BREEDING, MORPHOLOGY, AND GROWTH OF THE ENDANGERED DARK-RUMPED PETREL

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ABSTRACT.—Dark-rumped Petrels (*Pterodroma phaeopygia phaeopygia*) in the Galápagos archipelago breed on several islands. Life-history characteristics such as mate and site fidelity, large egg size, long incubation periods, long incubation bouts, and chick growth patterns are similar to those of other procellarids. Adults nest annually, but the timing of breeding is out-of-phase among the islands of Floreana, Santa Cruz, and Santiago. Banding data for 1,500 adults and juveniles indicated that little or no interbreeding occurs among islands. From adult morphological characteristics measured during five years on Floreana and one year on both Santiago and Santa Cruz, we found that on Floreana, adults were sexually monomorphic in all measured characteristics except bill height, and the adults from Floreana tended to be larger in both size and mass than adults from the other two islands. The possibility that each island's population is distinct should be considered when formulating management plans concerning this species. *Received 10 May 1989, accepted 6 November 1989.*

THE DARK-RUMPED Petrel (*Pterodroma phaeopygia phaeopygia*) breeds on at least four of the islands in the Galápagos archipelago: Floreana, Santa Cruz, Santiago, and San Cristóbal. They adhere to a rigid, annual breeding schedule; most other Galápagos seabirds breed semiannually or opportunistically (Harris 1977, Valle et al. 1987). Adult petrels return repeatedly to the same island-specific colonies to breed, and they probably disperse over broad areas of the eastern Pacific Ocean between breeding attempts (Murphy 1936). The Dark-rumped Petrel is endangered at all of its breeding sites (King 1981).

We studied aspects of petrel breeding biology including mate and site fidelity, egg size, and adult weight loss during incubation bouts. We also compared the breeding chronologies of colonies on Floreana, Santa Cruz, and Santiago; and we examined adult morphological characteristics and chick growth from all three islands.

The breeding biology of the Dark-rumped Petrel on Santa Cruz was studied previously by Harris (1970). Tomkins (1985) surveyed the archipelago in 1978-1979 and suggested that breeding was not synchronized among islands. This was supported by Coulter et al. (1981, 1982

unpubl.) who found differences in the initiation of breeding among different colonies on Floreana. We studied the breeding biology of the petrel on Floreana as a corollary to a conservation effort that alleviated petrel mortality through control of introduced mammalian predators (Cruz and Cruz 1987a, b; J. B. Cruz and F. Cruz 1987).

MATERIALS AND METHODS

Study areas.—We collected data from three locations in the Galápagos National Park in 1981, and 1983-1986 (Fig. 1). The colony on Floreana Island (1°13'S, 90°22'W) was located in a dormant volcano (Cerro Pajas) at 300-640 m above sea level (asl). We sampled petrels from the most accessible and least fragile nests along the interior walls of the volcano to minimize disturbance (J. B. Cruz and F. Cruz 1987). On Santa Cruz Island (0°9'S, 90°21'W), we sampled nests in the Media Luna colonies and their environs at 600-800 m asl. In these colonies, petrels frequently dig their burrows into the soft soil of water gullies (Harris 1970). We also studied petrels in the highlands of Santiago Island (0°8'S, 90°32'W), where colonies were widely scattered. Petrels on this island nest in small groups located in an area of at least 35 km². We monitored ca. 25 km². We found most nests deep in caves and other hard-to-reach areas at 500-900 m asl.

Field methods.—On Floreana we checked 43 nests (1981), 104 nests (1983), and 100 nests (1984, 1985, and 1986) from January through September. We assessed nests at least weekly, but more frequent checks were made in some years.

We banded all adults with 7-mm diameter num-

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Fig. 1. Map of the Galápagos archipelago with its location near the South American continent indicated in the upper right insert. The approximate locations of the colonies we studied are indicated by squares.

bered bands from the British Museum (Natural History). We followed pairs marked from previous years and documented losses or changes of partner. We captured adults by hand in burrows and determined their gender by cloacal inspection just after egg laying (Copestake et al. 1988). We measured 708 adults on Floreana, 25 adults on Santiago, and 52 adults on Santa Cruz. In 1985, we also measured chicks weekly and banded them before fledging (Floreana, $n = 15$; Santiago, $n = 14$; and Santa Cruz, $n = 10$).

