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FEEDING ECOLOGY OF THE DARK-RUMPED PETREL IN THE GALÁPAGOS ISLANDS[1]

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Abstract. During a study of Dark-rumped Petrel (*Pterodroma phaeopygia*) breeding biology in the Galápagos Islands, we collected over 80 samples of food regurgitated by petrel chicks. We identified the prey to the lowest possible taxonomic level and determined the relative importance of each food class in the petrel's diet. We also monitored the daily changes in mass of 14 chicks on Floreana Island to determine the quantity of food delivered as well as the food delivery rate. Dark-rumped Petrel hatchlings were fed a mixture of stomach oils, semi-digested fish, cephalopods and crustaceans. On the basis of mass composition, about 46% of the diet was cephalopods, about 37% fish, and about 17% crustaceans. Cephalopods, of at least 16 families, occurred with the greatest regularity. Fish were present in the samples more frequently than Crustacea: seven and five families, respectively. Feeding rates were highest in the month after hatching and lowest before fledging. Estimated food loads averaged 68 g and did not increase in size over the growth period. Dark-rumped Petrels fed on mainly mesopelagic prey, taken presumably at night, while ranging up to 2,000 km from the colonies, largely southwards.

Key words: Pterodroma phaeopygia; *nestling diet; feeding rate; feeding habits; Galapagos Islands.*

INTRODUCTION

The life-history characteristics of gadfly petrels *Pterodroma* spp. may be adaptations enabling them to make efficient use of food resources that are distant from the breeding colony, patchily distributed, and of relatively low nutritive value (Imber 1973, Croxall and Prince 1982). The diet of only a few *Pterodroma* species has been examined in any detail: Phoenix Petrel *P. alba* (Ashmole and Ashmole 1967, Ricklefs 1984), Grey-faced Petrel *P. macroptera gouldi* (Imber 1973), Great-winged Petrel *P. m. macroptera* and Soft-plumaged Petrel *P. mollis* (Schramm 1983), Bonin Petrel *P. hypoleuca* (Harrison et al. 1983), and Hawaiian Dark-rumped Petrel *P. phaeopygia sandwichensis* (Simons 1985). Prey species are mostly found in surface waters of the ocean at night.

The endangered Dark-rumped Petrel (*P. p. phaeopygia*) of the Galápagos Islands is a medium-sized gadfly petrel of about 420 g (Cruz and Cruz 1987). Little is known of its feeding biology, although the food of the Hawaiian subspecies has been documented summarily (Simons 1985). We report here the findings of a three-year study, amplifying what little is known about the diet of this petrel.

MATERIALS AND METHODS

FIELD METHODS

Data were collected from three locations in the Galápagos archipelago during 1984–1986 (Fig. 1): Cerro Pajas, Floreana Island (1°13′S, 90°22′W); Media Luna, Santa Cruz Island (0°29′S, 90°21′W) and Santiago Island (0°8′S, 90°32′W), all of which are within the Galápagos National Park. Samples of petrel prey were collected casually from chick regurgitates over three years from Floreana (1984, $n = 3$; 1985, $n = 13$; 1986, $n = 35$), two years from Santiago (1985, $n = 10$,

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1986, $n = 4$) and one year (1985, $n = 17$) from Santa Cruz. These were stored in formalin or 70% ethanol for up to seven months before analysis.

The samples were initially sorted into food classes and the total number of items in each class was recorded. We identified cephalopod and crustacean prey to the lowest possible taxonomic level using beaks and exoskeletons, respectively, and for fish prey using otoliths and skeletons. Estimated weights of cephalopods taken were calculated from beak measurements, using formulae given by Wolff (1984) and Clarke (1986). Noting the findings of Imber (1973) and Furness et al. (1984) on the persistence of larger mature cephalopod beaks in seabirds' stomachs, we excluded from calculations of the cephalopod mass component samples containing only beaks and/ or eye lenses.

On Floreana Island in 1986 we followed 20 petrel nests from the pre-laying season through fledging. We weighed the chicks daily at these nests from hatching to fledging to estimate feeding rate and meal size. A recurring problem in collection and analysis of the regurgitates involved the portion of oil in the sample. Several samples were composed largely of oil and, in some cases, much of this was lost on the ground and was impossible to quantify. Consequently, no attempt was made to measure the amount of oil in each sample. We did not obtain the total stomach or proventriculus contents from either chicks or adults due to the birds' status as an endangered species. Nor was it possible to sample directly the food organisms from the marine environment in the area of the Galápagos archipelago.

