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Food and feeding ecology of Wilson's storm petrel *Oceanites oceanicus* at South Georgia

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At South Georgia, the diet of Wilson's storm petrel was studied using the regurgitates of adults arriving to feed chicks. Feeding frequency and meal size were estimated by weighing chicks twice daily, or in some cases every 3 h during daytime. Crustaceans contributed 98% of the total number of individual items and 68% of the total weight consumed; fish, I% of the number of items and 28%, of the weight. The most abundant crustacean was the amphipod *Thernisto gaudichaudii,* which accounted for 90% of the total number but only 44% of the total weight of crustaceans eaten. Most (79%) of the *Thernisto* were juveniles. Euphausiids were much less numerous in the diet (5% by number) but were the main group by weight (55%); most (52%) were Antarctic krill, with juveniles and sub-adults (25-50 mm long) predominating. Mysids, copepods and barnacle larvae were also present. Fish were all myctophids (lanternfish), *Protomyctophum normani* and *P. bolini* being identified; specimens were 50-85 mm long and weighed 1-4 g. Meal sizes averaged 6·5-7·5 g (14-22% adult body mass); about 75% of chicks were fed each day (mainly at night), about 10% probably receiving meals from both parents. A review of storm petrel diets emphasizes the importance of fish to *Oceanodrorna* species and of crustaceans to *Oceanites, Garrodia* and *Pelagodroma.* Euphausiids and amphipods (chiefly *Themisto* and *Hyperia)* are the main crustacean prey and range from 5-50 mm and 0·005-0·7 g. Myctophids are the main fish prey and range from 20-100 mm and 1-5 g. Meal size ranges from 15-25% adult body mass and chicks are fed on 50-85% of days. This low delivery rate is mainly responsible for the disproportionately slow growth and long fledging period of storm petrel chicks.

Contents

Introduction

Wilson's storm petrel, *Oceanites oceanicus*, is one of the most characteristic and widespread of pelagic seabirds. It breeds in considerable numbers on the Antarctic Continent, Antarctic Peninsula and sub-Antarctic islands in the South Atlantic and South Indian Oceans (Copestake & Croxall, 1985) and in the austral winter migrates into the North Pacific and North Atlantic Oceans, being especially abundant in the North American Gulf Stream (Roberts, 1940).

Despite its abundance and wide distribution and the fact that it has been studied in some detail in six breeding areas-Terre Adelie, Antarctic Continent (Mougin, 1968; Lacan, 1971), Argentine and Anvers Islands, Antarctic Peninsula (Roberts, 1940; Obst, 1986; Obst, Nagy & Ricklefs, 1987), **King** George Island, South Shetland Islands (Wasilewski, 1986) Signy Island, South Orkney Islands (Beck & Brown, 1972) and Bird Island, South Georgia (Copestake & Croxall, 1985; Copestake, Croxall & Prince, 1988)-data published on its diet and feeding ecology have been mainly anecdotal, only Ainley, O'Connor & Boekelheide (1984) providing estimates of composition by mass. This paper reports the results of the first detailed quantitative evaluation of the diet of Wilson's storm petrel, based on regurgitations collected from adults arriving to feed their chicks at South Georgia. It also estimates provisioning rate (meal sizes and frequency of delivery) and compares this and the dietary information with data for other storm petrel species.

Methods

Study site

The study was carried out in the austral summer of 1984-85 at Bird Island, South Georgia (54°00S, 38"02'W), of which the topography and habitats are described by Hunter, Croxall & Prince (1982). Wilson's storm petrels breed in consolidated scree and rocky debris slopes and their total Bird Island breeding population is estimated to be *c.* 60 000 pairs (Copestake, Croxall & Prince, 1988). The main study site was the scree slope on the north side of Stejneger Peak, described in detail by Copestake, Croxall & Prince (1988), who estimated its population to be *c.* 5200 pairs. The occupants of a few burrows on the south slope of Gazella Peak were also studied.

Collection and analysis of food samples

Adult Wilson's storm petrels bringing food to their chicks were caught at night in mist nets (see Copestake, Croxall & Prince (1988) for details ofnetting techniques). Many birds regurgitate stomach contents on impact or on removal from the net. Where possible, these regurgitates were collected in plastic bags fixed to the end of plastic funnels 15 cm in diameter. On Bird Island the liquid ('oil') fraction was drained, weighed and discarded. Any fish otoliths present in the rest of the sample were removed and stored dry. The remainder was preserved in 5% formaldehyde in sea water and shipped to the UK. Here, material was sorted, identified to the lowest possible taxonomic category (using extensive reference collections for help with fragmentary material) and weighed to 0·01 g. Crustacean total lengths (TL) were measured (to 0·1 mm) from the anterior edge of the eye to the tip of the telson. Because many euphausiids were insufficiently intact to permit this, carapace lengths (CL: tip of rostrum to posterior end along mid-dorsal line) were also measured and converted to TL using the relationships: male TL=2·32CL+ 11·09; female TL=3·15CL+3·58; juvenile TL=2·88CL+2·28 (Morris, Watkins, Ricketts, Buchholz & Priddle, 1988). Identity offish was established by comparing otoliths with published illustrations and reference material (Adams & Klages, 1987; Hecht, 1987; British Antarctic Survey, unpubl. data). Otolith length, breadth, thickness and weight were measured and these were used to estimate the size of the whole fish (see Croxall & North (1988) for full details).

Feeding rate and meal size

Feeding rate and meal size were estimated by weighing chicks. Nine chicks were weighed to 0·5 g twice daily (07: 00-09:00 and 18:00- I 9: 00 local time) from hatching to fledging, giving a total of 717 weights. These data were supplemented by weighing (to 0·1 g) 16 chicks, 37-58 days old and 25-65 g in weight, at 3-h intervals during daytime on 3-7 days in mid-to-late March-a total of 399 weights. The three-hourly daytime weighings were used to calculate an average rate of weight loss. This was used in conjunction with the morning weights to determine whether a chick had been fed since being weighed the previous evening. The meal mass delivered was also estimated by comparing morning and evening weights.