We weighed birds with 300 (± 2 g), 500 (± 5 g) or 1,000 g (± 10 g) Pesola spring scales. Wing length was measured (± 1 mm) from the wrist joint to the tip of the longest primary or feather sheath, if primaries had not erupted. We measured the length of the tarsometatarsus (± 0.1 mm), and the culmen (± 0.1 mm) from the tip of the upper mandible to the edge of the forehead feathers (we referred to this value as bill length in the remainder of the paper). Bill height and width were measured at the nostrils. We measured tail length (± 1 mm) from the tip of the longest rectrix to the point between the middle rectrices where they emerged from the skin (Baldwin et al. 1931).

We measured egg length and width (± 0.1 mm) once during the incubation period. In 1981, we weighed eggs weekly with a 100-g balance (± 1 g). In other years we weighed eggs once only. Because petrels are burrow nesters, it was difficult to find newly laid eggs and follow them at frequent intervals. Therefore, we used egg density (g/cc) to estimate egg-laying and hatching dates. Eggs lose mass during incubation, and egg mass varies with egg size. However, egg density is much less variable. We calculated egg density using the following formulas: density = mass/ volume, egg volume = $\pi l w^2 / 6$, and therefore, egg density = $6m / \pi l w^2$, where l = egg length, w = egg width, and m = egg mass (Furness and Furness 1981).

We made morphological observations through the nestling period. The data were analyzed for chicks of known age (to within 3 days) that lived beyond 85 days, or were known to have fledged successfully. In 1986, we followed an additional 20 nests daily from the prelaying season through fledging. Here we banded each adult as it returned to the nest. We marked one of each pair with additional black spots on the neck and gular region in order to more easily distinguish between members of a pair. This reduced disturbance during daily observations. We documented the length of incubation bouts taken by each adult, and we measured mass loss twice a week. Incubation bout length for both birds is underestimated because of missing observations.

On Santa Cruz we followed 100 nests weekly from July to November in 1985 and 1986. On Santiago we monitored 205 nests from February to August and again in October of 1985. We monitored 50 nests during a 14-day visit in June 1986. Different workers made observations on each island, but the same observer took measurements at each nest to assure uniformity. In 1986 a single observer collected data from adult petrels on all three islands.

Data analysis.—We analyzed all quantitative data with the SAS statistical package on an IBM VM370 computer at the University of Connecticut. Length of incubation period was compared among years with a one-way ANOVA. We tested for correlation between estimated length of incubation bouts and loss of adult mass using Pearson's correlation coefficients followed by the Kruskal-Wallis test.

We analyzed adult petrel measurements from 1986 for interisland differences using a two-way ANOVA, followed by Scheffé, Bonferroni, Kruskal-Wallis, and Mann-Whitney tests (Snedecor and Cochran 1980). We also analyzed differences among islands and between genders using a multivariate MANOVA, standardized to the same scale for purposes of comparison. We used 0.05 probability levels for all tests of adult morphology, except where noted. Means ($\bar{x}$) are followed by one standard deviation (SD).

We estimated chick growth rates using iteration to fit the logistic, Gompertz, and von Bertalanffy equations to the data for each variable. We then analyzed for goodness-of-fit by nonlinear least squares regression (Ricklefs 1967). The Richards growth model was an attractive alternative to these methods, but it may be sensitive to small errors in determination (Brisbin et al. 1986). We therefore used the logistic equation which provided the best approximation to the data: $M = A(1 + be^{-Kt})^{-1}$, where M is the measured variable, A approaches the maximum measure, b is the proportional gain from the initial measure to the final measure, t is time, and K is a constant which is proportional to the overall growth rate.

We omitted from analysis the data on body mass for chicks undergoing prefledging mass recession. We then compared the derived growth constants for interisland differences using the Kruskal-Wallis test. Because chick mass declines from its maximum for about a month before fledging, we were able to ap-

proximate the maximum mass and size of chicks on all islands. On both Santa Cruz and Santiago, however, there were too few observations at the end of the breeding season to analyze fledging ages or fledging mass.

