

BIOLOGY AND BEHAVIOR OF THE ENDANGERED HAWAIIAN DARK-RUMPED PETREL

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ABSTRACT.—The Hawaiian Dark-rumped Petrel (*Pterodroma phaeopygia sandwichensis*), or 'Ua'u, is an endangered gadfly petrel that nests in the Hawaiian Islands and ranges throughout the central Pacific. The species was once common in Hawaii with large colonies located on all the main islands, but its numbers have recently been reduced to several small relict populations. Over 85% of the breeding birds known today nest in and around Haleakala National Park on the island of Maui, the site of a three-year study begun in 1979. I studied the breeding biology, behavior, and conservation needs of this poorly known species using specially designed event recorders and a closed circuit television system employing a night vision scope. The study also documented variations in the birds' reproductive success that occurred naturally and as a result of varying levels of predation by introduced mammals. Predation is the primary threat to the birds' survival, so if it can be controlled, the remaining populations should thrive.

The Dark-rumped Petrel (*Pterodroma phaeopygia*) breeds only in the Hawaiian and Galapagos islands (King 1981). A unique subspecies breeds in each location and both populations are endangered. The Galapagos subspecies (*P. p. phaeopygia*) has been studied by Harris (1970), but, prior to my study, little was known about the Hawaiian subspecies (*P. p. sandwichensis*). This paper reports some of the results of a three-year study of the Hawaiian population initiated in 1979 (Simons 1983). The purposes of my study were to document the bird's breeding biology, to identify the factors currently threatening its survival, and to develop a management plan to guide future conservation efforts.

The limited historical evidence available suggests that Dark-rumped Petrel populations have declined substantially over the last century (Banko 1980). Perkins (1903) noted that the birds were common in many parts of the islands and that they nested in large colonies high in the mountains. The first Polynesians arrived in Hawaii about 1,400 years before Perkins' observation (Kirch 1974). Until recently, the Polynesians were thought to have had little impact on native ecosystems, and it has been generally assumed that the early European explorers, led by Cook in 1778, found Hawaii in a nearly pristine state. The subsequent decline of the native avifauna was believed to have been caused by a combination of factors, including predation by introduced mammals (Atkinson 1977), disease (Warner 1968), and habitat destruction (Berger 1972). A re-examination of the historical evidence, and archaeological research by Olson and James (1982a, b) now suggests that the Hawaiian ecosystem was substantially modified by

the prehistoric Polynesians, and that a sizable segment of the native avifauna was exterminated in the process. Seabird populations were no exception. Dark-rumped Petrels were probably abundant on all of the main Hawaiian Islands, including Oahu (Olson and James 1982a, b) and it now appears that the Oahu population was exterminated before the arrival of Europeans. Lowland petrel populations were probably extirpated as a result of predation by the dogs, pigs, and rats (*Rattus exulans*) that the Polynesians brought with them, and by the Polynesians themselves. Henshaw (1902:120) reported, "It is said that years ago the nestlings of the 'Ua'u were considered a great delicacy, and were tabooed for the exclusive use of the chiefs. Natives were dispatched each season to gather the young birds which they did by inserting into the burrows a long stick and twisting it into the down of the young which then were easily pulled to the surface." The abundant remains of adult and nestling Dark-rumped Petrels found in middens and lava tubes throughout the islands (Olson and James 1982a; C. B. Kepler, J. M. Scott, pers. comm.) document the large-scale harvesting of the birds.

The decline initiated by the Polynesians was accelerated after Europeans introduced cats (*Felis catus*), black rats (*Rattus rattus*), Norway rats (*Rattus norvegicus*), disease-carrying mosquitoes, and, in 1883, mongooses (*Herpestes auropunctatus*; Tomich 1969). These predators, which pose the primary threat to the remaining populations, may represent only a small portion of the decimating influences of the past 1,500 years. The pattern of decline in Hawaii has been repeated in populations of gadfly petrels all over the world. The combined

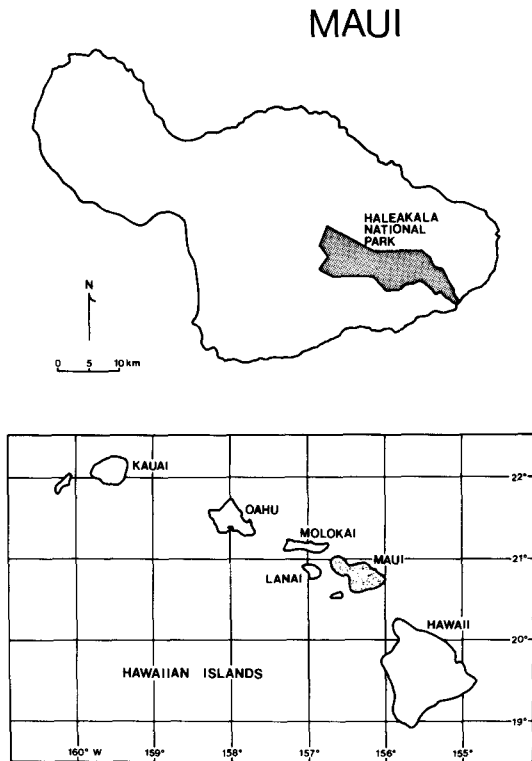


FIGURE 1. Haleakala National Park and the Hawaiian Islands.

effects of hunting by man and predation by introduced mammals have driven many populations to the brink of extinction and, today, only a few species with healthy, undisturbed populations remain. Most populations of gadfly petrels are surviving today like the Dark-rumped Petrel: outside their preferred habitats, at high elevations, or on remote offshore islets (see reviews by Bourne 1965, Harris 1970).

I found few records of the Dark-rumped Petrel from about 1910 to the late 1940s. Apparently, many ornithologists during that period feared that the species was on the brink of extinction in Hawaii (Munro 1941, 1944). The species reappeared on the island of Hawaii in November 1948 when a bird was grounded near Kilauea caldera during a storm (Baldwin and Hubbard 1949). Since that discovery, evidence of the birds has been reported from the islands of Maui (Richardson and Woodside 1954), Lanai (Shallenberger 1974, Hirai 1978), Kauai (Banko 1980; T. Telfer, pers. comm.), and Molokai (C. B. Kepler, J. M. Scott, pers. comm.).

Records of these petrels at sea are scarce. King (1967, 1970) reported birds in very limited numbers over a range from 42°N to 5°N latitude, and 148°W to 158°W longitude, and, more recently, Pitman (1982) reported the birds

to be widespread over the eastern tropical Pacific. His observations suggest that the Hawaiian population may be "thinly continuous" with the Galapagos population at sea. Sightings were primarily of solitary birds, but Pitman noted that the species often joined in mixed species foraging flocks.

The largest nesting colony of the Hawaiian Dark-rumped Petrel known today is located in and around Haleakala National Park on the island of Maui (Fig. 1). Haleakala is the only place where active breeding has been found in recent years, and the fate of the Hawaiian population largely depends on the future of that colony.

STUDY AREA

Haleakala National Park encompasses most of the summit of Haleakala, a mountain that rises 3,055 m above the Pacific Ocean and comprises over half of the land area of Maui. Haleakala is a dormant shield volcano, with a large erosional depression at its center. This depression forms a 52-km² crater that lies over 1,000 m below the rim of the volcano. The soils on Haleakala are primarily lithosols and regosols (Cline 1955). The regosols are formed of volcanic ash and cinders, and are not used by nesting petrels. The lithosols, found primarily along the steep (50–70% slope) walls of the crater, are characterized by a mixture of boulders and erosional debris associated with bedrock, and they provide the primary nesting substrate for the Dark-rumped Petrels. The nesting areas are located between elevations of 2,500 and 3,000 m, making Haleakala one of the highest colonies of nesting seabirds in the world.

The vegetation associated with the nesting areas is characterized primarily as sub-humid, sub-alpine. In these dry habitats, vegetative cover is generally less than 10%, and the plant community is dominated by several shrubby species, including pukiaawe (*Styphelia tameiameia*), kukaenene (*Coprosma montana*), ohelo (*Vaccinium reticulatum*), and kupaoa (*Dubautia menziesii*).

The climate atop Haleakala is marked by the extremes typical of many sub-alpine areas. Precipitation averages approximately 125 cm per year (Schroeder et al. 1977, Lyons 1979). Most rain falls during the winter months, and the petrel nesting period coincides closely with a pronounced dry season from May to August. Relative humidity at the summit is typically less than half that at sea level, and, during the dry summer months, daytime levels can drop to 5%. Summer temperatures average ca. 10.0°C (range 0–25°C). Winter temperatures average ca. 8°C lower than those in the sum-

mer. The summit is buffeted by tropical storms with winds occasionally exceeding 100 km/h, and winter snowfall is regularly recorded at elevations above 2,500 m.

METHODS

Field work was conducted from early April to early November, 1979, and from early March to mid-November in 1980 and 1981. I monitored the birds' burrow attendance patterns using specially designed event recorders at 10–12 nests each season. The device consisted of a switch mechanism placed over the burrow entrance, and a 20-channel Esterline Angus recorder (Simons 1981a, b, 1983). I studied approximately 40 accessible nests each season, and monitored an additional 125 nests indirectly through the use of toothpick barriers. These burrows were checked every 7–10 days to determine which nests had been visited during the interval. I also made over 280 h of behavioral observations using a night vision scope at one nest in 1981. The nest was illuminated by an infrared light source, and the scope was attached to a closed circuit television camera, monitor, and video-tape deck. Six hours of activity within the burrow were recorded on video-tape.

All birds were weighed with 500- or 1,000-g Pesola scales to the nearest 1.0 g. Eggs were weighed on a triple beam balance accurate to 0.01 g. Other measurements were made with a steel ruler or dial caliper accurate to 0.1 mm. Wings were measured according to the methods outlined by Warham (1977). Tarsus length was measured by depressing the foot and measuring the distance from, and including, the end of the tibiotarsus to the end of the tarso-metatarsus. Culmen length was measured from the edge of the forehead feathers to the tip of the upper mandible, and culmen width was measured at its widest point below the nostrils.