Results

Diet

About 80 regurgitations were collected on eight sampling occasions between 6 and 15 March on Gazella Peak (mean fledging date 26 March± 4 days, range 23 March- I April, $n=8$) and between 19 March and 1 April on Stejneger Peak (mean fledging date 15 April± 18 days, range 26 March-6 May, $n=5$). Only 51 samples contained solid material, the rest (*c.* 36%) comprising only oily liquid. The average weight of each of the 51 samples was 2·0 ± 1·3 g (range 0·5--6·4 g) and their overall composition by mass was 13% liquid, 52% identifiable material and 35% unidentifiable material. The general composition of the identified material, totalling 53·4 g, is summarized in Table I.

TABLE I

Composition by weight.frequency of occurrence and number of individuals of prey in 51 samples regurgitated by Wilson's storm petrels at Bird Island, South Georgia

Group	Frequency of occurrence (%)	Individuals		Weight (g)	
		Number	%	Total	%
Crustaceans	100	1983	98·5	36·3	68·0
Fish	41	26	1·3	15·1	28·3
Squid	2	1	0·1	1·0	1·9
Insects	6	3	0·1	1·0	1·9

TABLE II

Size and composition by weight.frequency <Jf occurrence and number of individuals, in 51 samples <Jf crustacean prey regurgitated by Wilson's storm petrels at Bird Island, South Georgia

	Frequency of occurrence	Individuals		Weight (g)		
Group	(%)	Number	o;;i	Total	%	Size range• (mm)
Euphausiacea						
Euphausia superba	51	68	3·4	18·8	51·8	24 51
E. triacantha	4	8	0·1	0·2	0·5	
E.frigida	2	I	0·l	0·2	0·5	
Thysanoessa sp.	22	33	1·7	0·7	1·9	6-12
Amphipoda						
Themisto gaudichaudii (adult)	71	364	18·4	11·7	32·2	8-22
T. gaudichaudii (juvenile)	49	1411	71·2	4·5	12·4	2-7
Vibilia sp.	4	3	0·l	0·l		9--12
Cyphocarus sp.	2	1	0·1	0·1		
Mysidacea						
Antarctomysis sp. (adult)	2	I	0·l	0·1		
Antarctomysis sp. (larvae)	4	2	0·l	0·I		
Copepoda						
Rhincalanus gigas	4	2	0·1)			8-10
Ca/anus simillimus	6	5	0·3)	0·I	0·5	3-4
C. *propinquus*	12	13	0·7)			4-5
Cirripedia						
Cypris larvae	33	76	3·8	0·l	0·5	2-5

• Total length: see methods section for details

Overall, crustaceans dominated the samples, both numerically and by bulk, though the few fish made a large contribution by mass. The samples contained remains of only one squid.

Tiny pieces of pumice were present in 27 samples (53%) and fragments of plastic in five samples (10%). Fur seal hair occurred in five samples (10%); this might have been ingested together with scraps of blubber which would be digested rapidly, contributing to the oil fraction but not being recognizable in the solid material. Tiny pieces of unidentifiable tissue that might represent bird or seal flesh were recorded in ten samples (20%) but their total contribution by weight was less than 5%. Small fragments of plant material occurred in 35 samples (69%); their provenance is unknown, as is that of the five insects, three of which were the mite *Podocarus auberti.* There were no significant variations in overall diet composition between any of the sampling occasions or sites.

Crustaceans

Wilson's storm petrels took a diverse selection of small crustaceans (Table 11) but two species, Antarctic krill *Euphausia superba* and the hyperiid amphipod *Themisto gaudichaudii,* accounted for 96% of the weight of crustaceans in the diet; *Themisto* alone comprised almost 90% of individual prey items. The only other taxa which contributed more than I% of the diet by numbers or mass were the euphausiid *Thysanoessa* and barnacle cypris larvae. Of the 20 krill which could be sexed and measured, six were sub-adult males (42-51 mm total length), three were sub-adult

TABLE III

Estimated total length and weight (from otolith measurements) of fish regurgitated by Wilson's storm petrel at Bird Island, South Georgia. Values are mean± S.D. with range in parenthesis

Species	Sample size	Otolith length (mm)	Fish size	
			Length (mm)	Weight (g)
Protomyctophum normani	5	2·01 ±0·08 (l·90-2·10)	78·2±4·4 (72-84)	3·3±0·5 (2·6-3·9)
P. bo!ini		1·80±0·02 (1·79-1·82)	63	l·8

females (42-49 mm) and 11 were juveniles (24-43 mm). Because a disproportionate number of large krill are likely to be intact, it is probable that well over half the krill portion of the diet consisted of juveniles. Most *Themisto* were sufficiently intact to be classified and measured; 79% were juveniles, but the 21% of adults comprise 72% of the total mass of this species ingested by the storm petrels. Although copepods are very abundant around South Georgia and several species are at least as big as the barnacle larvae, surprisingly few were present in the samples. Both *Rhincalanus gigas* were adults (one male, one female); four of the five *Calanus simillimus* were adult males, the other being a juvenile (copepodite stage V); ten *Ca/anus propinquus* were stage **V** copepodites, the other three being adult females. These three copepod species are by no means the commonest around South Georgia, but they are amongst the largest species **(A.** Atkinson, pers. comm.).

Fish

Fish were present in 42% of samples, though only five samples contained remains of more than one fish. No fish was sufficiently intact to be identified below family level and identifications, measurements and estimates oflength and weight rely almost exclusively on otoliths. The detailed results of these data were discussed by Croxall & North (1988). Eleven otoliths were sufficiently intact to be identified to family; all belonged to lanternfish Myctophidae. Eight (representing six separate indivdiuals) could be identified to species (Table III). Five of the six fish, representing 87% of the estimated mass of identified fish, were *Protomyctophum normani.* The remaining specimen was the smaller congener *P. bolini.* Both species are fairly common members of the Scotia Sea epipelagic zooplankton. All identifiable flesh remains were of myctophids. Post-cranial skeletons of these were 16-45 mm long *(n* = 14) and reasonably intact fish (lacking heads) weighed l·1-2·5 g *(n* = 5). These measurements are consistent with those estimated from otolith size. *Protomyctophum normani* probably becomes sexually mature from about 48 mm standard length (Hulley, 1981), so most of the specimens taken were likely to have been adult fish.

Squid

The single beak was too badly damaged to be identifiable.

