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BIOLOGY AND CONSERVATION OF THE ENDANGERED HAWAIIAN DARK-RUMPED PETREL (PTERODROMA PHAEOPYGIA SANDWICHENSIS)

University of Washington

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Biology and Conservation of the Endangered Hawaiian Dark-rumped Petrel (*Pterodroma phaeopygia sandwichensis*)

by

Theodore Raymond Simons

A dissertation submitted in partial fulfillment
of the requirements for the degree of

Doctor of Philosophy

University of Washington

1983

Approved by David A Manuwal
(Chairperson of Supervisory Committee)

Program Authorized
to Offer Degree Forest Resources

Date 3 June 1983

Doctoral Dissertation

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Date 6 June 1983

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To Pam and Jits

CHAPTER 1

INTRODUCTION

This work reports the results of a three year study of the endangered Dark-rumped Petrel initiated in 1979. The purposes of the study were to document the biology of this poorly known species, to identify the factors currently threatening its survival, and to develop a management plan to guide future conservation efforts.

Taxonomic background

The Dark-rumped Petrel (Pterodroma phaeopygia sandwichensis) or 'Ua'u is one of two endangered subspecies. The other, Pterodroma phaeopygia phaeopygia, nests in the Galapagos Islands (Harris 1970). The name Pterodroma is derived from the Greek words pteron, refering to feathers or wings, and dromos which refers to a race course or any quick movement. Phaeopygia is derived from the Greek phaios, for dusky or brown, and puge, for rump or buttocks (Gotch 1981). Thus, the name describes a fast flying dark-rumped bird. The Dark-rumped Petrel is a member of a large order of seabirds, the Procellariiformes. These are long-winged pelagic birds that are characterized by their tube-shaped nostrils. Most come to land only to breed and are highly adapted to an ocean existance (Alexander 1954, Tuck and Heinzel 1978). The Dark-rumped Petrel is a gadfly petrel and belongs to the family Procellariidae, which also contains the shearwaters and the fulmars. The gadfly petrels are most commonly found in tropical and sub-tropical zones and it appears that they feed primarily on cephalopods which they catch near the sea surface at night (Ashmole 1971, Serventy et. al 1971, Imber 1973, Warham 1977, Chapter 2).

Adult birds are stocky in appearance and approximately 40 cm in length (Figure 1). Their upperparts are grayish-black, including their nape, wings, back, rump and wedge-shaped tail. The forehead and underparts are white including the underwings which posess prominent dark margins. The bill is black. The legs are pink and the feet are pink with mostly black webs. Measurements of adult birds are summarized in Chapter 2.

Prior Distribution of the Dark-rumped Petrel in Hawaii

The definitive work on the history and distribution of the Dark-rumped Petrel in Hawaii has been compiled by W.E. Banko

Figure 1. Adult Dark-rumped Petrel.

(1980). I will not recount his findings here but I will review his major conclusions, incorporating additional observations and work that have come to light in the last few years.

The limited historical evidence available indicates that Dark-rumped Petrels were once abundant throughout the main Hawaiian Islands (Figure 2). Early reports of their distribution and numbers are scarce but they all reflect large pre-historic populations. Perkins (1903) noted that the bird was "common in many parts of the islands, nesting in the high mountains, where it forms large colonies" . Munro (1955) commented on the populations on Molokai stating, "I was told that on its arrival at Pelekunu Valley, Molokai, in the evening it darkened the sky". Bryan (1908, 1914) collected birds in the upper valleys of Molokai in the early 1900's and Banko (1980) discussed a report of the birds nesting at lower elevations, including Makukooniki, a small offshore islet. Munro (1941) collected specimens of the Dark-rumped Petrel and observed birds flying inland in the evening on Kauai in 1895 and, he also described several nesting colonies on Lanai. Evidence of nesting colonies on Maui is scarce but Banko (1980) discussed several reports of birds nesting on the lower slopes of Haleakala near Olinda and Polipoli. Henshaw (1902) was told by natives on the Island of Hawaii that the

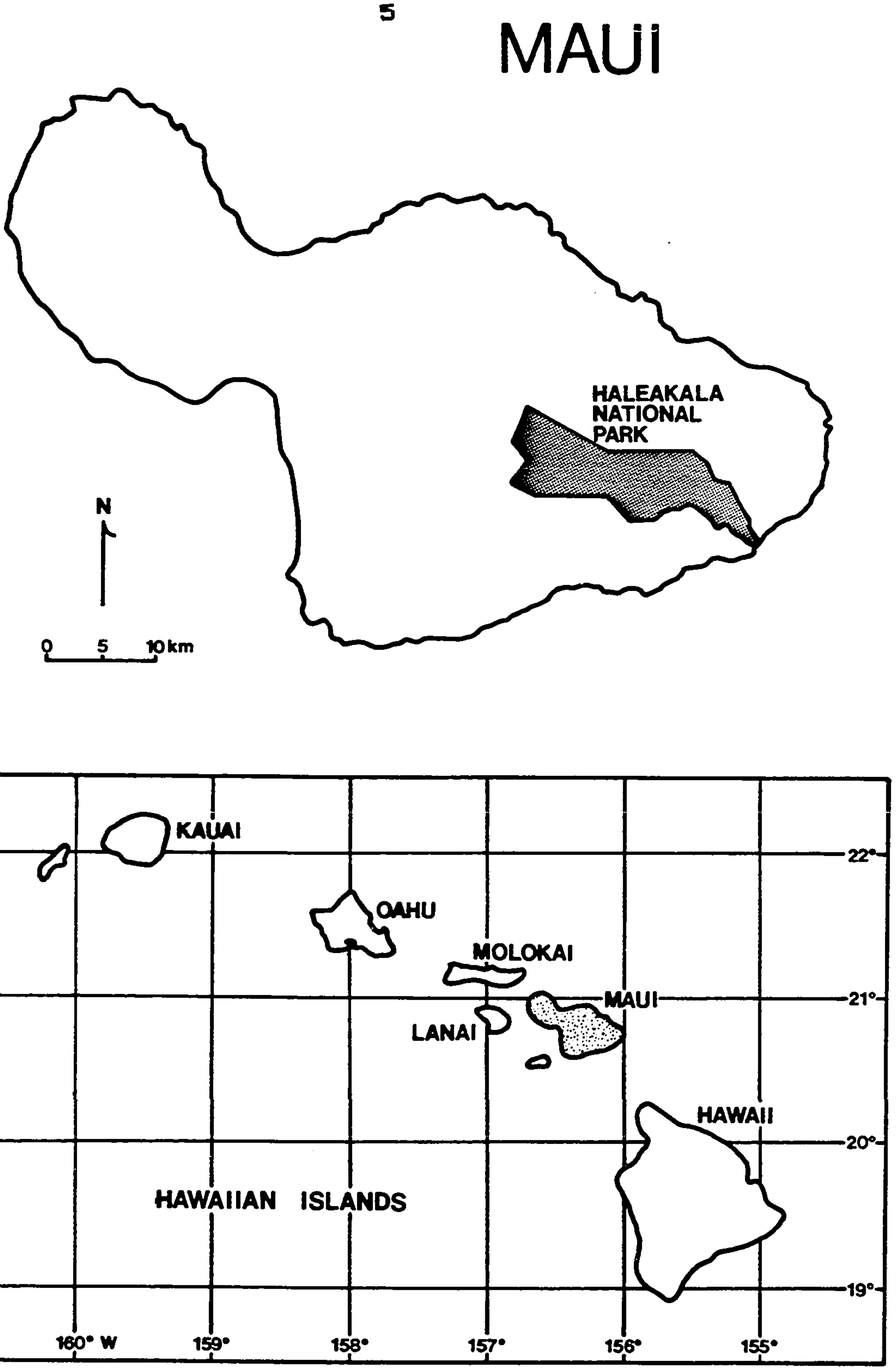

Figure 2. Principal Hawaiian Islands and Haleakala National Park.

birds formerly "nested in great numbers in the lava between Mauna Kea and Mauna Loa". Thus, although reports of the birds did not appear until almost a century after the arrival of the first European explorers, sizable populations of the birds may still have existed on all of the main islands except Oahu at that time. It is now clear that the Dark-rumped Petrel was once a common breeding seabird on Oahu (Olson and James 1982a, 1982b) and its history on that island is indicative of the decline of the species throughout Hawaii.

It is generally believed that the first Polynesians arrived in Hawaii about 1500 years ago (Kirch 1974). Until recently it has also been generally accepted that the Polynesians had little impact on native ecosystems. Ornithologists (Amadon 1950) as well as biogeographers (Juvik and Austring 1979) have almost universally assumed that the early explorers, led by Cook in 1778, found Hawaii in a near pristine state. Most ornithologists have assumed that the native avifauna did not begin to decline until after the arrival of the Europeans, and that this decline was caused by a combination of factors including predation by introduced mammals (Atkinson 1977), disease (Warner 1968), and habitat destruction (Berger 1972). A reexamination of the historical evidence, and archeological research by Olson and James (1982a, 1982b) now suggests that the Hawaiian ecosystem was substantially modified by the prehistoric Polynesian populations and that a sizable segment of the native avifauna was exterminated in the process. The Polynesians imported a variety of predators including dogs, pigs, and the Polynesian Rat (Rattus exulans), and they extensively modified the native plant communities by cultivating taro, sweet potatoes, and bananas. In addition, Olson and James (1982a) have pointed to evidence that the Polynesians were responsible for converting large areas of forest habitat into grassland by burning. The impact of these activities on the endemic avifauna was substantial. Olson and James (1982a, 1982b) have now identified at least 39 extinct species of endemic land birds in Hawaii, and they propose "it is likely that well over half of the species of endemic land birds that were present in the archipelago before the arrival of Polynesians became extinct between that event and European contact." There is evidence that the seabird populations were decimated as well. Recent archeological work suggests that Dark-rumped Petrels were abundant on all of the main Hawaiian Islands, including Oahu. It now appears that the Oahu population was exterminated prior to the arrival of Europeans. Olson and James (1982a, 1982b) also found evidence that Audubon's Shearwaters (Puffinus lherminieri), Bonin Petrels (Pterodroma hypoleuca) and a previously unknown Pterodroma species once bred on the main islands. All of the birds disappeared before the historic period.

Although the Dark-rumped Petrel is now restricted to breeding sites at high elevations, it may have once bred much closer to sea level. Munro (1944) reported that the species could be found at elevations of between 1500 and 5000 feet, and Banko (1980) proposed that birds may have also nested on off-shore islets near sea level. Indeed most of Olson and James' (1982a, 1982b) archeological sites were located near sea level, and it seems likely that some birds were breeding in the vicinity. It now appears likely that most Dark-rumped Petrels nesting at lower elevations were exterminated prior to European contact. These populations may have been reduced as a result of predation by the dogs and pigs that the Polynesians brought with them, and by hunting of the birds by the Polynesians. Henshaw (1902) 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." It appears that both adults and nestlings were harvested on a large scale and the remains of Dark-rumped Petrels have been found in abundance in middens and lava tubes throughout the islands (Olson and James 1982a, Kepler and Scott in prep.).

Thus, the decline of the Dark-rumped Petrel populations in Hawaii may have been well underway by the time the first Europeans arrived two centuries ago. The introduction of cats, black rats (*Rattus rattus*), Norway rats (*Rattus norwegicus*), disease-carrying mosquitos, and in 1883 mongooses (*Herpestes auropunctatus*) certainly accelerated the decline so that the birds survive today in only a few high-elevation sites. The predators that threaten the remaining populations today probably represent only a small portion of the decimating influences that have reduced the populations over the last 1500 years. This pattern of decline has been repeated in populations of gadfly petrels all over the world, so that today only a few species with healthy, undisturbed populations survive. The combined effects of hunting by man and predation by introduced mammals have driven many populations to the brink of extinction. Like the Dark-rumped Petrel, many of those populations are surviving outside of their preferred habitats, at high elevations, or on remote offshore islets (See reviews by Bourne 1965, Harris 1970).

Present Day Distribution of the Dark-rumped Petrel

There are few records of the Dark-rumped Petrel from about 1910 to the late 1940's, and many ornithologists during that time feared that the species was on the brink of extinction in Hawaii (Munro 1941). 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 Maui (Richardson and Woodside 1954), Lanai (Shallenberger 1974, Hirai 1978), Kauai (Banko 1980, J.Sincock, D. Boynton pers. comm.), and Molokai (Kepler and Scott in prep.).

Considerable effort has been expended searching for Dark-rumped Petrels on the Island of Hawaii since the discovery of five active burrows near Puu Kole on the southeast slope of Mauna Kea in 1954 (Richardson and Woodside 1954). Banko (1980) surveyed the island extensively from 1968 to 1978 and concluded that the "The only known breeding group extant on the island of Hawaii is a small scattered group which nests on the Southwest Rift of Mauna Loa. Another small scattered population may exist in or near Hawaii Volcanoes National Park and/or along the flanks of the northeast rift where recent indications have been found." These indications were reported by Conant (1980) based on surveys of the Mauna Loa Summit Trail in July 1978. Conant reported hearing Dark-rumped Petrels in a small (approximately 2 ha) area at about 2449 m elevation, although no active burrows were found. Recent surveys by the U.S. Fish and Wildlife Service on Hawaii have failed to detect any evidence of the Mauna Kea population, although an estimated 34 - 45 calling birds were heard along the southwest rift of Mauna Loa (Kepler and Scott in prep.). It appears therefore that only a small breeding population survives on the island of Hawaii. Only a handful of active burrows have been located since the rediscovery of the birds in 1954, and no active burrows have been found in recent years.

On Lanai, a potentially sizable population may exist along the ridges of Kumoa Gulch at an elevation of 825 m (Shallenberger 1974, Hirai 1978). An estimated 50 birds were heard calling in the area in May, June, and July but, in spite of several attempts to locate the colony, the steep terrain and dense vegetation have precluded the location of any active burrows.

It also appears that a small number of birds are still breeding on Molokai and Kauai. Five to ten calling birds were heard by a U.S. Fish and Wildlife Service survey crew along the upper southeast corner of Wailau Valley, Molokai in 1980. The birds appeared to be congregating along the cliffs below Puu Ohelo at an elevation of approximately 1000 m (Kepler and Scott in prep.). On Kauai, several grounded Dark-rumped Petrel fledglings have been collected in recent years as part of the Newell's Shearwater recovery program (J.Sincock pers. comm.). Most birds have been found near the mouth of Waimea Canyon indicating that some birds still breed in the vicinity.

Observations of the Dark-rumped Petrel at sea are scarce. Henshaw (1902) reported "The natives inform me that the 'Ua'u is common on the fishing grounds, some five to ten miles off the windward side of Hawaii.", but there appear to be no other early reports of the distribution of the birds at sea. Records of the birds at sea were collected by the Smithsonian's Pacific Ocean Biological Survey Program in the late 1960's (King 1967, 1970). Observers collected information on the distribution of seabirds during 34,384 miles of cruising in the vicinity of the Hawaiian Islands. Dark-rumped Petrels were recorded in very limited numbers as far north as 42°N and as far south as 5°N latitude, as far east as 148°W, and as far west as 158°W longitude. In addition, a specimen from the Moluccas Islands in the Southwest Pacific suggests that the birds may migrate to the Western Pacific in the non-breeding season. Banko (1980) recounts a conversation with the skipper of a fishing boat who told him that "'Ua'u were present in Hawaiian waters (from South Point, island of Hawaii to

French Frigate Shoals, Northwestern Hawaiian Islands) from May to October, and were absent from about November to April." Banko also notes that R.S. Crossin reported seeing Dark-rumped Petrels flying toward and away from Kauai in the 1960's. Pitman (1982) reported over 1200 sightings of Dark-rumped Petrels at sea and found the birds to be widespread over the eastern tropical Pacific. Sightings were primarily of solitary birds but Pitman noted that the species often joined in mixed species foraging flocks.

The largest and most important nesting colony of the Dark-rumped Petrel remaining today is located in and around Haleakala National Park on the island of Maui. It is clear that the fate of the Hawaiian population to a large extent depends on the future of this colony.

Early Work and the Scope of the Present Study

Kjargaard (1978) reported that Civilian Conservation Corps personnel and National Park Service employees were aware of the Haleakala Dark-rumped Petrel population in the 1930's, although the breeding population was not "rediscovered" by science until 1954 (Richardson and Woodside 1954). Censusing and study of the population was initiated by Larson (1967) and continued by W.B. King, K.Buxbaum, and for most of the past 15 years, by J.Kunioki. Kunioki and his coworkers have now mapped over 600 burrows, most of which are located along the heavily eroded west rim of Haleakala at an elevation of almost 3000 m. The Maui population is currently estimated to be approximately 900 pairs of which about 430 pairs are breeding adult birds (Chapters 2 and 4).

Field work was conducted from April to November 1979 and from early March to November in 1980 and 1981. A two week visit was also made to the colony in August 1982.

The methods employed in the study will be presented in conjunction with the relevant results. All statistical tests were taken from Sokal and Rohlf (1981).

CHAPTER 2

BREEDING BIOLOGY AND BEHAVIOR OF THE DARK-RUMPED PETREL

In this chapter I will discuss the breeding biology and behavior of the Dark-rumped Petrel. After beginning with an overview of the birds present distribution and abundance on the island of Maui, I will trace their nesting cycle from arrival through fledging. Relevant material presented in other chapters will not be repeated here and in those cases the reader will be referred directly to the pertinent chapter.

THE PRE-LAYING PERIOD

Nesting Habitat and Environment

Virtually all of the known Dark-rumped Petrel nest sites remaining today can be found in and around Haleakala National Park (Figure 3). The park encompasses most of the summit of Haleakala, a mountain which extends 3,055 meters above the Pacific Ocean and comprises over half of the land area of Maui. Haleakala is a dormant shield volcano with a

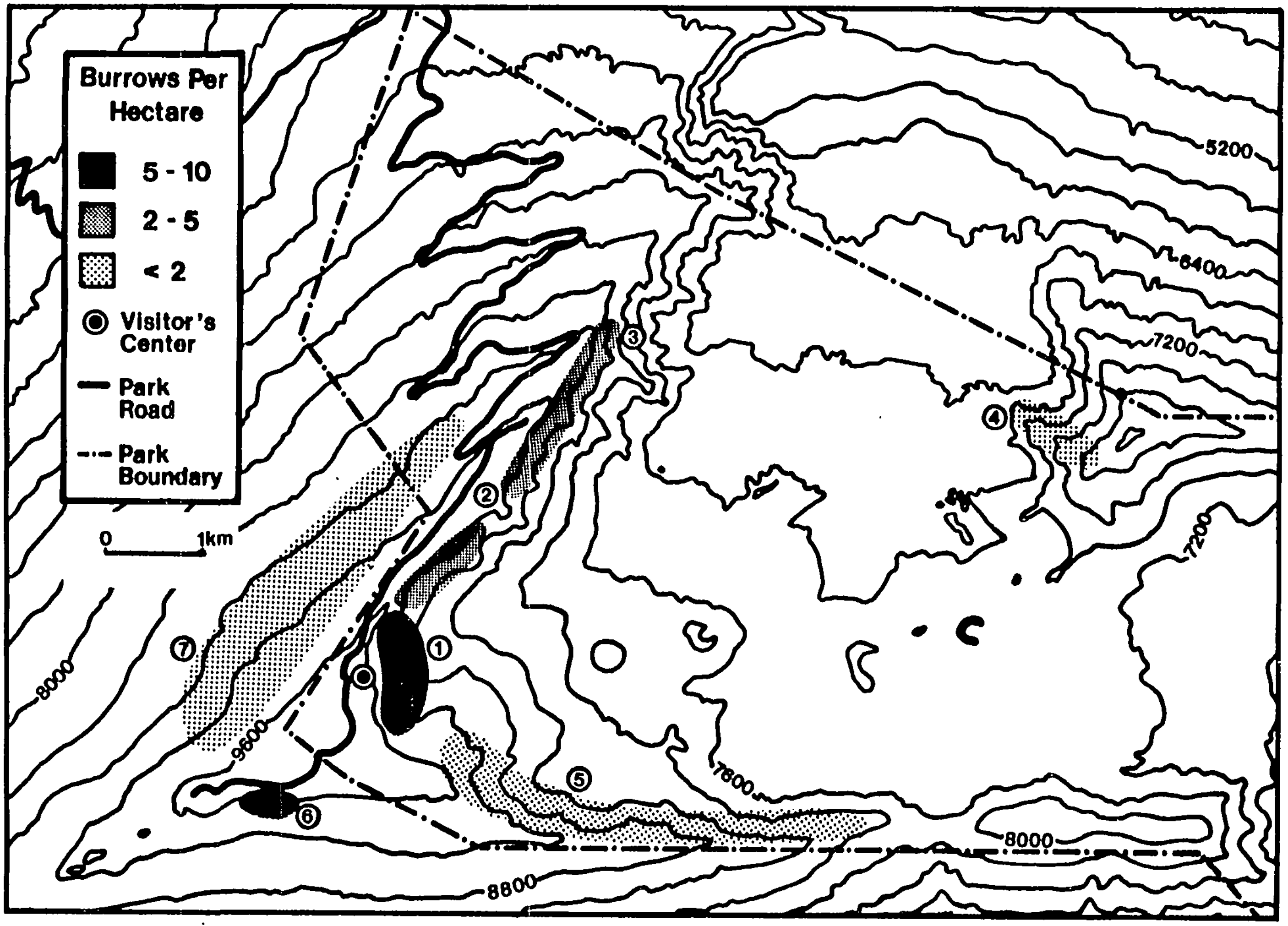

Figure 3. Dark-rumped Petrel nesting areas on East Maui. Numbers refer to the primary sub-colonies; (1) White Hill, (2) West Rim, (3) Holua, (4) Hana Mountain, (5) South Rim, (6) Science City, (7) West Slope.

large erosion depression at its center. This depression forms a 20 square mile crater which lies over 1000 meters 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. They are often undifferentiated and continuous, and form much of the central crater area. These soils are not suitable for burrowing and are not utilized by nesting petrels. The lithosols are characterized by a mixture of boulders and erosional debris in an association with bedrock, and they provide the primary nesting substrate for the Dark-rumped Petrel. These soils are found primarily along the steep, (50 - 70% slope) walls of the crater between an elevation of 2500 and 3000 meters, and it is in these areas that most petrel nesting habitat is concentrated. Dark-rumped Petrels are nevertheless eclectic in their choice of nesting sites, and some burrows have been located in almost every habitat associated with the summit areas of Haleakala.

The vegetation associated with Dark-rumped Petrel nesting areas is characterized primarily as sub-humid, sub-alpine in nature. In these dry habitats vegetative cover is generally less than 10%, and the plant community is dominated by several shrubby species including Pukiawe (<u>Styphelia tameiameiae</u>), Kukaenene (<u>Coprosma montana</u>), Ohelo (Vaccinium reticulatum), and Kupaoa (Dubautia menziesii). Other common species include Tetramalopium (Tetramalopium humile), and the Haleakala Silversword (Argyroxiphium sandwicense). In areas at lower elevations, which receive slightly more precipitation, petrels burrow extensively in soil covered slopes. Where goats are not present these slopes are blanketed with several species of native grasses (Trisetum glomeratum, Deschampsia australis, Agrostris sandwicensis), and Bracken Fern (Pteridium aquilinum). A small sub-colony has also been located along the more densely vegetated south rim of the crater, where birds nest in a shrub community composed primarily of Ohelo, Pukiawe, Kupaoa, and Mamane (Sophora chrysophylla).

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, Figure 4). Most rainfall occurs during the winter months, and the pronounced dry season coincides closely with the petrel nesting period. Relative humidiy at the summit is typically less than half that at sea level, and during the dry summer months daytime levels can drop as low as 5%. Summer temperatures average approx. 10.0°C and range from 0 to 25 °C. Winter temperatures average approximately 8°C lower than those in the summer. The

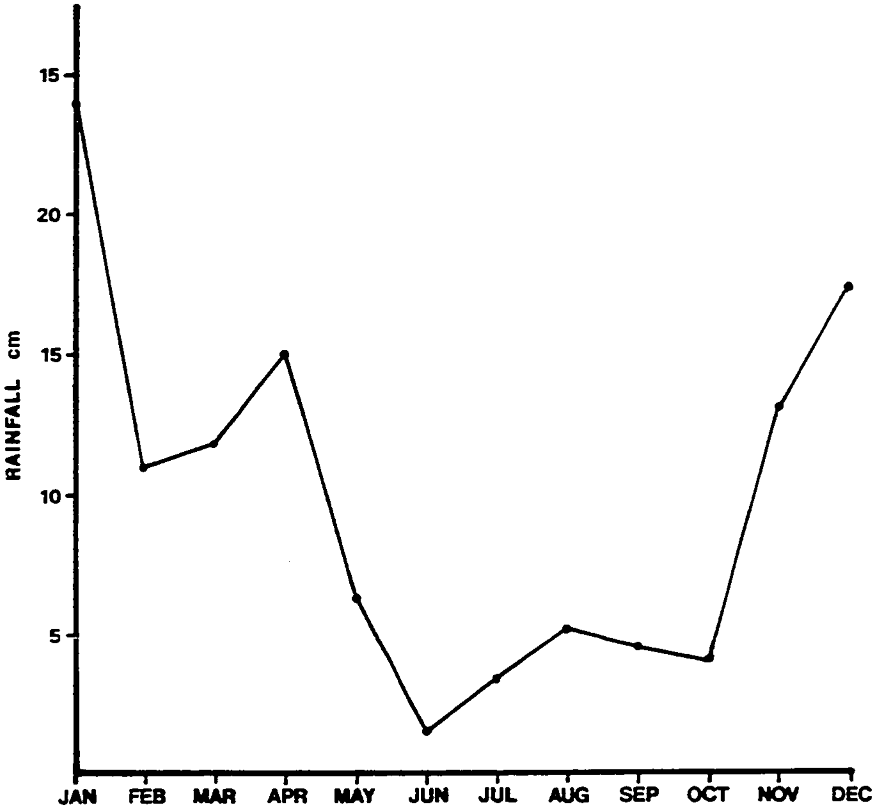

Figure 4. Summit rainfall on Haleakala, 10 year average 1963 - 1973 (From Lyons 1979).

summit is buffeted by tropical storms with winds occasionally exceeding 100 km per hr during the year. Winter snowfall is regularly recorded at elevations above 2500 meters.

Population Estimates

Following the rediscovery of the nesting grounds of the Dark-rumped Petrel (Richardson and Woodside 1954), a record of the distribution and abundance of the remaining populations has been slowly compiled. Beginning in 1966 systematic surveys of the Haleakala population were conducted each summer to determine the number, distribution, and status of petrel burrows located in and around Haleakala National park. The results of these surveys, incorporating data collected during this study, have been summarized in Table 1. These results may vary slightly from those reported by earlier investigators (Kunioki 1968 - 1980, Kjargaard 1978) because some ambiguous and redundant data were eliminated. There are currently 659 mapped petrel burrows distributed around the summit area of East Maui. The percentage of active burrows varied from year to year averaging 78.1% (S.D.11.0 %) and ranging from just over 63% to 95%. The highest densities occur along the inner walls of the crater's west rim (Figure 5). Approximately 77% of all the known burrows are

Table 1. Results of Dark-rumped Petrel colony surveys 1966 - 1981. Data from 1966 - 1978 were collected by National Park Service personnel.