All temperatures were measured with a Wescor model TH-65 digital thermocouple thermometer, calibrated against a laboratory mercury thermometer in a water bath. Core temperatures were measured by inserting a thermister probe into the lower esophagus. Burrow temperatures were measured at the nest. Incubation temperature was estimated at one nest by fitting a chicken egg with a thermister probe and substituting it for a petrel egg. Relative humidity was recorded with a Psychrodyne wet-dry hygrometer.

I banded adult birds during the nestling period by trapping them with Havahart traps at their burrow entrances. Nineteen food loads regurgitated by trapped adult birds during the banding study were collected, preserved, and analyzed to the lowest possible taxon.

Growth equations were obtained by employing the graphical method described by Ricklefs (1967, 1968) and a computer model. In Ricklefs' terminology, the equation for the logistic growth equation is $dW/dt = KW(1 - W)$, where W is the weight of the growing bird, K is a constant related to the overall growth rate, and t is time. The model determined the best estimate of K in an iterative fashion by converting a large number of curves over a range of assumed asymptotes. The curves were then compared via linear regression, and the best estimate of K was calculated from the curve with the highest correlation coefficient. Two other factors were also calculated for making growth comparisons. The values, $Ka/4$ and $KR/4 \times 100$, represent the maximum instantaneous growth rate of the chick at the inflection point of the fitted logistic curve, and they may estimate the overall growth rate better than K (Hussel 1972). All growth rate calculations were made using the linear portion of the growth curve, including measurements from day 0 to day 65.

I examined 22 individual blood smears from adult birds for signs of avian malaria. The smears were fixed in 100% methanol, stained in Wright's Giesma, washed in distilled water, allowed to air dry, and examined under the oil immersion objective of a compound microscope.

Vocalizations were recorded on a Sony TCS 300 stereo cassette recorder with a Dan Gibson model P 650 parabolic microphone. Sonograms were made using Kay Elemetrics type B/65 Sona-graph. All statistical tests were taken from Sokal and Rohlf (1981).

RESULTS AND DISCUSSION

POPULATION ESTIMATES

Approximately 700 petrel nests have been found around the summit area of East Maui as a result of yearly surveys conducted by National Park Service personnel since 1966. The annual percentage of active burrows has ranged from 63–95%, averaging $78.1 \pm 11.0\%$. Approximately 77% of all the known burrows are located along the inner walls of the crater's west rim, making the area the most important nesting habitat remaining for the birds. The birds nest there at maximum densities of up to 6.7 burrows per ha, but densities in outlying areas are much lower. I frequently found individuals nesting hundreds of meters from their closest neighbors, and several active burrows were over a kilometer from another nest.

I estimated the size of the Maui population by combining census and activity data with estimates of reproductive success and an age

TABLE 1. Weights and measurements of adult Dark-rumped Petrels.

	<i>n</i>	Mean	SD
Weight (g)	38	433.8	52.9
Wing length (mm)	31	303.6	5.5
Wing span (cm)	8	98.0	2.6
Total wing area (cm ²)	8	798.11	33.52
Mean wing loading (g/cm ²)	8	0.54	
Aspect ratio	8	10.89	
Tarsus length (mm)	31	45.1	1.1
Culmen length (mm)	29	33.4	1.3
Culmen width (mm)	11	10.2	0.6
First primary remex length (mm)	12	193.3	8.5
Central rectrix length (mm)	12	139.3	6.1
Core temperature (°C)	9	38.6	1.1

structure derived from a matrix model of the population (Simons 1984). The current total population is estimated at ca. 900 pairs, of which ca. 430 pairs are breeding adults.

Weights and measurements of adult Dark-rumped Petrels. Adult Hawaiian Dark-rumped Petrels weighed an average of 433.8 g (Table 1), which was somewhat heavier than the birds studied in the Galapagos by Coulter et al. (1982; mean = 421.2 g, $t = 2.04$, $P < 0.05$) and Harris (1970; mean = 408.0 g, $t = 3.25$, $P < 0.01$). In contrast, the wings and tarsi of Hawaiian birds (303.6 mm and 45.1 mm) were shorter than those reported for Galapagos birds (314.5 mm and 46.7 mm; $t = 7.68$ and 6.40, $P < 0.001$; Coulter et al. 1982). The average bill of Hawaiian birds was shorter than that of Galapagos birds (33.4 mm vs. 35.8 mm; Coulter et al. 1982; $t = 7.50$, $P < 0.001$), but slightly wider (10.2 mm vs. 8.8 mm; $t = 2.69$, $P <$

0.02). Total wing area and wing loading were slightly higher in Hawaiian birds than the values reported by Warham (1977) for a single Galapagos specimen. This is consistent with the finding of higher weights and shorter wings in the Hawaiian birds, and conforms with the general trend throughout the order for larger species to have higher aspect ratio wings, higher wing loadings and, therefore, higher flight speeds and less agility (Warham 1977). It also suggests that the two subspecies may differ in their flight and foraging behavior.

Arrival of birds at the colony and the pre-laying period. Most of the adult population returned within a 7-day period in late February each year (Figs. 2 and 3). The event recorder was kept in operation over the winter in 1981 and 1982, and in those years, the first birds arrived on 23 and 24 February. Most birds visited their burrows regularly at night for several weeks following their return and spent their time removing debris, bringing in new nest material, or enlarging the burrow chamber. Individual birds and pairs were found in their burrows during the period, and although I never observed copulation, it probably occurs in the burrow as for the Bonin Petrel (*Pterodroma hypoleuca*; Grant et al. 1983).

A distinct pre-laying absence began in late March. This pattern is characteristic of procellariiforms and is thought to allow females time to acquire the nutrient reserves necessary for egg production, and for males to store energy for incubation (Harris 1966, Perrins and Brooke 1976). Most of the birds that continued to visit the colony during April were subsequently found to be non-breeders. I never found both members of a breeding pair in their bur-

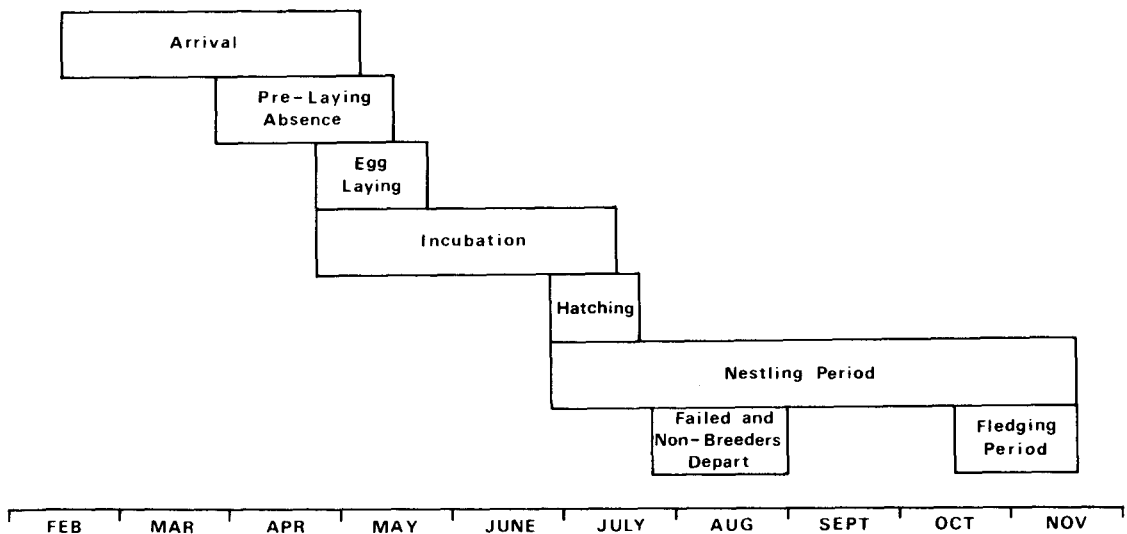


FIGURE 2. Dark-rumped Petrel breeding chronology.

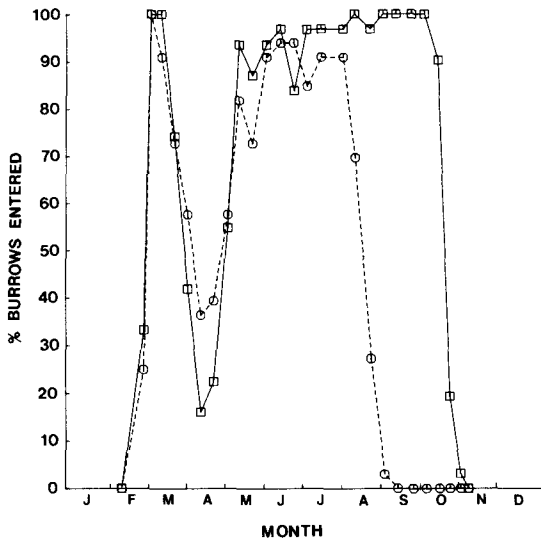


FIGURE 3. Colony attendance patterns of Dark-rumped Petrels. The dashed line represents attendance by non-breeding birds and the solid line attendance by breeding birds.

row during the absence period, and in most cases, breeding males did not return until either just before or just after egg-laying. If copulation does occur before the absence period, female Dark-rumped Petrels must be capable of storing sperm for several weeks, as are Northern Fulmars (*Fulmarus glacialis*; Hatch 1983).

Characteristics of nest sites. Dark-rumped Petrel burrows were commonly situated at the bases of rock outcrops where erosional debris provided an adequate substrate for burrowing. Nest sites were highly variable, ranging from crevices less than 1 m deep to cracks and lava tubes that penetrated over 10 m into the cliff face. Petrels also excavated extensive tunnels into softer substrates. Over 95% of the 419 burrows examined were at least partially excavated, most beneath rock outcrops or boulders, but a few were dug at the bases of shrubs or in sod-covered soil. Less than 10% of the burrows examined were shorter than 1 m, and at least 44% were over 2 m in length. Burrow entrances ranged from cracks only 4 cm in diameter to caves over 2 m across, averaging 19.14 ± 11.73 cm in diameter ($n = 402$). Most burrows were therefore accessible to mammalian predators, including mongooses, feral cats, and rats.