TABLE IV

Mean (±S.D.) rates of weight loss over different timespans for chicks of Wilson's storm petrel weighed at 3 h intervals

Timespan (h)	Sample size	Mean weight loss	
		g	gh-1
6	18	1·64±0·81	0·197
9	40	2·59±1·12	0·288
12	38	2-44±1·10	0·203
All	96		0·247±0·118

Feeding rate and meal size

Calculation, solely from daily or even twice-daily weighings, of the frequency and mass of meals delivered to chicks is not simple. This is because meals are relatively infrequent and small meals may be missed because of the high rates of mass loss characteristic of small, fasting chicks. Allowance can be made for this by conducting separate experiments to estimate size of meals and rate of mass loss between meals (e.g. Payne & Prince, 1979; Ricklefs, Day, Huntington & Williams, 1985). In our study the three-hourly daytime weighings allow estimation ofrates of mass loss. For 96 periods (lasting from 3-12 h) of mass loss, the overall average rate was 0·247±0·118 g h^{-1} (Table IV). However, mass loss was not constant with time, being significantly lower when measured over the first 6 h than over longer time spans and not significantly different between time spans of 9 and 12 h (Table IV). If this pattern typically reflects digestion of the previous night's meal and the mass loss at night is similar to that recorded during the day (probably a conservative assumption), we can reasonably assume that chicks lose *c.* 2·5 g between 18:00 and 09:00 h. However, we cannot simply assume that all chicks which lose less than 2·5 g overnight have been fed, because the relatively large variance (46% C.V.) associated with this estimate means that a significant proportion of errors would be introduced. Thus, we know from the three-hourly daytime weighings that no study chick was fed in the daytime during this experiment (though genuine daytime feeds do occur, albeit infrequently). If, however, we take 9-12 h losses of2 g, 1 g and 0·5 g, respectively, to indicate that meals have been delivered, then this results in estimates of feeding frequency (meals per chick days) of 41·7%, 18·5% and 6·3%, respectively, compared with the true answer of 0%. In estimating daytime feeding frequency it seems, therefore, best to use chick mass increases, or decreases of not more than 0·5 g, to indicate that meals have been delivered.

Because we have no three-hourly weighing data for night-time, we cannot perform a similar analysis. Accordingly, we use criteria similar to those applied to the daytime data (Table V). The most conservative, and certainly an underestimated, value for feeding frequency is 55% (comprising 50% of nights and 5% of days). Incorporating a modest correction (0·5 g criterion) for both day and night mass loss gives 85% (61% of nights and 24% of days); a larger correction (1·0 g criterion) gives 103% (65% of nights and 38% of days) and is certainly an overestimate. It is not clear why the same corrected threshold should result in a greater increase in daytime values than night-time ones, unless it is harder to detect daytime feeds (because they tend to be smaller). Probably the most we can conclude from this analysis is that typical feeding frequencies are between 70% and 90%. There is some suggestion (e.g. chicks 3 and 7) that chicks which failed to fledge received fewer feeds but this is not statistically significant.

Meal sizes estimated from twice-daily weighings (Table VI) are very consistent between chicks and average 4·7 g (**S.D.** 3·4 g; $n = 186$) overall. These estimates are based solely on increases in chick mass and do not take account of the mass loss between receiving a feed and the next weighing. If meals are delivered, on average, halfway between successive weighings (i.e. at 01:30 h) then the average mass loss would be 1·85 g (0·247 g h^{-1} (Table IV) times 7·5 h), giving a true meal size of 6·55 g. Estimates of the meal size from the three-hourly weighings give a value of 7·6 g (6·1 g plus 0·247 g h^{-1} times 6·0 h), so the true average is probably about 7·0 g.

For both data sets we can estimate the number of nights on which chicks received two meals, if we assume that any increase greater than 9·4 g (twice-daily weighings) or 12·2 g (three-hourly weighings) represents two meals. This gives 19 (10·2%) and three (6·7%) double visits, respectively.

Discussion

Diet and feeding ecology

Interpretation of results

In any study of diet there are numerous sources of bias relating to the way the samples are obtained and analysed and the type of material present (Ashmole & Ashmole, 1967; Croxall, Prince, Baird & Ward, 1985; Duffy & Jackson, 1986; Croxall, In press). The main potential sources of error in this study are:

1. Only part (c. 10-95%) of the average meal load brought to the chick by the adult is collected as regurgitate. The likely bias is against larger items (mainly fish, perhaps also squid) which would be less easily vomited.

2. The samples collected contained a high proportion (35%) of material which could not be easily allocated to fish, squid or crustacean sources. This will introduce biases if any of these classes were disproportionately represented in the unidentifiable material. Indeed, fish and squid material is digested particularly rapidly and crustacean fragments are, perhaps, more easily recognizable than minute remains of other taxa. However, if all the unidentifiable material in samples containing any fish (and it is very unlikely that fish would be totally overlooked in any sample that contained it) is assumed to be entirely fish-derived, then the proportion by weight offish in the diet would increase only from 28% to 37%, with crustaceans decreasing to 60%.

3. Our analysis of solid, identifiable material assumes that all prey in the sample are equally digested, which is unlikely because they will have been in the petrel's stomach for different lengths of time and different prey types may be digested at different rates (e.g. Jackson & Ryan, 1986). One way of avoiding part of this bias is to estimate the mass of each prey item when it was freshly ingested (see Croxall *et al.*, 1985; Duffy & Jackson, 1986). To do this requires: (a) identifying all the main prey taxa to species level, (b) having accurate size/weight relationships for whatever parts of these prey are available in the samples and (c) accurate estimates of the number of individuals in each prey taxon in the samples. If these criteria are not met the estimates ofingested weight of prey may be so inaccurate (e.g. squid of 35-40 g being ingested by Leach's storm petrel, *Oceanodroma leucorhoa;* Watanuki, 1985a) that greater biases are introduced than by recording accurately the composition of the prey that the chick actually receives. In our study difficulties in identifying

TABLE V

Estimated percentage of days and nights on which Wilson's storm petrel chicks received meals, based on twice-daily weighings and using various criteria of mass change