RESULTS

BREEDING

Behavior at the colony.—Dark-rumped Petrels are nocturnal at the colony, arriving at approximately 1845. Their loud calling and flying above the colony may last through the night, but more often activity is bimodal with a lull between 2200 and 0200. Because breeding adults have already established pair bonds and birds with eggs do not leave their burrows during incubation (Coulter et al. 1982 unpubl.), subadults appear to do most of the courtship flying and calling. Similar to Dark-rumped Petrels in Hawaii (*P. phaeopygia sandwichensis*), nonbreeders appear to desert the colony after several months, and levels of nocturnal vocalization then decrease (Simons 1985). Failed breeders do not attempt a second breeding, and lengthen the nest cavity for up to 3 weeks after egg or chick loss.

Mate and site fidelity.—During the study we banded both birds of 165 pairs on Floreana (or 40% of the total). Of these marked pairs, 11 birds (3%) changed nest cavities (3 male, 7 female, and 1 unsexed). At the new nest, we found that 1 male and 6 females had acquired new mates. At least seven of the birds that switched mates came from collapsed nesting cavities; the new nests were within 10 m of the old. We also documented another seven birds (2%) that changed partners but not nest sites.

By 1986, we had banded ca. 1,500 adults and juveniles out of an archipelago-wide population roughly estimated as 10,000 (Cruz and Cruz 1987a). Although we banded several hundred adults from each island (800 on Floreana, 250 on Santiago, and 250 on Santa Cruz), none were recovered away from the breeding or natal colony (i.e. at another colony). Most breeders were recovered at the same nest site with the same partner. We believe that little interchange occurs among the colonies.

Laying.—For several weeks after their return, birds visited their nesting cavities individually or in pairs to remove debris and add new nest material. Often the nest chamber was enlarged or the burrow elongated. Nests usually con-
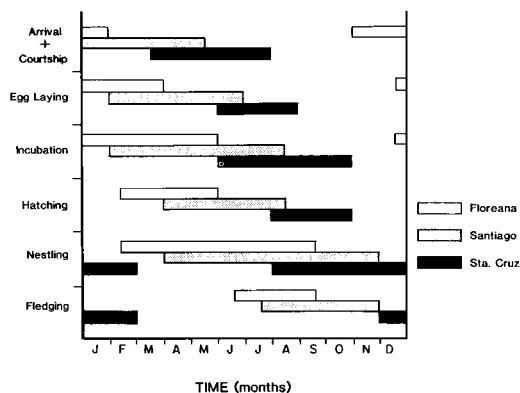
Fig. 2. Breeding chronology of petrels on Floreana, Santa Cruz, and Santiago is out-of-phase between islands and is not highly synchronized within each colony.

sisted of a few twigs, leaves, and moss. Birds were absent from the nest following renovation and before laying for ca. 34 ± 2.8 days (*n* = 4).

As time of laying approached, the male returned to the nest before the female 88% of the time (*n* = 20). He spent 2–3 days in the burrow, and if the female was not present during this time, he left and returned 5–10 days later. In most cases, the arrival of the female and subsequent laying of the egg occurred during the male's second visit.

Breeding phenology was not synchronous among islands (Fig. 2). Petrels arrived in January on Santiago where egg laying commenced by early February. Petrels that breed on Santa Cruz began to arrive in late April (Harris 1970), and egg laying commenced in early June. The earliest birds returned to Floreana in October and started laying by mid-December.

Adults laid a single egg per pair. On average the eggs weighed 65.5 ± 3.25 g (*n* = 40) when newly laid, and 57.8 ± 4.48 g (*n* = 9) at hatching (this study, Coulter et al. 1982 unpubl.). At laying the egg was ca. 16% of adult body mass and thus relatively large compared with body size (Rahn et al. 1975). Egg density decreased from laying until hatching almost linearly and was approximated by the regression equation, $y = ax + b$, where $a = -0.0028$, $b = 1.0479$, and $x =$ egg density. We estimated the dates of laying and hatching for eggs of unknown age and also for some eggs of known age using the regression equation. For eggs of known age, we found that 80% (*n* = 8) were laid within 5 days of the
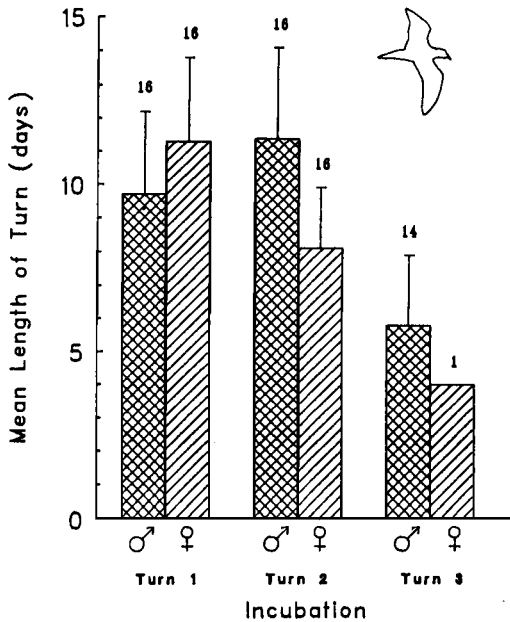
Fig. 3. Mean incubation bouts of males and females. We found no differences between the sexes. The first bouts were longer than those interrupted by hatching.