The composition of the nest was also variable. Birds in burrows situated near shrubs or clumps of bunch grass often built sizable dished nests, up to 10 cm thick and 40 cm in diameter, of grass or twigs. If nest material was scarce, birds either formed a modest nest of nearby debris or laid their eggs directly on bare soil or rock.

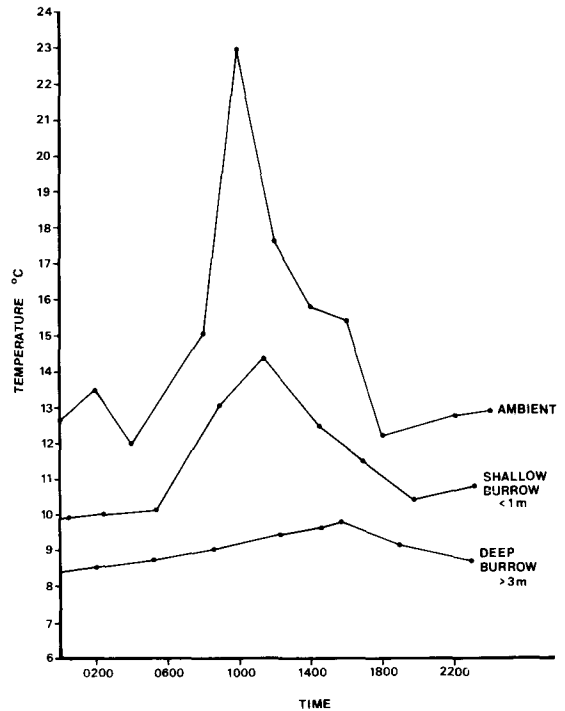


FIGURE 4. Dark-rumped Petrel burrow temperatures 23 October 1981.

Daily burrow temperatures varied over an average range of only 2.39°C , in contrast to the 25°C range in ambient temperatures during the breeding season. The average temperature inside petrel burrows ($9.59 \pm 2.39^\circ\text{C}$, $n = 108$) was close to the average summer ambient temperature of 9.5°C reported by Lyons (1979) for the summit of Haleakala. Thus, the burrow drastically reduced temperature fluctuations at the nest. The degree of this moderating influence depended on the depth of the burrow (Fig. 4).

Summer humidity atop Haleakala averages only 26% (Lyons 1979). The lowest levels of humidity coincide with the petrel's incubation period in May and June, and this may significantly constrain the water balance of the developing embryo (Whittow et al. 1984). I recorded relative humidities of less than 7% at some nest sites during incubation, and the average humidity measured at one nest over a 24 h-period during incubation was $20.3 \pm 7.4\%$ ($n = 12$).

Mate and nest-site fidelity. Eighteen pairs of breeding adults (36 birds) were banded out of 57 birds captured during the study. Of these eighteen pairs, five pairs and five additional individuals were recaptured in their burrows in subsequent years. In addition, one bird, banded as an adult by park personnel in 1975, was recaptured in the same burrow in 1981. I found no evidence that breeding birds changed

mates or nest sites during the two years of the banding study. This suggests that Dark-rumped Petrels, like most other large procellariiforms, show a high degree of fidelity to nest site and mate.

EGG-LAYING AND INCUBATION

Breeding frequency. Breeding frequency, the percentage of years in which adult females laid eggs, was estimated to be 89% from a sample of 15 undisturbed accessible nests for which I had three or more years of data. I assumed that the same birds were using the burrows each season. In order to ensure that only adult birds were sampled, I based the estimate on nests that were known to have fledged at least one chick. This estimate is on the high end of the range reported for similar species (Perrins et al. 1973, Fisher 1975a, b, 1976), but given the evidence that seabird populations in Hawaii have been reduced substantially over the past two centuries (Olson and James 1982a, b, S. Olson, pers. comm.), I would expect a higher than average breeding frequency owing to relatively abundant breeding resources.

Egg-laying. I monitored six color-marked pairs and saw no evidence that breeding females visited their burrows during the pre-laying absence. All three marked birds found in their burrows before egg-laying were males. Females always laid their eggs within 24 h of returning to the burrow. If the male was present at egg-laying, he always took the first incubation shift and the female departed before dawn. If the male was not present, the female remained and incubated the eggs until her mate returned.

The attendance patterns of the pair in the television-monitored burrow were typical of most birds. Both birds were seen together in the burrow for several days in mid-March. From mid-March to mid-April, they visited the burrow briefly at night on four occasions, but for the next three weeks, they did not visit the nest. On the evening of 6 May, the female returned to the burrow. She arrived shortly after 21:00, and after preening briefly, began preparing the nest site. She worked on the nest constantly for 1 h and 40 min, carefully arranging pieces of nest material, and dishing out the center of the nest by rocking forward and kicking alternately to the rear with both feet. At 22:39, the female settled down on the nest and began slowly raising and lowering her tail. This behavior continued for 10 min, during which her tail feathers appeared to be spreading farther and farther apart. I assume that the egg was laid at that time, although because the bird was facing the camera, I did not actually see the egg emerge. At 22:49, the female stood

up, turned slightly, and settled down on the nest in an incubating posture. She continued to incubate for the next four days until she was relieved by the male on the evening of 10 May.

Egg-laying dates, egg size, and incubation temperatures. Egg-laying began each year during the last week of April and continued until mid-May (Fig. 2). The mean laying date was 8 May in both 1980 (± 4.3 days, $n = 9$ nests) and 1981 (± 5.9 days, $n = 11$ nests).

Eggs of Hawaiian Dark-rumped Petrels are significantly larger and heavier than those of Galapagos birds (Coulter et al. 1982; *t*-test, $P < 0.001$; Table 2). This may be because Hawaiian birds weigh more, on average, than those in the Galapagos, but it may also represent an adaptation to high altitude nesting (Whittow et al. 1984).

The temperature of a chicken egg incubated steadily by a petrel for 85 min stabilized at 34.9°C. Typical of procellariiforms (Whittow 1980), this temperature is lower than the average incubation temperature of 35.6°C reported for 27 species by Ar and Rahn (1980).

Attendance patterns of adult birds during incubation. Non-breeding birds generally showed an abbreviated pre-laying absence and a regular attendance pattern throughout the incubation period in May and June (Fig. 5). Breeding birds were usually away from the colony for much of April and they returned to the nest for egg-laying in early May. Most breeding pairs divided the incubation period into four or five incubation shifts, and the male always took the first long shift. Of six pairs of color-marked birds, three pairs divided the incubation period into four shifts, and three pairs divided it into five shifts (Table 3). Males took only two shifts in all cases, but the average number of incubation days by males (31.33 ± 2.61 days) was significantly greater than the average for females (24.33 ± 1.75 days; $t = 6.14$, $P < 0.001$). This pattern is similar to that found in other procellariiforms (Richdale 1952, Rice and Kenyon 1962, Pinder 1966, Fisher 1971, Simons 1981a, and Croxall and Ricketts 1983). The male might be expected to take a greater role in incubation given the large energetic investment by the female in producing the egg.

The average duration of 27 incubation shifts (Table 3) recorded for both sexes was 12.37 ± 6.7 days. Eliminating the first and last shifts, which were shortened by the events surrounding egg-laying and hatching, yields an overall average shift of 16.47 ± 3.95 days ($n = 17$). The average shift duration for males, 16.18 ± 4.19 days ($n = 11$), did not differ significantly from that for females, 17.0 ± 3.79 days ($n = 6$). Males, however, took two shifts during that period while females took only one.

TABLE 2. Measurements of Dark-rumped Petrel eggs.

	<i>n</i>	Mean	SD
Egg length (mm)	30	64.65	2.88
Egg width (mm)	30	46.47	1.37
Egg volume (cm ³)	8	71.96	5.95
Fresh egg mass (g)	5	76.87	0.93
Shell mass (g)	10	3.987	0.532
Shell thickness (mm)			
Shell only	93	0.23	0.03
Outer shell membrane	3	0.08	0.01
Inner shell membrane	12	0.01	0.01
Shell + shell membranes	133	0.26	0.08

The average incubation shifts of the Dark-rumped Petrel are long, and the 23-day shift accomplished by one male is among the longest reported for any seabird (Burger 1980). The average incubation shift in these petrels exceeds that reported for most other seabirds, including albatrosses and penguins (Burger 1980). As has been argued elsewhere (Lack 1968, Burger 1980, Simons 1981a, and Ricklefs 1984), this suggests that the petrel's food supplies are scarce and/or widely distributed. Assuming that an adult Dark-rumped Petrel is capable of an average flight speed of 45 km/h (Pennycuik 1969), it is conceivable that an adult bird could range thousands of kilometers from the colony between incubation bouts.

I measured the weight of one adult petrel before and after a 12-day incubation shift, and determined the daily rate of weight loss to be 7.08 g/day. This amounted to an average daily weight loss of 1.54% of initial body weight, which is comparable to the rates reported in several species of albatrosses (Prince et al. 1981, Croxall and Ricketts 1983). At that rate, the bird, which remained on the nest for 11 more days, would have lost a total of 163 g or 35.5% of its initial weight during its 23-day incubation bout.

Behavior of incubating birds. Incubating adult Dark-rumped Petrels spent almost 95% of their time sleeping with their bills buried in their scapular feathers, just over 3% of their time resting quietly on the nest, and 2% of their time arranging nest material or preening (Table 4). Adult birds maintained close contact

TABLE 3. Incubation shifts of six pairs of color-marked Dark-rumped Petrels.

