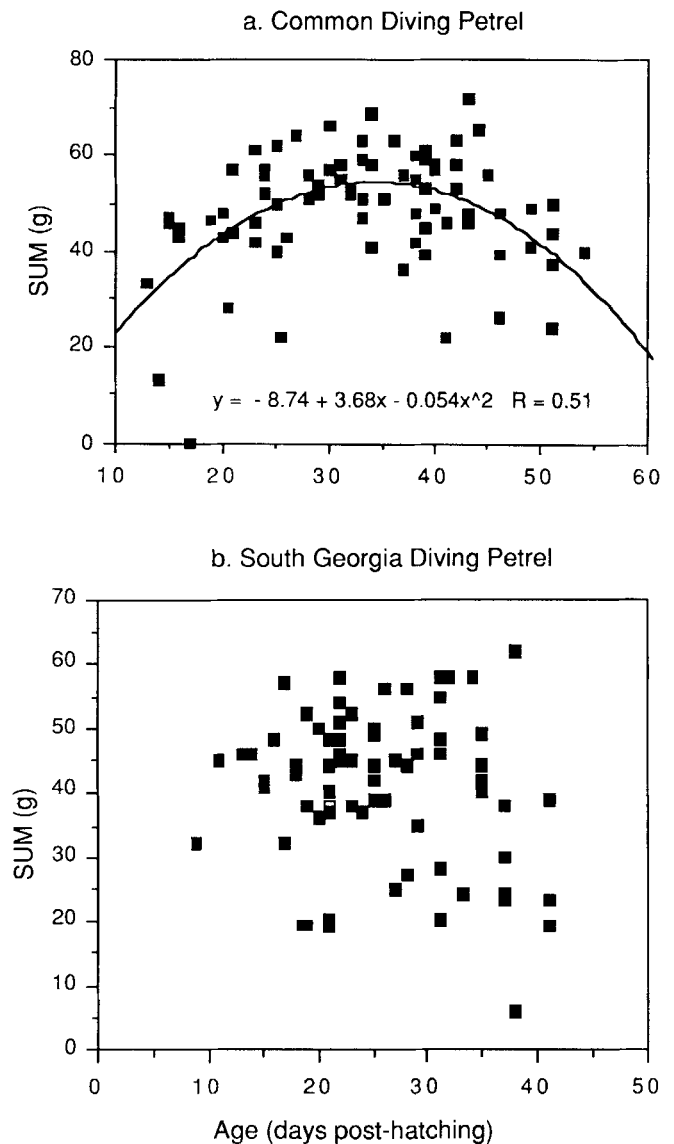


Fig. 2. Values of SUM (sum of the positive mass increments during overnight weighings) plotted against chick age for a. common diving petrels and b. South Georgia diving petrels. The line in Fig. 2a represents the fitted quadratic equation to the data.

this agreement, including weighing chicks at intervals of three hours and timing weighings so that most chick feeding occurred between two consecutive weighings (23:00 and 02:00). Diving petrels lend themselves particularly well to this technique as chick feeding occurs only at night and is relatively synchronized.

Payne & Prince (1979) used the mass increment technique to estimate the amount of food delivered to 11 South Georgia diving petrel chicks on one night. The average value of SUM (30.8 g, $sd = 15.82$, range = 1–56 g) was less than in the present study (41.6 g). However, Payne and Prince weighed chicks at 21:30, 24:00, 03:00, and 06:00 instead of 23:00, 02:00 and 05:00. Adults were present in seven of the 11 nests

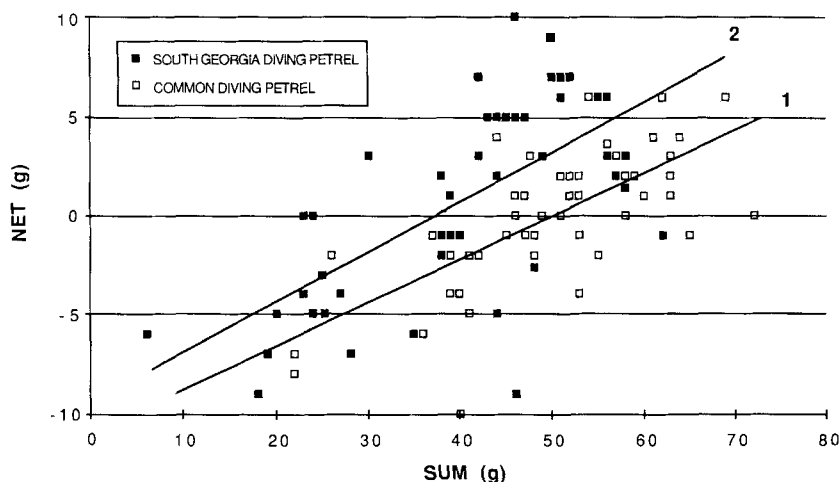


Fig. 3. Values of NET (net gain in mass over the 24-hour period) plotted against SUM (sum of the positive mass increments during overnight weighings) for diving petrel nestlings. Line 1 is the least squares regression for data from common diving petrel chicks and line 2 is the regression for data from South Georgia diving petrels.

at the 24:00 weighing and, as the authors pointed out, this probably curtailed some chick feeding. The values of SUM for two of the chicks in the 1979 study were 4 g and 1 g, indicating that an adult visited the nest but little food was transferred to the chick. Of the remaining nine chicks, all but one were apparently fed by both parents and the average value of SUM for these eight was 38.1 g, close to the average in the present study.