DATA ANALYSIS

Data were analyzed using the SAS statistical package on an IBM VM370 computer at the University of Connecticut, Storrs, CT. We separated the petrel's prey into three food classes and counted the number of items in each sample as an indication of the relative importance of each food class in the petrel's diet. The Kruskal-Wallis test was used for interisland comparisons of the proportion of each food class present in the samples. A frequency-of-occurrence analysis based on the number of samples containing each food class indicated whether a prey was consistently eaten. However, these data were not suitable for statistical tests of significance.

We assumed that increments in chick body mass during the growth period reflected food delivery rates. Although some food packets were undoubtedly small, we assigned mass gains of ≤ 5 g to measuring error. We partitioned the 120-day nestling period into 10-day segments and counted the number of feedings (mass increments) and number of mass losses in each period. Each increment of more than 5 g was counted as one feeding. To more accurately assess the mass of meals, mean daily mass loss of chicks during the same period was added to the daily mass gain when feeding occurred. Ten-day periods with less than eight observations were omitted from analysis. We calculated mean number of feedings per 10-day period, and mean number of feedings per month. Due to a few missing observations, the number of feedings during the chick period is underestimated and, therefore, the mean interval between feedings is slightly less than we estimate.

We averaged the mass gained or lost daily per chick during the previously assigned 10-day periods and also by months. Only increments or decreases from the previous day's mass were included in analysis. Both mass gains and losses were analyzed using a repeated measures design to clarify patterns of change in mass over time.

RESULTS

PREY

Initially, parents feed stomach oil to their chicks by regurgitation. The oil's primary function is nutritive (Boersma et al. 1980), but it may also be used as a defense against predators (Clarke 1977). As chicks age, partially digested fish, crustaceans and cephalopods are combined with the oil. Later in the nesting season, larger pieces or whole animals are fed to the chicks.

Regurgitates consisted of oil, fish parts (vertebrae, otoliths, scales, heads, jaws, clithrums, operculums, fin elements, flesh and mush), crustaceans (whole or carapaces, other exoskeletal parts and bits), and partially digested cephalopods (lenses, beaks, mantles, gladii, arms, spermatophores, hectocotyles, buccal bulbs, and mush). Thirty-six prey items of the Dark-rumped Petrel were identified in three classes including 21 species in 16 families of the Cephalopoda (Table 1), seven families plus one order of Pisces, and five genera in five families of Crustacea (Table 2). Because there were no differences between