Pair #		Shift #				
		1	2	3	4	5
1	Shift length (days)	1	18	21	16	2
	Sex	F	M	F	M	F
2	Shift length (days)	1	23	21	10	
	Sex	F	M	F	M	
3	Shift length (days)	20	15	12	8	
	Sex	M	F	M	F	
4	Shift length (days)	2	14	13	16	10
	Sex	F	M	F	M	F
5	Shift length (days)	6	10	19	21	
	Sex	F	M	F	M	
6	Shift length (days)	4	17	13	11	10
	Sex	F	M	F	M	F

with the egg throughout the incubation period, even while exchanging incubation duties. Direct observations and information from the event recorder indicated that adult birds only rarely left their nests for brief trips to the burrow entrance, and that the egg was exposed for at most a few minutes during an average incubation shift. This behavior would be adaptive in the bird's cold, arid, high-altitude nesting environment because it presumably reduces both the duration of the incubation period and the embryonic water loss (Whittow et al. 1984). The bird's behavior also appears to be tied to the energetic demands of long incubation shifts. Adult petrels, and nestlings undoubtedly reduce their metabolic demands substantially by sleeping (Simons and Whittow 1984); tucking the bill into the scapulars may reduce heat loss by as much as 12% (Deighton and Hutchinson 1940). The average respiratory rate of an alert resting bird was 23.7 ± 1.14 breaths/min ($n = 29$), which is close to the predicted value of 24.5 breaths/min, based on the equations of Calder (1968). The average respiratory rate of sleeping birds, 12.3 ± 1.20 breaths/min ($n = 66$), was significantly less ($t = 22.9$, $P < 0.0001$), indicating a substantial reduction in the metabolic rate of sleeping birds.

Twice I watched the exchange of incubation duties by adult birds. On the first exchange,

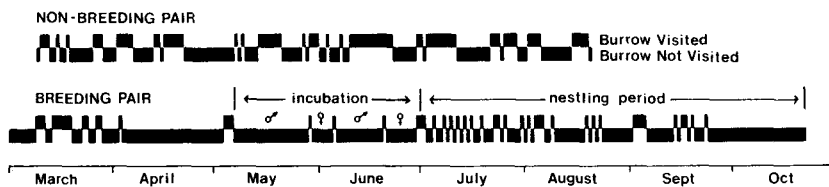


FIGURE 5. Burrow attendance patterns of individual breeding and non-breeding Dark-rumped Petrels. Upper marks for each pair indicate days when the burrow was entered. Data for breeding pair indicate pre-laying absence, incubation shifts, and feeding frequencies.

TABLE 4. Behavior of incubating Dark-rumped Petrels. Data are presented as percent total time, based on 107 h 12 min of observations during incubation and 76 h 3 min of observations prior to hatching.

Period	Behavior				
	Alert		Self-maintenance	Sleeping	Locomotion
	Resting quietly	Arranging nest material			
Incubation	3.4%	0.3%	1.7%	94.5%	0.1%
Hatching	64.6%	0.02%	1.2%	34.1%	0.0%

the male arrived at about 22:00 to relieve the female. He walked directly to the nest and settled down beside his mate. The female then preened the male's forehead and face for about 1 min before exchanging positions with him. The two birds remained together on the nest for several more minutes and preened each other continuously. Four minutes after the male's arrival, the female rose from the nest and walked out of the burrow. The behavior of the pair was similar during the second exchange. The female arrived at 22:12, walked directly to the nest, settled down next to the male, and the two birds engaged in mutual preening until 22:37. The male then rose off the egg, and the female began incubating. The male spent the next 15 min either preening himself or resting quietly next to his mate, and at 20:53, he stood up and walked out of the burrow.

The long pre-laying absence and long incubation shifts typical of these birds require a strong pair bond and closely synchronized attendance patterns. An ill-timed return to the burrow could result in an interruption in incubation and a failed breeding effort for the season. The importance of synchronization in breeding Dark-rumped Petrels is readily apparent, given that members of a pair may meet only briefly in their burrow on three or four occasions during the five to six months between egg-laying and fledging. Similar patterns have been seen in other species. Croxall and Ricketts (1983) determined that poorly synchronized pairs of Wandering Albatrosses (*Diomedea exulans*) suffered reduced reproductive success. Indeed, the need for closely synchronized breeding activities may be an important selective pressure favoring delayed breeding in many procellariiforms.

Behavior during the hatching period. I observed the television-monitored nest almost continuously for the four days before hatching (30 June–3 July). The adult's behavior during the period differed markedly from that seen earlier. Rather than sleeping most of the time, the bird spent most of the period in an alert posture on the nest (Table 4). About two days before hatching, the adult began to adjust the egg frequently with its bill, and it assumed a more upright posture on the nest, as if it were standing slightly, with its wings held out to each side. I saw no evidence that the adult assisted the chick directly in emerging from the shell, as can occur for the Fork-tailed Storm-Petrel (*Oceanodroma furcata*; Simons 1981a), but the adult indirectly assisted the chick by adjusting the position of the egg and by not restricting the chick as it emerged from the shell.

By 7:10 on 3 July, I could tell that the chick had hatched. The adult brooded the chick for several hours, and by 12:00, the chick's down was dry and it was resting quietly on the nest, partially covered by the adult's wing. The two birds remained close together throughout the next three days, although the adult never completely covered the chick after its down was dry. The adult initiated feeding regularly during the period by nibbling gently at the chick's bill and regurgitating small amounts of food.

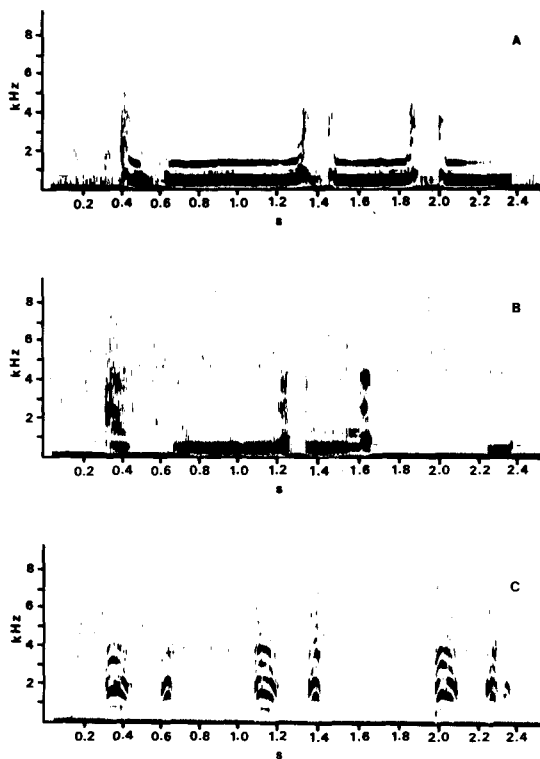


FIGURE 6. Sonograms of Dark-rumped Petrel calls.

TABLE 5. Dark-rumped Petrel reproductive success 1979–1981.*

Year	<i>n</i>	% Active burrows with eggs	Hatching success	Fledging success	% Predation on active burrows	Reproductive success
1979	41	75.6	67.8	57.1	34.0	38.7
1980	40	70.0	71.4	100.0	0.0	71.4
1981	47	66.0	70.9	86.4	6.4	61.3

* All data were collected from accessible burrows. "Hatching success" is percentage of eggs laid that hatched. "Fledging success" is percentage of chicks hatched that fledged. "Reproductive success" is percentage of eggs laid that produced fledglings.

Vocal behavior. Dark-rumped Petrels emitted a variety of sounds, although two call types predominated. The first was a penetrating and resonant call from which the birds presumably received their Hawaiian name, "'Ua' u'" (Fig. 6a). The call could be described as: *a'-uuuuu-a'-uu-a'-uu-a'*. The second common call was similar but its tone was raspy and nasal rather than resonant (Fig. 6b). In addition, the birds uttered various sharp squeaks and nasal clucks. A common form of this type of call could be imitated as *ee'-a, ee'-a, ee'-a* (Fig. 6c).

The birds occasionally called from their burrows if disturbed, but they usually vocalized only while flying. On several occasions, I heard birds calling at lower elevations as they flew to the nesting area, but most calling birds congregated over the steep cliffs in the main colony where the constant updrafts allowed them to soar back and forth for hours. Unlike the Galapagos birds, where the peak of calling occurs before dawn (Harris 1970), the Hawaiian birds began calling about 1 h after sunset, and the peak of calling occurred 2–3 h later. A few birds could usually be heard calling throughout the night, but most stopped calling by about 01:00. Typically, calling birds flew in pairs or small groups and called back and forth. A common pattern was for one bird to give the resonant call and be answered by another giving the raspy call. The frequency of calling throughout the season suggests a close association between calling and pair formation. Breeding adults returning to relieve their mates on the nest, or feed their chicks, always flew quickly and silently to their burrows and they did not appear to associate with the calling birds flying nearby. In addition, the pattern of calling appeared to coincide with the attendance patterns of non-breeding birds (Fig. 3). Calling began in March but dropped off, in conjunction with the pre-laying absence, in April. It increased again in May, continued steadily until mid-August, and then, with the departure of the non-breeders, dropped off to almost nothing.

Hatching dates and hatching success. Hatching, like egg-laying, was quite synchronous and extended for about two and one-half weeks. The median hatching date in 1979 was 2 July (± 5.3 days, $n = 10$ nests), and in 1980 and 1981, it was 1 July (± 3.8 and 4.9 days,

$n = 7$ and 11 nests, respectively). Hatching dates ranged during the study from 24 June to 11 July.

The incubation periods of 11 eggs averaged 55.27 ± 1.10 days (range 54–58 days). This is longer than the incubation period reported for birds nesting in the Galapagos (Harris 1970, Coulter et al. 1982), and may be related to the elevation at which the Hawaiian birds nest (Whittow et al. 1984). The egg that took 58 days to hatch was neglected for three days in the middle of the incubation period, during which it survived an average burrow temperature of 7.1°C. Egg neglect may be the primary factor responsible for variations in the incubation period in some procellariiforms (Boersma and Wheelwright 1979, Boersma 1982), but I found little evidence of it in the Dark-rumped Petrel. The low variance in the duration of the incubation periods also indicates that egg neglect is uncommon in this species.