predicted date while 90% ($n = 10$) hatched within 3 days of the prediction.

Incubation and hatching.—Length of incubation period did not significantly differ among years on Floreana. The average time was 50.2 ± 5.72 days ($n = 239$). Both members of a pair incubated the egg and exchanged nest duties 4–6 times during the period. Males incubated first, with only one exception in 16 pairs, and were relieved by their partners an average of 10 days later (mean of uninterrupted bouts = 9.97 ± 2.75 days, $n = 66$). The nonincubating adult was presumed to be foraging at sea. Males generally took three incubation bouts and females took two ($n = 12$). But there were exceptions to this pattern. In some, the egg hatched after two male and two female bouts ($n = 2$). In others, the female took three turns and the male took two ($n = 1$), or both male and female took three bouts ($n = 1$).

The length of bouts taken by either males or females was similar (Fig. 3). However, the last bout was abbreviated by hatching ($\bar{x} = 5.80 \pm 2.27$ days, $n = 15$), and was shorter than earlier bouts (Kruskal-Wallis $\chi^2 = 37.36$, df $= 5$, $P <$

0.0001). Length of incubation bout and rate of mass lost by the adult were not correlated. Males and females lost similar mass per day ($\bar{x}$ male loss = 6.3 ± 1.70 g/day and $\bar{x}$ female loss = 6.05 ± 1.61 g/day), and this rate did not vary over the incubation period. Males, however, spent an average of 26.8 ± 2.8 days at the nest, and lost ca. 168 g over the incubation period. Females spent an average of 19.4 ± 2.5 days at the nest and lost ca. 117 g over the incubation period. The difference, ca. 51 g, approaches the mass of the egg.

On Santiago hatching occurred between 8 April and 14 August 1985 (range = 129 days), and on Santa Cruz the period stretched from 8 August to 15 November 1985 (range = 99 days). On Floreana hatching extended from 23 February to 22 May. Fledglings left Santiago between mid-July and the beginning of December (range: ca. 130 days), and they departed Santa Cruz from early December to the end of February (range: ca. 90 days). On Floreana the young left the nest between 13 June and 7 September after remaining in the nest on average 112.1 ± 4.3 days ($n = 197$).

ADULT MORPHOLOGY

The two-way ANOVA on measurements of Floreana Island birds for 1981 and 1983–1986 indicated that adult birds were sexually monomorphic in all measured characteristics except bill height ($n = 150$ males and 166 females). Males had deeper bills than females ($\bar{x} = 11.9 \pm 0.04$ mm vs. $\bar{x} = 11.4 \pm 0.04$ mm; $F = 20.73$, df $= 1, 132, P < 0.001$).

On average, male petrels from Floreana ($n = 50$) were heavier and larger than birds of both sexes from other islands for all variables except bill width (Santiago, $n = 13$ males and 11 females; Santa Cruz, $n = 20$ males and 23 females). There was no difference in bill width among males from the three islands (Fig. 4). Females from Floreana ($n = 40$) were also heavier and larger than females from the other islands. Differences between birds from Santiago and Santa Cruz were less consistent than those between Floreana adults and adults from the other islands.