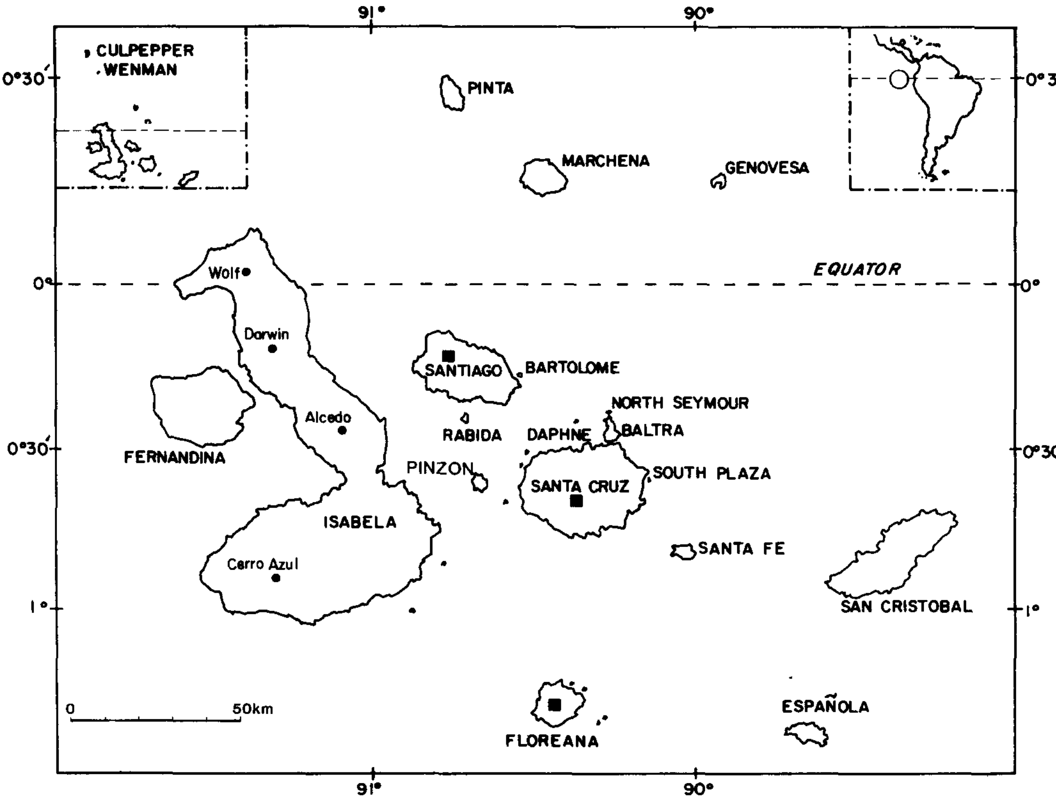

FIGURE 1. Map of the Galápagos archipelago with its location near the South American continent indicated in the upper right inset. The Dark-rumped Petrel colonies we studied are located on Floreana, Santa Cruz, and Santiago Islands; their approximate locations are indicated by solid squares. Dark-rumped Petrel colonies also exist on San Cristobal Island and possibly on the southern volcanoes of Isabela Island.

islands in the proportions of prey from each food class (Kruskal-Wallis test, $\chi^2 = 2.14$, df = 2, $P < 0.34$), the data were pooled for further analysis (Fig. 2).

Cephalopods occurred in 86% of the samples, fish in 59% and crustaceans in 46%. Seven samples contained only beaks and/or eye lenses of cephalopods, but 45% of samples containing cephalopod remains had no beaks, reflecting the prevalence of juvenile and small mature cephalopods in this petrel's diet. By estimating the percentage by mass of the three prey classes in each sample, excluding residual items (beaks, eye lenses) included in Figure 2, then pooling the data, we calculated the diet to comprise 46% Cephalopoda, 37% Pisces and 17% Crustacea. The most frequently captured fish were Sternoptychidae (hatchet fish), Exocoetidae (flying fish), Stomiatoid dragonfish and Macrouridae (rattails). Amphipods (*Eurythenes*), Isopods (*Anuropus*) and Decapods (Pasiphaeidae, Oplophoridae) were the most important crustacean prey. However, the Cephalopoda were the most important prey category; the most frequently encountered species were *Sthenoteuthis oualaniensis* juveniles, *Onychoteuthis banksii, Mastigoteuthis dentata, Pholidoteuthis boschmai* juveniles and *Chiroteuthis veranyi.*

FEEDING FREQUENCY AND MEAL SIZES

The intervals between feedings for some chicks were quite long and variable. Feeding frequency of 14 chicks on Floreana in 1986 decreased from a high of 3.75 ± 1.03 feeds during the first 10 days after hatching (that is, about once every 2.6 days) to a low of less than one feeding every 10 days over the last 20 days of the nestling period (Fig. 3). Feeding rates were highest during the first month after hatching (3.33 ± 1.01 feeds per

TABLE 1. Cephalopoda identified from beaks in 83 food samples from Dark-rumped Petrels of Galápagos Islands. Mass (g) determined from beak measurements: lower rostral length (mm) for squids, lower hood length (mm) for octopuses.

Species	n	Age	Beak measurement	Mass		
				$\bar{x}$	Total	%
Squids						
Ancistrocheirus lesueuri	1	Sub-ad.	3.8	96	96	2
Octopoteuthis nielseni	5	various	3.4–7.0	52	262	5
Taningia danae	1	Juv.	2.3	9	9	tr
Onychoteuthis banksii	19	Ad.	2.1–2.6	44	845	17
Discoteuthis sp.	2	Juv.	3.8	89	178	4
Gonatus antarcticus	1	Ad.	6.7	291	291	6
Pholidoteuthis boschmai	11	Juv.	1.7–3.3	35	383	8
Histioteuthis heteropsis	5	Ad.	3.0–4.2	109	548	11
Histioteuthis spp.	3	Ad.	2.5–2.9	53	160	3
Ctenopteryx sicula	5	Ad.	2.0–2.1	40	200	4
Eucleoteuthis luminosa	1	Ad.	4.1	99	99	2
Sthenoteuthis oualaniensis	33	Juv.	1.1–2.2	13	424	9
Chiroteuthis veranyi	7	various	1.5–4.3	17	117	2
Mastigoteuthis dentata	12	Ad. (1J)	2.0–3.8	44	528	11
Leachia sp.	1	Ad.	1.2	3	3	tr
Galiteuthis pacifica	6	various	2.3–4.8	56	333	7
Unidentified squid	1	Ad.	—	40	40	1
Octopuses						
Amphitretus pelagicus	1	Ad.	3.3	69	69	1
Vitreledonella richardi	1	Ad.?	2.0	33	33	1
Argonauta sp.	2	Ad.?	2.7	51	102	2
Alloposus mollis	1	Sub-ad.	6.5	184	184	4
Totals and mean mass	119			41	4,904	100

10 days or about 10 feeds per month) dropping to 2.88 ± 0.74 and 2.87 ± 1.13 feedings per 10 days (about 8.5 feeds per month) during the second and third months, and falling further to an average of 1.15 ± 1.01 feeds per 10 days (about 3.5 feeds per month) during the last month in the nest. Intervals between feedings averaged 3.3 days for the first three months of the development period but increased to 8.5 days in the month before fledging (Fig. 4). However, the number of feedings is probably underestimated in the last month, when small feeds are most likely (Imber 1976), causing the feeding intervals to be somewhat overestimated.