Hatching success averaged approximately 70% (Table 6), and it varied as a result of both natural and artificial influences. Some failed eggs appeared to be infertile, and in others the embryo died before hatching. Predation by feral cats and mongooses further reduced hatching success in 1979 and 1981. I also found several eggs during the study that appeared to have been crushed by the incubating adult. The thin shell of the Dark-rumped Petrel's egg (Table

TABLE 6. Estimated feeding rates in Dark-rumped Petrel nestlings.*

Chick age (days)	<i>n</i> **	Est. food delivered to chick (g)	% Total food	Avg. number chick feeding visits	Est. avg. food load size (g)
0–30	9	791.7 (53.0)	32	12.5 (1.8)	63.3
31–60	10	901.5 (173.77)	36	14.3 (4.03)	62.9
61–90	9	682.6 (79.70)	27	12.3 (3.28)	55.4
91–120	9	114.7 (67.5)	5	3.2 (1.9)	35.6
0–Fledging (total)	7	2,501.7 (94.6)	100	44.5 (7.6)	56.2

* Values in parentheses are one standard deviation.

** Chicks monitored by event recorder.

2) may be an adaptation to high altitude nesting (Whittow et al. 1984) and it is characteristic of procellariiforms (Whittow 1984), but other causes cannot be ruled out. Organochlorine compounds are known to induce eggshell-thinning and lower reproductive success in many species of birds (Hickey 1969, Ratcliffe 1970), including the endangered Bermuda Petrel (*Pterodroma cahow*; Wurster and Wingate 1968).

Unfortunately, I could not locate any Dark-rumped Petrel eggs from the era before the use of DDT, so I could not determine if the bird's egg shells were formerly as thin as they are today. Eight eggs and one nestling of the species have been analyzed for organochlorine contamination. An average level of DDE contamination of 0.43 ppm wet weight, considerably less than the level of 3.99 ppm reported by Wurster and Wingate (1968) for the Bermuda Petrel, was found in a chick and four eggs collected in 1970 (King and Lincer 1973). Two eggs collected by C. B. Kepler in 1978, and two eggs collected during this study also yielded low levels of contaminants. DDE levels averaged 0.32 ppm in the 1978 eggs and 0.49 ppm in the eggs collected in 1981. PCB levels averaged 0.18 ppm wet weight in 1978 and 0.67 ppm in 1981. No other detectable levels of organochlorine compounds were detected in the 1978 or 1981 eggs. Thus, Dark-rumped Petrels do not appear to have been contaminated with levels of organochlorine compounds that might lower reproductive success. On the other hand, because their egg shells are naturally thin, the level of contamination needed to reduce reproductive success may be considerably lower than it is in other birds. It may therefore be wise to closely monitor organochlorine residues in this population in the future.

THE NESTLING PERIOD

Attendance patterns during the nestling period. Most non-breeding birds continued to visit their burrows at night through early August. They generally remained for several hours and engaged in activities such as enlarging the nest chamber or constructing a nest. Pairs occasionally remained in their burrows during the day, some for periods of up to a week. In mid-August, non-breeding birds and most failed breeders departed the colony for the season. Their departure was rapid and, by September, the only birds visiting the colony were adults returning to feed their chicks (Fig. 3).

Chicks were capable of thermoregulation shortly after hatching, and they did not appear to require much brooding from their parents (Simons and Whittow 1984). Some adult birds

remained with their chicks for up to six days after hatching, although most departed within two days, some within 24 h. The primary determinant of the duration of the brooding period appeared to be the size of the adult's food reserves and, therefore, its ability to remain and feed the newly hatched chick.

I summarized the visitation patterns and estimated nestling feeding rates of Dark-rumped Petrels (Table 6), using the average weight loss of fasting chicks, weight changes of nestlings, and attendance data from event recorder-monitored burrows. Feeding rates peaked between 30 and 60 days, the period of maximum chick growth (the inflection point of the logistic chick growth curve; Ricklefs 1967, 1968). Adult visits became less frequent after the period of maximum growth, and chicks were fed only 3.2 times, on average, during the last quarter of the nestling period. Estimated food loads ranged from less than 10 g to over 110 g (about 26% of mean adult weight). Nestlings were fed almost 70% of their total food during the first half of the nestling period and about 95% of their total by the time they were 90 days old. This suggests that they must store and metabolize a large amount of fat before fledging, as is the case for Leach's Storm-Petrel (*Oceanodroma leucorhoa*; Ricklefs et al. 1980). There was, however, much variability in the feeding pattern. Some chicks were deserted entirely for up to three weeks before fledging, while others were visited and fed small amounts just before they fledged. The pattern of visitation at monitored nests and observations of a hand-raised bird suggest that most chicks began to refuse food one to two weeks before fledging. This behavior has been found in other species, including the Atlantic Puffin (*Fratercula arctica*; Harris 1976), Fork-tailed Storm-Petrel (Simons, 1981a), Wedge-tailed Shearwater (*Puffinus pacificus*; J. Sincock, pers. comm.), and the Rhinoceros Auklet (*Cerorhinca monocerata*; Wilson et al., in press). These observations suggest that in some species the nestling determines when it is ready to fledge; furthermore, they may explain much of the conflicting evidence concerning the "desertion period" in seabirds (Burger 1980). The best mechanisms for determining when a nestling is ready to fledge probably reside within the chick itself. If adults simply continued to feed their nestlings until they began to refuse food, we would expect to see a variety of attendance patterns by adult birds late in the nestling period. In nests where chicks have matured rapidly and stored large amounts of fat, the signal might result in a substantial desertion period before fledging. In nests where the parents have provided less food, chicks may continue to beg

for food right up to the time the adults depart the colony at the end of the season. Both patterns have been noted in the Dark-rumped Petrel.

Food habits of breeding adults. Ten different types of prey were identified from three classes of marine organisms. Squid predominated in the petrel's diet, followed by fishes and crustacea (Table 7). I did not attempt to measure prey volumes, but a visual estimate of the samples indicated that squid constituted 50–75% of the total sample volume. This is in agreement with the evidence available for other gadfly petrels of the genus *Pterodroma* (Ashmole 1971, Imber 1973), although Pitman (1982) saw Dark-rumped Petrels feeding diurnally on prey driven to the surface by tuna and porpoise.

Gadfly petrels are more aerial than procellariiforms that feed primarily by diving, and they lack the laterally compressed, streamlined legs that are characteristic of this group (Ashmole and Ashmole 1967, Warham 1977). For these reasons, they are generally thought to feed primarily by seizing their prey on the surface and by scavenging. They are also believed to frequently feed at night. The prey items identified in this study corroborate those beliefs. Flying fish and skipjack tuna are both pelagic forms that would be available to the petrels on or near the surface, and squirrelfish and goatfish both possess pelagic juvenile stages that frequent the surface layers, especially at night (Wheeler 1975, Nelson 1976). Lantern and hatchet fish are bathypelagic forms that spend the daylight hours as deep as 3,500 m, but often migrate to the surface layers at night. They would appear to be ideal prey for Dark-rumped Petrels because they are generally small (less than 15 cm) and both possess highly visible photophores (Grzimek 1974). Nightly vertical migration to the surface is characteristic of squid and the giant isopod *Anuropus*, which also suggests that the birds are feeding at night. The mantis shrimp is primarily a coastal bottom-dwelling species (George and George 1979), and it may have been obtained by scavenging. One petrel regurgitated about six spherical egg cases containing what appeared to be crustacean larvae. The cases were about 0.5 cm in diameter and they were unusual in that they were filled with orange oil resembling petrel stomach oil, which is assumed to be of dietary origin (Jacob 1982). The oil appears to be important as a concentrated energy source for breeding Dark-rumped Petrels (Simons and Whittow 1984).

Nestling growth and development. Nestlings typically gained weight steadily for the first three-quarters of the nestling period and then

TABLE 7. Prey items from 20 food samples regurgitated by adult Dark-rumped Petrels during the nestling period identified to the lowest taxon. One sample was collected by Larson (1967), the remainder were collected from 1979–1981.

Prey	Rank	# of organisms	# of samples in which occurred
Fishes			
Exocoetidae (flying fish)	6	2	2
Holocentridae (squirrelfish)	5	3	3
Mullidae (goatfish)	2	6	4
Myctophidae (lantern fishes)	4	4	4
Scombridae <i>Katcuwonus pelamis</i> (skipjack tuna)	7	1	1
Sternoptychidae (hatchet fish)	7	1	1
Unidentified fish	3	5	4
Mollusca			
Decapoda (squid)			
Loliginidae*	7	1	1
Ommastrephidae	2	6	5
Unidentified squid	1	108	8
Crustacea			
Isopoda			
<i>Anuropus</i> sp.	7	1	1
Unidentified isopod	7	1	1
Stomatopoda* (mantis shrimp)	7	1	1
Unidentified crustacea			
Globules of bright orange oil containing crustacean larvae	7	1	1

* Larson (unpubl.).

lost weight until they fledged (Fig. 7). The average maximum weight attained by chicks was slightly over 600 g, although some nestlings reached peak weights of over 850 g, or almost twice the average adult weight. The development patterns of individual nestlings may reflect the variability of food supplies and the foraging efficiency of individual adult birds (Fig. 8). Many nestlings showed a cyclic pattern of weight gain. Typically, they were fed regularly for five to ten days in a row, and then were deserted for periods of up to three weeks. Nestlings were capable of fasting for long periods when food was unavailable, and they could quickly consume large amounts of food when it was abundant, frequently doubling their weight in a single feeding. Fledgling weights averaged 434.3 ± 26.2 g ($n = 26$), which is close to average adult weight.