YEAR	# BURROWS KNOWN	# BURROWS CHECKED	# BURROWS ACTIVE	% BURROWS ACTIVE
1966	14	14	14	100.0
1967	14	0	?	?
1968	15	15	13	86.7
1969	36	36	24	66.7
1970	210	210	200	95.2
1971	223	167	136	81.4
1972	344	299	268	89.6
1973	353	240	197	82.1
1974	371	265	171	64.5
1975	388	300	218	72.7
1976	428	336	226	69.3
1977	469	399	298	74.7
1978	535	448	325	72.5
1979	567	452	354	78.3
1980	624	511	384	75.1
1981	659	563	355	63.1
				Mean 78.1 ±11.0

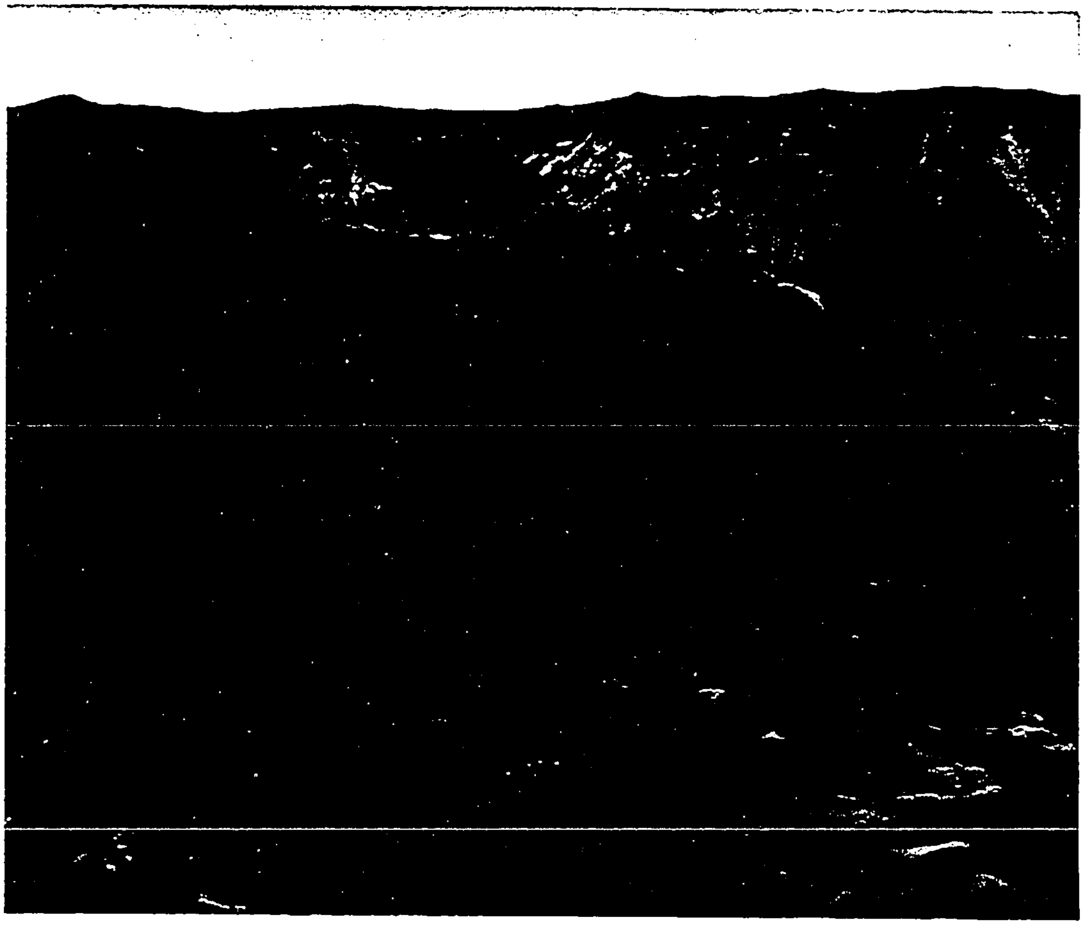

Figure 5. Principle Dark-rumped Petrel nesting habitat along the west rim of Haleakala.

located in this area which makes it the most important nesting habitat remaining for the species. Another 10% of the known nest sites are found along the outer west slope of Haleakala in a wide band extending from Kalahaku to the Science City complex. The remainder of the burrows are scattered throughout the central crater area with approximately 5% along the inner walls of the south rim, 5% in the Hana Mountain area and 3% in cinder cones along the crater floor. Maximum nesting densities of up to 6.7 burrows per hectare occur along the west rim, but in outlying areas the densities are much lower. Although some adjacent burrows are as close as 5 m, it is not uncommon to find individuals nesting hundreds of meters from their closest neighbors. Individual burrows have been located along the outer slope which are over a kilometer from another active burrow.

An estimate of the size of the Maui population was obtained by combining census and activity data with estimates of reproductive success and an age structure derived from a matrix model of the population (Chapter 4). In brief, the method assumes that there are approximately 575 active nests in the area of which 75% or 431 contain breeding adult birds. Since the predicted age distribution indicates that adults make up about 48.8% of the total population, the total breeding and nonbreeding population is estimated to be 431/.478 or 901 pairs of birds. The calculations also point out that over 50% of the total species population could be expected to be juvenile pre-breeding birds, and that approximately 70% of these birds will not be detected on the colony because they probably live exclusively sea.

Characteristics of Dark-rumped Petrel Nest Sites

Dark-rumped Petrel burrows are most commonly located at the base of rock outcrops where the accumulated erosional debris provides a high degree of local relief (Figure 6). Nest sites are highly variable and birds use natural crevices less than one meter in length as well as cracks and lava tubes that penetrate over 10 meters into the cliff face. Petrels also excavate extensive tunnels into softer substrate, usually beneath a large boulder or rock ledge. The characteristics of Dark-rumped Petrel burrows have been summarized in Table 2. Over 95% of the 419 burrows examined were at least partially excavated by the birds and were associated with a rock outcrop or boulder. Most burrows of this type were excavated along the edge of the outcrop or boulder so that the burrow was formed of soil on the sides and bottom and rock on the roof. A small number of birds use natural cavities, and a few burrows are

Figure 6. Typical Dark-rumped Petrel nesting habitat. Burrows are commonly located at the bases of rock outcrops where the accumulated erosional debris provides a high degree of local relief.

Table 2. Characteristics of Dark-rumped Petrel burrows.

	N	%
Burrow Type		
Excavated under rock outcrop	266	63
Excavated under boulder	132	32
Excavated at base of tree or shrub	8	2
Natural cavity	9	2
Excavated in soil	4	1
Burrow Length		
< 1 meter	32	9
> 1 meter	169	47
> 2 meters	121	33
> 3 meters	41	11
Burrow Entrance Diameter		
N = 402		
Mean = 19.14 cm		
S.D = 11.73 cm		
Range = 4 - 200 cm		

excavated at the bases of shrubs or in sod covered soil. Less than 10% of the burrows examined were shorter than one meter and at least 44% were over two meters in length. Burrow entrances ranged from cracks only four centimeters in diameter to caves over two meters across. Burrow entrances averaged 19.14 cm in diameter which makes most burrows accessible to the most serious mammalian predators: mongooses, cats, and rats.

The composition of the nest itself is highly variable. In some burrows a substantial nest is constructed, while in others the egg is laid directly on bare soil or rock and only a token effort is made at nest building. The amount of effort and material that goes into nest building appears to be related to the abundance of suitable nest material in the immediate vicinity of the nest. In burrows situated near clumps of bunch grass, birds often build sizable dished nests of grass up to 10 cm thick and 40 cm in diameter (Figure 7). If twigs are available near the burrow entrance they will often be used in a similar fashion. In burrows with no nest material nearby, birds often forego building any nest or they rather haphazardly assemble a few pieces of debris around the spot where the egg is laid (Figure 8).

I monitored the thermal environment of eight petrel nests

Figure 7. Adult Dark-rumped Petrel on a well insulated nest made of grass.

Figure 8. Dark-rumped Petrel nestling on a poorly insulated nest containing only a few twigs and feathers.

throughout the breeding season using a Wescor model TH-65 digital thermocouple thermometer. Thermistor probes were placed at the nest site so that they measured the air temperature immediately adjacent to the nest. Burrow temperatures varied over an average range of only 2.39 °C during the the course of a day, and although ambient temperatures at the summit ranged from 0°C to 25 °C during the breeding season, the range of temperatures recorded inside petrel burrows was considerably less (Table 3). The average temperature inside a petrel burrow (9.59°C) is very close to the average summer ambient temperature of 9.56°C reported by Lyons (1979) for the summit of Haleakala. Thus, the primary influence of the Dark-rumped Petrel's burrow on the thermal environment of the nest is as a moderator of fluctutaions in ambient temperature. The degree of this moderating influence depends on the depth of the burrow. The temperature in shallow burrows is much more closely tied to fluctuations in ambient temperature than it is in deep burrows (Figure 9).

Lyons (1979) reported that summer humidity atop Haleakala averaged 26%, which is less than 50% of the normal level at sea level. The lowest levels of humidity occur during May and June, which coincides with the incubation period of Dark-rumped Petrel, a fact which may have important

Table 3. Dark-rumped Petrel burrow temperatures °C.[1]

	N	Mean	S.D.	Range
Daytime 0600-1800	65	10.39	2.24	
Night-time 1800-0600	43	8.00	1.72	
Total	108	9.59	2.39	5.5 - 15.4

[1] Based on measurements at 8 burrows.

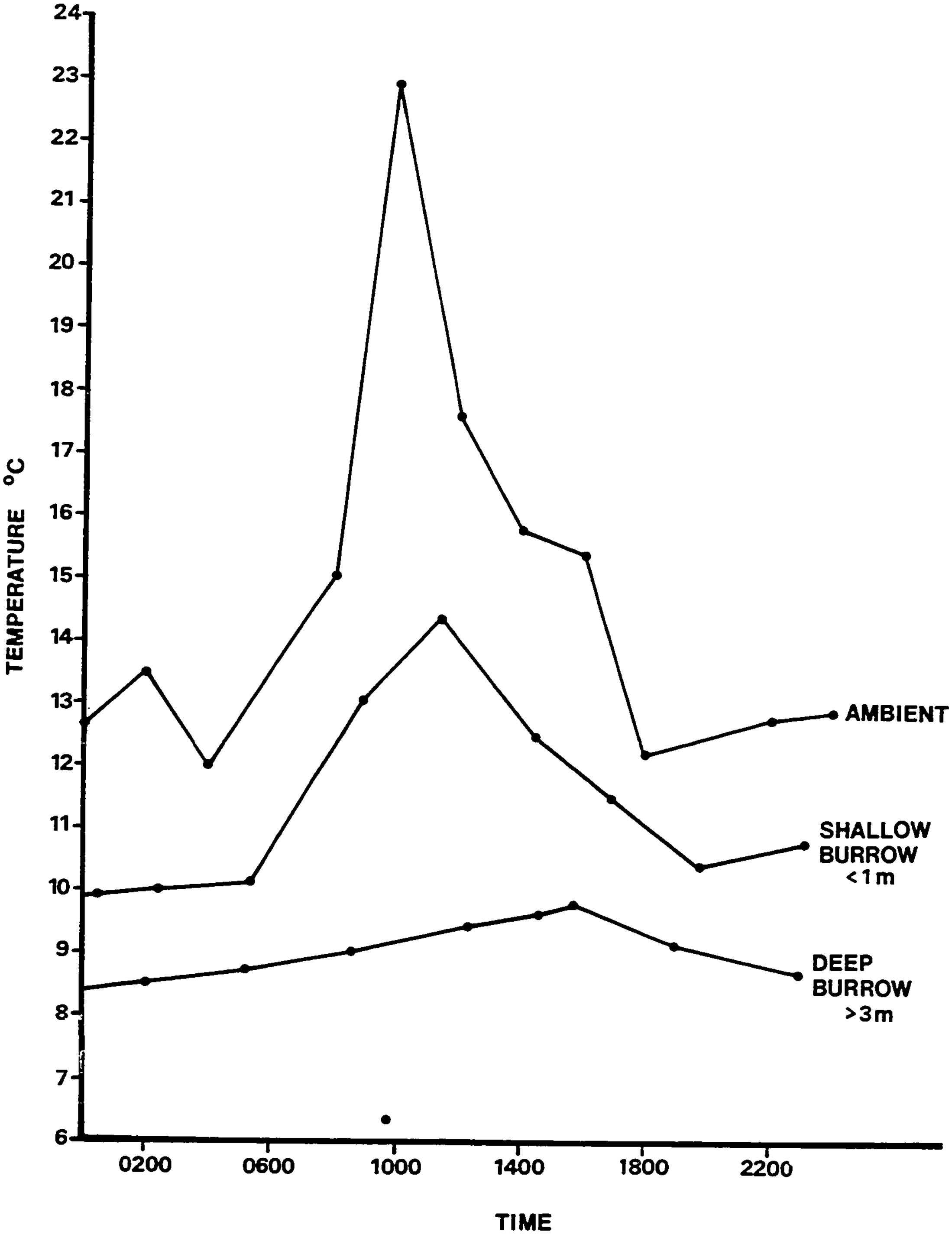

Figure 9. Dark-rumped Petrel burrow temperatures 23 October 1983.

implications for the physiology of the developing embryo (Chapter 3). I recorded relative humidities, with a Psychrodyne wet-dry hygrometer, of less than 7% at some nest sites during incubation, and the average humidity measured at one nest over a 24 hour period during incubation was 20.3% (S.D. 7.4%). Forty four measurements of burrow humidity made throughout the breeding season averaged 32.1% (S.D. 14.2%).

Weights and Measurements of Adult Dark-rumped Petrels

The weights and measurements of adult Dark-rumped Petrels are summarized in Table 4. Birds were weighed with 500 or 1000-g Pesola scales to the nearest 1.0 g. Wing measurements were made by measuring the distance from the proximal end of the wrist to the extreme tip of the wing with a steel ruler. The wing span is the distance between the tips of the fully extended wings. Total wing area, mean wing loading, and aspect ratio were calculated according to the methods described by Warham (1977). All other measurements were made with a dial caliper accurate to 0.1 mm. 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 tarsometatarsus. Culmen length was measured from the edge of the forehead feathers to the tip of the upper mandible and culmen width was

Table 4. Weights and measurements of adult Dark-rumped Petrels.

	N	Mean	S.D.
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 (cm²)	8	798.11	33.52
Mean wing loading (g/cm²)	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
1st primary length (mm)	12	193.3	8.5
Central retrix length (mm)	12	139.3	6.1
Core temperature (°C)	9	38.6	1.1

measured its widest point below the nostrils. Core temperature was recorded with a Wescor TH-65 digital thermometer by inserting a thermistor probe into the lower esophagus.

Hawaiian Dark-rumped Petrels weighed an average of 433.8 g, which is somewhat heavier than the birds studied in the Galapagos by Coulter et al. (1982)(mean = 421.2 g, $t = 2.04$, $p < .05$), and Harris (1970)(mean = 408.0 g, $t = 3.25$, $p < .01$). In contrast, the wing and tarsus lengths of Hawaiian birds (303.6 mm and 45.1mm) are less than those reported for Galapagos birds (314.5 mm and 46.7 mm) ($t = 7.68$ and 6.40, $p < .001$) (Coulter 1982). The average bill length of Hawaiian birds, 33.4 mm, was less than the length of 35.8 mm reported by Coulter (1982)($t = 7.50$, $p < .001$), while bill width was slightly larger, 10.2 mm versus 8.8 mm, ($t = 2.69$, $p < .02$). Total wing area and wing loading are slightly higher in the Hawaiian Dark-rumped Petrel than the values reported for a single Galapagos specimen by Warham (1977). This is consistant 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. It also suggests that the two subspecies may differ somewhat in their flight and foraging behavior.

Arrival of Birds at the Colony and the Pre-laying Period

I collected data on the behavior and attendance patterns of breeding Dark-rumped Petrels using a variety of methods. Approximately 40 accessible nests were observed directly each season, while a larger sample of about 125 nests were monitored indirectly through the use of event recorders and toothpick barriers. In addition, one breeding pair was observed continuously throughout the breeding season in 1981 using a closed-circuit television system which employed a night vision scope.

I used an event recorder to record activity at ten nests each breeding season. The device consisted of a switch mechanism (Figure 10) which was placed over the burrow entrance, and a twenty channel Esterline Angus recorder. This system was incorporated into a display about the petrels in the visitor center at the summit of Haleakala (Figure 11). The recorder kept a continuous record of the arrival and departure of birds at the monitored burrows throughout the breeding season. In addition, several other burrows in remote locations were monitored using the portable event recorder that I have described eleswhere (Simons 1981a, 1981b). Seven color-marked pairs in event recorder monitored burrows were observed to determine the

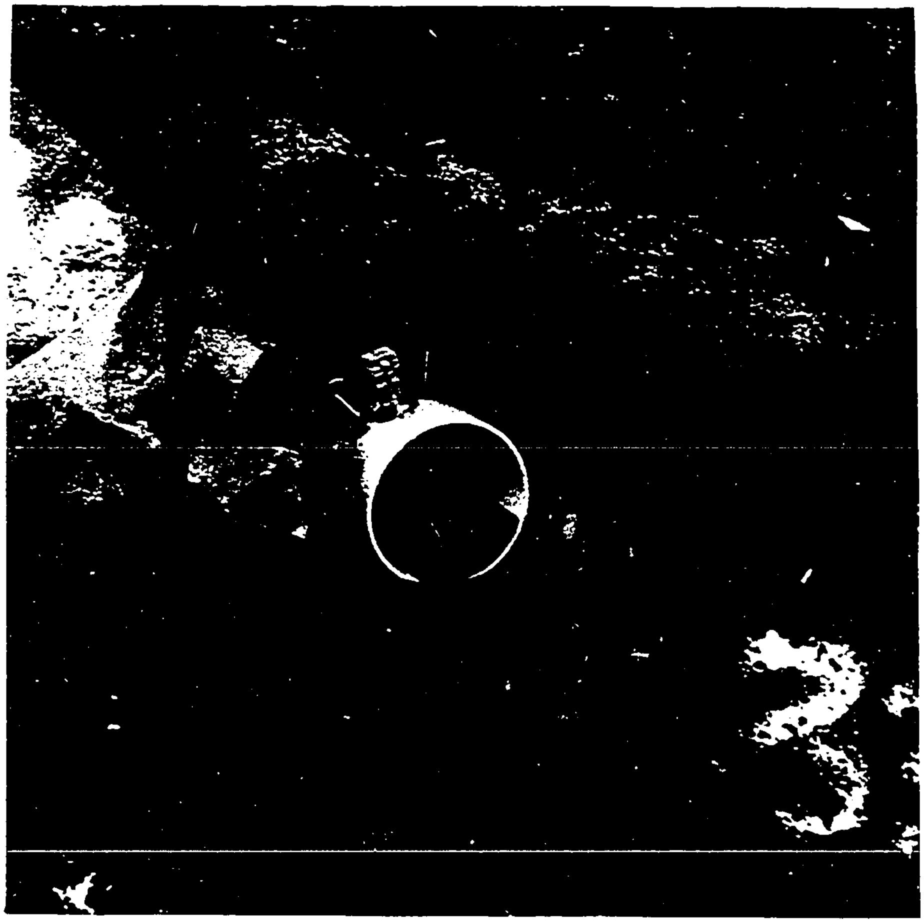

Figure 10. Event recorder switch mechanism.

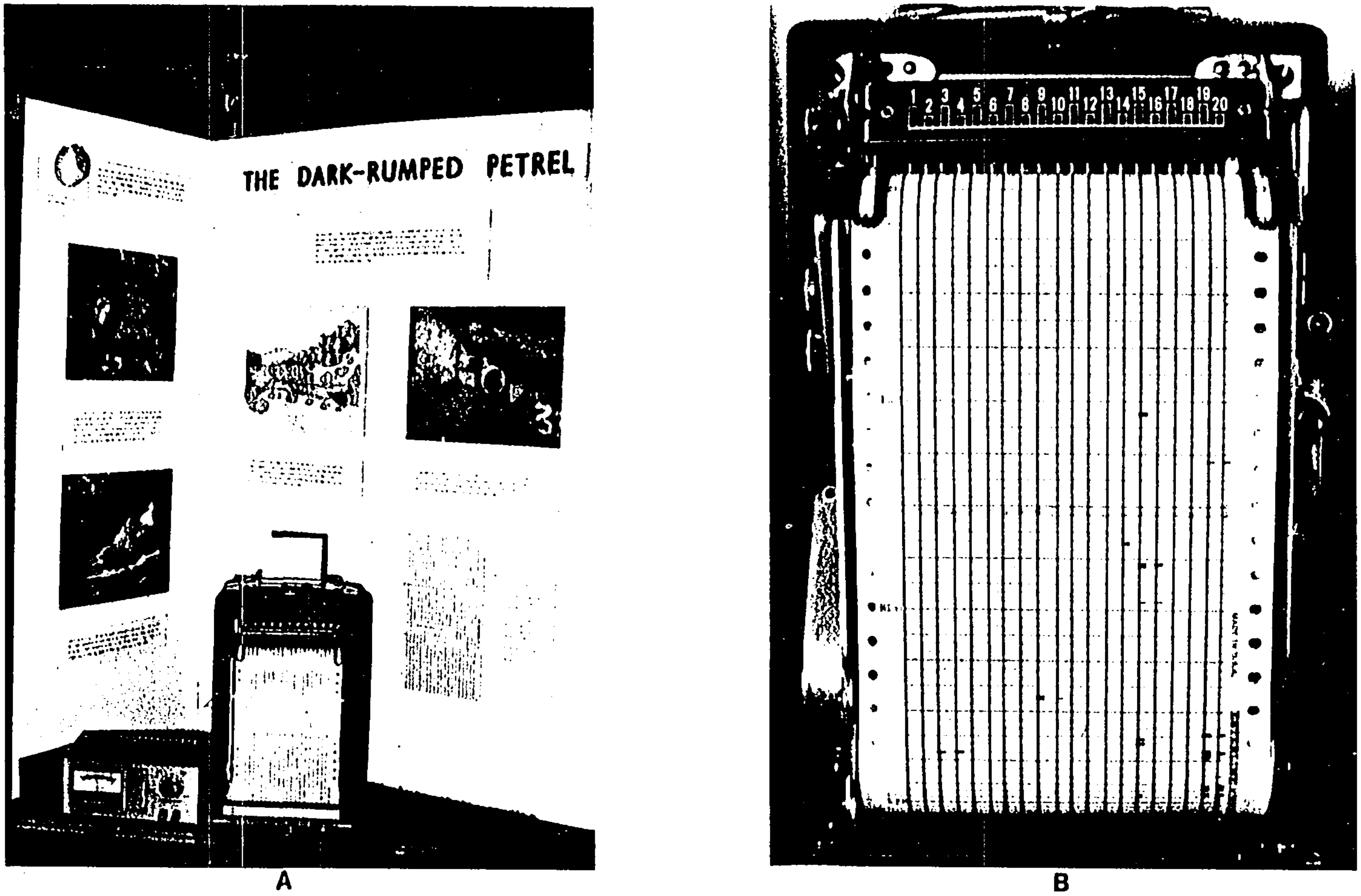

Figure 11. Event recorder used to monitor Dark-rumped Petrel. Photo A illustrates the location of the recorder and the interpretive display. Photo B illustrates signs of activity at several petrel nests.

attendance patterns of male and female birds.

A sample of 105 nest sites were also studied each season by placing toothpick barriers at their entrances. These burrows were checked every seven to ten days to determine which burrows had been visited during the interval. The checks provided information on the general attendance patterns of the birds, and as I will explain below, they also allowed me to estimate the relative proportion of successful breeders in the colony each season.

One nest was also observed directly throughout the 1981 breeding season. The nest was located in a lava tube approx. 150 m below the Haleakala visitor center. It was monitored with a Javelin brand night vision scope attached to a portable closed circuit television camera (Figure 12). The camera was connected to a monitor and video tape deck located in the visitor center. A dim infrared light source illuminated the interior of the burrow. Over 280 hours of observations and six hours of video tape were recorded during the breeding season. The entire breeding cycle was observed, including the arrival of the female, egg-laying, hatching, and the development and fledging of the chick.

The breeding chronology and general colony attendance patterns of Dark-rumped Perels are summarized in Figures 13

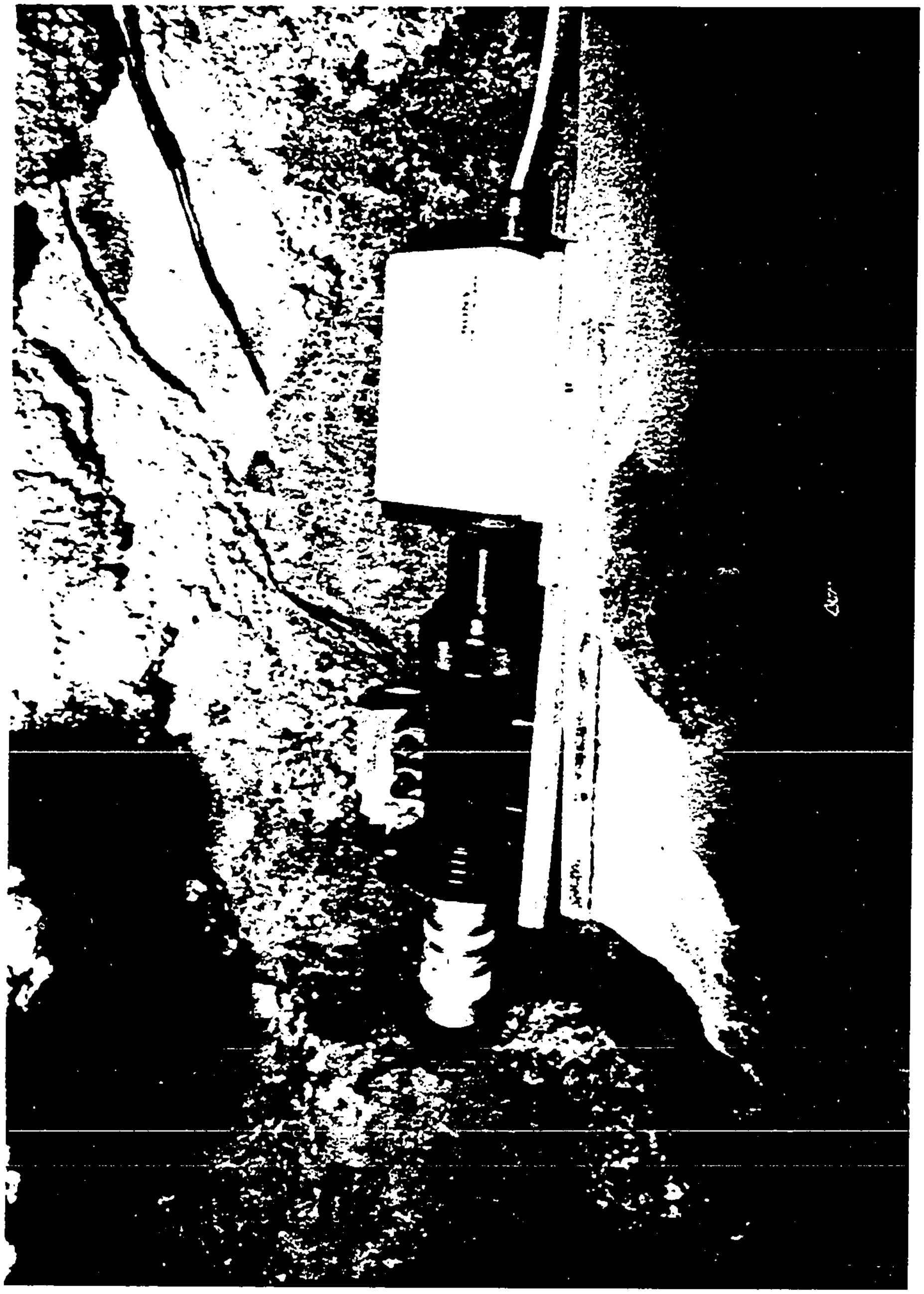

Figure 12. Night vision scope and closed circuit television camera mounted in a petrel burrow.