Using a MANOVA, we found that bill height, bill width, and bill length were the most important characteristics in distinguishing between the sexes. Males had deeper, broader, and
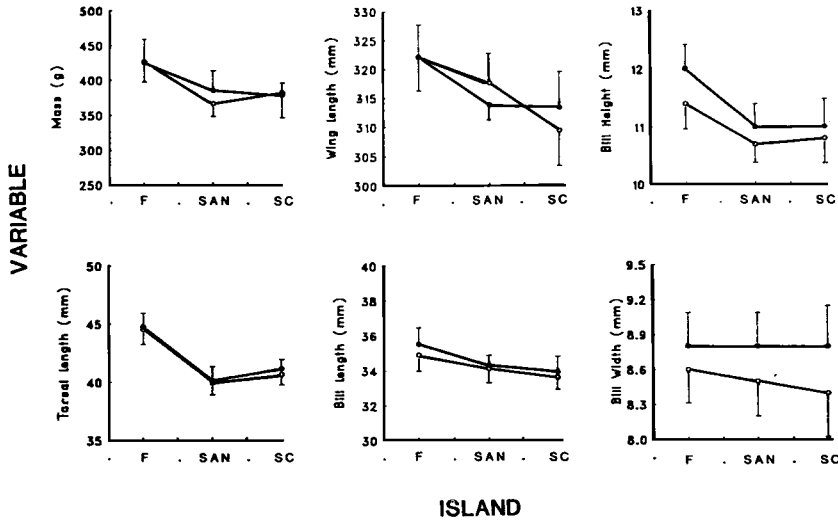
Fig. 4. Mean male (●) and female (○) adult measurements from Floreana, Santa Cruz, and Santiago in 1986.

longer bills than females. Differences among islands were distinguished most strongly by tarsal length (Fig. 5) followed by bill height (Fig. 6). Birds of Floreana had longer tarsi and deeper bills than other birds.

CHICK GROWTH

Chicks from all colonies followed similar growth patterns (Fig. 7). Chick mass increased rapidly for 10–11 weeks, and reached a maximum at ca. 134% of adult mass. Mass then remained constant for 2–3 weeks while feathers grew and down was lost from the face and wings. Mass was lost over the last few weeks, but feathers continued to grow. Tail feathers grew quickly after ca. 65 days. The bill and tarsus developed rapidly during the early chick stage, attaining close to their maximum size by day 60 and growing more slowly thereafter. Wing length increased throughout the nestling period. Primaries erupted at approximately day 40, and the wing was still growing when the chick fledged. Chicks on Santiago and Santa Cruz were not monitored long enough to determine fledging mass. On Floreana in 1985, the average fledging mass was 440.2 ± 31.2 g, similar to adult mass.

The fitted logistic curve of mass increments from all islands (Fig. 8) and the growth constants (*K*) derived from the curve fitting procedure (Table 1) indicated that tarsus and mass

increased more quickly in Floreana chicks than in chicks of the other islands.

DISCUSSION

Mate fidelity and adult survival.—Our banding data indicate that the Dark-rumped Petrel is a long-lived seabird. The life span is not known with certainty, but Simons (1984) estimated a maximum of 36 years. On Santa Cruz, we recovered petrels banded as breeding adults 20 yr previously, so Simons' estimate is not unrealistic. Mate fidelity is common among long-lived seabirds and has been observed in albatross (Rice and Kenyon 1962), shearwaters (Brooke 1978), and other petrels (Warham 1967).