Estimated food loads, which included considerable proportions of stomach oil, ranged from less than 30 g to over 150 g per feeding and averaged around 68 g. The estimated average mass of cephalopods taken (41 g) was not much less, indicating that these petrels prefer cephalopods as large as they can consume. Chicks gained the least mass per feeding during the first month after hatching (56.5 ± 24.0 g, n = 80), and gained the greatest mass per feeding during the second (74.9 ± 32.6 g, n = 69), lessening during the third (70.2 ± 26.4 g, n = 52) and fourth month (68.4 ± 33.6 g, n = 28). Combining this information with frequency of feedings per month, we found that chicks received on average an estimated 565 g of food during days 0–30, 647 g in days 31–60, 605 g in days 61–90, and 236 g in days 90–120. This indicates that chicks received at least 2,053 g of food: 59% of the total food was received during the first half of development, and 88% of the food was delivered by the end of the third month of the nestling period.

A repeated-measures analysis of the mass gained by chicks indicated that individuals received similar meal sizes by mass throughout development with the exception of days 60–70 ($F_{12,15} = 3.47, P < 0.01$) and 70–80 ($F_{11,11} = 3.57$, $P < 0.02$) when chick mass gain was more variable. Similarly, individual chicks appeared to lose mass between feedings in a constant manner with the exception of the 20–30 day ($F_{11,27} = 3.55$, $P < 0.004$) and 80–90 day periods ($F_{6,10} = 6.30$, $P < 0.006$) when mass loss was more variable.

Estimated loss of chick mass between feedings

TABLE 2. Fish and Crustacea in regurgitations or stomach contents from 83 Dark-rumped Petrels on Galápagos Islands.

Food item identification			*n*	Frequency in 83 samples
Fish		Total	62	
Clupeidae	*Harengula* cf. *peruvana*		1	1
Sternoptychidae	*Argyripnus* sp.		1	1
	unidentified		14	12
Stomiatoidea	unidentified		3	3
Stomiatidae	unidentified		3	3
Myctophidae	*Electrona* cf. *paucirastra*		1	1
	unidentified		3	3
Gadiformes	unidentified		5	4
Macrouridae	unidentified		2	2
Exocoetidae	*Hirundichthys* sp. or *Fodiator* sp.		6	6
	unidentified		1	1
Bramidae	unidentified		4	4
Unidentified			18	17
Crustacea		Total	52	
Mysidacea				
Lophogastridae	*Gnathophausia* cf. *zoea*		2	2
Amphipoda				
Lysianassidae	*Eurythenes* sp./spp.		18	16
Isopoda				
Anuropodidae	*Anuropus* sp.		6	5
Decapoda				
Oplophoridae	*Acanthephyra* sp.		5	5
	cf. *Notostomus* sp.		1	1
Pasiphaeidae	unidentified		5	4
	unidentified decapods		7	7
Unidentified			8	8

indicated that the greatest loss of mass ($F_{11,347}$ = 3.74, $P < 0.001$) occurred during the second and third months of the development period (26.3 ± 16.8 g per day and 27.7 ± 16.4 g per day, respectively). Least mass was lost during the month after hatching (18.1 ± 14.4 g per day) and the month before fledging (21.1 ± 17.9 g per day) (Fig. 5).

DISCUSSION

PREY

In common with the Galápagos subspecies, Simons (1985) found that the Hawaiian Dark-rumped Petrel took fish of the families Exocoetidae, Sternoptychidae and Myctophidae, squid of the Ommastrephidae, and also *Anuropus* isopods. Loomis (1918) reported pteropods and coelenterates in Galápagos Dark-rumped Petrel stomachs but we found no trace of these.