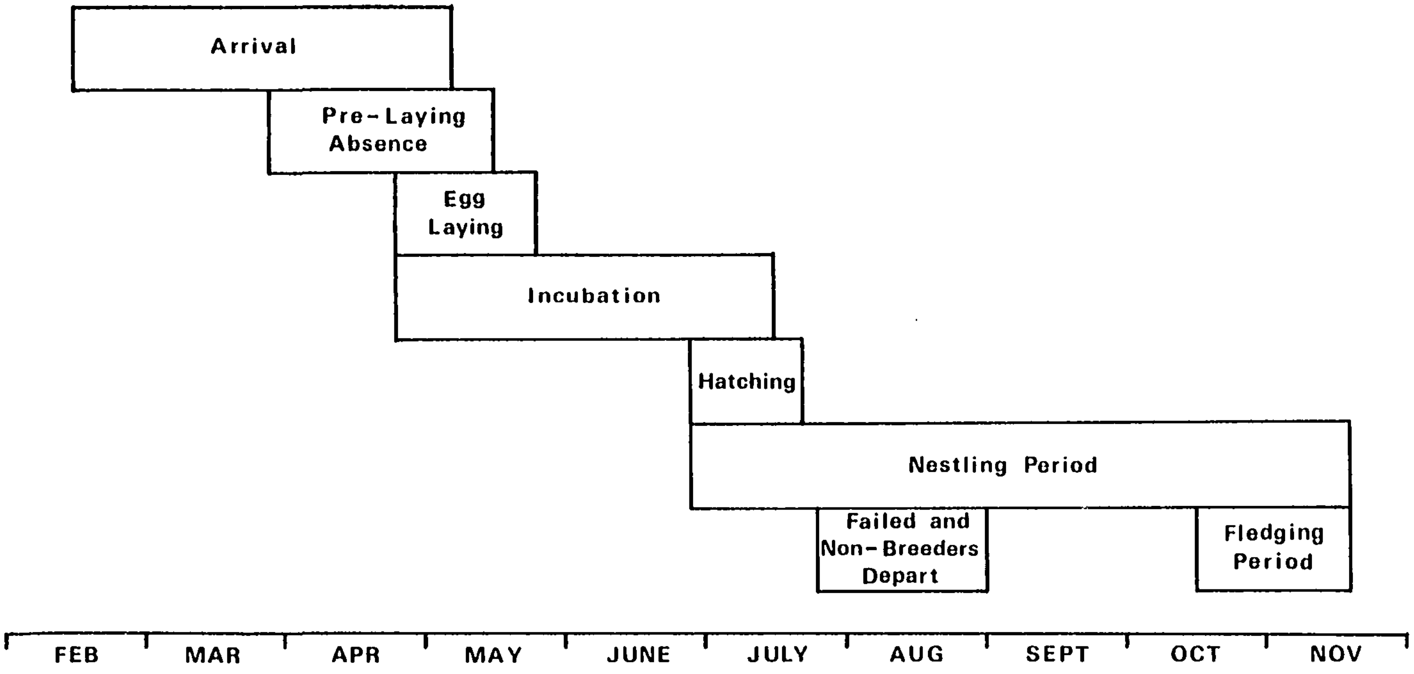

Figure 13. Dark-rumped Petrel breeding chronology.

and 14 . The pre-laying period is characterized by a rapid return to the colony by most of the adult population in late February. The event recorder was kept in operation over the winter in 1981 and 1982 and in those years the first birds arrived on 23 February and 24 February. Most birds visit their burrows regulary during the first one to two weeks following their return to the colony. During this period debris is removed from the burrow and the nest chamber is occasionally enlarged and new nest material brought in. Both individual birds and pairs can be found in their burrows during the period, and although it was never observed, copulation may occur at that time.

A distinct pre-laying absence begins in late March. The pattern is characteristic of other Procellariiformes and it is thought to enable female birds to acquire the necessary energetic reserves to produce the egg, and for male birds to store energy for incubation (Harris 1966a, Perrins and Brooke 1976). Most of the birds that continue to visit the colony during April were subsequently found to be pre-breeders (Figure 15). Ocassionally individuals in breeding burrows, perhaps males, return during the pre-laying absence, but they spend little time in the burrow. In many cases breeding males do not return until just prior to egg laying, or in some cases, just after the female has laid the egg.

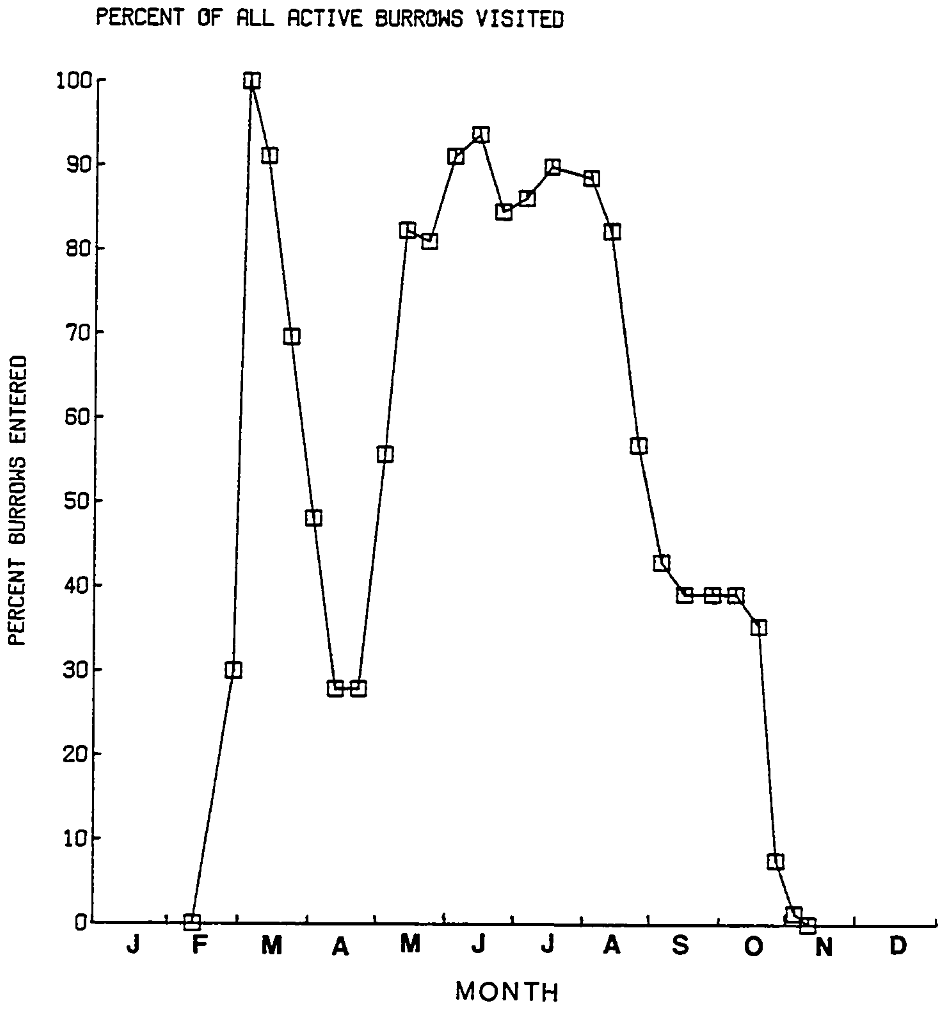

Figure 14. Colony attendance patterns of Dark-rumped Petrels.

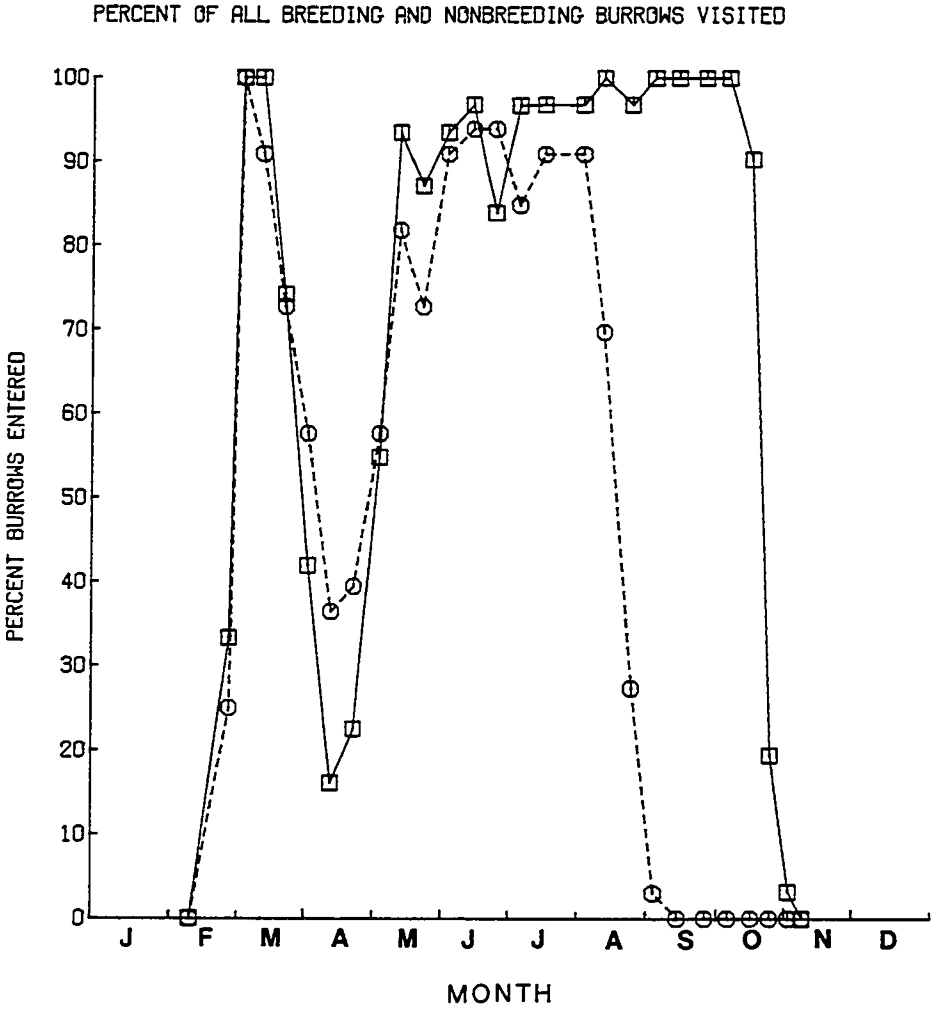

Figure 15. Attendance patterns of breeding and non-breeding Dark-rumped Petrels. The dashed line represents attendance by nonbreeding birds and the solid line attendance by breeding birds.

The pre-laying absence poses some interesting questions regarding the development of the Dark-rumped Petrel's egg. In most birds studied thusfar, the development of the egg takes from one to several days (Welty 1975). If Dark-rumped Petrels copulate in their burrows, as many other procellariiformes do (Harris 1966a, Warham 1964), then they must posess a mechanism by which the development of the egg can be delayed. In the domestic fowl sperm can remain viable in the oviduct for 10 - 12 days following copulation (Lofts and Murton 1973). Perhaps Dark-rumped Petrel sperm are capable of surviving for extended periods in the oviduct as well.

Mate and Nest-site Fidelity

A long-term banding project was initiated in 1980 to eventually provide estimates of juvenile and adult survival. As many nestlings as possible were banded each year before fledging, and adult birds were trapped and banded as they returned to feed their chicks (Chapter 5). A total of 92 birds were banded including 57 adults. Eighteen pairs of breeding adults were banded, and of these 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 of breeding birds changing mates or nest sites during the two years of the banding study. These results suggest that Dark-rumped Petrels, like most other large procellariiformes, exhibit a high degree of nest site and mate fidelity. The degree of this fidelity will only be determined by further banding efforts.

Vocal Behavior

Dark-rumped Petrels emit a variety of vocalizations, although two call types predominate. The first is a penetrating and very resonant call from which the birds presumably received their Hawaiian name 'Ua' u (Figure 16a). The call could be described as follows: a'-uuuuu-a'-uu-a'-uu-a'. The second common call is very similar but its tone is raspy and nasal rather than resonant (Figure 16b). In addition to these two primary calls the birds emit a variety of sharp squeeks and nasal clucks. A common form of this type of call could be immitated as ee'e-a, ee'e-a, ee'e-a in which the first sylable is accented (Figure 16c)

Birds will occasionally call from their burrows if disturbed, but normally birds only vocalize while flying. On several occasions I heard birds call at lower elevations

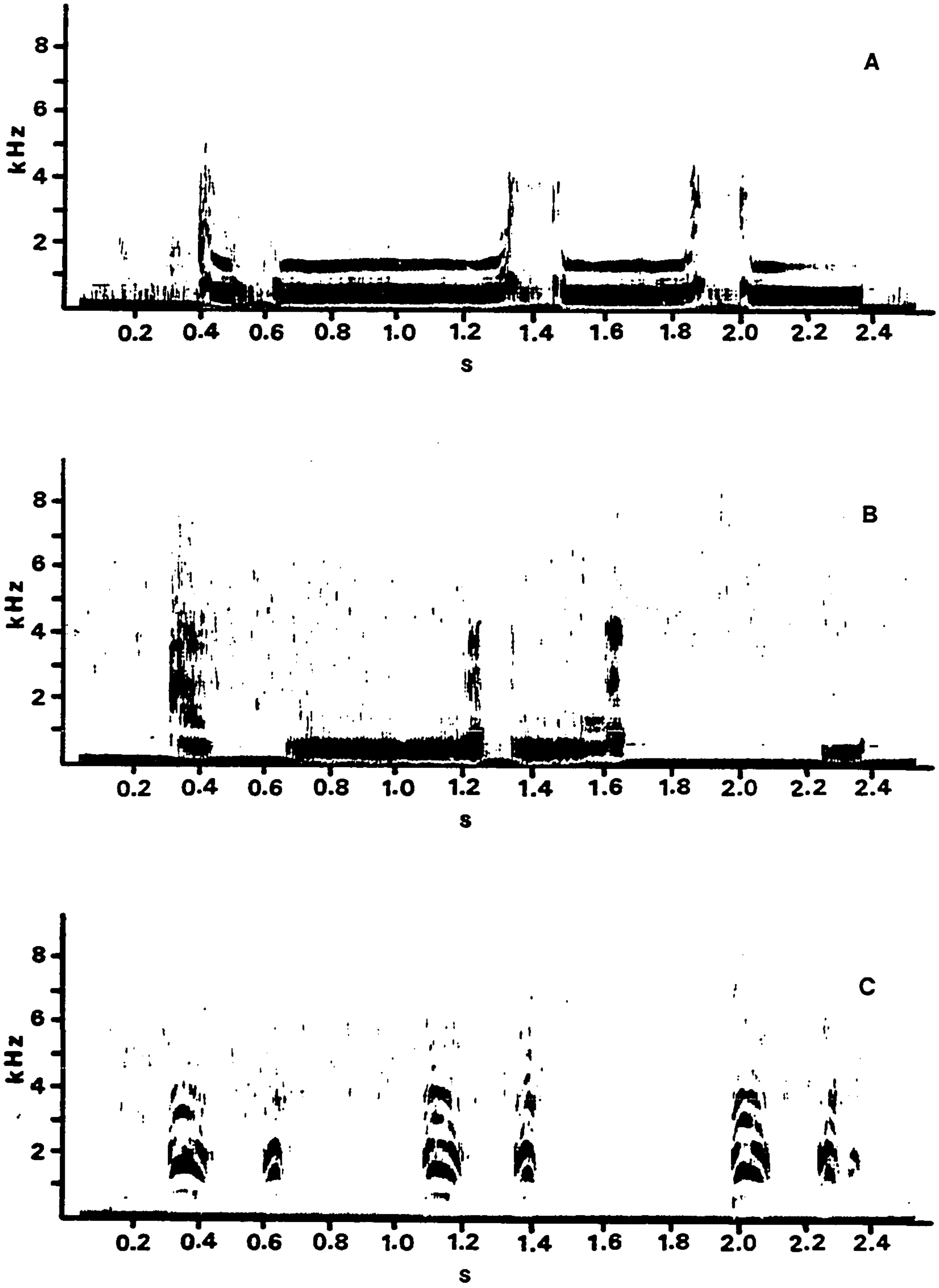

Figure 16. Sonagrams of Dark-rumped Petrel calls. (A) Resonant call. (B) Raspy call. (C) "eee - a" call.

as they flew to the nesting area but most calling occurs over the central portion of the colony. Birds often congregate where updrafts allow them to continuously circle over a section of the colony with little effort. Unlike the Galapagos where the peak of calling occurs before dawn (Harris 1970), Hawaiian birds begin calling about one hour after sunset, and the peak of calling occurs two to three hours later. Although birds can occasionally be heard calling throughout the night most birds stop calling by about 0100. Typically, calling birds fly in pairs or small groups and call back and forth. A common pattern is for one bird to give the resonant call and be answered by another giving the raspy call and it appears likely that the primary function of this behavior relates to pair formation or maintenance. I observed breeding birds returning to their burrows on many occasions, to relieve their mates on the nest, or feed their chicks. These birds always flew quickly and silently to their burrows and did not appear to associate with calling birds.

The frequency of calling throughout the season also suggests a close association between calling and pair formation. The pattern of calling generally follows the pattern of attendance by non-breeding birds (Figure 15). Birds begin calling in March but calling drops off in conjunction with the pre-laying absence in April. It increases again in May and continues steadily for the next three months. Calling starts to decline by August and very few calls are heard following the departure of the pre-breeders late in the month. By September calling has usually stopped entirely.

EGG-LAYING AND INCUBATION

Breeding Frequency

Breeding frequency, the percentage of years in which adult females laid eggs, was estimated from a sample of 15 undisturbed accessible nests for which I had three or more years of observations. To insure that only adult birds were sampled, I only included nests in which at least one chick had been successfully raised. I assumed that the same birds were using these burrows each season. Based on these assumptions I found that these birds attempted to breed in all but six of a possible 56 breeding periods. Thus, I estimate that the average breeding frequency of adult Dark-rumped Petrels is about 89%. This estimate is on the high end of the range reported for similar species (Perrins et. at 1973, Fisher 1975a, 1975b, 1976), but given the evidence that competition for the resources used by breeding seabirds in Hawaii may have been reduced substantially over the past two centuries (Chapter 1), we might expect higher than average rates of breeding.

Egg-laying

I found no evidence that breeding females returned to their burrows during the pre-laying absence. Each of three marked birds observed in their burrows before egglaying were males. The pattern of visitation by males is variable. Some return several times during the pre-laying period while others do not return until the time of egg-laying. The female does not return until she is ready to lay, and in all of the cases I observed the egg was laid within 24 hrs of the female's return. If the male was present in the burrow when the female returned, he took the first incubation shift and the female departed. If the male was not present, the female took the first incubation shift which usually lasted from one to four days.

The attendance patterns of the pair in the television-monitored burrow were typical of most birds. Both birds were observed together in the burrow for several days in mid-March. From mid-March to mid-April the burrow was visited briefly at night on four occasions but for the next three weeks the nest was not visited. On the evening of 6 May the female returned to the burrow. She arrived shortly after 2100 hrs and after preening briefly she began preparing the nest site. She worked on the nest constantly for an hour and forty minutes by carefully arranging pieces of nest material, and dishing out the center of the nest. The dishing was accomplished by rocking forward and kicking vigorously to the rear with both feet in alternation. At 2239 the female settled down on the nest and began slowly raising and lowering her tail. This behavior continued for ten minutes during which the tail feathers appeared to be spreading further and further apart. I assume that the egg was laid at that time although, since the female was facing the camera, I did not actually see the egg emerge. At 2249 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 in the Dark-rumped Petrel is quite synchronous (Figure 13). Egg-laying began during the last week of April during the three years of the study and continued until mid May. The mean laying date in nine nests observed in 1980 was 8 May (S.D. 4.3 days) and the mean laying date for 11 nests monitored in 1981 was also 8 May (S.D. 5.9 days).

The average weights and measurements of Dark-rumped Petrel eggs are summarized in Table 5. Eggs were measured with a dial caliper accurate to 0.10 mm and fresh egg weights were determined in the field using a triple beam balance accurate to 0.01 g. Dark-rumped Petrel eggs are significantly larger and heavier than the eggs of birds nesting in the Galapagos measured by Coulter et.al (1982)(t-test, $p < 0.001$). The larger eggs may be due to the fact that Hawaiian Dark-rumped Petrels are on average heavier than Galapagos birds, but they may also represent an adaptation to high altitude nesting (Chapter 3). The average fresh egg weight of 76.87 g amounts to about 18% of mean adult weight which is characteristic of most Procellariiformes (Rahn et. al 1975, Whittow 1980).

I estimated incubation temperature at one nest by fitting a chicken egg with a thermistor probe and substituting it for a petrel egg. The adult petrel incubated the chicken egg readily and after 85 min the temperature of the egg was steady at 34.9 °C. This temperature is lower than the average incubation temperature of 35.6°C for 27 species reported by Ar and Rahn (1980), which is also typical of Procellariiformes (Whittow 1980, 1983)(Chapter 3).

Table 5. Measurements of Dark-rumped Petrel eggs.

	N	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

Attendance Patterns of Adult Birds During Incubation

Typical attendance patterns of breeding and non-breeding birds are represented in Figure 17. Note the abbreviated pre-laying absence in the non-breeding bird and its regular pattern of attendance throughout the incubation period in May and June. Breeding birds, on the other hand, are usually away from the colony for much of April and they return 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.

The attendance patterns of six pairs of color-marked birds during incubation are summarized in Table 6. Three pairs divided the incubation period into four shifts and three pairs divided it into five shifts. Males took only two shifts in all cases, but the average number of days incubating by males (31.33 S.D. 2.61) was significantly longer than the average for females (24.33 S.D. 1.75)($t = 6.14$, p 0.001). This pattern is similar to that found in other procellariiformes (Richdale 1952, Rice and Kenyon 1962, Pinder 1966, Brown 1966, Fisher 1971 and Croxall and Ricketts 1983). We might expect the male to take a greater role in incubation given the large energetic investment by the female in producing the egg.

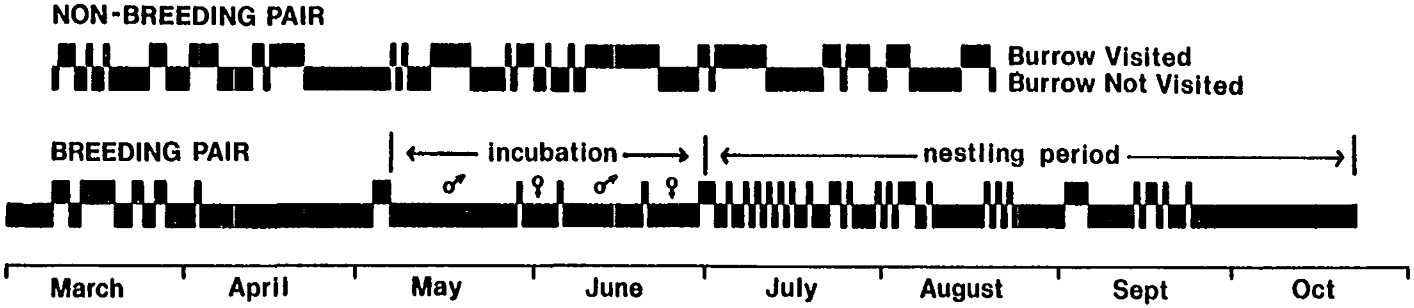

Figure 17. Burrow attendance patterns of individual breeding and non-breeding Dark-rumped Petrels. Upper marks for each pair indicate days when the burrow was entered. Data for breeding pair indicate pre-laying absence, incubation shifts, and feeding frequencies.

Table 6. 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

The average shift length of 27 incubation shifts recorded for both sexes was 12.37 days (S.D. = 6.7). If we eliminate the first and last shifts which were shortened by the events surrounding egg-laying and hatching, we find the overall average shift length to be 16.47 days (S.D.= 3.95 days, N = 17). The average shift length for males, 16.18 days (S.D. = 4.19, N = 11), was not significantly differant from that for females, 17.0 days (S.D. = 3.79, N = 6), during that interval. Of course, males took two shifts during that interval while the females took only one.

The average incubation shifts of the Dark-rumped Petrel are long, and the 23 day shift accomplished by one male is one of the longest reported for any seabird (Berger 1980). Lack (1968), Berger (1980), and Simons (1981) have discussed the relationship between food constraints and the length of the incubation shift in breeding seabirds. The average incubation shift length in Dark-rumped Petrels exceeds that reported for most other seabirds, including albatrosses and penguins (Burger 1980), which suggests that the petrel's food resources are scarce or widely distributed. Assuming that an adult Dark-rumped Petrel is capable of an average flight speed of 45 km/hr (Pennycuick 1969) it is conceivable that an adult bird could potentially range thousands of kilometers from the colony between incubation bouts.

I measured the weight loss of one adult petrel before and after a twelve 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. Based on this weight loss, the bird, which continued to incubate for 11 more days, would have lost a total of 163 g or 35.5% of its initial weight. Prince et al. (1981) reported that daily losses in Grey-headed (*Diomedia chrysostoma*) and Black-browed (*Diomedia melanophris*) Albatrosses ranged from 0.5% to 3.5% and averaged 1.2%, while Croxall and Ricketts (1983) estimated average daily losses in the Wandering Albatross (*Diomedia exulans*) to be 0.9%.

Behavior of Incubating Dark-rumped Petrels

I observed one pair of Dark-rumped Petrels in a television-monitored burrow for a total of 183 hours and 15 minutes during incubation. Observations were recorded both during the day and at night, and included several continuous 24 hr observation periods. The behavior of the adult during the four days prior to hatching was analyzed separately since it was clear that the activity of the adults changed significantly during that period. The activity of the incubating bird was tabulated on a continual basis using a stop watch.

Table 7 summarizes the behavior of adult birds during the incubation period. While incubating, adult Dark-rumped Petrels spend almost 95% of their time sleeping with their bills buried in their scapular feathers. They spend a little over 3% of their time resting quietly on the nest and another 2% arranging nest material or preening. They seldom leave the nest, and it appears that the eggs may be uncovered for only a few minutes during a typical incubation bout. It is likely that this pattern of behavior is related to the energetic demands on the incubating adult and to the physiological constraints on the developing embryo (Chapter 3). Adult petrels, like nestlings (Chapter 3), undoubtedly reduce their metabolic demands substantially by sleeping, and it has been demonstrated in other birds that tucking the bill into the scapulars can reduce heat loss by as much as 12% (Deighton and Hutchinson 1940). Clearly, the long incubation shifts that are characteristic of this species must require adaptations of this type to conserve energy. Adults also maintained close contact with the egg throughout incubation. This behavior is probably of considerable benefit to the developing embryo in maintianing a constant incubation temperature and minimizing water loss to the arid nesting environment (Chapter 3).

Table 7. Behavior of incubating Dark-rumped Petrels. Data are presented as % total time based on 107 hr 12 min of observations during incubation and 76 hr 3 min of observations prior to hatching.

Period	Behavior				
	Alert			Sleeping	Locomotion
	Resting Quietly	Arranging Nest Material	Self Maintenance		
Incubation	3.4%	0.3%	1.7%	94.5%	0.1%
Hatching	64.6%	0.02%	1.2%	34.1%	0.0%

I was able to count the respiratory frequency of incubating adults during incubation, and the results further illustrate the energetic benefits of the birds sedentary behavior. The respiratory rate of an alert adult bird was estimated on 29 occasions by averaging, from five or more counts, the amount of time required for the bird to take 10 breaths. I repeated the method on 66 occasions when the birds were sleeping. The average respiratory rate of an alert resting bird was 23.7 breaths/min (S.D.= 1.14), which is close to the predicted value of 24.5 breaths/min, for a bird of this size based on the equations of Calder (1968). The average respiratory rate of sleeping birds, 12.3 breaths/min (S.D. = 1.20), was significantly less ($t = 22.9$, $p < 0.0001$), which reinforces the view that the adult's behavior on the nest has substantial benefits related to energy conservation.