Growth rate constants varied little from year to year, averaging 0.058 (Table 8). The K values were not clearly correlated with the other growth rate parameters, perhaps a reflection of the extreme irregularity of the yearly growth data. Nevertheless, the duration of the nestling period appeared to be related to the magnitude of the asymptote attained in a given year. Overall, the nestling period averaged 110.6 ± 4.6 days (range 100–119 days). The asymptote

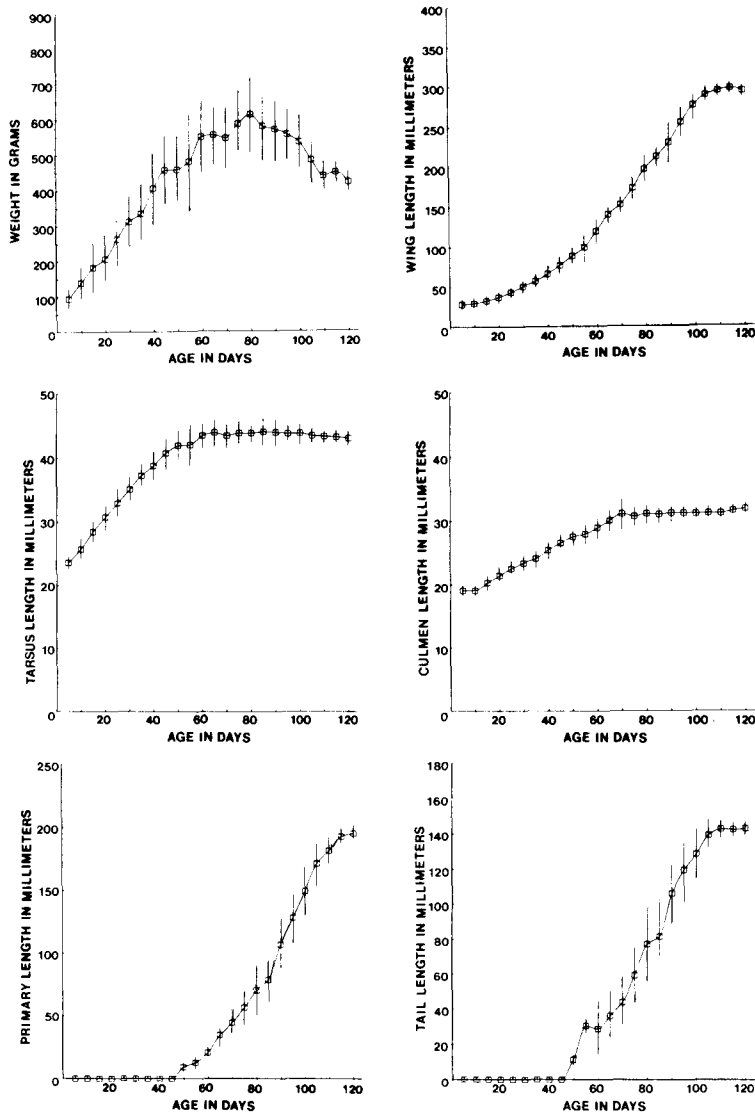


FIGURE 7. Growth patterns of Dark-rumped Petrel nestlings. Combined data 1979–1981 ($n = 31$). Vertical lines represent 1 SD on either side of the mean.

of chick weight averaged 629 g and higher asymptotes were associated with shorter nestling periods. The correlation again suggests that the duration of the nestling period is flexible, and may be regulated by the rate at which food is delivered to the nestling.

In contrast to weight, the growth of body parts and feathers was more uniform. The midpoint of the nestling period apparently represented an important turning point in the development of the chick (Fig. 7). Wing growth showed a typical logistic pattern with the inflection point occurring at approximately 60 days, and maximum length of about 300 mm was reached just prior to fledging. The tarsus and culmen both showed linear growth initially and reached an asymptote around day 60. The flight feathers emerged mid-way

through the nestling period and they grew at a constant rate until just before fledging. Thus, the first half of the nestling period was devoted to the development of tissue and body parts, while the remainder was dedicated to the maturation of that tissue and the development of the flight feathers.

Several other aspects of the chick's development can be used as criteria for aging the nestling. Nestlings opened their eyes shortly after hatching, and they retained their egg tooth for about one week. At hatching, they were covered by a layer of pale gray down which was distinctly whitish around the chest and belly. A denser second layer of down replaced the first during the second or third week. The first juvenal feather sheaths appeared along the spinal tract, and they began to emerge from

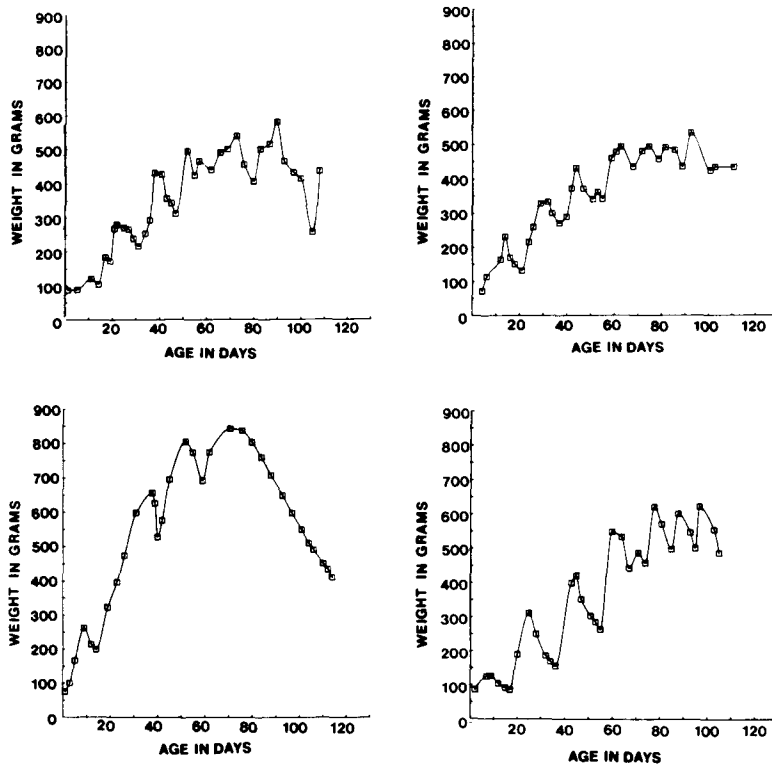


FIGURE 8. Growth patterns of four individual Dark-rumped Petrel nestlings.

the skin at about 13 days. These feathers erupted from their sheaths about day 45, and were fully developed by about day 60. The scapulars and belly feathers emerged between 30 and 35 days of age and were fully developed by day 65. The upper wing coverts emerged from the skin around day 40, and they began erupting from their sheaths about 10 days later. The feathers around the head and face developed more slowly, emerging on day 45 and erupting from their sheaths on day 65. The primary feathers emerged from their sheaths on about day 65 and the rectrices emerged on about day 55 (Fig. 7). By day 105, development of the juvenal plumage was usually complete, although some chicks retained small patches of down on their heads and bellies at fledging.

Nestling behavior. Nestling behavior differed from that of incubating adults in several important ways (Table 9). Chicks were more active on the nest than adults, and they spent a much smaller proportion of their time sleeping. This difference may be related to either the relatively higher thermoregulatory demands on the smaller nestlings or the importance of activity in stimulating muscle or feather development.

I observed feeding visits in the television-monitored burrow on several occasions. Typically, the adult arrived, walked directly to the nest, and began to preen the chick's face, head, and upper body. The chick responded with incessant cheeping and occasional nibbling at the adult's bill. The adult usually began to re-

TABLE 8. Growth rate constants and nestling periods of Dark-rumped Petrel nestlings 1979-1981.

	1979	1980	1981	Overall
<i>n</i>	17	6	8	31
Asymptote "a" (g)	590	718	650	629
Adult weight "W" (g)	430	430	430	430
$R = a/W$	1.37	1.67	1.51	1.45
K	0.065	0.054	0.067	0.058
Ka/4 (g/day)	9.59	9.69	10.88	9.12
KR/4 × 100 (%/day)	2.22	2.25	2.53	2.10
Nestling period (days)	112.8	106.9	110.1	110.6
(<i>n</i>)	(10)	(7)	(9)	(26)
(SD)	(2.90)	(3.70)	(4.51)	(4.60)

TABLE 9. Behavior of a nestling Dark-rumped Petrel. Data are presented as percent total time, based on 65 h 42 min of observations during the nestling period.

Portion of nestling period	Behavior				
	Resting quietly	Alert		Sleeping	Locomotion
		Arranging nest material	Self-maintenance		
First half	83.0%	0.6%	5.5%	9.1%	0.0%
Second half	57.2%	0.0%	6.3%	34.3%	2.2%
Total	65.8%	0.02%	6.0%	26.5%	1.5%

gurgitate food to the nestling within several minutes and continued feeding it until the adult decided to stop. Most visits lasted less than one hour. Occasionally, adult birds arrived late or they brought more food than their chicks could consume in an evening; in those cases, they often remained in the burrow the following day. I found adults with chicks as old as 65 days in burrows during the day.

Chicks became noticeably more active during the second half of the nestling period. About two months before fledging, the chick in the television-monitored burrow began to stretch and vigorously flap its wings as it rested on the nest. Chicks generally began to venture from their burrows at night two to three weeks before fledging. During these forays, they explored within about a 10-m radius of their burrow entrance, climbed rocks or other obstacles that could serve as take-off platforms, and exercised their wings. Chicks apparently continued this behavior until their exercising launched them into the air and they departed the colony on their first flight to the sea.

Fledging dates and overall reproductive success. The fledging period extended from 8 October to 30 October during the three years of the study. The median fledging date was 23 October ± 6.5 days in 1979, 19 October ± 6.7 days in 1980, and 19 October ± 6.1 days in 1981. Fledging success varied from 57.1% in 1979, a year with significant predation, to 100% in 1980, a year with no predation and high nestling growth rates (Table 5). Fledging success was reduced by predation in 1979 and, in both 1979 and 1981, by the death of several young nestlings, apparently from starvation. Active burrows containing fledglings were evident late in the season because they almost always showed traces of down around their entrances. This clue enabled me to estimate the percentage of active burrows that produced fledglings. Predation was severe in 1979, and approximately 24% of the active burrows produced fledglings. Predation was not significant in 1980 and 1981, and in those years, approximately 42% of the active burrows produced fledglings. Overall reproductive success ranged from 38.7% in 1979 to 71.4% in 1980.