Harris (1973) found that squid beaks regurgitated by chicks of the Waved Albatross (*Diomedea irrorata*) in the Galápagos included Ommastrephidae (some *Sthenoteuthis oualaniensis*), Histioteuthidae, Octopoteuthidae, Chiroteuthidae, Onychoteuthidae (*Onychoteuthis* sp. or *Moroteuthis* sp.), and Pholidoteuthidae (*Pholidoteuthis* sp.). Exocoetidae fish and the isopod *Anuropus pacifica* were also identified. There is much overlap in the prey species taken by the Waved Albatross and the Dark-rumped Petrel. Harris' data do not indicate the size of prey taken by the by the albatross, so the amount of overlap remains unknown. However, these prey species may be the most common or most easily obtainable for both bird species. Seasonal variation in availability of these prey to seabirds of the Galápagos is unknown, but Banse (1964) noted that at low latitudes massive nightly migrations to the surface occur throughout the year. However, the distribution of prey organisms around the Galápagos is not well documented. Many prey taken by Dark-rumped Petrels are mesopelagic species that migrate vertically from the deeper ocean layers (200 m–1,000 m) to feed at the surface at night and then return to depths during day. Im-

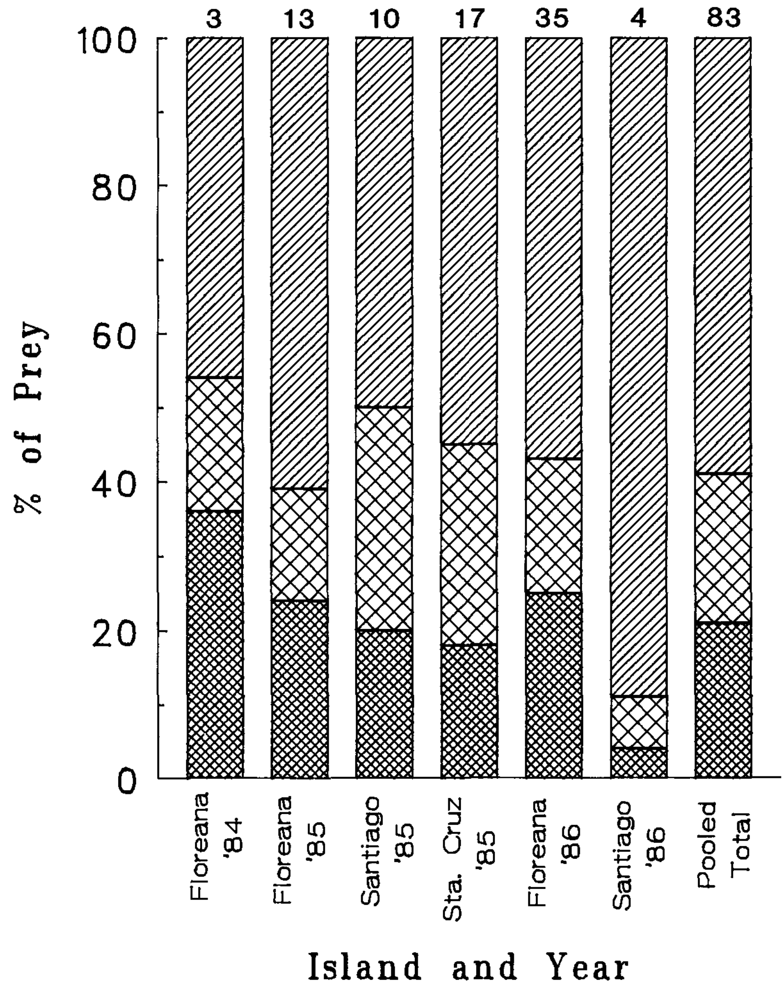

FIGURE 2. The percent of each prey class fed to chicks by Dark-rumped Petrel adults on three Galápagos Islands in 1984 to 1986. Samples were analyzed individually and then pooled for this comparison. In descending order: cephalopods, fish, crustaceans. Sample sizes at top.

ber (1973) discusses this aspect of Grey-faced Petrel feeding ecology. Of the cephalopods taken by Dark-rumped Petrels, 82% by number and 75% by mass are bioluminescent, which may aid the birds in detecting prey at night. As well as flying fish, a frequent squid prey (*Onychoteuthis*) is a "flying squid" (Barnes 1980). Both might be captured on the wing by this petrel, as its close relative the Juan Fernandez Petrel (*Pterodroma externa*) catches flying fish (Ainley and Boekelheide 1983).

Argonautids, ommastrephids and flying fish may be caught during the day (Ashmole and Ashmole 1967), particularly crepuscularly; and some large fragments of prey, such as eye lenses, came from large cephalopods that the petrels probably scavenged. However, the composition of regurgitates of Dark-rumped Petrels indicates that most foraging is nocturnal. Many of the fish prey, including unidentified ones, had less robust osteology indicating their deep sea origin. But the size of fish taken is also surprising. Standard length of one myctophid was 175 mm while the pectoral fin of one flying fish was at least 160 mm long. As these prey were consumed entire, the Dark-rumped Petrel is capable of capturing prey larger than previously supposed. Most cephalopods taken were one-meal-sized.