Long life may have several effects on breeding biology, particularly in a species where a high proportion of birds exhibit mate fidelity to the partner of the previous year (Coulson 1966). In this situation the pair bond can be reformed more quickly than with a strange adult, especially if both birds of the pair return to the same site. The high degree of philopatry and mate fidelity in Dark-rumped Petrels imply that both forms of tenacity improve petrel reproductive success. When fidelity is pronounced, however, the breaking of a pair bond due to unnaturally high adult mortality may delay rebreeding attempts because of the difficulty in forming a new pair bond (Van Ryzin and Fisher 1976).
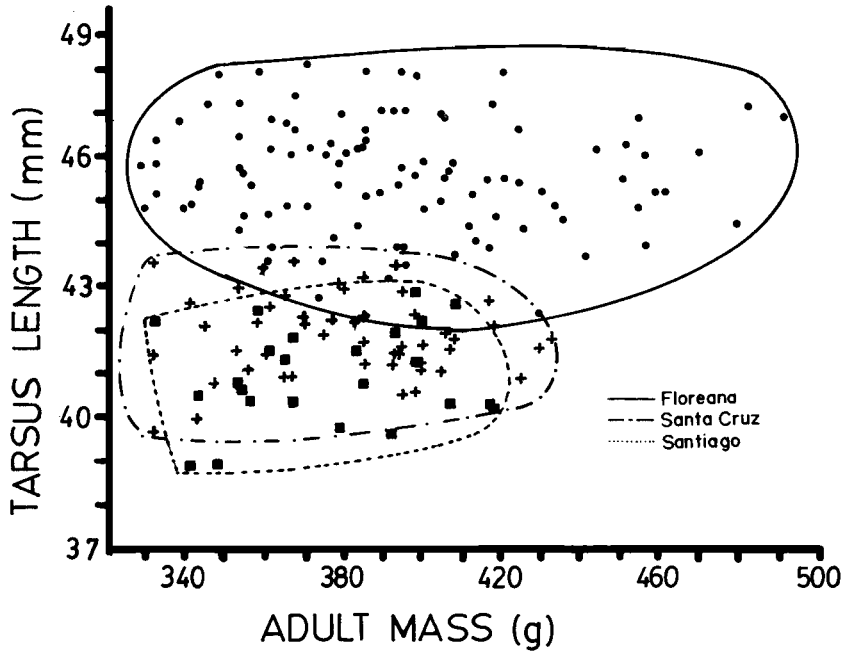
Fig. 5.   Tarsus length was one of the most consistently different characteristics between islands (ANOVA F = 249.3, df = 2, 146, P < 0.0001): Floreana (●), Santa Cruz (+), and Santiago (■) birds.
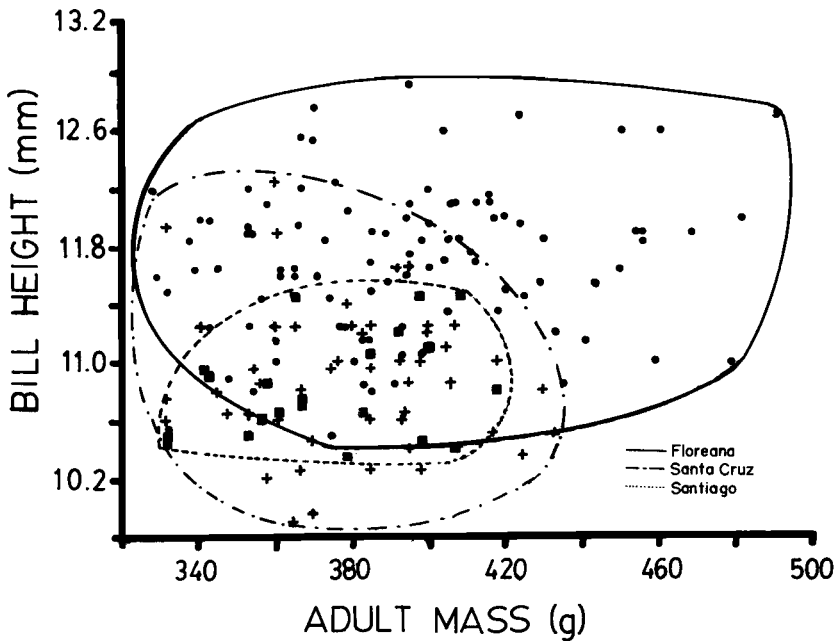
Fig. 6.   Bill height also distinguished strongly between adults of different islands (ANOVA F = 69.39, df = 2, 146, P < 0.0001). See Fig. 5 legend for explanation of symbols.
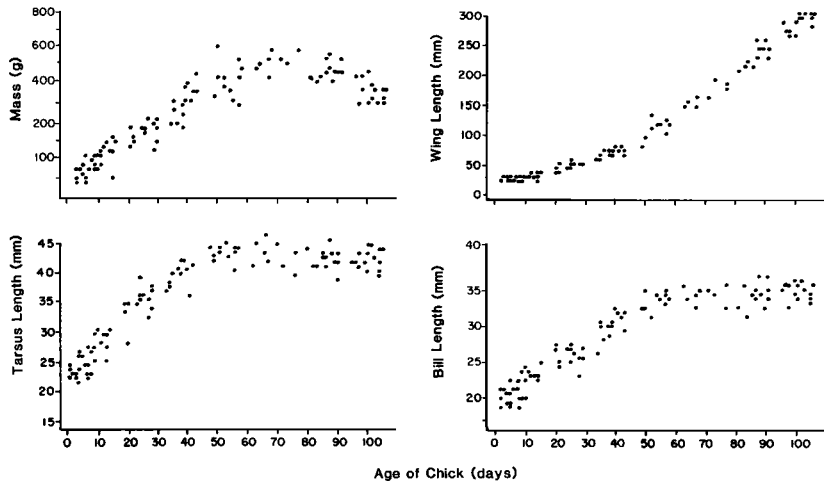
Fig. 7. Chick growth from Floreana Island in 1985 as a function of chick age. Mass increases over approximately the first 3 months in the nest and then declines before fledging. Wings are still growing at fledging, but both tarsus and bill approach maximum length by day 60.