The birds in the television-monitored burrow oriented themselves predominantly toward the rear of the burrow during incubation (Figure 18). This pattern may have been a peculiarity of this pair, but it was often observed in other incubating adults, and may therefore have more general significance. Adult Dark-rumped Petrels are certainly less visible when they turn their dark backs toward the burrow entrance, and the behavior may make them

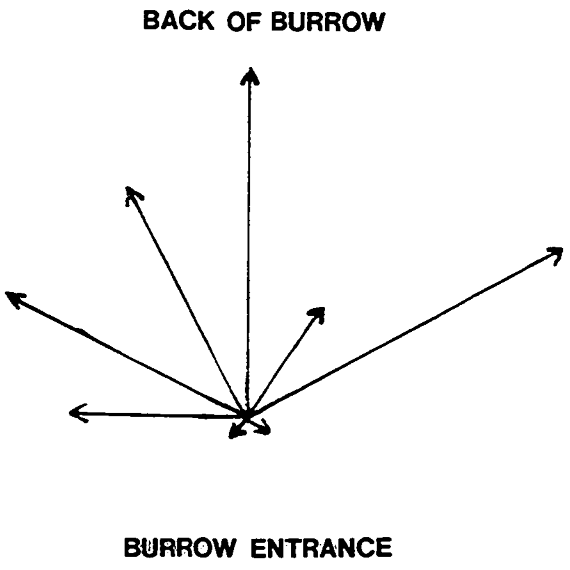

Figure 18. Orientation of incubating Dark-rumped Petrels. Vector length is proportional to the frequency of observations. Based on 10,774 min of observations.

less visible to nest predators. It may also have benefits related to thermoregulation, as has been suggested in the Fork-tailed Storm Petrel (Oceanodroma furcata)(Wheelwright and Boersma 1979).

I observed the exchange of incubation duties by adult birds on two occasions. In the first exchange, the female was incubating and the male arrived at about 2200 to relieve her. He walked directly to the nest and settled down beside his mate. The female then began to preen the male about the forehead and facial area, and after about a minute she rose off the egg and the male began incubating. The two birds remained together on the nest for several more minutes during which time they engaged in continuous bouts of mutual preening. Four minutes after the arrival of the male the female rose from the nest and walked out of the burrow. In the second exchange the female arrived at 2212 to relieve the male, and the behavior of the pair was similar. The female walked directly to the nest, settled down next to the male and the two birds engaged in mutual preening until 2237. At that point the male rose off the egg and the female began incubating immediately. The male remained in the burrow for another 15 minutes which he spent preening himself or resting quietly next to his mate. At 2053 he stood up and walked out of the burrow.

These observations illustrate two important aspects of the behavior of these birds during incubation. First, adult birds maintain close contact with the egg throughout the incubation period, even during the exchange of incubation duties. Direct observations and information from the event recorder indicate that although adult birds do occasionally leave their nests for brief trips to the burrow entrance, these occasions are rare and it is likely that the egg is exposed for at most a few minutes during an average incubation shift. Secondly, breeding Dark-rumped Petrels rely on a strong pair bond and well synchronized, mutually dependant behaviors in their breeding efforts. The long pre-laying absence and long incubation shifts typical of these birds require that the attendance patterns of adult birds be closely synchronized. A delayed or ill-timed return to the burrow could result in an interruption in incubation and a failed breeding effort for the entire season. Coxall and Ricketts (1983) determined that poorly synchronized pairs of Wandering Albatrosses (_Diomedes exulans_) suffered reduced reproductive success. Of 14 pairs that deserted fertile eggs in their study, nine deserted during incubation shifts that exceeded the 95% confidence limit for the duration of that shift, and the remaining five deserted during shifts that were significantly longer than average. In the Dark-rumped Petrel, close synchronization of the pair occurs in spite of the fact that adult birds spend little time together once the breeding effort has begun. Even though the entire breeding effort takes almost seven months, it is likely that adult birds spend less than two or three hours together in the burrow following the prelaying departure in early April.

Behavior During the Hatching Period

The television-monitored nest was observed almost continuously for the four days prior to hatching beginning on 30 June. The behavior of the adult was distinctly different during this interval. Rather than sleeping most of the time, as it had earlier, the bird spent most of this period in an alert posture on the nest (Table 7). About two days prior to 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 has been reported in the Fork-tailed Storm Petrel (Simons 1981), but it clearly assisted the chick indirectly by adjusting the position of the egg and not restricting the movement of the emerging chick.

By 0710 on 3 July it was evident that the chick had hatched. Even though it was not visible beneath the brooding adult, its activity jostled the adult frequently from side to side. By 1200 the chick's down was dry and it had emerged from underneath the adult and it could be seen resting on the nest partially covered by the adult's wing. The two birds remained in close association throughout the brooding period, although the adult never actually covered the chick once its down was dry. The adult initiated feeding on several occasions by nibbling gently at the chick's bill and regurgitating small amounts of food. It appeared that the chick was fed continuously throughout the brooding period.

Hatching Dates and Hatching Success

Hatching, like egg-laying, is quite synchronous. The median hatching date in 1979 was 2 July (S.D. = 5.3 days, N = 10), and in 1980 and 1981 it was 1 July (S.D. = 3.8 and 4.9 days, N = 7 and 11). Overall, hatching extends for about two and one half weeks. During the three years of the study the earliest egg hatched on 24 June and the latest hatched on 11 July.

The incubation periods of 11 eggs averaged 55.27 days (S.D. = 1.10). 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 (Chapter 3). Incubation periods ranged from 54 to 58 days. The egg which took 58 days to hatch was neglected for 3 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 procellariiformes (Boersma and Wheelwright 1979, Boersma 1982), but it does not appear to be common in the Dark-rumped Petrel. The low variance of the incubation periods is further evidence egg neglect is uncommon in this species.

Hatching success (Table 8), varied as a result of both natural and unnatural influences (Table 9). Normal hatching success averaged about 70% and it appears that there are a number of causes of hatching failure. Some eggs appeared to be infertile, while in others the embryo died prior to hatching. Predation by feral cats and mongooses in 1979 and 1981 reduced hatching success in those years even further.

Several eggs were discovered during the study which appeared to have been crushed by the incubating adult (Figure 19). The shell of a Dark-rumped Petrel egg is thin (Table 5). This thinning may be entirely related to high

Table 8. Dark-rumped Petrel reproductive success 1979 - 1981. 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.

YEAR	N	% ACTIVE BURROWS WITH EGGS	HATCHING SUCCESS	FLEDGING SUCCESS	REPROD. SUCCESS
1979	41	75.6	67.8	57.1	38.7
1980	40	70.0	71.4	100.0	71.4
1981	47	66.0	70.9	86.4	61.3

Table 9. Causes of breeding failures in the Dark-rumped Petrel 1979 -1981.

	1979	1980	1981
PREBREEDING ADULTS KILLED	2	0	0
EGGS LAID	31	28	31
EGGS FAILED TO HATCH	5	8	6
EGGS EATEN OR ADULTS KILLED	5	0	3
CHICKS DIED	2	0	3
CHICKS KILLED	7	0	0
CHICKS FLEDGED	12	20	19
% PREDATION ON ACTIVE BURROWS	34.0	0.0	6.4

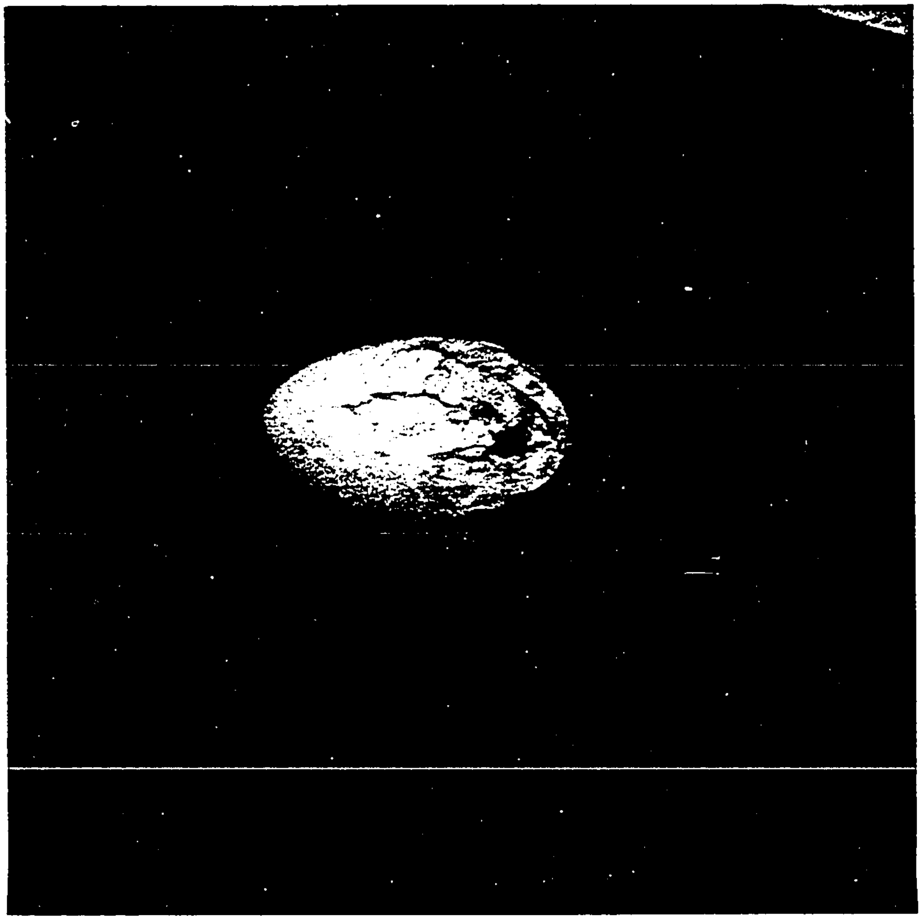

Figure 19. Dark-rumped Petrel egg crushed by an incubating adult.

altitude nesting (Chapter 3), 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). Wurster and Wingate (1968) concluded that DDE contamination was "a probable major cause of decline" in the endangered Bermuda Petrel (Pterodroma cahow) and Gress et al. (1971) have described a case of organochlorine contamination, eggshell-thinning, and reduced reproductive success in a California Common Murre (Uria aalge) population. Seven Dark-rumped Petrel specimens, six eggs and one nestling, have been analyzed for organochlorine contamination thus far. King and Lincer (1973) reported on the analysis of the chick and four eggs. They found an average level of DDE contamination of 0.43 ppm wet weight, which is considerably less than the level of 3.99 ppm reported by Wurster and Wingate (1968) for the Bermuda Petrel or 21.70 ppm reported by Gress et al. (1971) for the Common Murre. Kepler (unpbl. data) submitted two additional eggs for analysis in 1978 and these too yielded low levels of contaminants. DDE levels averaged 0.32 ppm and PCB levels averaged 0.18 ppm wet weight. No other detectable levels of organochlorine comounds were detected in the 1978 eggs. Thus, it does not appear that Dark-rumped Petrels have been contaminated with levels of organochlorine compounds that would be associated with lowered reproductive success. On the other hand, since the shells of these eggs may be thin to begin with, due to high altitude nesting, the level of contamination required to induce a reduction in reproductive success may be considerably lower than it is in other birds. Therefore, it would be wise to continue to monitor the level of organorchlorine residues in this population in the future. Unfortunately, no pre-DDT era eggs of these birds are available, so it is not possible to determine if the Dark-rumped Petrels egg shells have always been as thin as they are today.

THE NESTLING PERIOD

Attendance Patterns During the Nestling Period

The colony attendance patterns of adult Dark-rumped Petrels during the nestling period are summarized in Figures 15 and 17. One pattern that is immediately obvious is the early departure of non-breeding birds. Most non-breeders continue to visit their burrows during July and early August. During this time birds generally visit their burrows for several hours at night when they engage in burrow maintenace activities, such as enlarging the nest chamber or constructing a nest. Pair formation also continues during this period, and pairs occasionally remain in their burrows during the day. In mid-August non-breeding birds as well as most failed breeders depart the colony for the season. The departure is rapid and by September the only birds visiting the colony are adults returning to feed their chicks.

The attendance patterns of breeding adults vary as the nestling develops. Chicks are capable of thermoregulation shortly after hatching and they do not appear to require much brooding from their parents (Chapter 3). Some adult birds remained with their chicks for up to six days after hatching, although most departed within two days and some within 24 hrs. Adults that remain with their chicks often do not brood them directly, but rest next to them on the nest and feed them at regular intervals. It therefore appears that the ability of an adult to feed its newly hatched chick is the primary determinant of the length of the brooding period.

Table 10 summarizes the visitation patterns and estimated feeding rates of adult Dark-rumped Petrels. The table was derived from several sources including, the weight loss of fasting chicks, weight changes of nestlings, and data from event recorder monitored burrows (Chapter 3). Feeding rates are maximum between 30 and 60 days, which coincides with the period of maximum chick growth, the inflection point of the logistic chick growth curve (Ricklefs

Table 10. Estimated feeding rates in Dark-rumped Petrel nestlings[1].

Chick Age (days)	N[2]	Est. food delivered to chick (g)	% Total food	Avg. number chick feeding visits	Est. Avg. Food load size (g)
0 - 30	9	791.66 (52.98)	32	12.50 (1.77)	63.33
31 - 60	10	901.53 (173.77)	36	14.33 (4.03)	62.87
61 - 90	9	682.55 (79.70)	27	12.33 (3.28)	55.36
91 - 120	9	114.67 (67.54)	5	3.22 (1.92)	35.61
0 - Fledging (Total)	7	2501.71 (94.64)	100	44.50 (7.61)	56.22

[1] Values in parentheses are one standard deviation.

[2] Event recorder-monitored chicks.

1967,1968). The frequency of adult visits declines steadily after this point, and chicks are fed only 3.22 times, on average, during the last quarter of the nestling period. Maximum estimated food load sizes ranged from less than ten grams to over 110 grams, which is about 26% of mean adult weight. This is probably close to the maximum adult seabirds can carry (Ashmole 1971), especially in light of the altitude and distance from the sea of their nesting colonies. Nestlings are fed almost 70% of their total food during the first half of the nesting period and about 95% of their total by the time they are 90 days old. Because chicks on average are only fed a few times during their last month on the nest, it appears that like the Leach's Storm Petrel (Ricklefs et al. 1980), they must store a large amount of fat that they metabolize prior to fledging. However, there is much variability in the feeding pattern because some chicks are deserted entirely for up to three weeks before fledging, while others are visited and fed immediately prior to fledging. In most cases, chicks which were visited prior to fledging were only fed small amounts of food. Indirect evidence from the pattern of visitation at event recorder-monitored nests and direct observations of a hand-raised bird suggest that most chicks begin to refuse food one to two weeks prior to fledging. This behavior has been found in other species including the Common Puffin (Fratercula arctica)(Harris 1976), the

Fork-tailed Storm Petrel (Simons 1981), the Wedge-tailed Shearwater (*Puffinus pacificus*)(Sincock MS), and the Rhinoceros Auklet (*Cerorhinca monocerata*) (U. Wilson pers. com.). In contrast, Wingate (1972), found that a Bermuda Petrel that he hand fed for several weeks prior to fledging did not refuse food. If nestlings do indeed determine when they are ready to stop eating, this may explain much of the conflicting evidence concerning the "desertion period" in seabirds (Burger 1980). Clearly, the best mechanisms for determining when a nestling is ready to fledge reside within the chick itself. If adults simply continue to feed their nestlings until they receive a signal that the chicks are ready to fledge we would expect 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 with less efficient parents, chicks may continue to beg for food right up to the time the adults are forced to depart the colony at the end of the season. Both patterns have been observed in the Dark-rumped Petrel (see below). A careful analysis of chick development patterns and adult visitation frequencies may shed more light on this poorly understood aspect of seabird behavior.

Food Habits of Breeding Dark-rumped Petrels

Nineteen food loads were fortuitously collected during the study from breeding adults. The samples were regurgitated by birds that were trapped during the nestling period as part of a banding study, and they do not represent a systematic attempt to determine the food habits of the Dark-rumped Petrel. Nevertheless, they did contain a variety of prey items which give some indication of the feeding ecology of these birds. One sample collected by Larson (1967) and analyzed at the University of Hawaii has also been included, and all of the data are summarized in Table 11. The samples I collected were analyzed by Beatrice Burch of the B.P. Bishop Museum and Tom Hida of National Marine Fisheries Service, Honolulu, Hawaii. All specimens were identified to the lowest possible taxon.

A total of 10 different prey types were identified from three classes of marine organisms. Based on these data, it appears that squid predominate in the diet followed by fishes and crustacea. Although I did not attempt to measure volumes in this analysis, I would estimate that squid constituted 50 to 75% of the total volume of the samples I examined. This finding is in agreement with the evidence available for other gadfly petrels of the genus Pterodroma (Ashmole 1971, Imber 1973, Pitman 1982).

Table 11. List of 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 (squirrel fish)	5	3	3
Mullidae (goatfish)	2	6	4
Myctophidae (lantern fishes)	4	4	4
Scombridae Katcuwonus pelamis (skipjack tuna)	7	1	1
Sternoptychidae (hatchet fish)	7	1	1
Unidentified fish	3	5	4
MOLLUSCA			
Decopoda (squid)			
Loliginidae[1]	7	1	1
Ommastrephidae	2	6	5
Unidentified squid	1	108	8
CRUSTACEA			
Isopoda			
Anuropus sp	7	1	1
Unidentified isopod	7	1	1
Stomatopoda[1] (mantis shrimp)	7	1	1
Unidentified crustacea			
Balls of bright orange oil containing crustacean larvae	7	1	1

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[1] Larson (1967)

Gadfly petrels are more aeriel than procellariiformes 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 it is generally felt that they feed primarily by siezing their prey on the surface and scavenging. It is also generally believed that they frequently feed at night. The prey items identified in this study corroborate these beliefs. Among the fish, the Exocoetidae and Scombridae are both pelagic species which would be available to the petrels on or near the surface (Wheeler 1975, Nelson 1976). The Holocentridae and Mullidae are found nearshore as adults but they both posess pelagic juvenile stages which frequent the surface layers, especially at night (Wheeler 1975). The Myctophidae and Sternoptychidae are bathypelagic species that spend the daylight hours as deep as 3500 m, but often migrate to the surface layers at night. They would appear to be ideal prey for Dark-rumped Petrels since they are generally small (less than 15 cm) and they both posess highly visible photophores (Grzimek 1974). Daily vertical migration is also a characteristic of squid and the giant isopod, Anuropus, which suggests that the birds are feeding on these species at night. The Mantis Shrimp, may have been obtained by scavenging because these are primarily coastal bottom-dwelling species (George and George 1979). One adult regurgitated about a half dozen 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 very similar to the stomach oil of the birds. Little is known about the stomach oil of petrels but it is assumed to be of dietary origin and it appears to be an important energy source for breeding birds (Chapter 3). Crustacean egg cases of this type may be an important source of stomach oil in the Dark-rumped Petrel.

Nestling Growth and Development

The growth and development of Dark-rumped Petrel nestlings was recorded throughout the study by weighing and measuring nestlings at regular intervals. The methods used to make these measurements were identical to those described previously for adult birds. Seventeen chicks were measured in 1979, six in 1980, and eight in 1981. Growth equations were obtained by employing the graphical method described by Ricklefs (1967, 1968) and an itterative 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. With Ricklefs' method K is determined by repeatedly converting the logistic curve to a straight line on the basis of an assumed asymptote and conversion factors. Having done this, one then chooses the best approximation of K by visually inspecting the curves and choosing the one that gives the closest fit. With the computer model, the best estimate of K is determined in an itterative fashion by converting a large number of curves over a range of assumed asymptotes. These curves are compared via linear regression and the best estimate of K is then calculated from the curve with the highest correlation coefficient. Two other factors were also calculated for making growth comparisons. Ka/4 and KR/4 x 100 represent the maximum instantaneous growth rate of the chick at the inflection point of the fitted logistic curve and they may yield a better estimate of the overall growth rate than K (Hussel 1972). All growth rate calculations were made using the linear portion of the growth curve which includes measurements from day 0 to day 65.

The weight gain of developing Dark-rumped Petrel nestlings is summarized in Figure 20. On average, chicks gain weight steadily for the first three quarters of the nestling period and then loose weight until they fledge. The average maximum weight attained by chicks is slightly over 600 grams, but many chicks reach higher weights for short periods, and some nestlings reached peak weights of over 850 g or almost twice average adult weight. The development of the chicks is slow which presumably reflects the variable

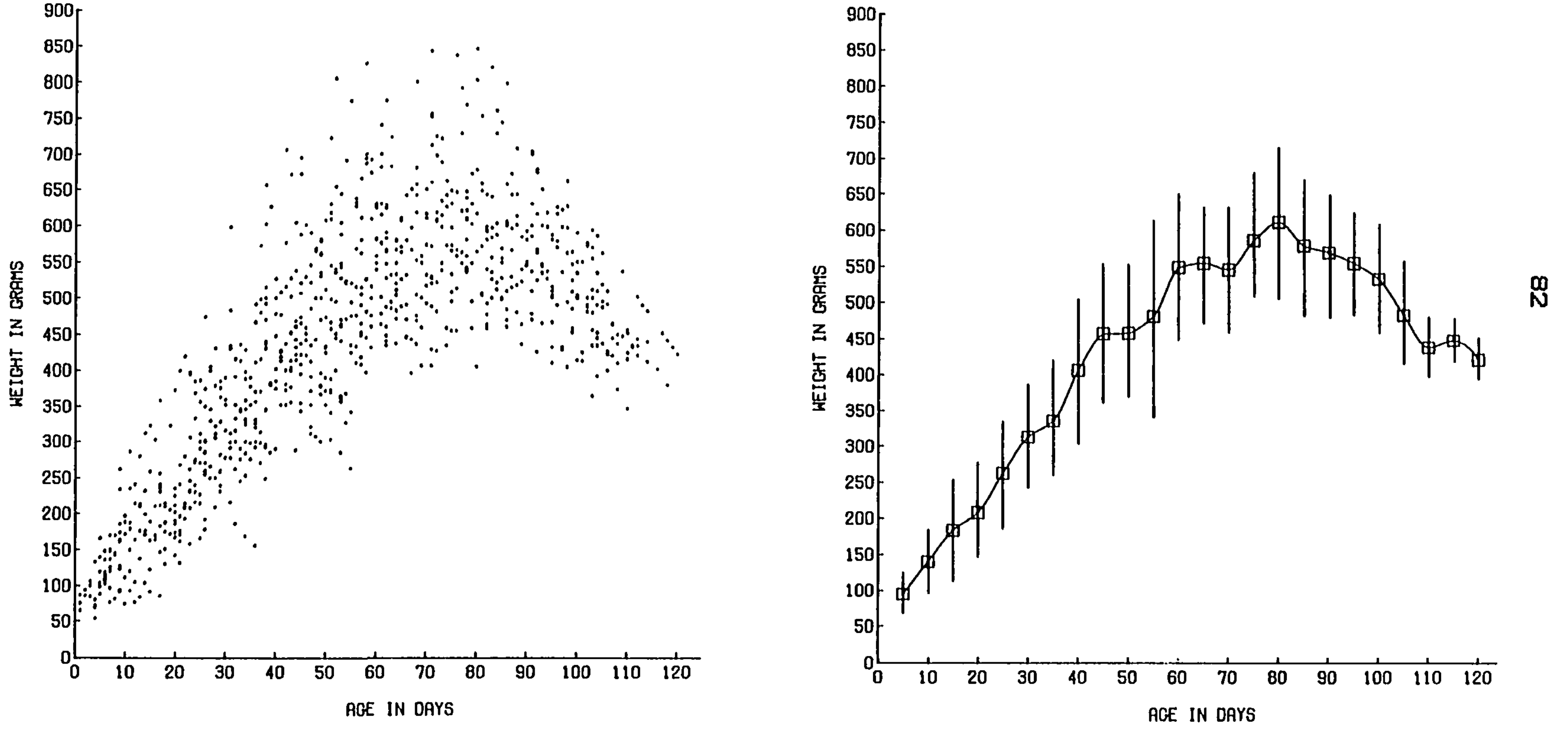

Figure 20. Weight gain of Dark-rumped Petrel nestlings. Combined data from 1979 - 1981 based on measurements of 31 nestlings.

and unpredicable food supply used by the adults. The development patterns of individual nestlings clearly reflect the variability of the food resources and the foraging efficiency of individual adult birds (Figure 21). Many nestlings show a cyclic pattern of weight gain and it is common for chicks to be fed regularly for periods of up to a week and then be deserted for periods of ten days to three weeks. Nestlings are capable of fasting for long periods when food is unavailable, and they can consume large amounts of food in a short time when food is abundant. Young chicks frequently doubled their weight in a single feeding. This pattern is typical of Procellariiform birds and has been reported in a number of related species (Roberts 1940, Richdale 1963, Harris 1966, Serventy 1967, and Simons 1981). Most chicks were fed less frequently and lost weight steadily prior to fledging, but some nestlings maintained a lower weight which varied little throughout the later half of the nestling period. In addition, while some chicks were clearly deserted by their parents for periods of up to six weeks prior to fledging, others were fed regularly until they fledged. Fledgling weights averaged 435 g overall, which is very close to average adult weight.

The growth rate constants varied little from year to year averaging 0.058 (Figure 22, Table 12). The K values were not clearly correlated with the other growth rate

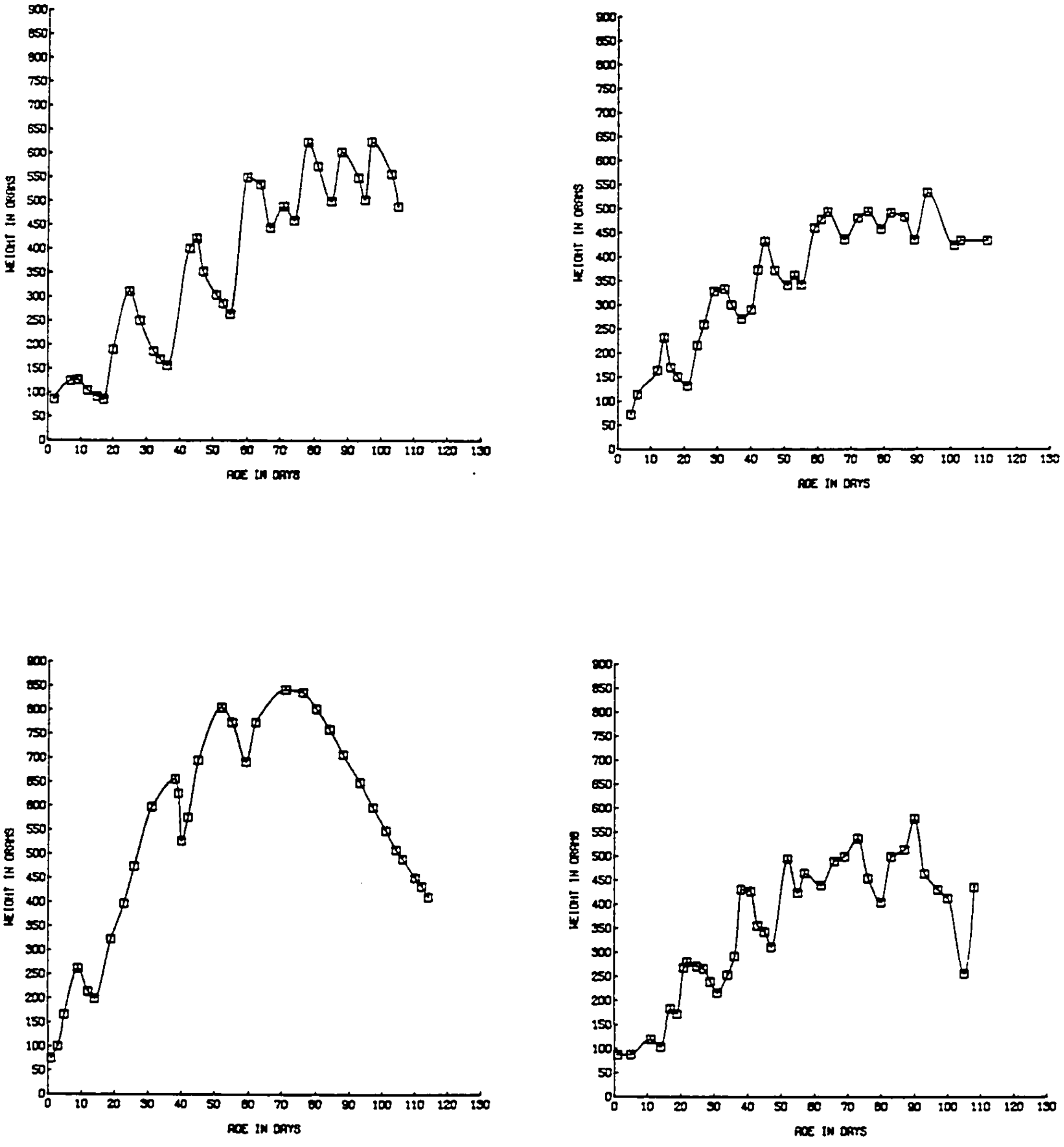

Figure 21. Growth patterns of four individual Dark-rumped Petrel nestlings.