			Day			Night			Overall		
Chick	Days studied	Fate"	Increases only	Including ..;0-5g	Decreases of ..;I·Og	Increases only	Including ..;0-5 g	Decreases of ..;I-0 g	Increases only	Including ..;0-5 g	Decreases of ..;1-0 g
2	43	S	2·3	14·0	18·6	60·5	72·1	79·1	62·8	86·1	97·7
4	58	S	*5·2*	24·1	32·8	50·0	63·8	*65·5*	55·2	87·9	98·3
5	50	S	6·0	16-0	32·0	54·0	70·0	74·0	60·0	86·0	106·0
8	58	S	1·7	15·5	29·3	58·6	60·3	63·8	60·3	75·8	93·1
IO	*59*	S	1·7	25·4	59·3	49·2	61·0	69·5	50·9	86·4	128·8
II	34	F(54)	14·7	29·4	50·0	44·1	50·0	58·8	58·8	79·4	108-8
3	35	F(53)	8·6	20·0	42·9	28·6	40·0	40·0	37·2	60·0	82·9
7	21	F(44)	4·8	57-1	66·7	38·1	52·3	57-1	42·9	109·4	123·8
1	17	F(SO)	O·O	11·8	11·8	70·6	76·5	76·5	70·6	88·3	88·3
Overall mean			5·0	23·7	38·2	50·4	60·7	64·9	*55-4*	84·4	103·1
S.D.			*4·5*	13·8	18·2	12·5	11·7	12·0	10·3	12·3	15·4
range			0--15	12-57	12-67	29-ll	40-76	40-79	37-71	60--109	83-129

• S: successful; F: failed, with percentage of normal fledging period (78 days) survived in parenthesis

TABLE VI

Meal size (mean positive mass increments (g) between successive evening and morning weighings) delivered to Wilson's storm petrel chicks at Bird Island, South Georgia

Chick	Fate•	Meal size			Sample size
		Mean	S.D.	Range	
2	S	5·6	3·5	1·0-14·0	27
4	S	5·1	3·9	0·5-15·0	27
5	S	4·8	3·5	0·5-15·0	27
8	S	4·4	3·2	0·5-10·5	33
10	S	4·4	2·5	0·5-II·5	27
I I	F	4·8	3·4	0·5-10·5	15
3	F	3·6	2·7	1·0-8·5	IO
7	F	3·9	2·9	0·5-9·0	8
I	F	4·9	3·3	0·5-12·5	12
All[b]		6·1	3'9	0·5-15·5	45

• S: successful; F: failed

[b] From three-hourly weighings

myctophid fish from otoliths and the paucity of data for estimating mass of crustaceans (other than *E. superba)* from carapace and other fragments meant that we did not attempt this approach.

4. Wilson's storm petrels are known to pick minute fragments of fat (blubber) from the water surface. Formerly, whaling operations were a rich source of this material. Nowadays the main sources are likely to be fish offal or seal and penguin carcasses, especially those killed or rendered available by the activities of natural predators, e.g. leopard seals *Hydrurga leptonyx*, or larger avian scavengers, e.g. giant petrels *Macronectes* (Bonner & Hunter, 1982; Hunter, 1983). Small pieces of blubber are likely to be digested and therefore unrecognizable in the identifiable material. It is impossible, therefore, to assess the contribution that scavenged material might make to the diet of Wilson's storm petrels at South Georgia.

Despite these problems, our results suggest that crustaceans were the main food of Wilson's storm petrels during the late chick-rearing period at South Georgia in 1984-85 and that myctophid fish also made an important contribution by weight. Numerically, amphipods, particularly juvenile *Themisto,* predominated, but adult *Themisto* and particularly juvenile and sub-adult krill made the main contribution by weight. The crustaceans eaten were small, ranging from 2-5 mm long copepods and cypris larvae to 10-20 mm amphipods and 25-50 mm euphausiids. The smallest prey weighed about 0·001 g; the largest (22 mm *Themisto* and 50 mm krill) weighed 0·2 g and 0·7 g each. By contrast, the fish taken were about 60-85 mm long and weighed 1·8-4·0 g. It is not clear how such relatively large fish are caught or why crustaceans much larger than those actually ingested are not eaten. However, adult *E. superba* of up to 65 mm length and weighing 1·3 g, which are eaten by penguins at South Georgia (Croxall & Lishman, 1987), may not be readily available in the surface waters to Wilson's storm petrels.

Comparison with existing information on Wilson's storm petrel

Most previous data on Wilson's storm petrel diet are anecdotal. Krill *(E. superba)* was the main component of food brought to chicks at Argentine Islands and Signy Island (Roberts, 1940; Beck

& Brown, 1972); at Anvers Island, Obst (1985) records that it formed 85% by weight of the diet. Elsewhere, however, he refers to the importance of wax-rich myctophids and squid in the diet (Obst, 1986). Squid (as beaks, which may be retained in the stomach for appreciable times) have been recorded from specimens taken at Iles Kerguelen (Paulian, 1953), near the Antarctic Continent (Falla, 1937; Mougin, 1968; Kamenev, 1977) and at sea in the South Atlantic (Bierman & Voous, 1950). The amphipod *Themisto* (as *Euthemisto} gaudichaudii*, was recorded as 'important' in the diet off Kerguelen (Falla, 1937).

There are two recent more quantitative studies. Wasilewski (1986) obtained samples from 82 adults during incubation and early chick-rearing and from 21 chicks. The latter contained only krill. Krill (95% *E. superba*, 5% *E. crystallorophias)* occurred in 96·4% of adult samples and formed 93·6% of 125 prey items recovered, amphipods (all *Themisto gaudichaudii;* 5·6%} and a single larval fish (0·8%), making up the rest. The krill averaged 42·8 mm long. Ainley *et al.* (1984) obtained 28 samples from birds caught in the Ross Sea (70°S}, off the Antarctic Continent (Table VII). Crustaceans and squid were the most abundant prey, in that order, which was reversed when composition by mass was estimated. The crustaceans were Antarctic krill (93% of individuals), averaging 35 mm in length (S.D. 0·5 mm, range 26-44 mm; $n = 14$) and lysianassid amphipods (7% by numbers). The only two squid identified were *Psychroteuthis glacialis* which, applying data from Offredo, Ridoux & Clarke (1985) to the beak measurements, were estimated to have weighed l·5 g and 9·7 g. Fish material included remains of a couple of *Pleuragramma antarcticum* (Nototheniidae), but no other details are given. Polychaetes occurred in 25% of samples and formed 7% of the number of prey items and 3% of the diet by mass. Obvious differences between the Ross Sea and South Georgia diets are the greater importance of squid in the former and fish in the latter. In both, however, *Euphausia superba* is the single most important species and the size range taken is very similar in both areas.