Harris (1970), Coulter et al. (1981), Tomkins (1985), and J. B. Cruz and F. Cruz (1987) blamed introduced mammalian predators for the low levels of reproductive success and abnormally high levels of adult mortality found in all the colonies. When exotic predators were not controlled in the Cerro Pajas colony, only 33% of the birds banded by Coulter and co-workers in 1981 returned (Coulter et al. 1982 unpubl.). In 1984 and 1985, with control of introduced predators, we found that 80–90% of previously banded birds returned and attempted to breed. This leads us to suspect that, currently, survival of adult birds is low in the absence of protection measures. Simons' (1984) population model for the Hawaiian Dark-rumped Petrel indicated that as little as a 10% reduction in adult survival might induce an annual population decline of ca. 5%. This estimate emphasizes the extreme vulnerability of these birds to introduced predators.

Timing of breeding.—Breeding occurred in the archipelago at all times of the year and initiation of breeding was not tightly synchronized on any island. Cues thought to synchronize the initiation of breeding in tropical regions (Immelman 1973), such as the timing of rainfall or changes associated with temperature, probably did not operate in this case. As food is thought to be available throughout the year in the Galápagos (Harris 1969), initiation of breeding may depend on when productive feeding grounds

are closer to each island. Unfortunately, documentation of fluctuations in marine productivity in the Galápagos is incomplete (Feldman et al. 1984), and we do not know the distribution of the petrel's prey in Galápagos waters.

Alternatively, social interactions coupled with endogenous rhythms may synchronize breeding in areas where environmental cues are lacking (Chapin 1954). Synchronization is favored because a bird that does not return to the archipelago when other birds return misses a reproductive opportunity. Perhaps separate colonization events, supported by the year-round food supply, and then reinforced by high mate and site fidelity, rigid annual breeding, and pair
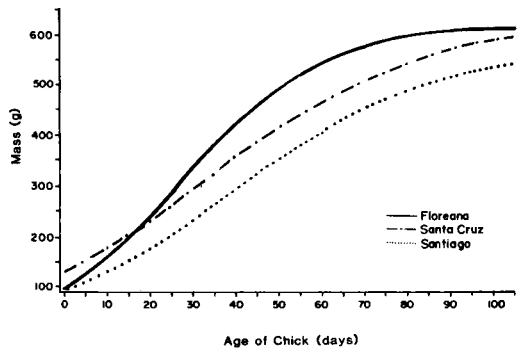
Fig. 8. Approximated growth of mass for the 1985 cohort of petrel chicks from three islands.

TABLE 1. Logistic analysis of growth variables for petrel chicks on three islands in 1985 (Kruskal-Wallis test, * = P < 0.006, ** = P < 0.0001). Values are $\bar{x} \pm$ SD.

Island	n	Growth constants (K)			
		Mass	Wing	Tarsus	Bill length
Floreana	15	0.060 ± 0.009	0.037 ± 0.009	0.070 ± 0.015	0.040 ± 0.010
Santiago	14	0.042 ± 0.016	0.039 ± 0.005	0.042 ± 0.016	0.040 ± 0.012
Santa Cruz	10	0.040 ± 0.001	0.041 ± 0.002	0.044 ± 0.002	0.041 ± 0.001
χ^2		23.97**	10.14*	21.33**	0.22

synchronization through social interactions, have led to the differences in time of breeding.

Laying and incubation.—Petrels have a much larger egg in relation to their body mass than many other seabirds. King (1973) suggested that egg production requires relatively large amounts of energy, so the long prelaying absence after copulation may be important to the female in acquiring the energy necessary for egg production. It would also allow the male to store sufficient energy reserves for the first incubation shift. A long absence before laying has also been reported in other petrels (see Warham 1967, Grant et al. 1983).