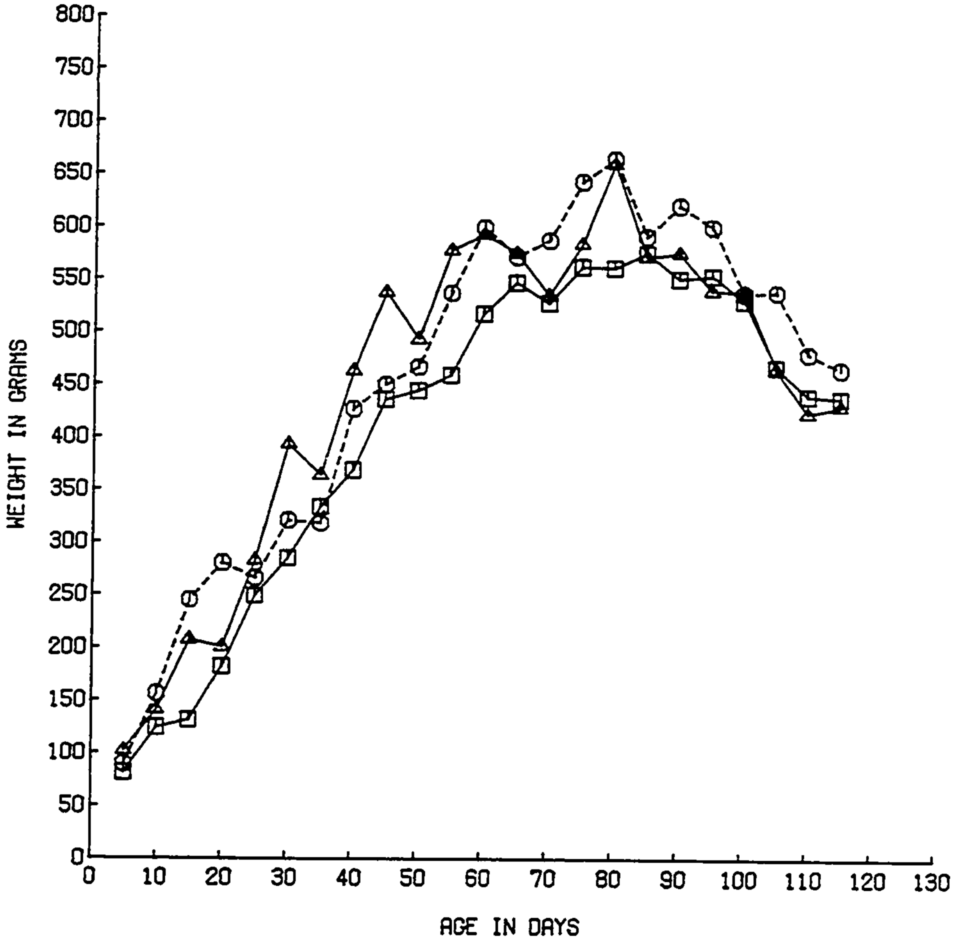

Figure 22. Dark-rumped Petrel yearly nestling growth patterns 1979 - 1981. Squares indicate data from 1979 (N = 17), circles data from 1980 (N = 6), and triangles data from 1981 (N = 8).

Table 12 . Growth rate constants and nestling periods of Dark-rumped Petrel nestlings 1979 - 1981.

	1979	1980	1981	Overall
N	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 x 100 (%/day)	2.22	2.25	2.53	2.10
Nestling period (days) (N) (S.D.)	112.8 (10)(2.90)	106.9 (7)(3.70)	110.1 (9)(4.51)	110.6 (26)(4.60)

parameters. This is probably related to the extreme irregularity of the yearly growth data. Nevertheless, the length of the nestling period does appears to be related to the magnitude of the asymptote attained in a given year. Overall, the nestling period averaged 110.6 days (range 100 - 119 days), and the asymptote of chick weight averaged 629 g. Higher asymptotes were associated with shorter nestling periods (Table 12). This pattern suggests that the length of the nestling period is flexible, and may be regulated by the total amount of food delivered to the nestling. As discussed previously, this process may be controlled to some extent by the nestling to maximize its development and vigor at fledging while minimizing the length of the nestling period.

In contrast to weight, the growth of body parts and feathers is much more uniform, and it appears that the mid-point of the nestling period represents an important turning point in the development of the chick. Wing growth (Figure 23) shows a typical logistic pattern with the inflection point occurring at approximately 60 days and maximum length of about 300 mm reached just prior to fledging. Tarsus growth (Figure 24) and culmen growth (Figure 25) are similar. Both show linear growth initially and reach an asymptote around day 60. The flight feathers do not begin to emerge until mid-way through the nestling

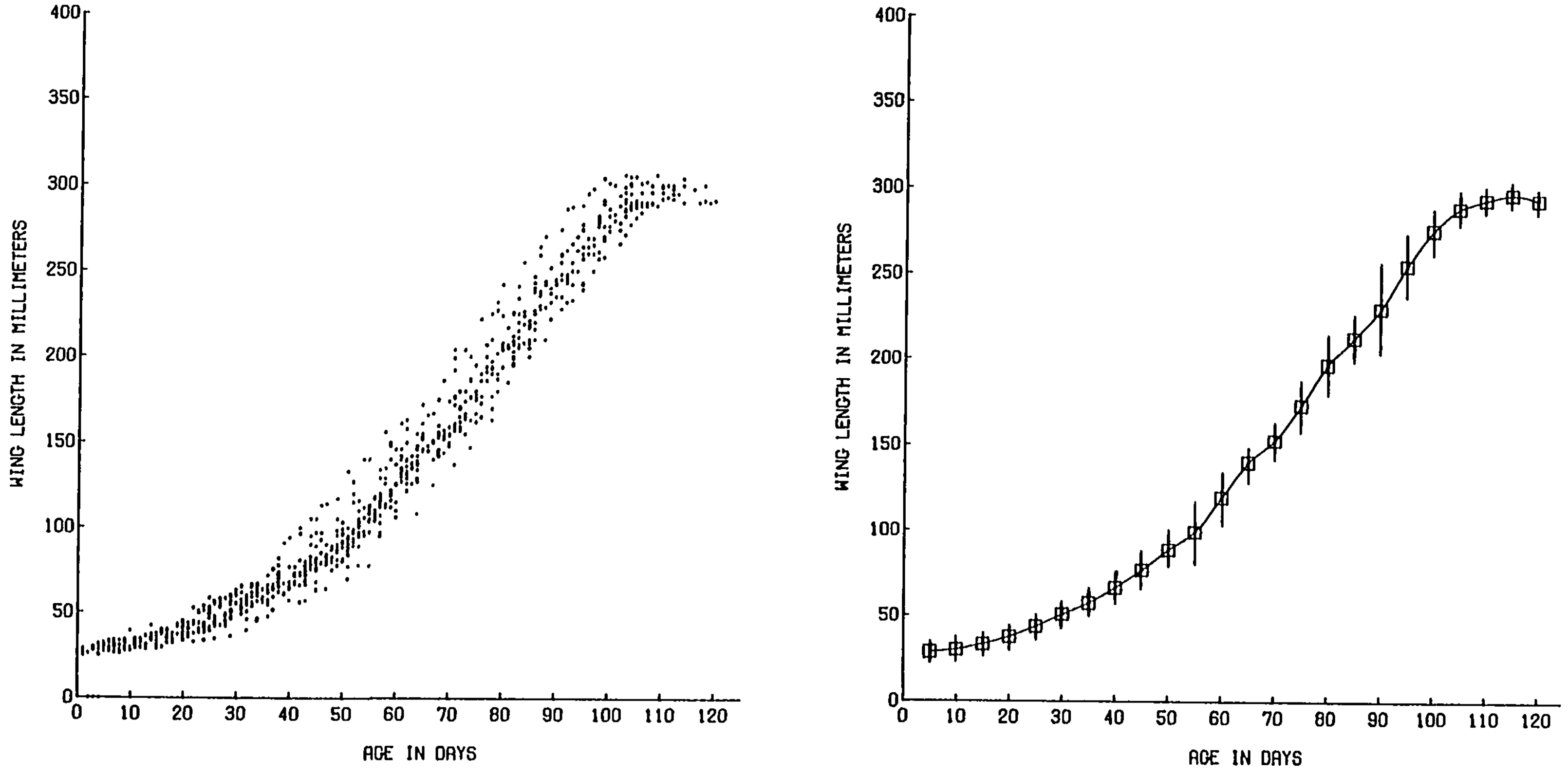

Figure 23. Wing growth of Dark-rumped Petrel nestlings. Combined data 1979 - 1981, N = 31.

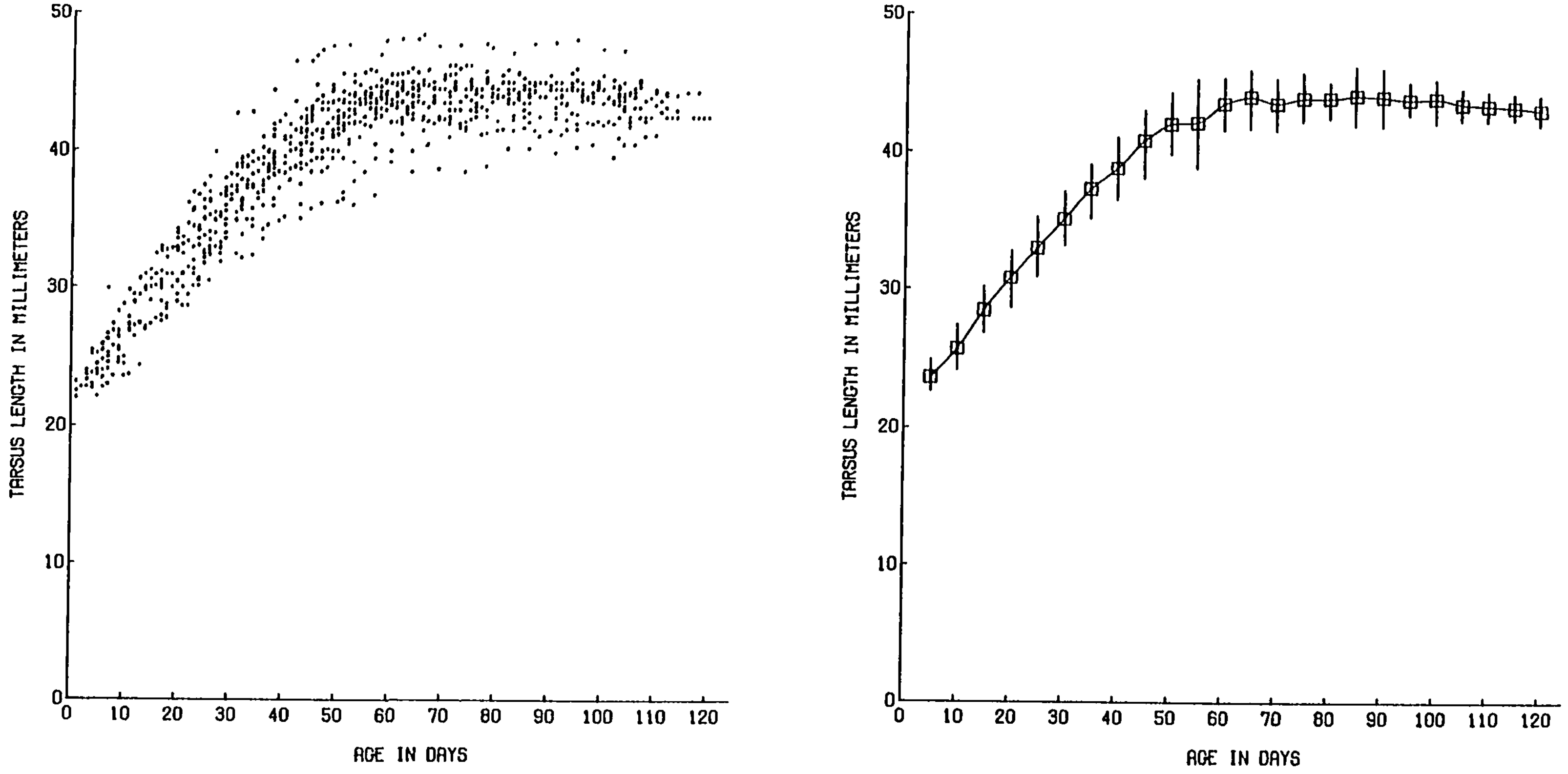

Figure 24. Tarsus growth of Dark-rumped Petrel nestlings. Combined data 1979 - 1981, N = 31.

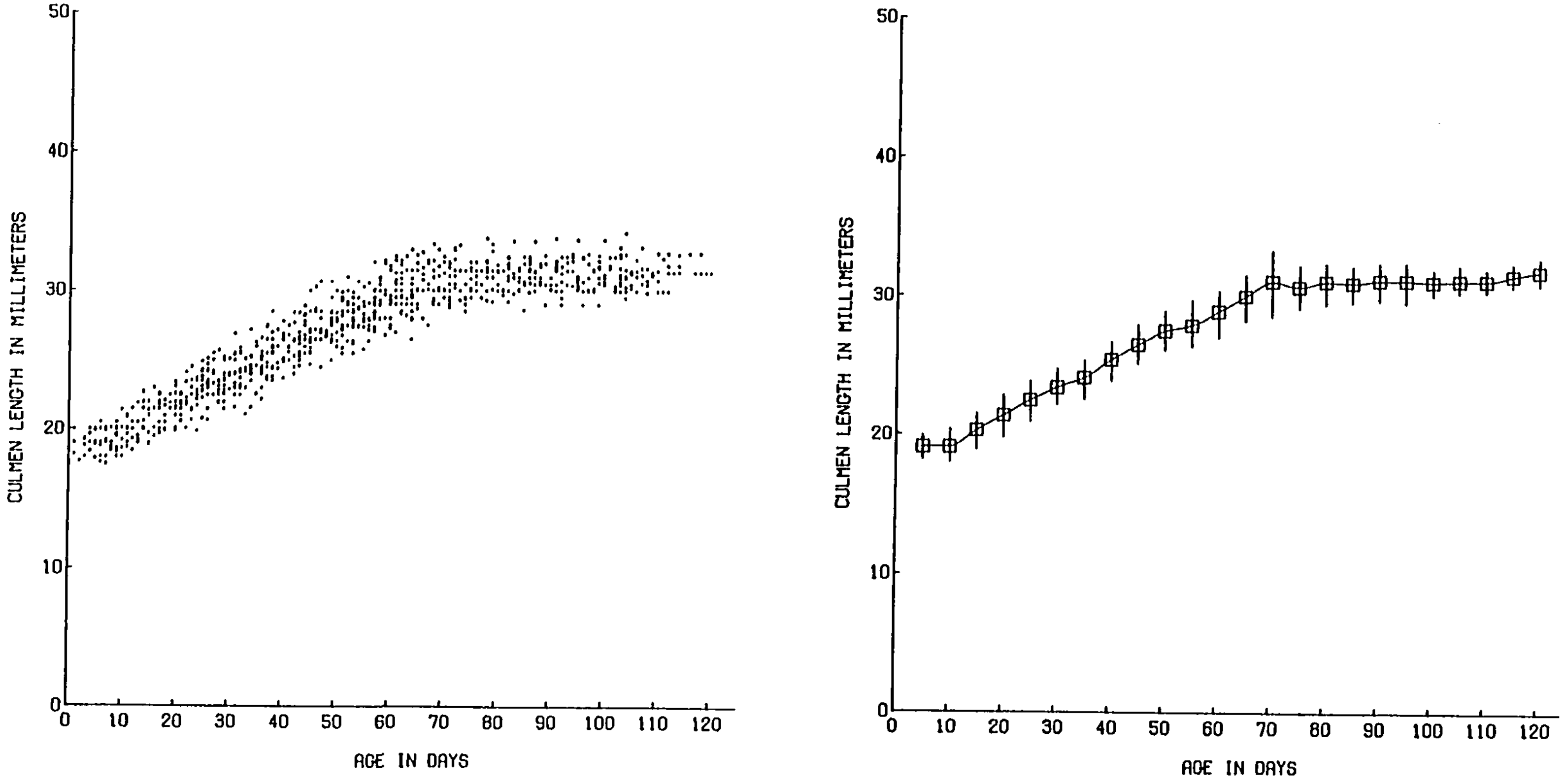

Figure 25. Culmen growth of Dark-rumped Petrel nestlings. Combined data 1979 - 1981, N = 31.

period and they grow in a nearly linear fashion until just prior to fledging (Figures 26 and 27). Thus, it appears that the first half of the nestling period is devoted to the development of tissue and body parts, while the remainder may be dedicated to the maturation of that tissue and the development of the flight feathers.

Several other aspects of the chicks development can be used as critera for aging the nestling. Nestlings open their eyes shortly after hatching, and they retain their egg tooth for about a week. At hatching they are covered by a layer of light grey down which is distinctly whitish around the chest and belly. A heavier second layer of down replaces the first during the second to third week of development. The first feather sheaths to appear are those along the spinal tract. These begin to emerge from the skin at about 13 days. They erupt from their sheaths on about day 45, and are fully developed by about day 60. The scapulars and the feathers along the belly emerge between 30 and 35 days of age and are fully developed by day 65. The upper wing coverts emerge from the skin around day 40, and they begin erupting from their sheaths about ten days later. The feathers around the head and face develop more slowly, emerging on day 45 and erupting from their sheaths on day 65. The primary feathers emerge from their sheaths on about day 65 and the the tail feathers on about day 55. By

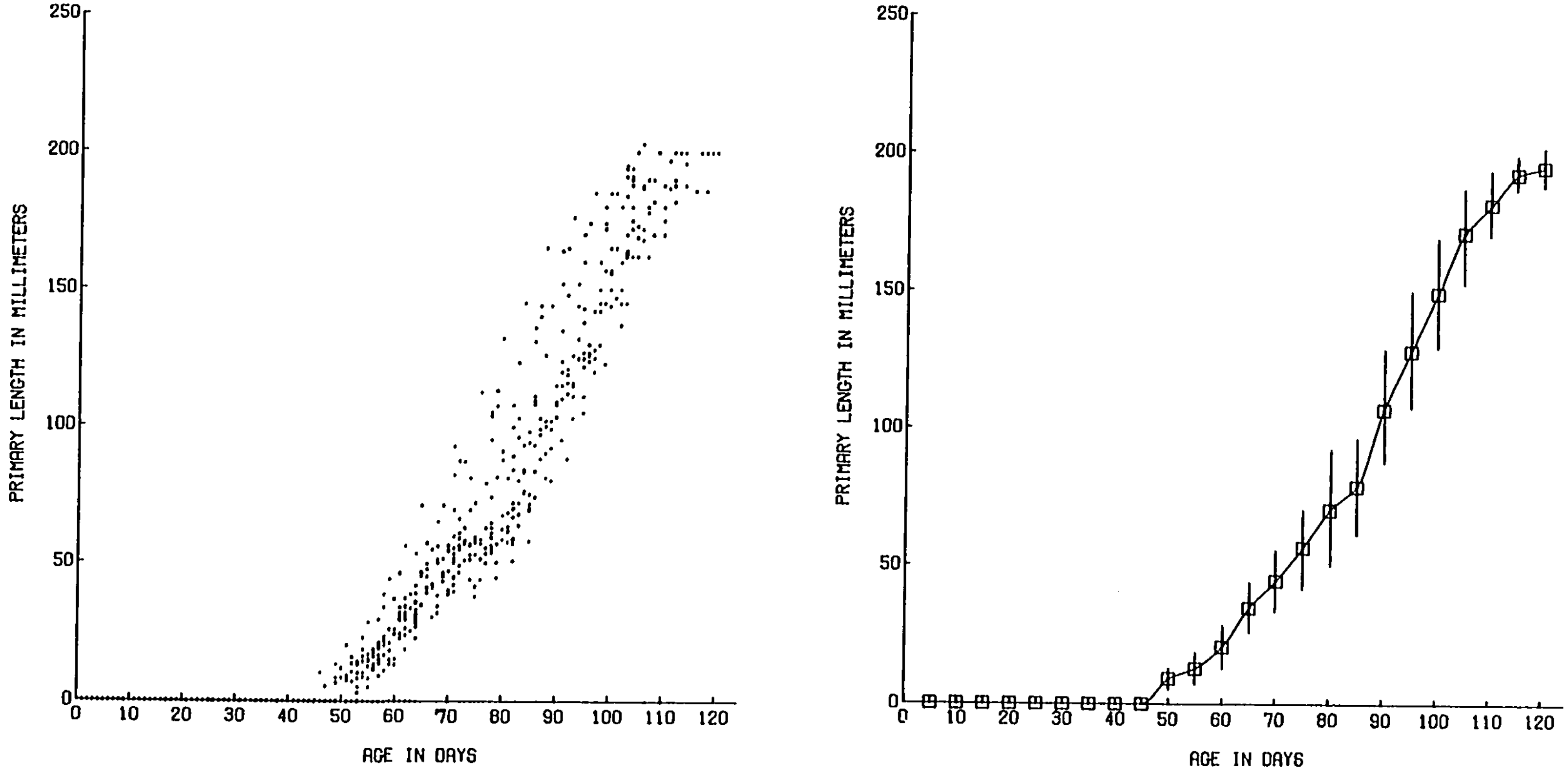

Figure 26. Primary growth of Dark-rumped Petrel nestlings. Combined data 1979 - 1981, N = 31.

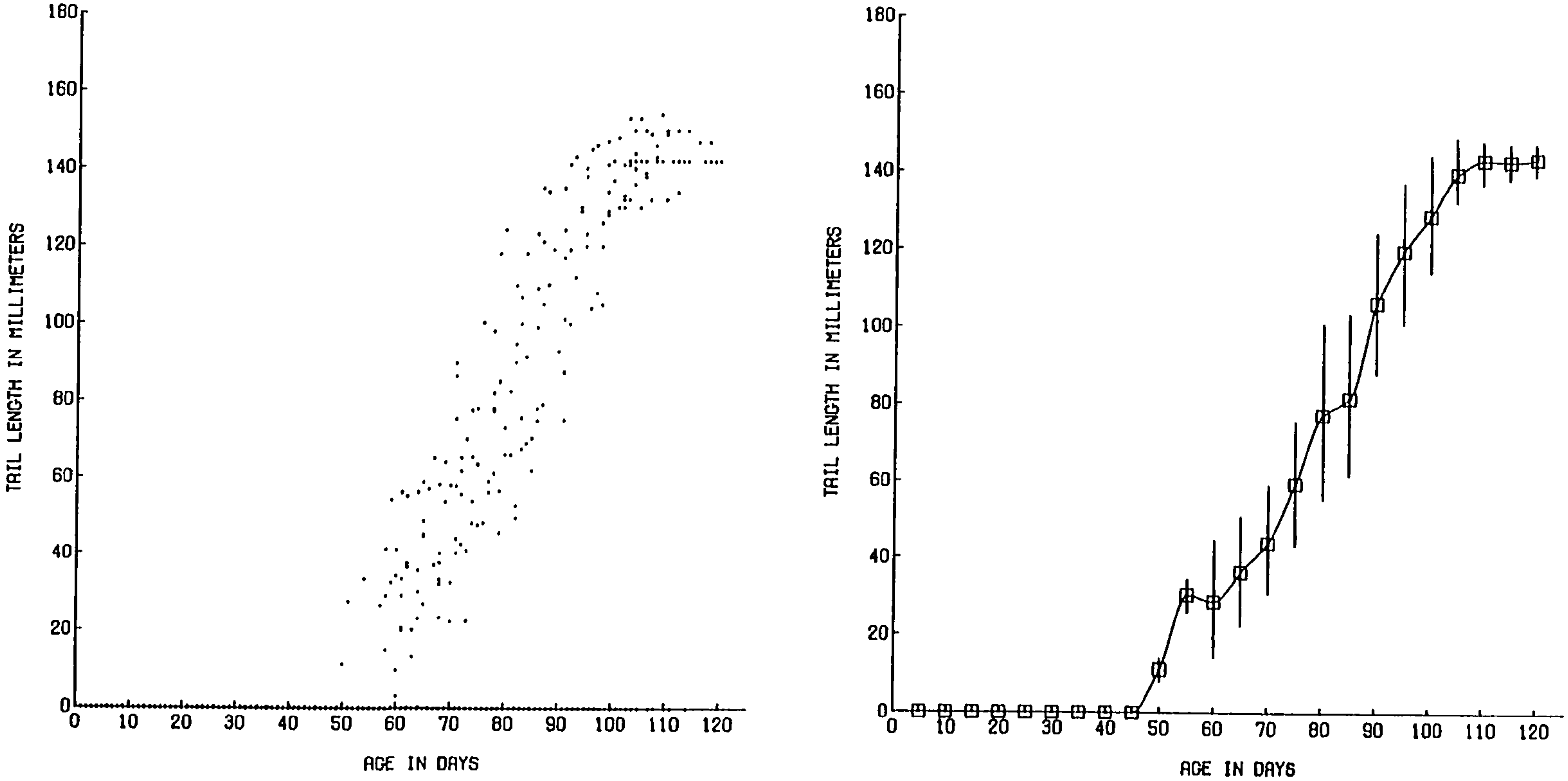

Figure 27. Tail growth of Dark-rumped Petrel nestlings. Combined data 1980 - 1981, N = 14.

day 105 feather development is usually complete, although some chicks retain small patches of down on their heads and bellies right up to fledging.

Nestling Behavior

The behavior of the nestling in the television-monitored burrow is summarized in Table 13. The behavior of the nestling differed from that of the incubating adult in several important ways. The chick was much more active on the nest than the adult, and it spent a much smaller proportion of its time sleeping. This may be related to several factors including the relatively higher thermoregulatory demands on the smaller nestling or the importance of activity in stimulating the proper development of the chick's strength and coordination. The chick also spent a larger portion of its time preening which may have been related to maintaining the insulative properties of its down or promoting proper feather development. The chick also spent more of its time off the nest. This occurred late in the nestling period when the nestling began to venture out of the burrow to exercise its wings in preparation for fledging. Like the adult the nestling faced away from the burrow entrance most of the time (Figure 28).

Table 13. Behavior of a nestling Dark-rumped Petrel. Data are presented as % total time based on 65 hr 42 min of observations during the nestling period.

Portion of Nestling Period	Behavior				
	Alert			Sleeping	Locomotion
	Resting Quietly	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%

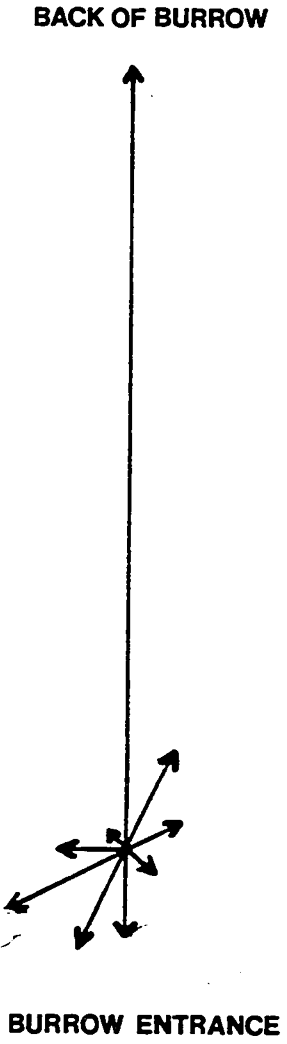

Figure 28. Orientation of a Dark-rumped Petrel nestling. Vector length is proportional to the frequency of observations. Based on 3800 min of observations.