Almost all authors mention the characteristic feeding method of dipping to pick items from the surface whilst skimming over the water, or, more often, hovering with feet touching the surface. This aerial pattering or 'hovering' is likely to be an important energy-saving mechanism (Withers, 1979; Obst, Nagy & Ricklefs, 1987). Birds are rarely seen floating or swimming on the sea but sub-surface seizing and surface plunging have been recorded (Harper, Croxall & Cooper, 1985; Prince & Morgan, 1987). Although aerial pattering enables the species to forage close to the sea surface, which must help it to prey on items like very small crustaceans, the presence of pumice (and plastics) in many samples suggest that there is little time or opportunity for the birds to discriminate between edible and inedible objects.

Comparison with other storm petrels

Of the quantitative data available on storm petrel diets (Table VII), those on five species are limited to information on frequency of occurrence. Interpreting this in the light of the other studies suggests, in very general terms, that fish are the main food for all *Oceanodroma* species, with squid probably of next importance for all Pacific Ocean species and populations. By contrast, crustaceans seem to be the main prey of the species in the other three genera. Only one squid (see above} and few fish have been identified from storm petrel stomachs. Sternoptychidae were identified in *Oceanodroma tristrami* stomachs; *Lampichthys procerus* (Myctophidae} and *Maurolicus muelleri* (Sternoptychidae) together formed 40% by weight of the fish in *Pelagodroma* samples. Cottoidea, Gadidae, Myctophidae and Scorpaeniformes were reported in Alaskan *Oceanodroma furcata* samples (Hatch, 1983), although juvenile capelin *Ma/lotus villosus* are

TABLE VII

General composition (%) of the diet of storm petrels

Species	Squid Frequency of occurrence	Squid Number	Squid Weight or volume	Fish Frequency of occurrence	Fish Number	Fish Weight or volume	Crustaceans Frequency of occurrence	Crustaceans Number	Crustaceans Weight or volume	Site and sample size	Reference
Oceanodroma leucorhoa	33	-		36	-	-	*c.50*		-	Japan (*n* = 178)	Watanuki (1985a)
Leach's storm petrel	5	0·6	5·6	78	13·5	68·8	c.95	85·8	35·7	Nova Scotia (n = 91)	Linton (1978)
	3	0·1	3·4	82	8·1	66·5	c.75	91·7	30·2	Newfoundland (*n* = 155)	Linton (1978)
O. furcata Fork-tailed storm petrel	9	-		100	-	-	82+		-	Alaska (n = 22)[a]	Hatch (1983)
O. monorhis Swinhoe's storm petrel	32	-		52	-		10		-	Korea (*n* = 178)	Won & Lee (1986)
O. castro Madeiran storm petrel	27	-		93	-		0		-	Galapagos (*n* = 15)	Harris (1966)
O. tethys Galapagos storm petrel	17			61	-	-	14		-	Galapagos (n = 66)	Harris (1966)
O. tristrami[b] Sooty storm petrel	60	-		50	-	-	60		-	Hawaiian Is. (n = 10)	Harrison, Hida & Seki (1983)
Oceanites oceanicus Wilson's storm petrel	2	0·1	1·9	42	1·3	28·3	100	98	68	S. Georgia (n = 51)	This study
	54	30·0	*45·5*	7	6·6	15·2	64+	56·7	36·3	Ross Sea (n = 28)	Ainley *et al.* (1984)
Ga"odia **nereis** **Grey-backed** storm **petrel**	0	0	0	4	0·1	0·3	100	100	99·7	Chatham **Is.** (*n* = 27)	**Imber (1981)**
Pelagodroma marina White-faced storm petrel	0	0	0	-	3	30·0	-	97	70·0	Chatham Is. (n = 22)	Imber (1981)

[a] Each sample comprised combined regurgitations of 15-20 birds

[b] **Also insects 40%, coelenterate *(Velella)* 40%**

TABLE VIII

Comparison of crustacean diets of storm petrels. Values are proportion (%) by weight" with size range (mm) in parenthesis. Data sources as in Table Vil

Taxon	Leach's storm petrel		Wilson's storm petrel	Grey-backed storm petrel	White-faced storm petrel
	Nova Scotia	Newfoundland	S. Georgia		
Euphausiacea	19	7	55	7	46
Euphausia	traceb		97 (24-51)<		0·7 (14-22)d
Nyctiphanes australis				100 (8-14)	75(7-15)
Nematosce/is mega/ops	9 (9-30)				23 (13-18)
Meganyctiphanes norvegica	88 (12-33)	12 (18-39)			
Thysanoessa		88 (6-30)"	2 (6-12)		0·9 (14-16}1
Amphipoda	3	20	45	7	10
Themisto	73 (6-2))8	6 (3-21)8	100 (8-22)h	4 (7-8)h.	8 (7-I0)h
Hyperia	13(3-15i	94 (3-18);		21 (6-l0)l	5 (9-16)i
Vibilia			trace (9-12)		18 (5-18)k
Cyllopus				*15* (6-10r	59 *(1-9r*
Decapoda	3 (24-66)"	3 (2!-63)m			trace (14)
Stomatopoda					4 (14-29)P
Copepoda	trace (3-6)q	trace (3-6)q	trace (3-10)		trace (3)'
Cirripedia			trace (2-5)	85 (2-5)8	0·5 (2-5)'

• For main groups, proportion of total diet; for species and genera, proportion by weight of main group

b *E. krohnii*

o *E. superba;* also *E. triacantha* and *E.frigida* as traces

d *E. lucens, E. similis*

• *Thysanoessa raschii,* also *T. longicaudata* and *T. inermis* as traces in Nova Scotia

r *T. gregaria*

8 *Themisto compressa* (formerly regarded as conspecific with *T. gaudichaudii;* see Schneppenheim & Weigmann-Haass, I986)

h *T. gaudichaudii*

i *H. galba*

i H. spinigera

kV. *armata*

m C. *macropis* and *C. magel/anlcus*

n Mainly *Sergestes arctlcus* and *Parapasiphaea sulcatifrons* larvae

P *Squilla armata* and *Heterosquilla spinosa* larvae

q *Anomalocera opalus,* also a few *Euchaeta norvegica* and *Calanus* sp. in Newfoundland and Nova Scotia, respectively

' *Calanus tonsus*

' *Lepas australis* larvae

apparently the main food of chicks in some parts of this region and walleye pollock *Theragra cha/cogramma* have also been recorded (Sanger, 1987). Myctophids (probably mainly *Electrona, Myctophum* and *Ceratoscopelus),* cod *Gadus morhua* and hatchet fish *Argyropelacus aculeatus* comprised, respectively, 50-55%, 30-40% and 3-11% by volume of fish diet of *0. leucorhoa* (Linton, 1978). Specimens of all these were typically 20-70 mm long, though the largest individuals recorded just exceeded 100 mm.