While common and South Georgia diving petrel adults delivered chick meals of similar size at similar frequencies, several interspecific differences are apparent. The larger relative size of South Georgia diving petrel chick meals (20.2% of average adult mass) compared with common diving petrel chick meals (17.6% of average adult mass) is consistent with the larger relative asymptotic chick mass for South Georgia diving petrels (133 g, 115% of average adult mass) compared with common diving petrel chicks (128 g, 89% of average adult mass). Despite the larger body mass of South Georgia diving petrel chicks, the average value of SUM and the predicted value of SUM when NET = 0 were less (40.0 g and 37.2 g, respectively) than for common diving petrel chicks (50.0 g and 50.6 g, respectively). This is consistent with the higher average lipid content of South Georgia diving petrel chick meals (8.7% of wet mass) compared with common diving petrel chick meals (4.6% of wet mass; Roby *et al.* 1986). The ability of South Georgia diving petrel adults to deliver large (relative to adult mass) and more energy-dense meals to their chicks may be related to the shorter nestling periods and higher fledgling weights compared with common diving petrel chicks.

There are few other published results from periodic weighings of procellariiform chicks. Harper (1976) found the average value of SUM for the fairy prion (*Pachyptila turtur* Gmelin) was 16.6 g ($n = 57$ chick nights), or 15% of average adult mass. Ricklefs (1984) reported average SUMs of 37.1 g ($n = 17$) and 54.8 g ($n = 30$) for the Phoenix petrel (*Pterodroma alba* Gmelin) and Christmas shearwater (*Puffinus nativitatis* Gmelin), respectively, or 13.6% and 16.1% of adult mass.

The average of SUMs for Leach's storm petrel (*Oceanodroma leucorhoa* Vieillot) was 8.8 g ($n = 62$), or 19.5% of adult mass (Ricklefs *et al.* 1985). For the two diving petrels in the present study, SUM relative to adult mass is twice what it is for those other procellariiform species.

The distribution of values of SUMs was used to estimate average mass of chick meals for the Phoenix petrel (49.4 g, coefficient of variation (cv) = 44%), Christmas shearwater (48.2 g, cv = 19%; Ricklefs 1984), and Leach's storm petrel (10.0 g, cv = 23%; Ricklefs *et al.* 1985). These meal masses are equivalent to 18%, 14% and 22% of average adult mass, compared with 18% in common diving petrels and 20% in South Georgia diving petrel. Thus meal size in diving petrels is similar to that of other procellariiforms when adjusted for differences in adult body mass. Variability in chick meal mass for the two diving petrels (cv = 18% and 17%) was similar to those of the shearwater and storm petrel, but less than for the Phoenix petrel. However, average adult feeding rates for the two diving petrels (0.95 and 0.92 day⁻¹) were considerably higher than for those for the shearwater (0.63 day⁻¹), petrel (0.36 day⁻¹), or storm petrel (0.43 day⁻¹).

Ricklefs (1984) calculated regression equations of NET on SUM for the Phoenix petrel (NET = $-34.6 + 0.765$ SUM, $r^2 = 0.76$) and Christmas shearwater (NET = $-19.4 + 0.421$ SUM, $r^2 = 0.54$). The regression equation for Leach's storm petrel was NET = $-6.04 + 0.92$ SUM ($r^2 = 0.88$; Ricklefs *et al.* 1985). The slopes of these regressions are steeper than those for common diving petrel ($b = 0.220$) or South Georgia diving petrel ($b = 0.251$). As Ricklefs (1984) pointed out, interspecific differences in regression slopes may be a consequence of differences in the energy density of chick meals. Similarly, the intercept of the regression of NET against SUM at the point NET = 0 is 17%, 14% and 15% of adult body mass in the petrel, shearwater and storm petrel, respectively, but in common diving petrel and South Georgia diving petrel the intercept is 35% and 32% respectively. This suggests that the conversion efficiency of food to biomass in diving period chicks is about half what it is in

other procellariiforms. Diving petrels are apparently unique among procellariiforms in that they do not feed their young stomach oils, an energy-dense food. The average water content of common and South Georgia diving petrel chick meals was 79.4% (sd = 1.4, n = 6) and 75.8% (sd = 1.0, n = 6), respectively (Roby *et al.* 1986). Consequently, most of the mass of a chick meal consists of water that is excreted following assimilation of the meal. This explains why the large relative values of SUMs for the two diving petrels result in no net gain in body mass on average.

The lower values of r^2 for the diving petrel regressions are attributable to smaller variances in both SUM and NET when compared with the petrel, shearwater, and storm petrel. The coefficients of variation in SUM for common diving petrel (cv = 27%) and South Georgia diving petrel (26%) were lower than those for the shearwater (43%), petrel (99%), and storm petrel (75%). Similarly, the standard deviation of NET as a percentage of SUM for common diving petrel (8.1%) and South Georgia diving petrel (12.6%) were lower than those for the shearwater (24.0%), petrel (90.0%), and storm petrel (68.3%). These differences reflect the fact that the diving petrel chicks were usually fed by both parents each night while shearwater, petrel and storm petrel chicks are not fed by either parent on approximately 13%, 41% and 36% of nights, respectively.

In summary, diving petrel chicks are fed meals at a higher frequency and with greater regularity than other procellariiforms. This is reflected in the lower variance in SUM, and the associated lower variance in NET, for diving petrels. From the chick's perspective, energy intake is far more reliable in diving petrels compared with other procellariiforms. These data are consistent with the hypothesis that diving petrels, like alcid, forage nearshore on a relatively dependable food supply. However, contrary to prediction, the mean and variance of relative chick meal mass was similar in diving petrels and other procellariiforms. This suggests that the frequency of meal delivery is determined more by proventriculus fill than by a set schedule of visitation to the nest site. Higher daily food consumption in diving petrels is associated with a lower conversion efficiency of food to biomass. The absence of stomach oils in chick meals necessitates that diving petrel chicks consume about twice the mass of food per day as other procellariiforms in order to meet their energy requirements.

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