CURRENT STATUS AND THREATS TO THE REMAINING POPULATIONS

Natural sources of mortality. The natural mortality rate of adult petrels on the colony appeared to be low, although I did find four adult birds that had apparently been killed by crashing into natural obstacles. Three of these birds were found along the steep cliffs of the west crater rim where they may have been caught by the normally strong winds there. Also, one adult bird was killed when the burrow it was excavating collapsed.

Introduced avian diseases are thought to have caused the decline and extinction of a large portion of the endemic Hawaiian avifauna (Warner 1968). Warner (1968) found avian malaria in Townsend's Shearwaters (*Puffinus auricularis newelli*) on Kauai (he erroneously called them Dark-rumped Petrels), which suggests that Dark-rumped Petrels may be susceptible. The disease is caused by infections of *Plasmodium*, and it is transported by the night-biting mosquito, *Culex quinquefasciatus* (Warner 1968). *Culex* is normally restricted to elevations below 600 m but may occur as high as 1,500 m (Williams 1931). I did not see any diseased birds during the study, and because all of the known petrel nesting locations are well above the range of the mosquito, it is unlikely that they are vulnerable to avian malaria. Nevertheless, I collected blood samples from five adult Dark-rumped Petrels in 1981 and examined them for signs of malaria. I found no evidence of developing *Plasmodium* schizonts or other signs of blood parasites in the blood smears. Van Riper (1978) reported similar results after examining a single adult bird on the island of Hawaii in 1977.

Finally, I found the remains of two birds, an adult in 1980 and a fledgling in 1981, that had apparently been killed by a Short-eared Owl (*Asio flammeus*). These owls are important predators of Dark-rumped Petrels in the Galapagos (Harris 1970), and they are common in Hawaii below elevations of approximately 2,000 m (Berger 1972). Most petrels nest well above that elevation, and both of the birds that were killed were found at the lower

limit of the petrel's breeding range. Short-eared Owls do not appear to prey significantly on Dark-rumped Petrels at this time, but they could become more of a threat if their range expands to higher elevations in the future.

Light-related groundings. Fledgling Dark-rumped Petrels occasionally become grounded after colliding with lights in urban areas, and although only five to ten birds are grounded on Maui in an average year, up to 20 fledglings have been recovered in the past, and many of these died (Simons 1983). The problem is much less than that involving Townsend's Shearwaters on Kauai (Telfer 1979), and it is not at present thought to threaten the remaining populations (Simons 1984). Nevertheless, the number of groundings on Maui can be expected to increase with growing urbanization on the island, and should be monitored closely.

Introduced mammals. The most serious cause of mortality and breeding failure in nesting Dark-rumped Petrels today is predation by introduced mammals. It was formerly thought that the remaining petrels nested above the range of feral cats and mongooses, and that the primary predator of the birds was the black rat (*Rattus rattus*; Larson 1967). Trapping prior to 1979 was mostly done with snap-type rat traps, which were ineffective on cats and mongooses. I began a trapping program in that year using live traps, and found that both cats and mongooses occurred in the petrel's nesting habitat (Simons 1983; Simons and Manuwal, unpubl.). Over 60% of the breeding failures in years with significant predation were caused by feral cats and mongooses (Simons 1983). In most cases, only a few vagrant individuals were responsible for the predation, but their long-term impact on the petrel population may have been significant. The Dark-rumped Petrel's intensely K-selected life history attributes make their populations very vulnerable to increased mortality rates, and they severely limit the recovery rate of a depressed population (Simons 1984). Fortunately, it appears that the trapping program, which has been expanded to areas surrounding the breeding colonies, has succeeded in controlling predation on breeding petrels. The number of predators caught in the nesting colony declined each year of the study, but there is a virtually unlimited source of predators at lower elevations in Hawaii, and it is likely that they will continue to threaten the remaining petrel populations indefinitely. In addition, predator populations, which appear to benefit from human activity, are likely to expand and increase in the future with growing urbanization on Maui, and increased visitation at Haleakala National Park. Nevertheless, there is reason

for cautious optimism regarding the future of the Hawaiian Dark-rumped Petrel. The bird's reproductive success increased dramatically in 1980, following the start of the predator control program (Table 5), and it has remained high in recent years (Simons and Manuwal, unpubl.). In addition, I found no evidence that food supplies or nesting sites are currently limiting the remaining populations. From a conservation standpoint, the requirements of the birds are simple. If they can be protected from mammalian predators, their populations should persist and possibly increase at a modest rate in the future.

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LITERATURE CITED

- AR, A., AND H. RAHN. 1980. Water in the avian egg: overall budget of incubation. *Am. Zool.* 30:373-384.
- ASHMOLE, N. P. 1971. Seabird ecology and the marine environment, p. 224-286. *In* D. S. Farner and J. R. King [eds.], *Avian biology*. Vol. 1. Academic Press, New York.
- ASHMOLE, N. P., AND M. J. ASHMOLE. 1967. Comparative feeding ecology of sea birds of a tropical oceanic island. *Peabody Mus. Nat. Hist. Yale Univ. Bull.* 24.
- ATKINSON, I. A. E. 1977. A reassessment of the factors, particularly *Rattus rattus* L., that influenced the decline of endemic forest birds in the Hawaiian Islands. *Pac. Sci.* 31:109-133.
- BALDWIN, P. H., AND D. H. HUBBARD. 1949. The Hawaiian Dark-rumped Petrel reappears on Hawaii. *Condor* 51:231-232.
- BANKO, W. E. 1980. History of endemic Hawaiian birds. CPSU/UH Avian History Report, CPSU/UH 026/10. Univ. of Hawaii, Manoa.
- BERGER, A. J. 1972. *Hawaiian birdlife*. The Univ. Press, of Hawaii, Honolulu.
- BOERSMA, P. D. 1982. Why some birds' eggs take so long to hatch. *Am. Nat.* 120:733-750.
- BOERSMA, P. D., AND N. T. WHEELWRIGHT. 1979. Egg neglect in the Procellariiformes: reproductive adap-