Only with the four detailed studies is it possible to make more critical comparisons, especially of the nature of the crustacean prey (Table VIII). Despite considerable differences in the importance of crustaceans and of the various constituents thereof and of the different geographical areas involved, there are striking similarities in the size and general identity of the zooplanktonic crustaceans eaten by storm petrels. In general, euphausiid crustaceans 15-50 mm long, weighing

0·1--0·7 g, and hyperiid amphipods, usually 7-20 mm long, weighing 0·005-0·2 g, make up the bulk of the prey by weight. Smaller prey (down to 2 mm long) can be taken, though only for *Garrodia* do they form the main resource. Larger prey are sometimes taken (e.g. by *0. leucorhoa)* but tend to contribute rather little to the overall diet. The main euphausiids and *Themisto* are all known to occur at high densities and this may be an important reason why they, rather than other euphausiids and amphipods, are taken. Copepods, despite their abundance, are of little importance to storm petrels, presumably because larger prey are usually equally readily available. *Garrodia* appears to specialize on the tiny barnacle larvae.

Finally, all workers who have collected food samples from storm petrels comment on the high proportion which contain only liquid ('oil'). This suggests either that storm petrels take prey that is especially easily digested (perhaps because small), or that the prey remains in the stomach for long periods. Both may be true. Most prey are small but, for many taxa, not much smaller than the prey of Antarctic prions (see next section), from which few food samples contain only liquid (P. A. Prince, unpubl. data). Later (p. 99) we show that storm petrel foraging trips are disproportionately long, so this may be the main cause. If the liquid fraction has a higher energy content than the solid portion (because energy is concentrated by selective absorption of water and protein), there may be additional advantages in maximizing energy density of meals in order to minimize the effect of the extra mass transported on flight speed and fuel consumption (Pennycuick, 1982; Ricklefs, Roby & Williams, 1986). This is a general point relevant to all procellariiforms but probably especially critical for storm petrels because of their small size and long trips.

Comparison with other seabirds at South Georgia

We have no data on the diet of grey-backed storm petrel *Garrodia nereis* and black-bellied storm petrel *Fregetta tropica* which nest in small numbers at South Georgia but can compare Wilson's storm petrel diet with that of two other small petrels (family Procellariidae) which feed mainly on zooplankton. Blue petrels *Halobaena caerulea* (190 g body mas) and Antarctic (dove) prions *Pachyptila desolata* (170 g) are abundant breeding species at Bird Island. The overall composition of their diets by weight and numbers, respectively, was, for blue petrels: crustaceans 91% and 94%, fish 8% and 6%, squid 0·2% and 0·8%; and for Antarctic prions: crustaceans 98% and 98%, fish 0·1% and 2%, squid 0·1% and less than 0·1% (Prince, 1980). This is not dissimilar to the general diet of Wilson's storm petrel (see Table I), with crustaceans predominating and squid being very rare. Depending on the allocation of unidentifiable material, the contribution by weight offish to Wilson's storm petrel diet was assessed at 28-33%. Prince (1980) also calculated the diet composition assuming that all unidentifiable material in samples containing fish, was fish. This gave results for blue petrel of crustaceans 43%, fish 56%, squid l % and for Antarctic prion of crustaceans 87%, fish 12%, squid 1%. In general terms, therefore, the diets of these three species are broadly similar. None of the fish remains in the blue petrel and Antarctic prion samples was identified, although it was 'probably myctophids' (Prince, 1980), so more critical comparison is limited to the crustaceans (Table IX). Antarctic krill *E. superba* is the principal prey of all species and there is substantial overlap in the size of the krill they take. Apart from krill, Antarctic prions eat mainly copepods and Wilson's storm petrels amphipods, and in both classes the size-range of prey taken by all three petrels is broadly similar. The composition of the amphipod prey, however, is rather different. Both blue petrels and Antarctic prions take a wide range of species, though the main prey are rather different. Thus *Themisto* and *Hyperiella* comprise 77% by weight of

TABLE IX

Comparison of crustacean diets delivered to chicks by blue petrels, Antarctic prions and Wilson's storm petrels at Bird Island, South Georgia. Values are proportion (%) by weight" with size range (mm) in parenthesis

Taxon	Blue petrel	Antarctic prion	Wilson's storm petrel
Euphausiacea	85-9	58·7	54·7
Euphausia superba	95·3 (10-59)	99·5 (5-60)	94·7 (24-51)
Thysanoessa macrura	4·7 (13-21)	0·5 (9-14)	3·5 (6-12)
Mysidacea[b]	3·5 (20-37)	0·8 (15-29)	trace
Decapoda[0]	4·3 (50-75)		
Amphipoda	4·9	8·2	44·6
Themisto gaudichaudii	10·2(5-1S)	56·1 (2-18)	100 (2-22)
Hyperia macrocephala	2·0(5-17)	1·2 (3-11)	
Hyperoche medusarum	38·8 (10-18)	4·9 (4-14)	
Hyperiella antarctica	10·2 (3-13)	20·7 (3-8)	
Vibi/ia antarctica	24·5 (4-8)	6·1 (4-11)	trace (5-18)
Cyllopus lucasii	10·2 (9-15)	11·0 (5-14)	
Eurythenes gryllus	4·1		
Copepoda	1·4	32·3 (1-11)[d]	0·5 (3-10)
Cirripedia			0·5 (2-5)

• For main groups, proportion of crustacean diet; for species, proportion of main group

[b] *Antarctomysis maxima*

[0] *Acanthephyra* sp.