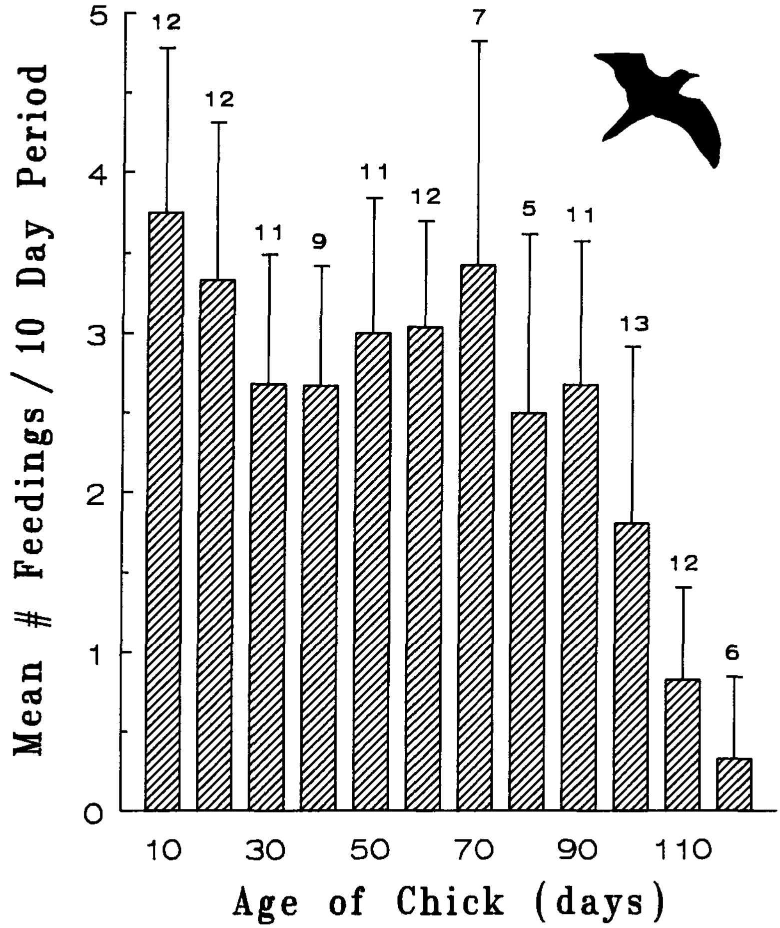

FIGURE 3. Rate of feedings delivered to Dark-rumped Petrel chicks on Floreana Island in 1986. Bars represent means per 10-day period, sample sizes are indicated over the error bars.

Among the problems in analysis of regurgitates is the danger of overestimating some types and sizes of prey while underestimating others. Furness et al. (1984) report that squid beaks can remain and collect for at least 50 days in the stomach of the Shy Albatross (*Diomedea cauta*) whereas fish remains are quickly digested. Small cephalopod beaks may also be completely digested (Imber 1973). Fish identifications were very difficult due to several factors including: (1) the material's advanced state of digestion, (2) scarcity of information on deep sea fish in Galápagos waters; and were complicated by (3) the normal changes in fish morphology with age. Because of these considerations, our analysis of the importance of prey types by their frequency of occurrence may overestimate the proportion of squid in the diet while underemphasizing the importance of fish and crustaceans.

STOMACH OILS

Cummins (1967), Clarke and Prince (1980), Croxall and Prince (1982) and Simons and Whittow (1984) found calorific values for some cephalopods, crustaceans and fish to range from 1.07–11.53 kJ per g of wet mass. Simons and Whittow analyzed several food samples from the Hawaiian Dark-rumped Petrel and found that fish and squid yielded 4.5–5.0 kJ per g, while stomach oil yielded 41.74 kJ per g. Energy content of oils from 12 species of Procellariiformes analyzed by Warham et al. (1976) ranged from 39.23–42.17 kJ per g. Stomach oils can therefore represent a 3.5 to 35 times more concentrated energy source