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 about the face, head, and upper body. The chick responded with incessant cheeping and occasional nibbling at the adult's bill. The adult usually began to regurgitate food to the nestling within several minutes. Feeding continued until it was terminated by the adult, and 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, and in those cases they often remained in the burrow the following day. Adults with chicks as old as 65 days were found in burrows during the day.

Chicks become noticeably more active during the second half of the nestling period. Beginning about two months before it fledged the chick in the television-monitored burrow began to stretch and vigorously flap its wings as it rested on the nest. Chicks generally begin to venture from their burrows two to three weeks before fledging. During these forays they explore within about a 10 m radius of their burrow entrances, climb rocks or other obstacles that could serve as take off platforms, and exercise their wings. Chicks apparently continue this behavior until at some point their exercising launches them into the air and they depart the colony on their first flight.

Fledging Dates and Overall Reproductive Success

The fledging period extended from 8 October to 30 October in the three years of the study. The median fledging date was 23 October (S.D. 6.5 days) in 1979, 19 October (S.D. 6.7 days) in 1980, and 19 October (S.D. 6.1 days) in 1981. Fledging success and reproductive success are summarized in Table 8, and the causes of breeding failures from 1979 to 1981 are tabulated in Table 9. 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. Fledging success was reduced in 1979 and 1981 due to the death of several young nestlings, apparently from starvation. Active burrows containing fledglings are evident late in the season since they almost always showed traces of down around their entrances. This clue made it possible to estimate the percentage of active burrows which produced fledglings each season. In 1979 when predation was severe, approximately 24% of the active burrows produced fledglings. In 1980 and 1981 predation was not significant, and in those years it appeared that about 42% of the active burrows produced fledglings. This finding was useful because it was used to determine the relative size of the adult petrel population, a key element in the population model (Chapter 4). Overall reproductive success varied from 38.7 % in 1979 to 71.4% in 1980. It should be noted however that the values in Tables 8 and 9 were derived solely from accessible burrows. Indirect evidence, such as feathers, or a sudden drop in activity, noted at many inaccessible burrows in 1979, suggested that the level of predation experienced by breeding birds that year may have been substantially higher than indicated in Table 8.

CAUSES OF MORTALITY IN BREEDING DARK-RUMPED PETRELS

Natural Sources of Mortality

The natural mortality rate of adult petrels at the colony appears to be low, although a small number of birds are killed each year in accidents related to their breeding activities. From 1979 to 1981 four adults were found which 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 down-drafts that occur there regularly. One adult bird was also killed when the burrow it was excavating collapsed (Figure 29). This type of mortality is difficult to detect but it may be fairly common since birds often burrow in loose, unstable, volcanic soils.

Figure 29. Adult Dark-rumped Petrel killed by a collapsing burrow.

Introduced avian diseases are thought to have been responsible for the decline and extinction of a large portion of the endemic Hawaiian avifauna (Warner 1968). Warner (1968) reported on a large grounding of Dark-rumped Petrels which occurred on Kauai in 1961 and he found that many of the debilitated birds were suffering from avian malaria. These birds were later determined to be Newell's Shearwaters rather than Dark-rumped Petrels (Banko 1980) but the finding of avian malaria suggests that other procellariiformes may be susceptible to the disease. The disease is caused by infections of Plasmodium, and it is transported by the night biting mosquito, Culex quinquefasciatus (Warner 1968, van Riper et al. 1980). Culex is normally restricted to elevations below 600 m but may occur as high as 1500 m (Williams 1931 (in Warner 1968)). I did not observe any birds with symptoms of avian diseases during the study, and because all of the known petrel nesting locations are well above the range of the night biting 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 avian malaria. Twenty two individual slides were prepared. The blood smears were fixed in 100% methanol, stained with Wrights Giemsa, washed in distilled water, and allowed to air dry. The smears were then individually examined under the oil immersion objective of a compound microscope. I found no evidence of developing Plasmodium schizonts or other signs of blood parasites in the blood smears.

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 2000 m. Most petrels nest well above this elevation, and both of the birds that were killed were found at the lower limit of the petrel's breeding distribution. It does not appear that Short-eared Owls inflict signigicant levels of predation on Dark-rumped Petrels at this time. But, if the owls range expands to higher elevations in the future, the predation threat could increase.

Predation by Introduced Mammals

Most procellariiformes, including the Dark-rumped Petrel, have evolved in ecosystems free from terrestial predators, and they are for the most part defenseless against them. Although many factors have contributed to the petrel population decline, the introduction to Hawaii of the black rat, the Norway rat, the domestic cat, and the Indian mongoose in the later half of the 19th century has certainly accelerated the process (Atkinson 1977, Berger 1972, Chapter 1). The most serious cause of mortality and breeding failure in nesting Dark-rumped Petrels today is predation by these introduced mammals (Chapter 5).

Prior to this study it was generally thought that the remaining Dark-rumped Petrels nested above the range of cats and mongooses, and that the primary predator of the birds was the black rat Rattus rattus (Larson 1967). Most trapping prior to 1979 was done using snap-type rat traps which are ineffective on cats and mongooses. I initiated a trapping program in that year using Havahart type live traps, and determined that both cats and mongooses could be found in the petrel's nesting habitat. Two trap lines, composed of live traps spaced 50 m apart and covering the main west rim colony, were establised in May 1979 and these were maintained throughout the study. The results of that trapping effort are summarized in Table 14. The number of individuals of each species caught declined each year, and it appears that the trapping program was successful in controlling predation on breeding petrels (Tables 8 and 9). The program was expanded in 1980 and 1981 to include the park road and crater cabins, and this may have reduced the influx of predators into the petrel colonies. In those years both species were caught in small

Table 14. Mammals trapped within the west rim petrel colony from April to October 1979 - 1981.

Year	Species				
	Rattus rattus	*Rattus exulans*	*Felis catus*	*Mus mus*	*Herpestes auropunctatus*
1979	79	5	2	30	3
1980	23	0	0	3	0
1981	15	1	0	0	0

numbers outside of the petrel nesting areas. There is a virtually unlimited source of these predators at lower elevations in Hawaii and it is likely that they will always pose a threat to the remaining petrel populations. Black rats are the only potential predators that exist within the petrels nesting habitat year round, but like Wingate (1964) I found no direct evidence of rat predation on breeding petrels. A stomach content analysis of 17 roof rats performed by Christa Russell of the Hawaii Field Research Center, Hawaii Volcanoes National Park, determined that rats captured in the summit area of Haleakala were subsisting primarily on green plant material, insects, insect larvae, and seeds.

In summary, feral cats and mongooses were found to pose a substantial threat to the remaining petrel populations. Over 60% of the breeding failures in years with significant predation were caused by these animals, and it appears that only a few vagrant individuals are responsible for the damage in most cases. The problem is serious because the life history attributes of the Dark-rumped Petrel make the species very sensitive to changes in its mortality rate (Chapter 4). In addition, the problem is likely to persist indefinitely because a large, low elevation, population of predators surrounds the remaining petrel habitat. As outlined in Chapter 5, it is clear that we need to know more about the biology, behavior, and population dynamics of these predators so that effective predator-specific control methods can be developed.

CHAPTER 3

THE PHYSIOLOGICAL ECOLOGY OF BREEDING DARK-RUMPED PETRELS

Physiololgical ecology has been defined by Whittow (1983) as the study of "the exchange of materials and energy between an organism and its natural environment". Knowledge of these exchange processes is essential to understanding the ecological role of an organism, and it can shed light on the adaptive nature of many aspects of an organism's biology and behavior. There are relatively few studies of the physiological ecology of seabirds, and most of these have been carried out over the last few years. Nevertheless, this early work has greatly improved our understanding of the ecology of seabirds and their role as marine organisms.

Much of the work thus far has centered on the physiology of the developing embryo. Rahn and Ar (1974) stimulated much of this work by pointing out the relationship between incubation time and egg water loss. This relationship has been examined in detail in a number of species including

Cassin's Auklets (Ptychoramphus aleutica) (Roudybush et al. 1980), Wedge-tailed Shearwaters (Whittow et al. 1982), and Bonin Petrels (Grant et al. 1982). Additional studies have focused on the relationship between embryonic oxygen consumption and growth (Ackerman et al. 1980, Vleck and Kenagy 1981, Pettit et al. 1981, 1982a,b). Most recent work has been reviewed by Whittow (1983), and the ecological correlates of prolonged incubation in seabirds have been discussed by Whittow (1980,1983) and Boersma (1982).

Other researchers have looked at the energetics of reproduction in seabirds by determining the metabolic demands of adult birds and nestlings. Ricklefs et al. (1980a, 1980b), and Ricklefs and White (1981), have analyzed the energetics of reproduction in Leach's Storm Petrels and Common (Sterna hirundo) and Sooty (Sterna fuscata) Terns. Prince et al. (1981) have estimated the energetic requirements of incubating albatrosses utilizing weight loss data, and Grant and Whittow (1983) have measured the energetic demands of incubating Laysan Albatrosses (Diomedia immutabilis) and Bonin Petrels (Pterodroma hypoleuca).

Recently, other workers have examined the caloric content and composition of the food consumed by several species of seabirds, primarily procellariiformes (Warham 1976, 1977, Clarke and Prince 1980). More studies of this type will be required before an overall picture of seabird energetics can be developed.

Despite our incomplete understanding of the physiological ecology and energetics of seabirds, some attempts to develop seabird energetic models have been made (Wiens and Scott 1975, Furness 1978). These models are invaluable in helping to develop management policies related to seabirds, particularly in cases involving seabird-fisheries conflicts. These conflicts have become more intense in recent years as fisheries turn to prey species upon which seabird populations depend (Straty and Haight 1979, Solomonsen 1979 Brown and Nettleship 1981). A better understanding of the physiological ecology of seabirds is essential if resource conflicts of this type are to be resolved intelligently.

The Dark-rumped Petrel, like most procellariiformes, exploits what is generally assumed to be a marginal and unpredictable food resource (Lack 1967, 1968). This food resource places important energetic constraints on these birds, and these constraints must shape much of the petrel's ecology. In addition these birds breed at an elevation of almost 3000 m in one of the highest seabird nesting colonies in the world. I have examined several aspects of the physiological ecology of the Dark-rumped Petrel in the hope of gaining insights into the adaptive significance of aspects of the birds breeding biology and behavior that are shaped by these constraints. In addition, it is hoped that this information will improve our understanding of seabird energetics in general, which will be essential if these birds are to be managed successfully in the future.

Metabolic Rates of Dark-rumped Petrels

The metabolic rates of nestling and adult Dark-rumped Petrels were estimated by measuring their rates of oxygen uptake. A portable system using an air tight chamber and a manometer was used, and most measurements were made at the nest sites. The device (Figure 30), consisted of a chamber containing soda lime (to absorb carbon dioxide) a calibrated manometer, and a source of oxygen. A bird's oxygen uptake was measured by placing the bird in the chamber with the soda lime, and flushing the entire system with oxygen. The system was then sealed, a timer started, barometric pressure and temperature recorded, and the chamber connected to the manometer by opening a valve. Inside the chamber the oxygen consumed by the bird caused a slight drop in pressure and movement of the manometer.

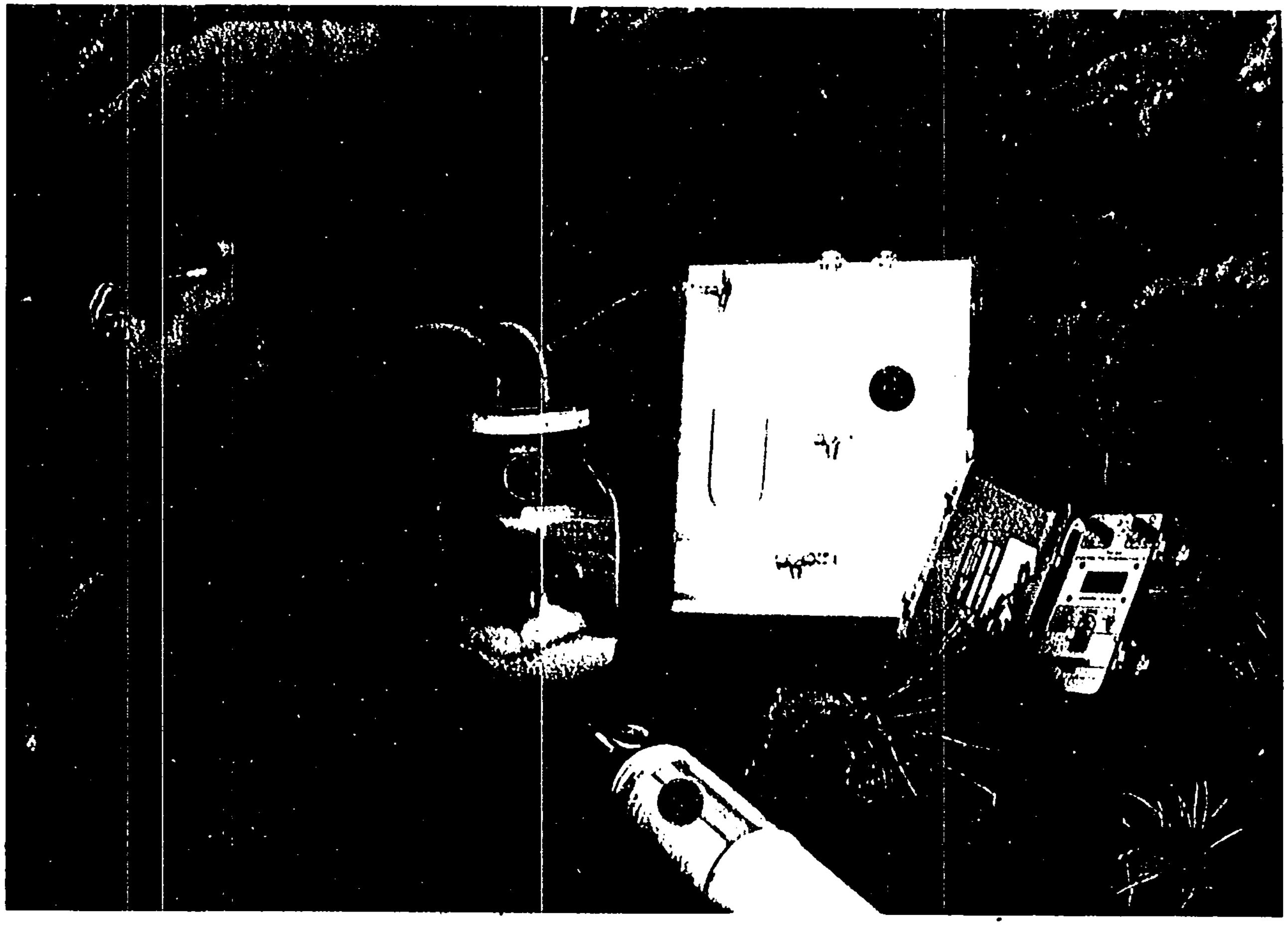

Figure 30. Portable aparatus for measuring oxygen uptake in Dark-rumped Petrels. The following components are visible: (A) metabolism chamber, (B) manometer and calibrated syringes for introducing oxygen, (C) source of oxygen.

After about 30 sec a second valve was opened and enough oxygen was reintroduced into the chamber with a syringe to return the manometer to its starting position. At that point the timer was stopped and the time and amount of oxygen used were recorded. A minimum of five measurements were made on each occasion, and these values were averaged to obtain a final estimate. A small chamber of aproximately 4 l in size was used for small nestlings and a larger 10 l chamber was used for larger nestlings and adults. The system was calibrated in the laboratory by measuring the oxygen uptake of a Rock Dove (*Columba livia*), and the estimates obtained were within 10% of those reported by other authors (Dawson and Hudson 1970). It was assumed that the air within the chamber was saturated with water vapor due to the respiration of the bird, and based on this assumption, measurements were converted to standard temperature and pressure, dry, as follows:

ml Oxygen used x BP - VP at ambient Temp/BP = Volume of Dry Oxygen used

ml Dry Oxygen used x BP/760 = Volume Dry Oxygen used at Standard Pressure

ml Dry Oxygen used x 273/(Temp+273) = Volume of Dry Oxygen used at Standard Temperature

Where BP = Barometric Pressure, VP = Water Vapor Pressure of Saturated Air

Therefore:

ml Oxygen used/Time (sec.) x 60 sec/min x 60 min/hr x 273/(Temp+273) x (BP-VP)/760 x 1/bird weight (g)

= ml Oxygen used/g hr Standard Temperature and Pressure Dry

Measurements were made on 72 occasions on seven nestlings and five adult birds. The results have been summarized by age class and are presented as total oxygen uptake and mass specific rates (Table 15). The high variance in the metabolic estimates for nestlings is probably related to the extreme variance in chick weights (Chapter 2). Nestlings of the same age can vary in their body weight by a factor of three or more. It is interesting to note that nestlings reach their highest total energy expenditure near the middle of the nestling period, and that energy demands decline during the latter half of their growth period. This probably reflects the sharp decline in body mass towards the end of the nestling period. The mass-specific metabolic rate is highest in very young chicks and then declines. This pattern is common in precocial or semi-precocial birds (Ricklefs 1974) although petrels are generally thought to be semi-altricial (Nice 1962). It is not clear why the estimates of adult metabolic rates are higher than those of nestlings just prior to fledging, although a high percentage of metabolically active tissue such as muscle in adult birds could be a contributing factor (G.C. Whittow pers. com.). The values for adult

Table 15. Oxygen consumption of Dark-rumped Petrel nestlings at ambient temperatures 5-25 degrees centigrade.

	Age (days)								
	1-15	16-30	31-45	46-60	61-75	76-90	91-105	106+	Adult
Total [a]									
n	4	13	8	6	10	11	11	4	5
x	419.1	576.8	1061.7	1021.4	1046.9	965.8	854.2	668.4	940.6
S.D.	53.5	306.7	201.7	133.3	183.1	193.6	204.6	128.3	170.8
Mass-specific [b]									
n	4	13	8	6	10	11	11	4	5
x	2.6	2.2	2.3	1.9	1.8	1.6	1.8	1.6	2.3
S.D.	0.79	0.82	0.59	0.47	0.43	0.25	0.44	0.13	0.43

a Units are ml O_2/hr.
b Units are ml O_2/g hr.

birds may have been inflated for several other reasons. First, all of the measurements on nestlings were made on birds that were accustomed to being handled. The adult birds on the other hand were captured on the ground as they returned at night to feed their nestlings. Although the birds were allowed to settle down prior to measuring their oxygen uptake, they were clearly more nervous than the nestlings. Second, the adults had recently flown from the warm lowlands to the cold summit of Haleakala and this may also have increased their rates of oxygen uptake. The two calmest adults measured yielded uptake rates of 760 and 768 ml/hr which suggests that the actual adult rate is probably lower than the average value reported in Table 15. The average BMR of adult birds is approximately twice the predicted value based on the equations of Aschoff and Pohl (1970). This is similar to the findings of Ricklefs et al. (1980a) for the Leach's Storm Petrel.

Energy Budget

I have calculated an energy budget for Dark-rumped Petrel nestlings following the methods outlined by Ricklefs et al. (1980a). I applied Ricklef's values for the rate of accumulation of lipid and nonlipid dry matter in Leach's Petrel to the Dark-rumped Petrel. I assumed that these components accumulated, as a percentage of body weight, at approximately the same rates in both species and used these estimates in conjunction with my data for oxygen consumption to estimate the total energy expenditure of growth and maintenance in a developing nestling. Like Ricklefs et al. (1980a), I assumed that the energy requirement of in burrow activity and the energy excreted in feces were negligible so I ignored them in these calculations. The completed energy budget is shown in Table 16 and Figure 31. The cost of biosynthesis is assumed to be about one-third the energy equivalent of tissue accumulation (Ricklefs 1974). Therefore, total energy for growth is 1.33 times the energy equivalent of tissue accumulation. Maintenance energy is the energy equivalent of oxygen consumption minus the energy cost of biosynthesis and total energy is the sum of growth and maintenance. Energy demands increase during the early nestling phase, reaching a peak of about 600 kJ/day by day 30. Energy demands remain at about that level during development until the last third of the nestling period when they decrease to less than 500 kJ/day. The energy requirement for growth decreases from almost 50% of total energy demands early in the nestling period to less than 25% in older nestlings. It is likely that a substantial percentage of the energy expenditure of young nestlings is devoted to thermoregulation given their small size, limited insulation, and the generally low burrow temperatures

Table 16. An energy budget for Dark-rumped Petrel nestlings.

Age interval (days)	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)
0-15	419.1	1.90	1.10	72.2	22.0	94.2	202.2	125.3	171.1	296.4
16-30	576.8	1.90	1.00	72.2	20.0	92.2	278.2	122.6	247.8	370.4
31-45	1061.7	1.90	1.20	72.2	24.0	96.2	512.2	127.9	480.5	608.4
46-60	1021.4	1.90	0.93	72.2	18.6	90.8	492.7	120.8	462.7	583.5
61-75	1046.9	1.90	0.67	72.2	13.4	85.6	505.0	113.8	476.8	590.6
76-90	965.8	1.90	0.40	72.2	8.0	80.2	461.6	106.7	435.1	541.8
91-105	854.2	1.90	0.38	72.2	7.6	79.8	412.1	106.1	385.8	491.9
105-110	668.4	1.90	0.36	72.2	7.2	79.4	322.4	105.6	296.2	401.8

(1) Oxygen consumption (cc O_2/hr) from Table .
(2) Rate of accumulation of lipid (g/day) estimated from Ricklefs et al. (1980).
(3) Rate of accumulation of nonlipid dry matter (g/day) estimated from Ricklefs et al. (1980).
(4) Energy equivalent of lipid accumulation (kJ/day) = (2) x 38 kJ/g lipid.
(5) Energy equivalent of accumulation of nonlipid dry matter (kJ/day) = (3) x 20 kJ/g.
(6) Energy equivalent of tissue accumulation (kJ/day) = (4) + (5).
(7) Energy equivalent of oxygen consumption (kJ/day) = ((1) x 24 hr/day x 20.1 kJ/l O2) / 1000 ml/l.
(8) Total energy requirement for growth (kJ/day), assuming production efficiency of 75% = (6) x 1.33.
(9) Total energy expenditure for maintenance (kJ/day) = (7) - 0.33 x (6).
(10) Total energy expenditure for growth and maintenance (kJ/day) = (8) + (9).

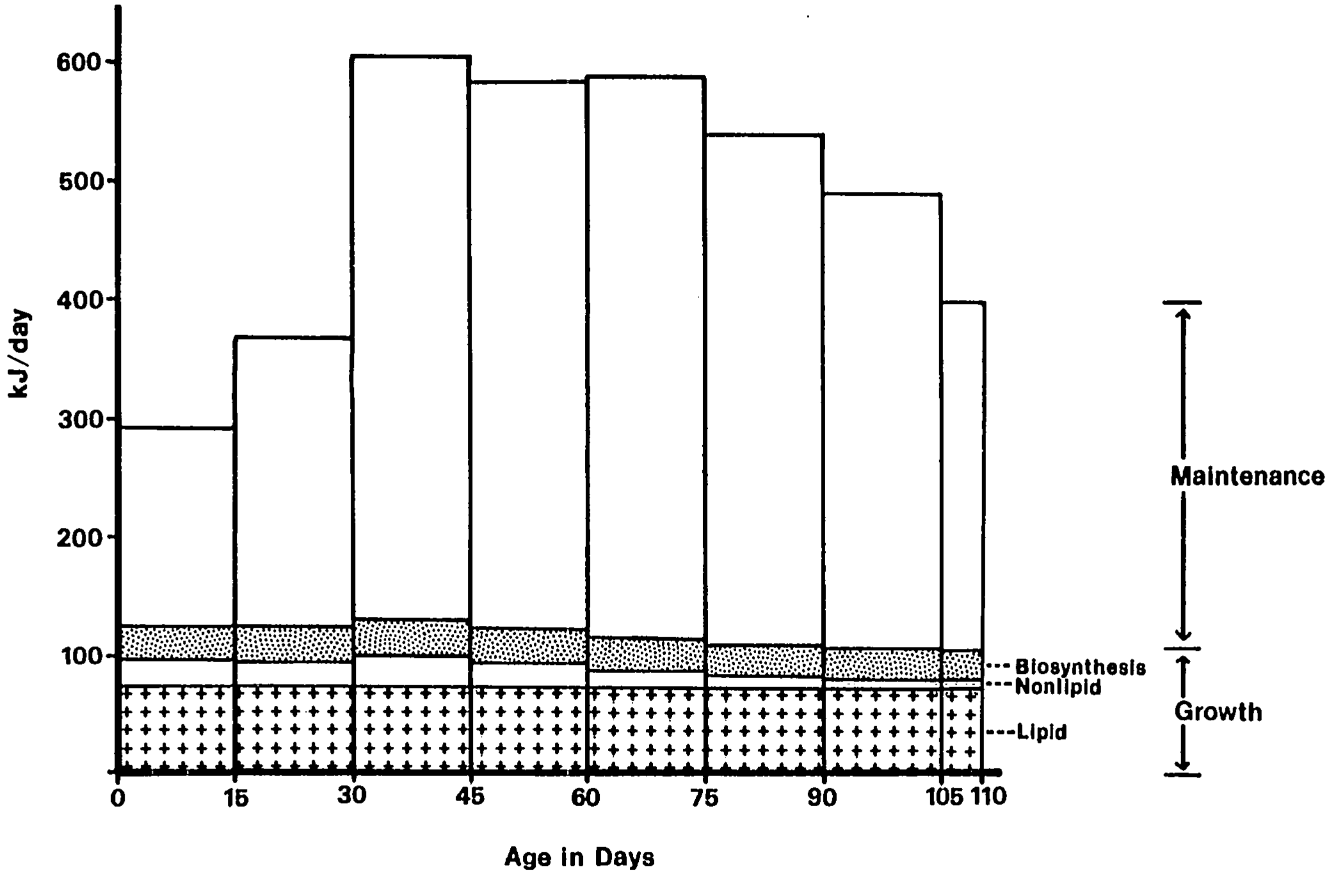

Figure 31. Energy budget of Dark-rumped Petrel nestlings. Rates were estimated from the accumulation of lipid and nonlipid matter (Ricklefs et al. 1980) and oxygen consumption.

(Chapter 2). Based on these calculations, the total energy requirement of a developing Dark-rumped Petrel nestling is estimated to be approximately 54,000 kJ.

The actual energy demands of nestling Dark-rumped Petrels are probably somewhat less than indicated by the oxygen uptake data. Behavioral observations (Chapter 2) indicate that chicks are inactive in the burrow, and spend most of their time resting quietly or sleeping on the nest. This behavior has obvious energetic benefits. Because chicks measured in the field never rested as quietly as they did in their burrows two chicks were monitored regularly for 24 hour periods to obtain some indication of the relationship between a chick's behavior and its energetic demands. The chicks were each about three months old and weighed aproximately 550 g. They were placed in a large ventilated chamber in a darkened room and their oxygen uptake was measured every two to three hours. The oxygen consumption of these chicks varied considerably depending the birds activity (Table 17).

These data give some indication of the relationship between a chicks activity and its metabolic rate. The rates for resting chicks are similar to those obtained for other nestlings of about the same age (Table 15). What is of significance though, is the reduced level of oxygen

Table 17. Nestling behavior and oxygen uptake in the Dark-rumped Petrel.

NESTLING AGE	BEHAVIOR	OXYGEN UPTAKE	
		ml/g hr	ml/hr
99 days	Active	2.8	1540.0
	Resting	1.8	990.0
	Sleeping	1.4	770.0
77 days	Active	3.0	1677.0
	Resting	1.8	1006.2
	Sleeping	1.2	670.8

consumption in sleeping chicks. It indicates that nestlings can reduce their metabolic rates by 20 to 30% below their alert resting rate by sleeping. Since chicks spend most of their time sleeping in the burrow it is probable that the energy budget calculated from field measurements may overestimate the actual energy demands of a developing Dark-rumped Petrel nestling.