[d] *Rhincalanus gigas* (5-11 mm) and *Calanoides acutus* (1-5 mm)

amphipods taken by Antarctic prions, whereas *Hyperoche* and *Vibilia* total 53% of the weight of those taken by blue petrels. Blue petrels take significantly larger specimens of *Hyperia, Hyperiella* and *Hyperoche* than Antarctic prions do (Prince, 1980). In contrast, Wilson's storm petrel almost exclusively takes *Themisto* of much the same average size (12·2±3·8 mm) as those taken by blue petrels (10·2 ±3·0 mm) and Antarctic prions (11·0 ±3·1 mm).

Prince (1980) related many of the differences between the diets of blue petrels and Antarctic prions to differences in feeding habits. Thus Antarctic prions use their palatal lamellae to filter copepods, whereas blue petrels have no morphological specializations for taking such small prey. Furthermore, they characteristically fly high above the sea and feed by swooping to pick prey from the surface (dipping) as well as by surface-seizing, which is also typical of prions (Prince & Morgan, 1987). Only relatively large prey items are likely to be taken by dipping, which might explain why the blue petrel takes larger prey of several taxa than the Antarctic prion does. Apart from this, all three species take a similar size-range of prey, but it appears that only Wilson's storm petrel specializes on *Themisto.* This is by far the most widespread and abundant amphipod around South Georgia, often occurring in considerable concentrations; but it is not clear why Wilson's storm petrels do not take a greater diversity of amphipods.

Chick growth, feeding rate and meal size

Information on chick growth and provisioning rate for storm petrels, summarized in Table X, enables us to make intra- and interspecific comparisons and also, briefly, to compare storm petrel provisioning with that of other Procellariiformes.

TABLE X

Comparison of aspects of chick-rearing biology in storm petrels

Species	Fork-tailed storm petrel *Oceanodromaf,ucata*	Madeiran storm petrel *0. castro*		Galapagos storm petrel *0. tethys*	Leach's storm petrel *0. leucor/wa*		Wilson's storm petrel ***Oceanites oceanicu.s***			British storm petrel *Hydrobates pelagicw*	White-faced storm petrel *Pelagodruma marina*
Site	**Alaska;** 58°SS'N	Galapagos; 0'30'S	Ascension; 7"57'S	Galapagos; 0°30'S	Japan; 42°52'N	NE USA; 44°40'N	S. Georgia; 54°00'S	Signy; 60"40'S	Adelie Land; 66°40'S	Wales; 51°42'N	S. New 7.ealand; 46°55'N
Reference•	I, 2, 3,4	*5*	6	*5*	7	8	9	to	II	12, 13	14
Adult mass (g)	59	40	44	25	49	*c.45*	35	38	43	28	47
Fledging period (days)	58 (Sl-66)	69; 71 (60-72)	64 (59-72)	66, 86	61	63-70	78 (64-97)	60 (54-@)	48 (46-51)	70(61-86); 70 (61-86)	58 (53--68)
Peak mass:											
(g)	85	**68**	75	-	70	75	49	61	76	42	65--67
age in days	*c.45*	46	48		51	52	48	57	31	**SO**	35-SO
% adult mass	144	170	170	-	143	167	140	157	177	ISO	138-143
Fledge mass:											
(g)	73	*c.SO*	49	-	*S1*	*c.60*	35	*55*	*c.64*	34	58
% adult mass	124	125	111	-	116	133	100	145	149	121	123
Growth rate (110-190) in days	33	*c.38*	*c.40*		44	*c.35*	*c.40*	43	*c.29*	c.42	?
Meal size:											
(g)	8·0±4 (3-19; *n*= 160)b 7-4±2 (n=82)° 11·6 (4-24, n= 18)b	*5·6* (n= 160/ 7·2 (11=75)	6·6 (*n*= 15)'	-	-	10·0 (n=l6f	*4·1* (0-15; *n*= 16) c.7·0	-	-	6·5 (2-23; *n=902f*j	6·4 (0-25; n=314)i 13·6
	12·8±7 (*n*= 14)°				-	22·2	13-4-20·0	-	-	23·2	
% adult mass	13·6-21-7	14·0-18·0	15·0								
Feeding frequencr, (chicks fed -d)	0·73d 0·68--0·79"	0·44; 0·65r	0-47'	O·Sr	0·6 +0	0·59 0·76	0·55r 0·84;	-	-	o-8if·i	0·72 (0·6S--0·82);
Delivery rate (adult visits d- 1)	0·7-1-13°	-	0·59	-		0·72 1·02	0·61 0·92	-	-	-	-

• I. Boersma, Wheelwright, Nerini & Wheelwright (1980); 2. Boersma (1986); 3. Hatch (1983); 4. Simons (1981); *5*. Harris (1966); 6. Allan (1962); 7. Watanuki (1985b); 8. Ricklefs *eta/.*(1985); 9. Copestake&Croxall(l985); this paper; 10. Beck& Brown(l972); I1. La n(l971); 12. Davis(l957); 13. Scott(l970); 14. Richdale (1965)

b Using weighings immediately before and after chick fed

c No method given

d Mass increases, plus decreases :E:; 3·0 g (Hatch, 1983)

• Using visit-recording device

r Using mass increments based on twice-daily weighings

8 Using mass increments based on daily weighings

h *7·6* g recorded for younger chicks (Ricklefs, J983); 10·0 g includes *l*·2 g for mass loss between three-hourly weighings

i Using -0·5 gas threshold mass change between successive evening and morning weighings to indicate meal delivered

i Allows some (unspecified) decrease between evening and morning weighings to represent feeds (and to add to meal size)

TABLE XI

Comparison of fledging period, chick growth and provisioning rate in three proce/lariiform species at South Georgia

Species	Adult mass (g)	Fledging period (d)	Chick peak mass (%)·	Meal size (%)"	Feeding frequency (meals d^{-1})
Black-browed albatross	3800	116	132	15	0·85
Antarctic prion	170	51	128	c.15	1·33
Wilson's storm petrel	35	78	100	15-20	0·75

• Percentage of adult mass

Intraspecific variation

The latitudinal gradient in body size of Wilson's storm petrel (Copestake & Croxall, 1985) is accompanied by a strong trend in chick parameters. Thus the duration of the chick fledging period differs greatly in Adelie Land, Signy and South Georgia birds, the last taking 62% longer than the first. There is a similar trend in absolute and proportionate peak mass (South Georgia birds being 64% and 55%, respectively, lighter than Adelie Land birds) and fledging mass (South Georgia birds 55% and 67% lighter). It is likely that there are similar differences in provisioning rate but no data are available from the other studies. At the Crozet Islands (46°S), Jouventin, Mougin, Stahl & Weimerskirch (1985) estimated that chicks were fed on 56% of nights, which is similar to our data from South Georgia (56°S).