- tations in the Fork-tailed Storm Petrel. *Condor* 81: 157-165.
- BOURNE, W. P. R. 1965. The missing petrels. *Bull. Br. Ornithol. Club* 85:97-105.
- BURGER, J. 1980. The transition to independence and postfledging parental care in seabirds, p. 367-447. *In* J. Burger, B. L. Olla, and H. E. Winn [eds.], *Behavior of marine animals*. Vol. 4. Plenum, New York.
- CALDER, W. A. 1968. Respiratory and heart rates of birds at rest. *Condor* 70:358-365.
- CLINE, M. G. 1955. Soil survey of the territory of Hawaii. U.S. Dep. Agric. Soil Survey Ser. No. 25.
- COULTER, C., F. CRUZ, AND T. BEACH. 1982. The biology and conservation of the Dark-rumped Petrel, *Pterodroma phaeopygia*, on Floreana Island, Galapagos, Ecuador, Unpubl. report to the Charles Darwin Research Station, Guayaquil, Ecuador.
- CROXALL, J. P., AND C. RICKETTS. 1983. Energy costs of incubation in the Wandering Albatross *Diomedea exulans*. *Ibis* 125:33-39.
- DEIGHTON, T., AND J. C. D. HUTCHINSON. 1940. Studies on the metabolism of fowls. II. The effect of activity on the metabolism. *J. Agric. Sci.* 30:141-157.
- FISHER, H. I. 1971. The Laysan Albatross: its incubation, hatching, and associated behavior. *Living Bird* 10: 19-78.
- FISHER, H. I. 1975a. The relationship between deferred breeding and mortality in the Laysan Albatross. *Auk* 92:433-441.
- FISHER, H. I. 1975b. Mortality and survival in the Laysan Albatross, *Diomedea immutabilis*. *Pac. Sci.* 29:279-300.
- FISHER, H. I. 1976. Some dynamics of a breeding colony of Laysan Albatrosses. *Wilson Bull.* 88:121-142.
- GEORGE, J. D., AND J. J. GEORGE. 1979. *Marine life: an illustrated encyclopedia of invertebrates in the sea*. J. Wiley, New York.
- GRANT, G. S., J. H. WARHAM, T. N. PETTIT, AND G. C. WHITTO. 1983. Reproductive behavior and vocalizations of the Bonin Petrel. *Wilson Bull.* 95:522-539.
- GRZIMEK, B. 1974. *Grzimek's animal life encyclopedia*. Van Nostrand Reinhold, New York.
- HARRIS, M. P. 1966. Breeding biology of the Manx Shearwater *Puffinus puffinus*. *Ibis* 108:17-33.
- HARRIS, M. P. 1970. The biology of an endangered species, the Dark-rumped Petrel (*Pterodroma phaeopygia*) in the Galapagos Islands. *Condor* 72:76-84.
- HARRIS, M. P. 1976. The present status of the Puffin in Britain and Ireland. *Br. Birds* 69:239-264.
- HATCH, S. A. 1983. Mechanism and ecological significance of sperm storage in the Northern Fulmar with reference to its occurrence in other birds. *Auk* 100: 593-600.
- HENSHAW, H. W. 1902. *Birds of the Hawaiian Islands, being a complete list of the birds of the Hawaiian Possessions, with notes on their habits*. Thos. G. Thrum, Honolulu.
- HICKEY, J. J. 1969. *Peregrine Falcon populations: their biology and decline*. Univ. of Wisconsin Press, Madison.
- HIRAI, L. T. 1978. Possible Dark-rumped Petrel colony on Lanai, Hawaii. *'Elepaio* 38:71-72.
- HUSSEL, D. J. T. 1972. Factors affecting clutch size in arctic passerines. *Ecol. Monogr.* 42:317-364.
- IMBER, M. J. 1973. The food of Grey-faced Petrels (*Pterodroma macroptera gouldi* [Hutton]), with special reference to the vertical migration of their prey. *J. Anim. Ecol.* 42:645-662.
- JACOB, J. 1982. Stomach oils, p. 325-340. *In* D. S. Farner, J. R. King, and K. C. Parkes [eds.], *Avian biology*. Vol. 6. Academic Press, New York.
- KING, W. B. 1967. *Seabirds of the tropical Pacific Ocean*. Smithsonian Institution, Washington DC.
- KING, W. B. 1970. The trade wind zone oceanography pilot study. Part VII: Observations of sea birds. March 1964 to June 1965. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish. No. 586.
- KING, W. B. 1981. *Endangered birds of the world: the ICBP bird red data book*. Smithsonian Institution Press, Washington, DC.
- KING, W. B., AND J. L. LINCER. 1973. DDE residues in the endangered Hawaiian Dark-rumped Petrel (*Pterodroma phaeopygia sandwichensis*). *Condor* 75:460-461.
- KIRCH, P. V. 1974. The chronology of the early Hawaiian settlement. *Archeo. Phys. Anthropol. Oceania* 9:110-119.
- LACK, D. 1968. *Ecological adaptations for breeding in birds*. Methuen, London.
- LARSON, J. W. 1967. The Dark-rumped Petrel in Haleakala Crater, Maui, Hawaii. Unpubl. report to the National Park Service, U.S. Department of the Interior.
- LYONS, S. W. 1979. Summer weather on Haleakala. Univ. of Hawaii, Department of Meteorology. Publ.# UHMET 79-09.
- MUNRO, G. C. 1941. Birds of Hawaii and adventures in bird study. The Dark-rumped Petrel. *'Elepaio* 2:24-27.
- MUNRO, G. C. 1944. *Birds of Hawaii*. Tongg Publ. Co., Honolulu.
- NELSON, J. S. 1976. *Fishes of the world*. Wiley, New York.
- OLSON, S. L., AND H. F. JAMES. 1982a. Fossil birds from the Hawaiian Islands: evidence for wholesale extinction by man before western contact. *Science (Wash. DC.)* 217:633-635.
- OLSON, S. L., AND H. F. JAMES. 1982b. Prodrum of the fossil avifauna of the Hawaiian Islands. *Smithson. Contrib. Zool.* No. 365.
- PENNYCUICK, C. J. 1969. The mechanics of bird migration. *Ibis* 111:525-556.
- PERKINS, R. C. L. 1903. *Fauna Hawaiiensis*. Cambridge Univ. Press, Cambridge.
- PERRINS, C. M., AND M. DE L. BROOKE. 1976. Manx Shearwaters in the Bay of Biscay. *Bird Study* 23:295-299.
- PERRINS, C. M., M. P. HARRIS, AND C. K. BRITTON. 1973. Survival of Manx Shearwaters *Puffinus puffinus*. *Ibis* 115:535-548.
- PINDER, R. 1966. The Cape Pigeon, *Daption capensis* Linnaeus, at Signey Island, South Orkney Island. *Br. Antarct. Surv. Bull.* 8:19-47.
- PITMAN, R. L. 1982. Distribution and foraging habits of the Dark-rumped Petrel (*Pterodroma phaeopygia*) in the eastern tropical Pacific. *Bull. Pacific Seabird Group* No. 9.
- PRINCE, P. A., C. RICKETTS, AND G. THOMAS. 1981. Weight loss in incubating albatrosses and its implications for their energy and food requirements. *Condor* 83:238-242.
- RATCLIFFE, D. A. 1970. Changes attributed to pesticides in egg breakage frequency and egg-shell thickness in some British birds. *J. Appl. Ecol.* 7:67-115.
- RICE, D. W., AND K. W. KENYON. 1962. Breeding cycles and behavior of Laysan and Black-footed albatrosses. *Auk* 79:517-567.
- RICHARDSON, F., AND D. H. WOODSIDE. 1954. Rediscovery of the nesting of the Dark-rumped Petrel in the Hawaiian Islands. *Condor* 56:323-327.
- RICHDALE, L. E. 1952. The post-egg period in Albatrosses. *Biol. Monogr.* 4 Dunedin, New Zealand.
- RICKLEFS, R. E. 1967. A graphical method of fitting equations to growth curves. *Ecology* 48:978-983.
- RICKLEFS, R. E. 1968. Patterns of growth in birds. *Ibis* 110:419-451.

- RICKLEFS, R. E. 1984. Some considerations of the reproductive energetics of pelagic seabirds. *Stud. Avian Biol.* 8:84-94.
- RICKLEFS, R. E., S. C. WHITE, AND J. CULLEN. 1980. Post-natal development of Leach's Storm Petrel. *Auk* 97: 768-781.
- SCHROEDER, T. A., B. J. KILONSKY, AND B. N. MEISNER. 1977. Diurnal variation in rainfall and cloudiness. UHMET 77-03. Tech. Rep. No. 112, Water Resources Research Center, Univ. of Hawaii, Manoa.
- SHALLENBERGER, R. J. 1974. Field notes. *'Elepaio* 35:18-20.
- SIMONS, T. R. 1981a. Behavior and attendance patterns of the Fork-tailed Storm Petrel. *Auk* 98:145-158.
- SIMONS, T. R. 1981b. A simple event recorder for monitoring cavity-dwelling animals. *Murrelet* 62:27-30.
- SIMONS, T. R. 1983. Biology and conservation of the endangered Hawaiian Dark-rumped Petrel (*Pterodroma phaeopygia sandwichensis*). National Park Service, Cooperative Park Studies Unit, Univ. Washington, CPSU/UW83-2, Seattle.
- SIMONS, T. R. 1984. A population model of the endangered Hawaiian Dark-rumped Petrel. *J. Wildl. Manage.* 48:1065-1076.
- SIMONS, T. R., AND G. C. WHITTO. 1984. Energetics of growth in the Dark-rumped Petrel, p. 159-182. *In* G. C. Whitto [ed.], *Seabird energetics*. Plenum, New York.
- SOKAL, R. R., AND F. J. ROHLF. 1981. *Biometry*. 2nd ed. W. H. Freeman and Co., San Francisco.
- TELFER, T. C. 1979. Successful Newell's Shearwater salvage on Kauai. *'Elepaio* 39:71.
- TOMICH, P. Q. 1969. Mammals in Hawaii: a synopsis and notational bibliography. B. P. Bishop Museum Publ. No. 57, Honolulu.
- VAN RIPER, C., III. 1978. Dark-rumped Petrel at Hawaii Volcanoes National Park. *Bird-Banding* 49:372.
- WARHAM, J. 1977. Wing loadings, wing shapes, and flight capabilities of Procellariiformes. *N. Z. J. Zool.* 4:73-83.
- WARNER, R. E. 1968. The role of introduced diseases in the extinction of the endemic Hawaiian avifauna. *Condor* 70:101-120.
- WHEELER, A. 1975. *Fishes of the World*. Van Nostrand Reinhold, New York.
- WHITTO, G. C. 1980. Physiological and ecological correlates of prolonged incubation in sea birds. *Am. Zool.* 20:427-436.
- WHITTO, G. C. 1984. Physiological ecology of incubation in tropical seabirds. *Stud. Avian Biol.* 8:47-72.
- WHITTO, G. C., T. R. SIMONS, AND T. N. PETTIT. 1984. Water loss from the eggs of a tropical seabird (*Pterodroma phaeopygia*) at high altitude. *Comp. Biochem. and Physiol.* 78:537-540.
- WILLIAMS, F. X. 1931. Notes and exhibits at 310th meeting of Hawaii Ent. Soc. 8:29.
- WILSON, U., D. A. MANUWAL, AND L. LESCHNER. In press. The natural history of the Rhinoceros Auklet (*Cerorhinca monocerata*) in Washington, with notes on inter-colonial variations. *Condor*.
- WURSTER, C. F., AND D. B. WINGATE. 1968. DDT residues and declining reproduction in the Bermuda Petrel. *Science (Wash. DC.)* 159:979-981.

Wildlife Science Group, College of Forest Resources, University of Washington, Seattle, Washington 98195. Present address: U.S. National Park Service, Gulf Islands National Seashore, 3500 Park Road, Ocean Springs, Mississippi 39564. Received 6 April 1984. Final acceptance 24 December 1984.

RECENT PUBLICATIONS

Pattern, mechanism, and adaptive significance of territoriality in Herring Gulls (*Larus argentatus*).—Joanna Burger. 1984. Ornithological Monographs No. 34. American Ornithologists' Union, Washington, DC. 92 p. Paper cover. \$9.00 (\$7.00 to AOU members). Source: Frank R. Moore, Assistant to the Treasurer, AOU, Department of Biology, University of Southern Mississippi, Southern Station Box 5018, Hattiesburg, MS 39406; all orders must be prepaid and include a \$0.50 handling charge. Thoughts on the evolution of territorial behavior in birds usually rest upon certain assumptions on the relationship of territory size to reproductive success on the one hand and to aggression on the other. These factors and their relationships are examined in this monograph, based on field work over several seasons at five Herring Gull colonies in New Jersey, New York, and Maine. Burger concludes that territory size and rates of aggression affect reproductive success in these gulls, but that the relationships are not linear. Her study yields important new insights into territoriality in larids. Diagrams, references.

The interpretation of aerial surveys for seabirds: some effects of behaviour.—A. J. Gaston and G. E. J. Smith. 1984. Occasional Paper No. 53, Canadian Wildlife Service. 18 p. Paper cover. Catalogue No. CW69-1/53E. No price given. Source: Minister of Supply and Services, Ottawa, Canada. Seabird biologists in the Canadian Wildlife Service have been exceptionally attentive to the accuracy and adequacy of their survey procedures (e.g., Gaston and Nettleship 1982, noted in *Condor* 85:207). The authors of this paper point out, however, that even if censuses are wholly accurate (or the degree of bias estimated precisely), differences in the numbers of birds seen in different areas or at different times will be variously interpreted owing to the birds' behavior. They consider here the effects of colony attendance, travel time between colony and feeding grounds, relative motion of birds and aircraft, and duration and frequency of dives. Their examples show how the proposed correction factors may improve the interpretation of the raw data. Some mathematical ability is required. Illustrations, references.