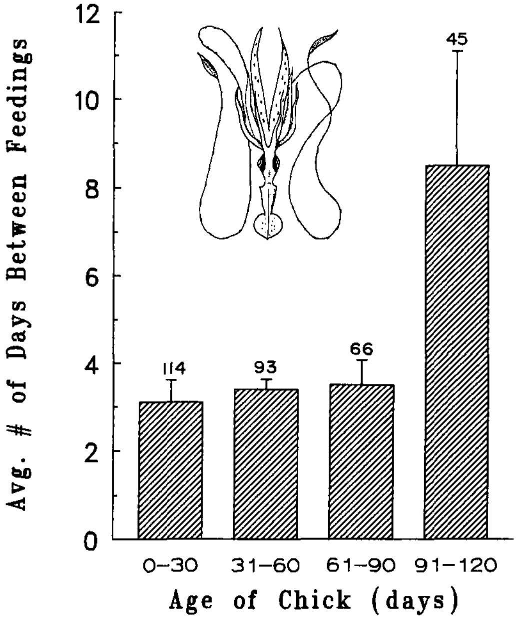

FIGURE 4. Average intervals between feedings of Dark-rumped Petrel chicks on Floreana in 1986. Error bars and sample sizes are given for each 30-day period.

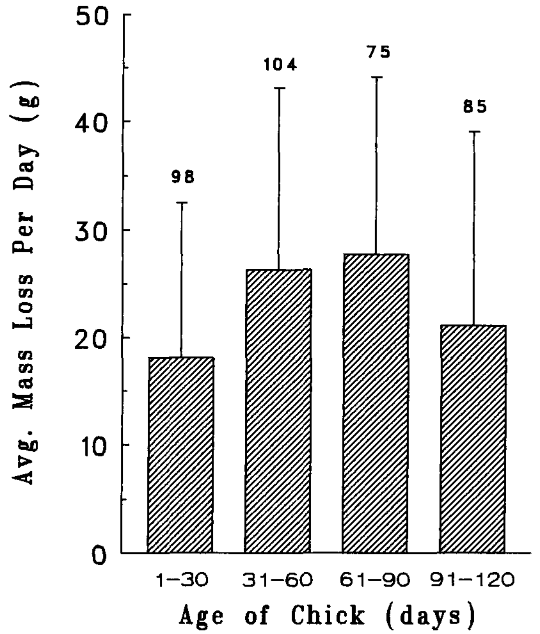

FIGURE 5. Estimated average loss of mass between feedings for Dark-rumped Petrel chicks on Floreana in 1986. Sample sizes are given above the error bars.

than prey at the time of capture. Oils may be the main source of energy and water for small chicks (Warham et al. 1976) as they form the bulk of material regurgitated by young Dark-rumped Petrel chicks. Simons and Whittow (1984) suggested that 30–50% of the energy requirements of Dark-rumped Petrel chicks in Hawaii were met through stomach oil fed to them.

FORAGING RANGE

Systematic sightings from ships have been made by several observers, and observations by R. L. Pitman (1986) on Dark-rumped Petrel density and distribution at sea are presented in Figure 6. Petrel density is greatest in and around the islands, and to the southeast, south, and southwest of the archipelago (from 2°N to 13°S, a range of 300–1,700 km). The northern and southern areas coincide with the productive waters resulting from the upwelling and deflection of the Equatorial Undercurrent. Concentrations of petrels to the southwest of the archipelago also coincide with the productive waters where cetaceans are principally located (Whitehead 1987). Juvenile *Pholidoteuthis boschmai* are a component of Dark-rumped Petrel regurgitate, while adult *P. boschmai* are taken by sperm whales (Clarke 1980).

From Pitman's data on petrel distribution around the Galápagos, we suggest that Dark-rumped Petrels take the more abundant prey found within 15° of the equator (King and Iversen 1962). Because the upwelling currents tend to vary in strength seasonally there may be accompanying shifts in petrel foraging zones.

FEEDING FREQUENCY AND MEAL SIZES

The infrequent feedings in the period before fledging suggest that, like Leach's Storm-petrel (*Oceanodroma leucorhoa*) (Ricklefs et al. 1987) and the Hawaiian Dark-rumped Petrel (Simons and Whittow 1984), the chicks metabolize and store much fat some time before they fledge (Lill and Baldwin 1983). Because meal size is fairly constant over the nestling period and because feeding rate decreases during the last month before fledging, a decrease in chick mass during the last month is not surprising. We found no pronounced starvation period in these birds, but the decreased frequency of food delivery was marked. The average meal size of about 68 g (16% of adult mass) is similar to that reported for the Grey-