A second estimate of the relationship between a chick's behavior and its metabolic rate was made by monitoring the heart rates of two nestlings over a 24 hour period. The chicks were fitted with a small ECG transmitter (E M Telemetry Transmitter #FM-1100-E1), returned to their burrows, and their heart rates were monitored regularly for at least 24 hours. Observations of the chicks activity were made in conjunction with the heart rate counts and the results (Table 18) show a relationship between behavior and metabolic rate similar to that derived from the measurement of oxygen uptake. Resting heart rates were slightly higher than the predicted value of 192 beats per minute obtained from Calder's (1968) predictive equation ($f_H = 763 \times W^{-0.23}$) based on bird weight (W).

Both of these measurements indicate the clear relationship between a chick's behavior and its metabolic demands. They suggest that inactive and sleeping nestlings use up to 30%

Table 18. Nestling behavior and heart rate in the Dark-rumped Petrel.

NESTLING AGE	BEHAVIOR	AVERAGE HEART RATE (Beats/Min.)
107 days	Active	251
	Resting	201
	Sleeping	195
105 days	Active	249
	Resting	203
	Sleeping	171

less energy than active chicks, a fact that must to a large extent explain their subdued behavior in the burrow. A similar relationship probably holds for incubating adults. The large percentage of time spent sleeping by incubating birds may permit the extremely long incubation shifts characteristic of this species. Estimates of the energetic demands of wild birds will always tend to be slightly inflated due to the unintentional agitation of the birds being measured. This problem is a factor in all field studies and data should always be viewed in that context.

Two recent studies have attempted to measure the true resting metabolic rate of wild birds by making the entire nest site into a metabolism chamber. Cavity nesting species are particularily suitable to this type of approach because their nests can be modified with a minimum of disturbance. Gessaman and Findell (1979) measured the metabolic rate of incubating American Kestrels (Falco sparverius) and Grant and Whittow (1983) estimated the energetic cost of incubation in the Laysan Albatross and the Bonin Petrel. Grant and Whittow's work on the Bonin Petrel is particularly relevant to the Dark-rumped Petrel since the two species are closely related. They measured the metabolic rates of a pair of adult petrels in one modified nest and found that the rate of oxygen uptake in incubating adults resting quietly on the nest was 18% less than the resting rate recorded in the laboratory. Thus, like the nestlings measured in this study it appears that adult petrels reduce their metabolic demands significantly when they are on the nest.

Grant and Whittow (1983) also estimated the respiratory quotient (RQ) of incubating Bonin Petrels and from it they derived a convincing theory of the metabolic processes and water balance of incubating procellariiformes. Their reasoning can be summarized as follows: They assumed that incubating birds were burning fat since their RQ was aprox. 0.7. This figure is similar to values for fasting bears (<u>Ursus</u> <u>americanus</u>) during winter sleep (Nelson et al. 1973) and fasting chickens (<u>Gallus</u> <u>gallus</u>) (Henry et al. 1934). They point out that when fat is burned the mass of oxygen used is equal to the mass of carbon dioxide lost. Thus, assuming that incubating birds do not eat, drink, or defecate, weight loss during incubation must be due entirely to water loss from the bird. This water could come from both the oxidation of fat (metabolic water production) and from body water stores. They found that birds did not become dehydrated during incubation, and they concluded that the water lost from the birds (ie weight lost) was equal to the metabolic water production over the interval. Metabolic water production is known to to be equal to 1.07 times the quantity of fat consumed

(Schmidt-Nielsen 1975). Therefore, the amount of fat burned by an incubating bird equals metabolic water loss divided by 1.07 which equals body mass loss divided by 1.07. That is, given these assumptions, if we divide the weight loss of a bird during an incubation shift by 1.07 we can estimate the amount of fat oxidized by the bird over the interval. Since fat produces approximately 39.7 kJ/g (Petrusewicz and Macfayden 1970), we can estimate the metabolic rate of the incubating bird.

This is a very handy method for estimating the metabolic rate of an incubating procellariiform and it can be compared to estimates obtained by other methods. For example, it provides a useful comparison with the estimates of metabolic rate in the Dark-rumped Petrel made from measurements of oxygen uptake. Dark-rumped Petrel incubation shifts can extend for up to 23 days, perhaps the longest of any procellariid, and it is likely that they also metabolize fat over those intervals. One adult bird was weighed over a twelve day incubation shift and it lost 85 g or an average of 7.08 g/day. This value is equivalent to an estimated loss of 1.7% of body weight per day which is slightly higher than average daily loss of 1.2% reported for two species of albatross (Prince et al. 1981). Given the assumptions just discussed, this bird would have used 7.08/1.07 or 6.62 g of fat per day. This is equivalent to an energetic demand of 6.62 g/day x 39.7 kJ/g or about 263 kJ/day. If we assume, as discussed previously, that alert resting adult petrels use about 760 ml oxygen/hr we then find that they burn about .760 l/hr x 24 hr/day x 20.1 kJ/l = 366.6 kJ/day. Thus, it appears that incubating Dark-rumped Petrels metabolize about 28% (263/366) less energy than they do in an alert resting state. These data suggest that both adults and nestlings are capable of substantially reducing their energetic needs while they are on the nest. These findings correlate well with the behavioral observations of nestlings and incubating adults (Chapter 2).

The proventricular temperatures of birds were measured with a Wescor model TH-65 digital thermocouple thermometer calibrated against a laboratory mercury thermometer in a water bath. Adult Dark-rumped Petrels have an average core temperature of 38.6 °C (Table 19). This is very close to the average of 38.78 °C reported by Warham (1971) for 31 species of petrels. Chicks are capable of thermoregulation from shortly after hatching, but their temperatures are quite variable for the first two weeks (Table 19). They do not appear to require much brooding by their parents, and although some adults remain in the burrow for up to six days after their chicks hatch, most depart within two days. Those that remain with their

Table 19. Body temperatures of Dark-rumped Petrels in degrees centigrade.

AGE	N	AVERAGE TEMPERATURE	S.D.	RANGE
ADULT	9	38.6	1.1	36.8 - 40.5
LESS THAN TWO WEEKS	13	35.2	2.1	31.7 - 38.4
MORE THAN TWO WEEKS	14	37.5	0.96	36.4 - 39.7

chicks often do not brood them directly, but rest next to them on the nest and feed them at regular intervals.

It appears that the ability of an adult to feed its chick may determine the length of the brooding period. Chicks that are only brooded for a short period develop normally as long as they are fed regularly. Well fed chicks can maintain near adult internal temperatures shortly after hatching, but changing food reserves can cause their temperatures to fluctuate over a range of several degrees. Chicks with low body temperatures are characteristicly light in weight, often shivering, and in extreme cases show signs of hypothermia such as closed eyes and lethargic semi-conscious behavior. As in other procellariiformes, (Boersma et al. 1980, Ricklefs et al. 1980a, Simons 1981a), Dark-rumped Petrel chicks are capable of remaining in this state of partial torpor for periods of several days, occasionally longer, and they recover quickly when they are brooded and fed by their parents.

Nestling Feeding Rates

Knowledge of the metabolic requirements of adult and nestling Dark-rumped Petrels can be helpful in understanding the adaptive significance of other aspects of the bird's breeding biology, such as the attendance and chick feeding patterns of breeding adults. I monitored 10 - 12 active Dark-rumped Petrel nests during each year of the study using an event recorder (Simons 1981a,1981b). The recorder provided information on the frequency of visitations at each burrow which, when combined with other data, can be helpful in understanding several patterns in the reproduction of these birds.

Table 20 summarizes the estimated feeding rates in the Dark-rumped Petrel. The table was derived from several sources, including, the weight loss of fasting chicks, weight changes of nestlings, and data from event recorder monitored burrows. Because the only accurate way to determine food load size, ie. weighing chicks before and after each feeding, was not possible, I used average chick weight loss during periods of fasting (Table 21), and changes in chick weight to estimate the size of the food loads delivered by adult birds. The weight loss of chicks between feedings is variable, and depends on the initial size and age of the chick, the size of the most recent feed, and the duration of the fast. The rate of weight loss is high following a large feed and declines throughout the fasting period. The values in Table 21 indicate average rates from fasts lasting from one to eight days. For simplicity, the following average values were used as average rates of weight loss; 15 g/day in chicks age 0 -

Table 20. Estimated feeding rates in Dark-rumped Petrel nestlings[1].

Chick Age (days)	N[2]	Est. food delivered to chick (g)	% Total food	Avg. number chick feeding visits	Est. Avg. Food load size (g)
0 - 30	9	791.66 (52.98)	32	12.50 (1.77)	63.33
31 - 60	10	901.53 (173.77)	36	14.33 (4.03)	62.87
61 - 90	9	682.55 (79.70)	27	12.33 (3.28)	55.36
91 - 120	9	114.67 (67.54)	5	3.22 (1.92)	35.61
0 - Fledging (Total)	7	2501.71 (94.64)	100	44.50 (7.61)	56.22

1 Values in parentheses are one standard deviation.
2 Event recorder-monitored chicks.

Table 21. Weight loss in fasting Dark-rumped Petrel nestlings.

Age (days)	N	Average fasting weight loss (g/day)
0 - 15	14	14.6 (8.6)
16 - 30	18	18.6 (11.2)
31 - 60	25	17.2 (9.5)
61 - 90	17	23.7 (8.9)
91 - 120	38	13.1 (4.0)

15, 20 g/day in chicks age 16 - 60, 25 g/day in chicks age 61 - 90, and 13 g/day in chicks older than 90 days. These are rough estimates, but on average they fit well with the nestling weight data. By combining these estimates with event recorder information on the rate of burrow visitation by adult birds and chick weights, I was able to estimate the feeding rates of adult birds. I did this for 12 chicks that were monitored over the three years of the study. An example of the calculations for a single chick is shown in Table 22. Table 20 summarizes all of the data and breaks it down by age interval. Of interest in this data is the fact that feeding rates are maximum between 30 and 60 days which coincides with the period of maximum chick growth, the inflection point of the logistic chick growth curve (Ricklefs 1967,1968). Maximum estimated food load sizes ranged from less than ten grams to over 110 grams which is about 26% of mean adult weight. This is probably close to the maximum adult seabirds can carry (Ashmole 1971). This is especially likely in the Dark-rumped Petrel in light of the altitude and distance from the sea of their nesting colonies. Nestlings were fed almost 70% of their total food during the first half of the nesting period and about 95% of their total by the time they are 90 days old. Chicks, on average, are only fed a few times during their last month on the nest which suggests that, like the Leach's Storm Petrel (Ricklefs et al. 1980), they must store and

Table 22. Chick weight changes, burrow visitation, and estimated chick feeding rates at one Dark-rumped Petrel nest.

Nestling Age (days)	Date	Nestling weight (g)	Interval length (days)	# Feeding visits	Nestling weight gain/ loss (g)	Estimated metabolic weight loss (g)	Estimated total food delivered in interval (g)
0	6/30	60					
2	7/2	94	2	1	34	30	64
3	7/3	85	1	0	-9	15	-
4	7/4	80	1	0	-5	15	-
7	7/7	148	3	1	68	45	113
9	7/9	234	2	1	86	30	116
11	7/11	286	2	1	52	30	82
15	7/15	323	4	2	37	60	97
17	7/17	359	2	1	36	40	76
20	7/20	373	3	1	14	60	74
23	7/23	395	3	1	22	60	82
24	7/24	385	1	0	-10	20	-
25	7/25	386	1	1	1	20	21
26	7/26	375	1	0	-11	20	-
27	7/27	405	1	1	30	20	50
28	7/28	379	1	0	-26	20	-
29	7/29	363	1	0	-16	20	-
30	7/30	352	1	0	-11	20	-
33	8/2	413	3	1	61	60	121
37	8/6	572	4	3	159	80	239
44	8/13	538	7	2	-34	140	106
49	8/18	470	5	0	-68	100	-
52	8/21	654	3	2	184	60	244
58	8/27	687	6	2	33	120	153
61	8/30	630	3	0	-57	75	-
64	9/2	580	3	0	-50	75	-
68	9/6	800	4	4	220	100	320
71	9/9	712	3	0	-88	75	-
74	9/12	662	3	0	-50	75	-
77	9/15	792	3	1	130	75	205
80	9/18	846	3	2	54	75	129
83	9/21	820	3	1	-26	75	49
86	9/24	798	3	1	-22	75	53
91	9/29	700	5	0	-98	85	-
98	10/6	662	7	1	-38	91	53
103	10/11	594	5	0	-68	65	-
105	10/13	562	2	0	-32	26	-
109	10/17	537	4	0	-25	52	-
112	10/20	502	3	0	-35	39	-
113	10/21	490	1	0	-12	13	-
114	10/22	482	1	0	-8	13	-
117	10/25	452	3	0	-30	39	-
118	10/26	442	1	0	-10	13	-
119	10/27	432	1	0	-10	13	-
120	10/28	422	1	0	-10	13	-
121	10/29	Fledged					
							Total 2447 g

metabolize a large amount of fat prior to fledging. However, there is much variability in the fledging pattern since chicks are deserted entirely for up to three weeks before fledging, whereas others are visited and fed immediately prior to fledging (Chapter 2).

Caloric Analysis of Nestling Food

In August and September 1981 I collected six Dark-rumped Petrel food samples for caloric analysis. All of the samples were obtained from adult birds returning to feed their chicks. The samples were frozen soon after weighing, and at a later date, they were thawed and dried to a constant mass in an oven at 45°C. The water content of the samples was determined by subtracting the dry mass fraction from the initial weight. Dried samples were homogenized by blending with a mortar and pestle, and the caloric content of approximately 10 mg samples was determined using a Phillipson micro-bomb calorimeter, with a benzoic acid standard. Duplicates of each sample were assayed. The ash content was determined by burning 6 aliquots of each dried sample in a muffler furnace at 600°C for 6 hours. The caloric content of the stomach oil was determined by adding a known amount (approximately 3 mg) to 10 mg pellets of enriched baking flour with a predetermined caloric content (16.73 kJ/g dry S.D. 0.020).

The total caloric content of the stomach oil and flour pellet was measured with the micro-bomb calorimeter, and the caloric content of the oil was determined by subtracting the caloric content of the flour.

The caloric analysis is summarized in Table 23. Combining this information with the physiological and behavioral data discussed previously provides several additional insights into the feeding ecology of these birds. Using the information in Table 16 and Figure 31, I have estimated that adult petrels need to deliver about 54,000 kJ of energy to raise their chicks. From Table 23 we find that the fish and squid that petrels feed on provide between 4.5 and 5.0 kJ of energy per gram. These values are similar to those reported by other authors. Clarke and Prince (1980) reported wet weight caloric values of 4.51 kJ/g for krill, 4.64 kJ/g for squid, and 5.61 kJ/g for fish from food samples of two species of albatross. Assuming an assimilation efficiency of 80% (Wiens and Scott 1975), the caloric analysis leads us to the conclusion that if adult petrels were only feeding their chicks fish and squid, they would have to deliver over 14,000 grams of food during the nestling period. This estimate conflicts with the feeding data obtained from event recorder monitored chicks (Table 20), and in fact it is more than five times the amount of food adult birds are estimated to bring to their chicks.

Table 23. Analysis of Dark-rumped Petrel food samples.

Sample #	Description	Fresh Weight (g)	%H_2O	%Ash[1]	kJ/g[2] dry	kJ/g ash-free	kJ/g wet
1	Oil and digested food	49.38	78.7	6.21	24.38	25.90	5.19
2	Digested fish-squid	49.96	79.4	7.71	22.01	23.70	4.53
3	Digested squid	34.99	78.0	8.23	21.82	23.62	4.80
4	Digested squid	23.00	76.2	8.41	20.95	22.72	4.99
5	Squid pieces	40.40	78.1	8.78	21.63	23.53	4.74
6	Oil	-----	-----	----	41.74	-----	-----

1 Six determinations per sample
2 Two determinations per sample

The missing factor appears to be stomach oil.

The Ecological Significance of Petrel Stomach Oil

The stomach oil of petrels has puzzled and intrigued researchers for decades. The oil, which is peculiar to birds in the Order Procellariiformes, is a fine light transparent oil varying in color from light yellow to a deep red, and is stored by the birds, often in large quantities, in the fore-gut or proventriculus (Warham 1976,1977, Jacob 1982). Many species are capable of regurgitating their oil for defensive purposes, and there are numerous accounts of the effectivness of this anti-predator behavior (Warham 1977, Jacob 1982). Some of the species that are thought to have died as a result of plumage contamination by petrel stomach oil include, eagles (Dennis 1970), owls, herons and gulls (Broad 1974), ravens, and even Peregrine Falcons (*Falco peregrinus*)(Booth 1976, Clarke 1977).

The nutritive value of stomach oil was suspected by early researchers because it is fed to nestlings, and it is found in many species that do not use it extensively for defensive purposes. Early workers concluded that the oil was secreted by special glands in the proventriculi of adult birds (Mathews 1949). Subsequent work has shown that this is not the case, and it is now generally agreed that stomach oil is strictly of dietary origin (Lewis 1966,1969; Cheah and Hanson 1970a,b; Clarke and Prince 1976; Imber 1976; Warham 1976,1977). The oil is composed mostly of wax esters and/or triglycerides which are thought to be concentrated from the fish, squid and crustaceans that constitute the principal prey of most procellariiformes (Warham 1976,1977). The caloric value of the oil is high (slightly less than that of commercial diesel oil), and in eleven species studied by Warham (1976), it ranged in value from 39 - 41 kJ/g and averaged 40.3 kJ/g. Stomach oil of the Laysan Albatross analyzed by Pettit and Whittow (unpbl. data) ranged in caloric value from 34 - 61 kJ/g averaging 46.0 kJ/g.

Procellariiformes, in general, rely on a food resource that is unpredictable in time and space and often dispersed at considerable distances from their breeding grounds (Lack 1966,1967,1968). Ashmole was one of the first authors to speculate on the role of stomach oil in allowing these birds to utilize such a food resource (Ashmole and Ashmole 1967, Ashmole 1971). They postulated that stomach oil would provide adult birds with an efficient vehicle for the transportation of a highly concentrated, high-energy food supply to their nestlings. Warham (1977) and others have also speculated that stomach oil is important in allowing adult birds to maintain the long incubation shifts that are characteristic of procellariiformes, and in allowing nestlings to survive extended fasting periods between feedings.

Some indirect evidence can be found to reinforce these views. We might expect that oil would be most important to chicks early in the nestling period when their relative energetic demands are highest. Rice and Kenyon (1962) found that oil was an important component in the diet of young Laysan and Black-footed Albatrosses and Boersma et al. (1980) found that Fork-tailed Storm Petrel adults delivered more oil to their chicks during the first half of the nestling period. Warham (1962) reported that Giant Petrel (Macronectes giganteus) chicks contained stomach oil up to 14 days after their last meal, suggesting that it may be acting as an energetic reserve, although it is not known if nestling procellariiformes are capable of concentrating stomach oil from the raw food fed to them by their parents. Dark-rumped Petrel chicks have been observed to requrgitate oil more than ten days after their last feeding. Finally, it is interesting to note that the only procellariiform that does not appear to utilize stomach oil is the Common Diving Petrel (Pelecanoides urinatrix) (Warham 1977). This species is ecologically very different from the rest of the procellariiformes. It is a near-shore feeder that feeds its chicks daily, and it apparently does not require a concentrated food supply like the rest of the petrels.

This study provides evidence that stomach oil plays a key role in the reproduction of the Dark-rumped Petrel. The stomach oil of the Dark-rumped Petrel is over nine times richer in calories than the fish, squid, and crustaceans from which it is derived (Table 23). Since it is clear that adult birds are not feeding their chicks anything near the 14,000 or so grams of raw food that they would require during their development, the adults must be making up the caloric deficit with stomach oil. These data indicate that if 40 - 50% of the food adult petrels delivered to their chicks was oil they would be able to meet their chicks energetic demands and still deliver only about 2500 g of food during the nestling period. I have no data on the percentage of oil in the nestlings diet, but based on a visual estimate of the regurgitations I've seen, this percentage of oil seems reasonable. Thus, the use of stomach oil in the Dark-rumped Petrel can be viewed as an adaptation to the unpredictable and widely dispersed food supply upon which the birds rely. In one sense the adaptation is ecologically equivalent to the production of milk by pigeons, or mammals for that matter, or the storage of high energy oils by crustaceans for use when food supplies dwindle.

These findings raise a number of questions that remain to be answered. We still know nothing about how stomach oil is metabolized by the birds nor do we know how or with what efficiency it is extracted from raw food the petrels eat. Is the oil stored by adult birds prior to the breeding season or is it synthesized on a continual basis? Would adult birds be capable of raising a chick entirely on raw food or would this require too many and too frequent feeding trips to the colony? Is stomach oil essential for adult birds maintaining long incubation shifts? Much work remains to be done, but it is becoming clear that stomach oil is an important ecological adaptation for breeding in procellariiformes and understanding its role will provide significant insights into the overall ecology of these birds.

Reproductive Energetics of Four Species of Seabirds

In Table 24 I have compared the results of this study with recent work on Leach's Storm Petrels (Ricklefs et al. 1980) and Common (*Sterna hirundo*) and Sooty Terns (*Sterna fuscata*) (Ricklefs and White 1981). The purpose of the comparison is to determine if any patterns exist that distinguish the two procellariiformes with their relatively

Table 24. Reproductive energetics of four species of seabirds.

Species	Brood Size	Mass of newly hatched chick (g)	Adult mass (g)	Adult - neonate mass (g)	Fledgling period /fledgling mass (days/g)	Fledgling period (days)	Total energy required (kJ)	Energy /g. fledgling (kJ/g)	Energy delivery rate (kJ/day)
Leach's Petrel[1]	1	7.3	45.0	37.7	1.59	60	4811.97	127.63	80.20
Dark-rumped Petrel[2]	1	60.0	425.9	365.9	0.30	111	52222.50	142.7	470.50
Common Tern[3]	3	14.9	111.5	(289.8)	(0.01)	30	(13228.68)	45.65	(440.96)
Sooty Tern[3]	1	20.5	176.7	156.2	0.32	50	5864.06	37.54	117.28

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1 Ricklefs et al. 1980

2 This study

3 Ricklefs and White 1981. Values in parentheses for the Common Tern represent the total expenditure for a brood of three.

long development periods from the more rapidly developing terns. In addition, it allows the comparison of the Common Tern, with relatively rapid growth, and the Sooty Tern with relatively slow growth, to the other species studied to date.

Both the Leach's Storm Petrel and the Dark-rumped Petrel are slow growing procellariiformes that raise at best a single chick to fledging each season. Both are thought to utilize a variable offshore food resource. The two species of terns develop more rapidly but the breeding biology of the Sooty Tern resembles that of the petrels. Sooty terns lay a single egg, they are offshore feeders, and they develop slowly when compared to other terns. Common Terns, on the other hand, raise two to three chicks each season and the chicks develop rapidly. They are nearshore feeders and their food supply appears to be more abundant and predictable. For the purpose of emphasis it was assumed in Table 24 that Common Terns fledged three chicks each season although in some seasons fledging success is lower (Langham 1972).

Several trends are suggested. When the fledgling period is expressed as fledgling period/fledgling mass or days/gram the Leach's Storm Petrel has the highest ratio by a factor of at least five. The Dark-rumped Petrel and the slow growing Sooty Tern are similar in this respect with a ratio of about 0.30 while the Common Tern has a ratio of only about 0.10. Thus the species with the shortest fledgling period also accumulates fledgling tissue most rapidly. It has been demonstrated that procellariiformes produce eggs that are high in yolk and therefore energetically expensive (Ackerman et al. 1980; Grant et al. 1982). It is also clear that the petrels require considerably more energy to produce a gram of fledgling than other seabirds such as terns. This may relate to the fact that the petrels deposit more fat than the terns or be due to a lower requirement to produce heat for thermoregulation in the terns. Thermoregulation costs may also explain the values for energetic cost/gram of fledgling produced in the two tern species which are opposite to what we might predict on the basis of fledgling period. The Dark-rumped Petrel has the highest energy delivery rate followed by the Common Tern, the Sooty Tern and the Leach's Storm Petrel.

Without additional information, it is difficult to interpret these figures any further. It is important to understand that the breeding biology of these birds is molded to a large extent by their feeding ecology. Until we understand where and how these birds feed, what they eat and its caloric value, and how efficient they are at converting that food into tissue, the patterns in these data will continue to be obscured.

Adaptations of the Egg of the Dark-rumped Petrel

The Haleakala Dark-rumped Petrel population survives today because the birds nest at an elevation of almost 3000 meters. This is one of the highest nesting sites known for any seabird and it offered protection to the birds since, until very recently, it was above the normal range of most predators. The survival benefits of this nesting location are coupled with physiological and energetic costs. In this section I will discuss the results of a joint study with Dr. C.G. Whittow (Whittow et al. 1983) which examined the adaptations of the Dark-rumped Petrels's eggs to the unusual environment in which the birds reproduce.

At this altitude, the low barometric pressure poses two fundamental problems for bird eggs. The problems stem from the high diffusion coeficients of gasses at low pressure, and the reduced partial pressure of oxygen at high elevations. At the summit of Haleakala, the partial pressure of oxygen is less than 70% of that at sea level (Folk 1974). In addition, the diffusion coeficients of all gasses at that altitude are significantly higher than they are at sea level (Paganelli et al. 1975; Carey 1980). High diffusion rates help offset the reduced partial pressure of oxygen in the atmosphere by increasing the rate of diffusion of oxygen into the egg, but they are also responsible for a more rapid loss of water from the egg. Therefore, the eggs of the Dark-rumped Petrel must strike a balance between the conflicting requirements of providing oxygen to the embryo and conserving water. These requirements are intensified since, like all procellariiform birds, the incubation period of the egg is long in relation to the size of the egg. Long incubation periods have been shown to be associated with reduced rates of gas transfer, including water vapor, between the egg and its surroundings (Whittow 1980). We studied the regulation of water loss in Dark-rumped Petrel eggs to determine how the eggs have been influenced by the combined selective pressures of high altitude nesting and prolonged incubation.

The following predictive equations were taken from the literature and used to evaluate the results of this aspect of the study: MH_2O (mg/day) = 13.243 x $W^{0.754}$ (Ar and Rahn 1980), GH_2O (mg/day torr) = 0.843 x $W^{0.814}$ (Ar and Rahn 1978), Shell Thickness (mm) = 0.05126 x $W^{0.456}$ (Ar et al. 1974), Pore area (mm^2) = 0.0092 x $W^{1.236}$ (Ar et al. 1974), # of Pores = 1449 x $W^{0.42}$ (Tullet and Board 1977), Nest Ventilation (l/day) = $MH_2O/(C\ nest - C\ air)$ (Rahn and Dawson 1979), Incubation Period (days) = $12.03 \times W^{0.217}$ (Rahn and Ar 1974), Egg Surface Area (mm^2) = $4.853 \times W^{0.662}$ (Paganelli et al. 1974); Where W stands for fresh egg weight, C nest and C air stand for the water vapor content of the air in the nest microclimate and ambient air, respectively.

During the study I recorded the incubation period of 11 eggs. The average incubation period, 55.27 days (S.D.= 1.1 days). is significantly longer than the incubation periods for 22 eggs reported by Coulter (1982) for Dark-rumped Petrels breeding at lower elevations in the Galapagos Islands (Mean = 50.0 days S.D. 4.65 days, $t = 4.82$, $p < 0.001$). I also recorded the mass of five freshly-laid eggs which averaged 76.87 g (S.D. 0.93 g) (Table 1). According to the predictive equations of Rahn and Ar (1974) the incubation period of an egg this size should be 30.87 days. Therefore, the incuabtion period of the egg is 179% longer than predicted. This is characteristic of most procellariiform birds, but these data suggest that in the Hawaiian Dark-rumped Petrel the incubation period is further prolonged by high altitude nesting.