A large egg enables the chick to hatch with a food reserve and probably increases the rate of survival through the initial post-hatching period until the first meal (Drent and Daan 1980). Another benefit of a large egg may be a slower rate of cooling when unattended during incubation. Although we did not quantify length or frequency of egg neglect, Floreana birds temporarily deserted eggs that hatched successfully after incubation was resumed. Tomkins (1985) and Harris (1970) also reported egg neglect at the Santa Cruz colony. Temporary desertion of the egg is usually associated with failure of the partner to relieve its sitting mate (Gardner et al. 1985). It is widely reported among the Procellariiformes and is associated with distant foraging habits and long incubation bouts (Warham 1956, 1977; Boersma and Wheelwright 1979).

Incubation bouts of 10 days were similar to those reported for other *Pterodroma* species (e.g. $\bar{x}$ = 8.8 ± 0.7 days in the Bonin Petrel, *P. hypoleuca* [Grant et al. 1983], and $\bar{x}$ = 9.3 ± 1.0 days in the Herald Petrel, *P. arminjoniana* [Gardner et al. 1985]). Because both sexes of the Dark-rumped Petrel were of similar size, it is not surprising that incubation duties were shared almost equally.

On average, adults lost 6.2 g/day during incubation, or ca. 1.5% of their body mass. An average incubation bout would therefore result in a loss of 62 g (ca. 15% of body mass). The longest bout was 17 days, with a loss of ca. 105 g (ca. 25% of adult mass). Bout length and mass loss were below the maxima reported by Simons (1985) for the Hawaiian subspecies, where the longest bout was 23 days with a loss of 7.08 g/day or a total of 163 g (35.5% of initial mass). The shorter bout length and lower mass loss of the Galápagos petrel may, in part, reflect the lower elevation at which this subspecies nests. Alternatively, it may reflect shorter traveling times to foraging areas.

Differences among islands.—Adults from Floreana tended to be larger in both size and mass than adults from the other two islands. Adults from Santiago were larger than Santa Cruz adults for some characteristics, and smaller in some others. Tarsal length was the best indicator of island of origin, and the shape and length of the bill also tended to vary between genders and among islands. The small measurable differences of these characteristics, however, make them inconvenient for distinguishing among birds of different islands in the field. The differences in bill size might be involved in pair formation, or they might reflect differences in foraging behavior or in types and sizes of prey captured.

In our analysis of chick growth, we found K values which indicated some interisland differences in rates of growth; but, sample sizes were small and measurements across the three islands were taken during a single year. Growth approximations from a larger sample taken over a 5-yr period are available for Floreana Island. The between-year variation in chick growth on Floreana was greater than the interisland variation in a single year (Cruz and Cruz 1990). Because fluctuations in food resources can affect

growth, especially in species with slow-growing chicks (Lack 1968), it is difficult to generalize about observations over a single season. The differences in growth could be an artifact of a variable food supply or differences in the distance to foraging areas from the different islands. Alternatively, the differences in growth may reflect real differences between the populations.

Coulter et al. (1982 unpubl.) and Tomkins (1985) discussed the possibility of distinct populations of petrels based on interisland differences in morphology, egg size, breeding chronology, and vocalizations. Our data support their conclusions on differences in time of breeding, differences in size of adults on different islands, and lack of interchange among breeding adults from different colonies. However, interchange is less likely to occur between breeding adults that have already developed pair bonds and nest-site tenacity, than among prebreeding sub-adults. We have not documented if interchange occurs for this age class of petrels. Perhaps the best test of the hypothesis that these populations are indeed isolated is through genetic analysis.

The life-history traits of Dark-rumped Petrels (including a one-egg clutch, egg neglect, long incubation period, and long incubation bouts) are like those of other procellarids. Other aspects of their biology (including age of first breeding and genetic similarities or differences among populations) remain unknown. Differences in timing of breeding, and lack of interchange among colonies, suggest that petrels may form distinct populations on different islands. A species subdivided into several populations is sometimes less susceptible to global extinction than a species consisting of only one population (Slobodkin 1986). From the standpoint of breeding populations, however, each colony should be considered individually. Managers must incorporate this factor into their conservation plans and, if feasible, make an effort to maintain breeding colonies on all of the islands so that existing diversity is not lost.

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