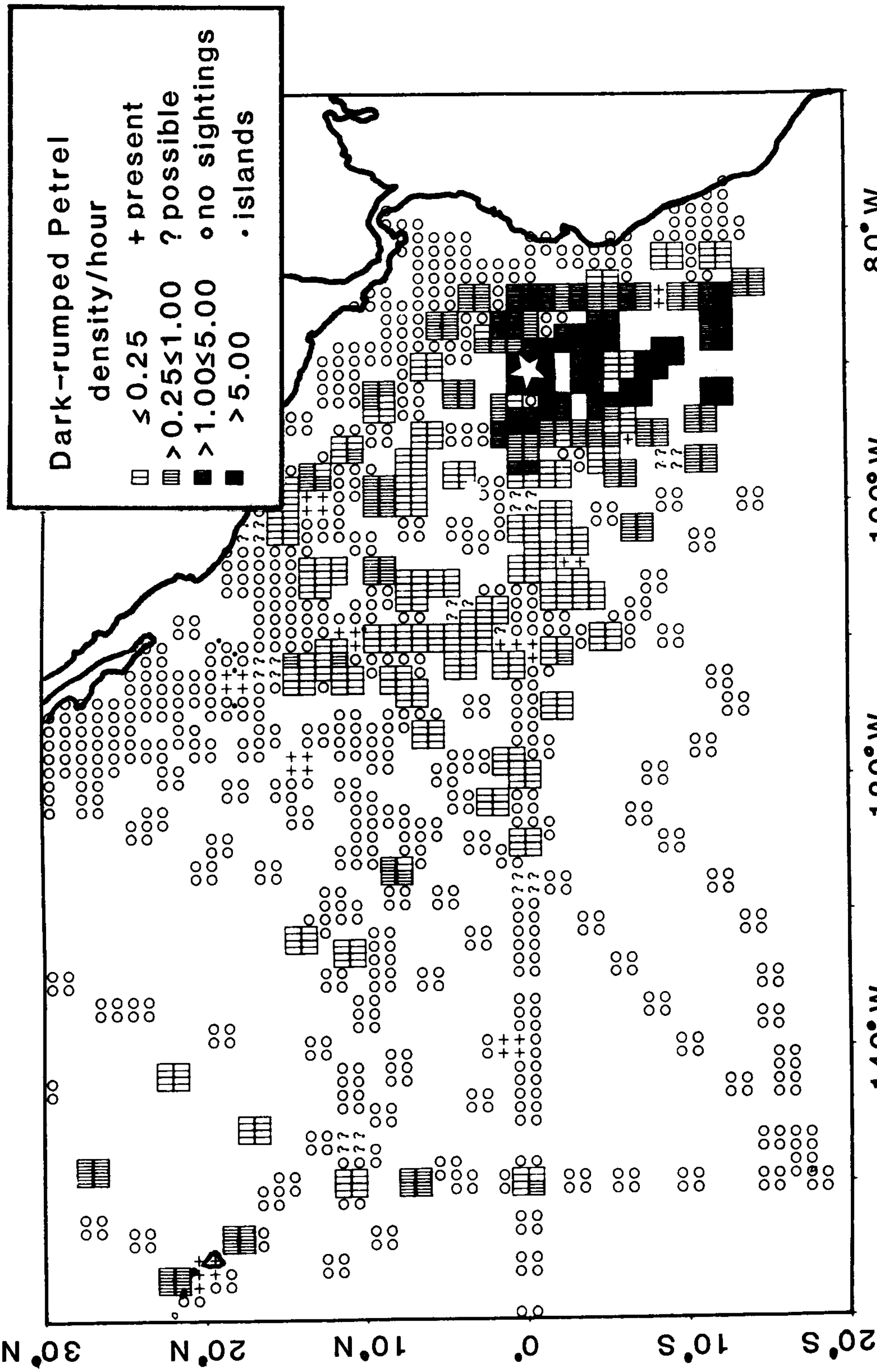

FIGURE 6. Dark-rumped Petrel sightings in the eastern Pacific Ocean, from Pitman (1986).

faced Petrel (97 g, 18%) (Imber 1973), Great-winged Petrel (86 g, 14%) (Schramm 1983), Soft-plumaged Petrel (74 g, 20%) (Schramm 1983) and Phoenix Petrel (49.4 g, 18.2%) (Ricklefs 1984).

The mass-specific metabolic rate and the energy requirement for growth in Hawaiian Dark-rumped Petrels are highest in very young chicks (Simons and Whittow 1984). This pattern has also been found in three burrow-nesting petrels on Marion Island (Brown 1988). This suggests that much energy in the early nestling period is devoted to developing the thermoregulatory ability just after hatching. The increased mass loss during the 30–90 day period in the Galápagos Dark-rumped Petrel chick is consistent with the highest total energy expenditures found during this same period in the Hawaiian Dark-rumped Petrel. During this period the chick may be more sensitive to limitations of food delivery. Variable food resources may reduce the energy diverted to growth and development during this period, thus extending the total time to fledging.

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