Such a high degree of intraspecific variation is not entirely unexpected, given the major environmental differences between the Antarctic continent, where conditions are only suitable for breeding for a short period each year, and the much milder conditions at sub-Antarctic South Georgia. They illustrate, however, that considerable variation in chick growth rate is possible, presumably accompanied by similar variation in feeding frequency, because there cannot be much scope for increasing meal size beyond about 20-25% of adult body mass.

Comparison with other storm petrels

The substantial intraspecific variation in Wilson's storm petrel and the relatively few data for other species urge caution in interspecific comparisons. Nevertheless, the general picture is one of similarities rather than differences. Thus, despite a range of adult mass of 25-60 g, mean fledging periods are 58-70 days. However, the intraspecific variation in this is proportionately the greatest yet recorded for any group of Procellariiformes; notably the range of Wilson's storm petrel (48-78 days), which spans those for all other species. Chicks reach peak weights (of 140-170% adult mass at 40-50 days of age), which are amongst the highest recorded for Procellariiformes; again the range for Wilson's storm petrel (140-180% at 31-60 days) spans all other storm petrels. The southernmost populations of Wilson's storm petrel have chick fledging masses (145-150% adult weight) considerably greater than in other species (110-130%) and the South Georgia population of Wilson's storm petrel (100%). Chick growth rates appear to be broadly similar but the data are not really adequate for critical comparisons.

There are also problems in comparing meal size and feeding frequency, mainly because the various studies have collected, analysed and presented their data in many different ways. As

Ricklefs *et al.* (1985) note, there is an urgent need for standardization of field techniques for such studies and also for similar approaches to data analysis and presentation of results. Allowing for the present differences, meal sizes are probably typically between 15 and 23% of adult body mass and chicks of most species are fed on between 50 and 80% of nights. There is a suggestion that lower values may be associated with tropical species and that chicks of temperate species may usually receive food on about 75% of nights. Only for three species are there estimates of the number of nights on which both adults may deliver meals. For *Oceanodroma furcata* this was recorded on 18 of 52 nights (35%; Simons, 1981: fig. 6), for *0. leucorhoa* on 16 of 62 nights (26%; Ricklefs *et al.*, 1985) and for *Oceanites* on 19 of 186 nights (10%; this paper) with delivery rates of adults being 1·13, 1·02 and 0·92 visits per night, respectively. The lower value for Wilson's storm petrel is not surprising considering that its fledging period is 15-20 days (20-25%) longer than the other two species.

Comparison with other Procellariiformes

Data on growth and provisioning rates of storm petrels (e.g. Ricklefs, White & Cullen, 1980a, *b;* Ricklefs *et al.*, 1985) have been central to the issue of whether foraging rates in Procellariiformes are limited by food supplies or are closely adjusted to chick requirements. Lack (1968) argued that slow growth rates of Procellariiformes were consequences of low provisioning rates caused by the difficulty adults experience in locating unpredictably distributed prey which is of restricted availability to birds that can only forage in surface waters. Ricklefs (1983), Ricklefs, White & Cullen (1980b) and Ricklefs *et al.* (1985), however, maintained that growth rates were typical of other birds of similarly extreme developmental precocity and that significant increases in growth rate could be achieved by relatively small increases in provisioning rate, suggesting that adults were typically operating at well below capacity.

There are few experimental data with which to evaluate these hypotheses. Twinning experiments (e.g. Huntington, 1963; Harris, 1966, 1969) have indicated that the upper limit to feeding rate in Procellariiformes is less than twice the food requirement of a single chick but these and other manipulation experiments (Prince & Ricketts, 1981; Shea & Ricklefs, 1985) also show that significant increases in provisioning and/or growth rate are possible, though usually within well-defined upper and lower limits. None of this is very surprising, because growth and provisioning rates are likely to operate as compromises between the maximum rate of food supply, above which chicks cannot absorb more, and a minimum rate below which chick growth is too slow for successful fledging. However, as Pennycuick, Croxall & Prince (1984) showed, both the smallest and largest Procellariiformes (storm petrels and great albatrosses) have disproportionately lower provisioning rates than medium-sized species, suggesting that they may face more rigorous constraints.

There are now enough data available for storm petrels to state that in comparison with other Procellariiformes: (a) they have disproportionately long fledging periods (e.g. Croxall, 1984); (b) they have disproportionately slow chick growth (Ricklefs, 1973; Croxall, 1984), even though chicks generally attain proportionately similar (or even higher) peak and fledging masses. The slower growth seems to be due chiefly to less frequent parental visits rather than to smaller meals, which are similar to, or proportionately larger than, average values for other procellariiforms (Croxall & Prince, 1980; Pennycuick, Croxall & Prince, 1984). This can be illustrated simply by comparing Wilson's storm petrel with Antarctic prions and black-browed albatrosses *(Diomedea melanophrys)* (Table XI; data from Bird Island, South Georgia; see Croxall, Ricketts & Prince, 1984; Croxall, Prince & Ricketts, 1985; Croxall & Prince, 1987). Thus black-browed albatrosses, which are one hundred times the mass of Wilson's storm petrel, only take half as long again to rear a chick and have a slightly higher provisioning rate. Antarctic prions, nearly five times the mass of Wilson's storm petrel, rear a chick in two-thirds of the time with double the provisioning rate. These comparisons do not indicate the extent to which the provisioning rate of Wilson's storm petrel is adjusted to food availability on the one hand or to chick requirements on the other. They do, however, emphasize that storm petrels cannot simply be regarded as typical Procellariiformes. That some of their chick-rearing adaptations are extreme in the family while other features (e.g. free-living energy costs) are relatively economic (Obst, Nagy & Ricklefs, 1987) may not be paradoxical but, rather, essential complementary adaptations for ensuring the success of these smallest of seabirds in the Antarctic environment.

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