I determined the water loss (MH_2O) of six naturally-incubated eggs according to the methods of Rahn and Ar (1974) by weighing the eggs at the nest site with an

Ohaus triple beam balance. All eggs were weighed twice at intervals of 26-34 days. The average daily water loss from these eggs (Table 25) was only 78.5% of the predicted value based on the equations developed by Ar and Rahn (1980). This reduction could be the consequence of two factors, because egg water loss is determined by the water vapor conductance of the shell (GH_2O) and the water vapor pressure differential between the inside and the outside of the shell (ΔPH_2O) according to the following relationship:

$$MH_2O = GH_2O \times \Delta PH_2O \qquad \text{(Rahn and Ar 1974)}$$

The influence of each of these factors will be discussed separately. The first factor, the water vapor conductance of the shell (GH_2O) is a function of the ease with which water vapor may pass through the shell. Over the course of the study I was able to collect five intact eggs which had been ejected from petrel nests by unsuccessful breeders, and these eggs were used to measure GH2O in the laboratory. The eggs were placed in a dessicator containing silica gel, and they were weighed daily for five days. Based on these measurements, the water vapor conductance (Table 25) was calculated according to the methods of Ar et al. (1974). This value was only 67% of the

Table 25. Physical characteristics and water loss of Dark-rumped Petrel eggs.

	N	Mean	SD
Rate of water loss, MH_2O (mg/day)	6	275.08	65.96
Shell water vapor conductance GH_2O, (mg/(day x torr))	5	8.82	1.62
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
Number of pores (pores/cm^2)	6[*]	52.77	7.36

[*] 720 measurements on 6 eggs

predicted value for an egg of this size based on the equations derived by Ar and Rahn (1978). Therefore, the rate of water loss from these eggs must, to a significant degree, be the result of the low water vapor conductance of the shell.

Water vapor diffuses out of the egg through pores in the shell, and for this reason the water vapor conductance of the shell is a function of the shell thickness, the number of pores in the shell, and the total pore area of the shell. Each of these factors was estimated in an effort to determine their relative importance in the eggs of the Dark-rumped Petrel. Egg shell measurements were made on shells from 19 eggs which failed to hatch . The eggs were dried in a dessicator for at least ten days, and measurements were made using a Starrett model 230 micrometer calipers, which could be read to an accuracy of 0.0245 mm. The average shell thickness (Table 25) was only 70.1% of the predicted value for an egg of this size based on the equations of Ar et al. (1974). It is not yet clear why the egg shell in this species is as thin as it is. Rahn et al. (1977) reported only a slight reduction in shell thickness with altitude in the Red-winged Blackbird (Agelaius phoeniceus) and the native Indian Chicken (Gallus gallus). In addition, there is no evidence of chlorinated hydrocarbon contamination in this species. All of the egg and tissue samples analyzed thus far have shown extremely low levels of both chlorinated hydrocarbons and PCB (Chapter 2; King and Lincer 1973). Nevertheless, because the shells of these eggs are almost 30% thinner than predicted, shell thickness does not explain the low values for water vapor conductance in these eggs. Therefore, conductance must be related to the number or size of the pores in the shell.

Ar et al. (1974) have derived a formula based on Fick's law of diffusion for calculating the total functional pore area (Ap) of an egg. Their formula incorporates shell thickness and water vapor conductance. The total functional pore area calculated from this formula is 1.1 mm^2, which is only 79% of the predicted value for an egg of this size. This low functional pore area could be the result of a smaller number of pores or of pores that are of smaller than normal diameter. To determine which was the cause, we counted the number of pores in a sample of eggs using the method described by Tyler (1953). We then calculated the average number of pores per egg based on average egg surface area (Paganelli et al. 1974) which yielded a average value of 4,520 pores per egg. This value is only 50.4% of the predicted value based on egg weight (Tullett and Board 1977). In contrast, the mean area of an individual pore, which is calculated by dividing the number of pores into the total pore area, yielded a value of 208.7 um^2 which is very close to the predicted value for an egg of this size (Whittow 1983). Therefore, we concluded that the low water vapor conductance and low pore area of the Dark-rumped Petrel egg shell was due to a smaller number of pores in the shell.

Measurements of Dark-rumped Petrel eggs are summarized in Table 26. Eggs were measured with a dial calipers accurate to 0.0254 mm. Egg volume was determined by weighing the eggs in air and in water according to the method described by Rahn et al. (1976). Shell mass was measured on eggs that had been dried in a desiccator for at least one week. The eggs of the Hawaiian Dark-rumped Petrel are significantly larger ($p < 0.001$) than those of the Galapagos race, which nests at lower elevations (Harris 1970, Coulter 1982). This is similar to the finding of Rahn et al. (1977) who reported that the eggs of Red-winged Blackbirds were larger at higher nesting sites. The average value for shell mass was only 60.7% of the predicted value for an egg of this size based on the equations of Paganelli et al. (1974). This appears to be a consequence of the thinness of the egg shell.

If we know the rate of water loss from an egg and the water vapor conductance of the egg shell, we can also calculate

Table 26. Measurements of Dark-rumped Petrel eggs.

	N	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

the water vapor pressure difference between the inside of the egg and the micro-climate surrounding the egg by employing the equation discussed previously. In order to do this, the water vapor conductance of the egg (GH_2O), which was calculated in the laboratory, must be converted to the conditions of temperature and pressure that prevail at the nest site. Barometric pressure at the summit of Haleakala is quite constant during the summer months averaging 537.0 mm Hg. I estimated the incubation temperature of a petrel egg by fitting a chicken egg with a thermistor probe and substituting it for a petrel's egg. The temperature was recorded on a Wescor model TH-65 thermocouple thermometer which had been calibrated in the laboratory. The adult petrel incubated the chicken egg readily, and after 85 min. the temperature of the egg was steady at 34.9 °C. This incubation temperature is slightly lower than the average of 35.6°C for 27 species reported by Ar and Rahn (1980) which is typical of procellariiformes (Whittow 1980, 1983). Using these estimates for the pressure and temperature at the nest site, the corrected value of GH_2O is estimated to be 12.68 mg/day torr. By dividing this figure into the value for egg water loss we obtain an estimate for ΔPH_2O of 21.69 torr. ΔPH_2O is a measure of the water vapor pressure gradient between the egg and the nest site. This gradient is determined by the micro-environment of the nest site itself and the behavior of the incubating adult petrel. We can estimate the the water vapor pressure at the nest site (PH_2O nest) if we know the incubation temperature of the egg. If we assume that the contents of the egg are saturated with water vapor, then at an incubation temperature of 34.9°C the water vapor pressure inside the egg (PH_2O egg) would be 41.9 torr. Because (PH_2O egg) − (PH_2O nest) = ΔPH_2O we can estimate the water vapor pressure of the nest by subtracting the water vapor pressure difference (ΔPH_2O =21.69) from the water vapor pressure inside the egg (PH_2O egg =41.90). This gives us an estimate of 20.21 torr for the water vapor pressure of the nest which is close to the average value of 19 torr for 23 species of birds reported by Ar and Rahn (1978). Therefore, the low value for water vapor pressure gradient (ΔPH_2O) in this species cannot be explained by the incubation temperature of the egg or the water vapor pressure at the nest site. Other factors may be involved such as the climate at the summit of Haleakala or the incubation behavior of adult birds.

The summer climate at the 3000 m summit of Haleakala is cool and dry. I made 93 measurements of burrow temperatures which averaged 10.39 °C (S.D. 2.24) in the daytime and 8.00 °C (S.D. 1.72) at night (Chapter 2).

Lyons (1979) reported that humidity at the summit averaged less than 50% of that at sea level with the lowest levels occurring during May and June, which coincides with the incubation period of the Dark-rumped Petrel. I recorded relative humidities, with a Psychrodyne wet-dry bulb hygrometer, of less than 7% at nest sites during incubation. The average humidity measured at one nest over a 24 hr period during incubation was 20.3% (S.D. = 7.4%, N = 12). Whittow (pers. comm.) made nine measurements adjacent to petrel nests during incubation which averaged approximately 3 torr. These measurements suggest a water vapor pressure gradient between the nest site and the surrounding environment of about 17 torr, which is considerably higher than that reported for any other seabird (Whittow 1983).

Thus, although the vapor pressure gradient between the bird's nest and the surrounding atmosphere is high, the gradient between the egg and the nest is surprising low. Rahn and Ar (1974) have pointed out that ΔPH_2O can be influenced by the nest type, the incubation behavior of the bird, or climatic conditions. In addition, Rahn and Dawson (1979) have shown that the degree of nest ventilation required of the incubating bird is a function of the water vapor pressure differential between the nest and the surrounding air. In birds with a low differential, a considerable degree of nest ventilation is required of the incubating bird. Given the large differential, and potentially dessicating environment, encountered by the eggs of the Dark-rumped Petrel, we might expect low levels of nest ventilation in this species. Calculation of the nest ventilation rate for the Dark-rumped Petrel, using the equation of Rahn and Dawson (1979), yielded a value of 17.2 l/day, lower than that for any other seabird (Whittow 1983). This low level of nest ventilation should be reflected in the incubation behavior of the adult birds. There is some evidence of this in the Dark-rumped Petrel. A study of the behavior and attendance patterns of incubating birds, utilizing direct observations from a television-monitored nest, and indirect observations from event recorder monitored burrows, indicated that incubating adults spent almost the entire incubation period in close contact with the egg (Chapter 2). Adult birds maintain continuous incubation shifts of up to 23 days (some of the longest recorded for any seabird), and aside from the three or four occasions on which they exchange incubation duties, and infrequent brief trips to the burrow entrance by incubating adults, the eggs are covered continuously. Exposure of the eggs to ambient conditions occurs rarely, and I estimated that the egg is unattended for less than 10 minutes during an average incubation shift (Chapter 2).

In summary, we found that the eggs of the Dark-rumped Petrel had lower rates of water loss from the egg, lower rates of water vapor conductance through the shell, thinner shells, and a smaller number of pores in the shell than would be predicted on the basis of the size of the egg. All of these characteristics are associated with prolonged incubation (Whittow 1980,1983), and high altitude nesting (Rahn et al. 1977; Carey 1980). We attempted to distinguish the relative importance of these two factors by employing the predictive equations of Ar and Rahn (1978) and Rahn and Ar (1980) which incorporate both egg mass and incubation period (Figure 32). This analysis points out that the adaptations of the Dark-rumped Petrel's eggs are primarily adaptations to the long incubation periods characteristic of most procellariiformes. On the other hand, the fact that the rates for water loss, shell conductance, and estimated pore area were all higher than the predicted values which incorporated incubation period suggests that the eggs morphology may also be influenced by the constraints of high altitude nesting.

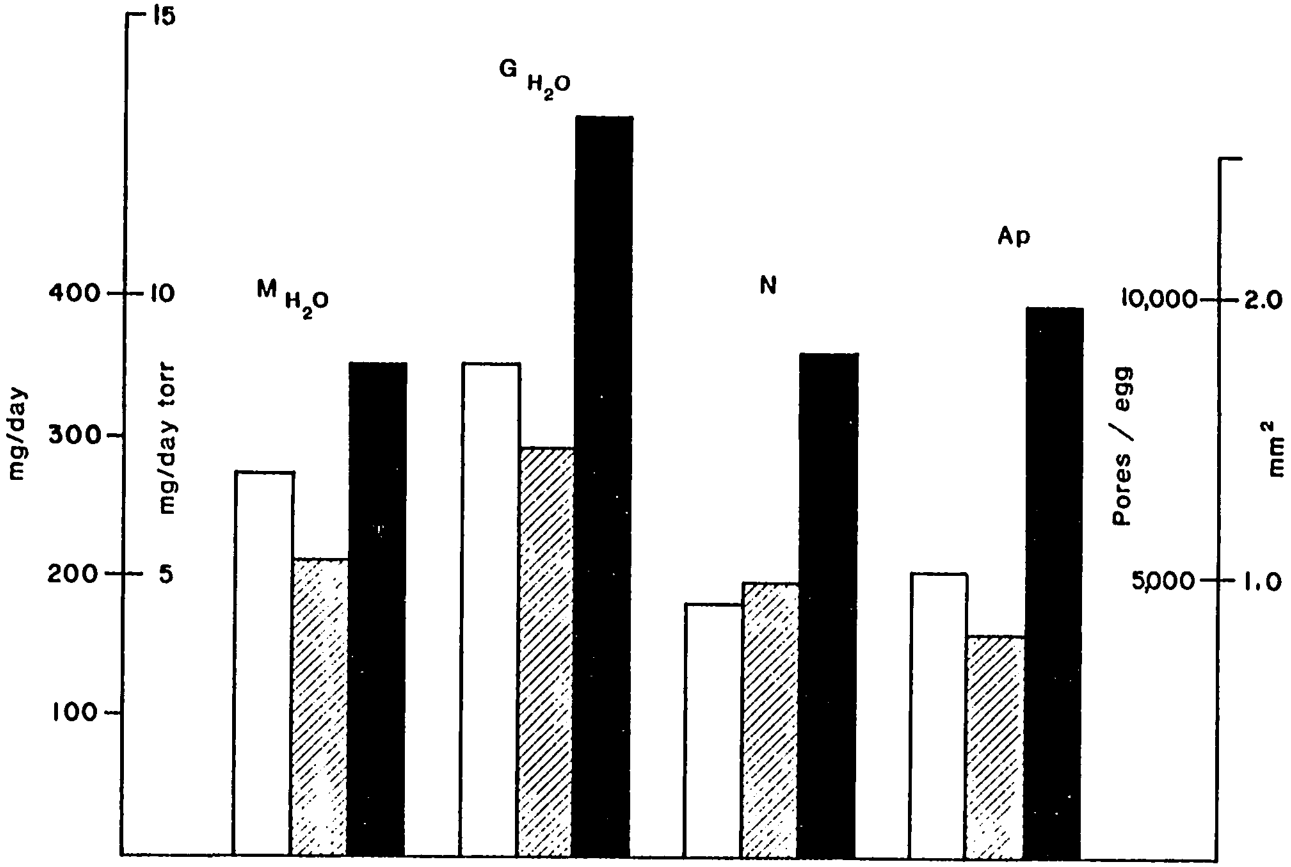

Figure 32. Measured and predicted values for water loss (MH_2O), water vapor conductance (GH_2O), number of pores, and fuctional pore area (Ap), of Dark-rumped Petrel eggs. Shaded area represents predicted value based on egg weight (Ar et al. 1974; Tullet and Board 1977; Ar and Rahn 1978,1980). Unshaded area represents measured values. Hatched areas represent predicted values based on egg weight and incubation period (Ar and Rahn 1978; Rahn and Ar 1980)

CHAPTER 4

A SIMULATION MODEL OF THE POPULATIONS OF THE DARK-RUMPED PETREL

Modeling can be used to gain insight into the relative importance of factors influencing a population and to make predictions on potential rates of increase or decrease. All models are simplifications of the systems they simulate, but they can help us to understand some of the influences which shape those systems. They are also useful in generating hypotheses, evaluating assumptions, and optimizing our management efforts (Hall and Day 1977, Miller 1978).

The Leslie Matrix Model

Matrix models were first proposed independently by Lewis (1942) and Leslie (1945,1948). These models provide a simple method by which specific fecundity and survival rates can be manipulated and their effects on population age structure and growth rate examined. Leslie (1966) is the only author to apply the technique to a seabird population, and he did so by determining the intrinsic rate of increase in a population of murres and examining the influence of overlapping generations on the distribution of two plumage morphs within the population. More recently, Miller et al. (1972) have used a similar method to develop a management plan and hunting quotas for Sand Hill Cranes (*Grus canadensis*). Mertz (1971) used Leslie's model to study the mathematical demography of the California Condor (*Gymnogyps californianus*), and used his findings to evaluate management priorities for the species.

Matrix models are well-suited to applications involving endangered or threatened species. Their real value lies not in their ability to make specific predictions, but in their usefulness in evaluating the relative importance of factors determining fecundity and survival. Given the multitude of factors that can influence a population it should not be surprising that even in the best of cases it is still not possible to make accurate long term predictions of the dynamics of a population. On the other hand, given a basic understanding of a species life history, we can assess the relative impact of varying rates of survival, mortality, and fecundity on a given population. With this knowledge, management efforts can be optimized.

Simply stated, the Leslie matrix consists of columns of survival and fecundity values for each female age class in the population. The first row of the matrix represents the fecundity rates of each age class of females, and the primary subdiagonal represents the survival rates for females in each of these classes. This matrix can then be used to make projections of the future population size and age structure. This is done by multiplying the fecundity-survival matrix by a vector which represents the age structure of the population. For example, a simple matrix representing an organism with six age classes could be depicted as follows.

$$\begin{array}{cccccccc}
F(0) & F(1) & F(2) & F(3) & F(4) & F(5) & & N(0) \\
S(0) & 0 & 0 & 0 & 0 & 0 & & N(1) \\
0 & S(1) & 0 & 0 & 0 & 0 & & N(2) \\
0 & 0 & S(2) & 0 & 0 & 0 & & N(3) \\
0 & 0 & 0 & S(3) & 0 & 0 & & N(4) \\
0 & 0 & 0 & 0 & S(4) & 0 & & N(5) \\
0 & 0 & 0 & 0 & 0 & 0 & &
\end{array}$$

The model deals exclusivly with the female component of the population, and the variables in the matrix represent the fecundity and survival rates of individuals in each age class. Each column of the matrix represents an age class. That is, F(1) represents the fecundity of one year old females and S(0) represents the survival rate of females during their first year. In the Dark-rumped Petrel, I used

36 age classes because it is unlikely that individuals live for more than 36 years (Botkin and Miller 1974). The age distribution vector (N(0)-N(35)) contains 36 elements with each element representing the number of individuals from the population in each age class at a given point in time. The product of this vector with the fecundity-survival matrix yields an age distribution vector for the population during the next time interval. This new vector when multiplied by the original survival-fecundity matrix yields the size and age distribution of the population during the next time interval and so on. Because Dark-rumped Petrels are annual breeders, the time interval used is one year. We know the size of the petrel population today, and we can use this method to examine how variations in the birds survival and fecundity will affect the rate of growth or decline of the population in the future.

Input Parameters

The demographic characteristics of a bird population can only be obtained through long-term banding studies. Although a banding study of the Dark-rumped Petrel was started in 1979 it will still be many years before some aspects of their life history are understood. Initial results confirm the high degree of nest site and mate fidelity that is typical of procellariiformes, but many more years of banding and recapturing adult birds will be needed before accurate estimates of adult survival can be made. In addition, it will be at least 1985 before we could expect any of the chicks banded during the last few years to return as breeding adults. Fortunately, some of the best long term banding studies that have been done on birds have involved procellariiformes with life histories very similar to the Dark-rumped Petrel. Some of these banding studies have extended over thirty years and involve a variety of species from the small storm petrels to the largest members of the order, the albatrosses (Table 27). These studies indicate some clear patterns in the life history of the procellariiformes.

In general, the birds show high rates of adult survival which range from a little over 90% up to 97%. Juvenile survival is similarly high and ranges from 65% to 93%. All species show delayed maturity with the age of first breeding ranging from three to nine years. The data suggest that the largest species breed latest and have the highest juvenile and adult survival. Survival rates and age at first breeding appear to decline in a regular manner with the size of the bird. Using these findings and the results of this study, I have constructed a table of the life history parameters of the Dark-rumped Petrel (Table 28). This species is a medium-sized procellariiform, about

Table 27. Procellariiform life history parameters.

SPECIES	WING SPAN (CM)*	AGE AT FIRST BREEDING	FLEDGLING SURVIVAL	ADULT SURVIVAL	SOURCE
Diomedea exulans	324			.96	Tickell (1968)
Diomedia epomophora	305	8-9		.97	Lack (1954) Richdale (1950,1952) Richdale and Warham (1973)
Diomedea irrorata	208	5-6	.93+	.95	Harris (1973)
Diomedea immutabilis	203	7-9	.92	.91-.95	Rice and Kenyon (1962) Fisher (1975a,1975b,1976) Van Ryzin and Fisher (1976)
Diomedea melanophris	229			.93	Tickell and Pinder (1975)
Diomedea bulleri	213			.89	Richdale and Warham (1973)
Diomedea chrysostoma	203			.93	Tickell and Pinder (1975)
Phoebetria polpebrata	208	7			Kerry and Colback (1972)
Macronectes giganteus	213	5-6			Warham (1962)
Fulmarus glacialis	107	9.2	.88-.93	.97	Dunnet and Ollason (1978a,1978b) Dunnet et al. (1979)
Daption capense	89	4-5	.65-.70	.94-.95	Pinder (1966) Hudson (1966)
Pagodroma nivea				.93-.95	Hudson (1966) Guillotin and Jouventin (1980)
Puffinus griseus	109	6		.92-.94	Richdale (1963)
Puffinus tenuirostris	97	5-7	.85+	.91-.95	Serventy (1956,1957,1967) Palmer (1962)
Puffinus puffinus	78	5-8	.80-.82	.90-.96	Orians (1958) Harris (1966) Perrins et al. (1973) Brooke (1977)
Oceanites oceanicus	41			.91	Beck and Brown (1972)
Oceanodroma leucorhoa	48	3-5		.94	Gross (1947) Morse and Bucheister (1977)

*(From: Tuck and Heinzel 1978, Warham 1977)

Table 28. Dark-rumped Petrel life history parameters.

PARAMETER	VALUE	SOURCE
Wing span[1]	98 cm.	This study
Age at first breeding[2]	6 yr.	Table 1
Juvenile survival[3]	.8034	Table 1
Adult Survival	.80-.93	This study, Table 1
Reproductive success[4]	.35-.72	This study
Breeding frequency[5]	.89	This study

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1 Tip to tip distance of the fully extended wings.
2 Birds start breeding at six years of age but turn seven during their first nesting season.
3 Yearly survival rate of pre-breeding birds.
4 Percentage of eggs laid the produce fledglings.
5 Percentage of adult birds that attempt to breed each season.

the same size as the Short-tailed Shearwater. We might expect their life history parameters to be intermediate as well. I have estimated several parameters from the literature, and given the rather narrow range of values across the entire order, it is likely that these estimates are reasonably accurate. It is not essential to have strictly accurate estimates for all of these parameters because I am not using the model to make specific predictions but rather to examine the relative influence of varying rates of survival and fecundity on the population. Several parameters were estimated from the literature, and those values will remain as constants in all of the calculations that follow. The average age at first breeding will be assumed to be six years. That is, it is assumed that when these birds start nesting for the first time they are well into their sixth year and they turn seven during that breeding season. Fledgling survival, the yearly survival rate of young birds from the time they leave the nest until they begin to breed, will be set at 80.3%. This parameter is the most difficult one to estimate in wild populations and good estimates from field studies are rare. The estimate used in the model is well within the range reported in similar species, and was chosen because it yields a stable population when combined with the other parameters assumed in the model. Based on this estimate, approximately 27% of the chicks that fledge each year will return to breed. Normal yearly adult survival is estimated to be 93%, but if predation similar to that experienced by the birds in 1979 were the norm, it is likely that it could drop to 80% or even lower. In that year over 34% of all nests suffered some form of predation. The predation rate also influences reproductive success which varied from 35% to 70% depending on the severity of predation. Reproductive success averaged 66% in the two years without significant predation and this value will be assumed as an average rate in the model. The Sex ratio of embryos at egg laying is assumed to be 50:50. Breeding frequency, the percentage of adult birds that attempt to breed each year, was found to be 89%. This estimate was based on fifteen accessible, undisturbed, unpredated, burrows for which I had three or more years of data. In addition, each of these nests raised at least one chick in three years indicating that the birds were established breeders. Mate and nest fidelity is assumed in this estimate which is the norm in closely related species. Fisher (1975a,1975b,1976) estimated that 90% of adult Laysan Albatrosses breed each year and Perrins et. al (1973) determined that just over 80% of the adult Manx Shearwaters on Skolkholm attempt to breed each season. Clearly the values in Table 28 are estimates of average values, and it is likely that they are subject to considerable yearly variation in real populations. For example, in most species the age of first breeding shows some variability and may be different for males and females (Serventy 1967, Perrins et al. 1973); newly formed pairs and inexperienced birds have lower reproductive success than established pairs (Brooke 1978); and adult survival varies from season to season (Van Ryzin and Fisher 1976).

To construct the survival-fecundity matrix it is necessary to first calculate the survival and fecundity values for each of the six age classes in the matrix. The initial matrix will assume values that yield a stable population. Although there is evidence that in some species fecundity varies with the age of the breeding birds (Fisher 1976, Brooke 1978), there is no information on this for the Dark-rumped Petrel and it will not be incorporated into the model. It also appears that seabirds do not exhibit a senescent decline in fecundity, and it will be assumed that adult birds reproduce at a constant rate until they die. Thus, remembering that the model deals exclusivly with the female component of the population, the number of female chicks fledged in an average year can be calculated as follows:

$$(0.89) \times (0.50) \times (0.66) = 0.294$$

That is, 89% of the eligible adult females breed each year, they have a 50% chance of producing a female egg, and that egg has a 66% chance of producing a fledgling. Thus an average female has a 29.4% chance of producing a female fledgling in an average year. The fecundity of birds in the first six age classes is assumed to be zero since these are all pre-breeding birds. Now all that remains is to calculate the survival rates for birds in each of the six age classes. In this example yearly fledgling survival is taken to be 80.3% for a total juvenile survival of $(.8034^6)$ = 26.89%. Adult survival is assumed to be constant averaging 93% per year. These values form the basis of the orignial survival-fecundity matrix shown below.

		AGE			
0-5	6-11	12-17	18-23	24-29	30-35
0	0.294	0.294	0.294	0.294	0.294
.8034	0	0	0	0	0
0	.93	0	0	0	0
0	0	.93	0	0	0
0	0	0	.93	0	0
0	0	0	0	.93	0
0	0	0	0	0	0

The survival-fecundity matrix can be used to calculate two useful measures of a population's growth potential, Lambda (L), the yearly rate of population growth, and the individual or intrinsic rate of population growth (r) (Pielou 1969). The two variables are related by the following equation $L = e^r$. In a population of constant size Lambda equals 1, in a growing population it is greater than one, and in a declining population it is between zero and one. Conversion of the fecundity survival matrix yields the following equation (Pielou, 1969):

$$(L^{k+1}) - (F0 \times L^k) - (S0 \times F1 \times L^{k-1}) - (S0 \times S1 \times F2 \times L^{k-2}) - \ldots (S0 \times S1 \ldots Sk-1) \times Fk = 0$$

In this equation Lambda (L) is solved for by iteration using the fecundity and survival values in the matrix. In this case, F0 refers to the fecundity value in the first age class, S1 refers to the survival rate in the second age class and so on. Using the values in this initial matrix and solving for Lambda we find that (L) equals 0.99998, indicating that given these initial conditions the population will decrease by a factor of only 0.99998 each year and will remain approximately constant in size as long as these conditions hold.

Procellariiforms are some of the longest-lived birds in the world. Several extreme cases of longevity have been reported, including a Laysan Albatross over 53 years old, a Fulmar over over 41 years old, and a Manx Shearwater over 23 years old (Nelson 1979). These examples are probably extremes (Botkin and Miller 1974). Banding studies provide a reasonable although conservative estimate of natural longevity, and they suggest that few mid-sized procellariiformes live to be older than 35 years (Perrins et al. 1973). For this reason it seems reasonable to eliminate age classes older than 35 years as I have done in this model. Although a small percentage of birds may live beyond that age it is unlikely that they make a significant contribution to the breeding population.

Before continuing with the model it is essential to establish the initial age distribution vector. This vector summarizes the number of individuals in the population in each age class with the top element in the vector indicating the number of individuals in the youngest age class, the second element indicating the number of individuals in the second age class, and similarly to the last age class. Sharpe and Lotka (1911) proved, and Leslie (1945,1948) has illustrated that regardless of the initial age distribution, a population under constant rates of survival and fecundity will eventually establish a stable age distribution. By experimenting with the range of values used in this model I determined that, at stability, this population will always approach a distribution close to the following:

52.2% of the population will be less than 6 years old
19.0% of the population will be 6 to 11 years old
12.3% of the population will be 12 to 17 years old
7.9% of the population will be 18 to 23 years old
5.2% of the population will be 24 to 29 years old
3.4% of the population will be 30 to 35 years old

Using this age distribution in conjunction with census and breeding success data from the Haleakala population it is possible to construct an initial age distribution. There are currently 659 known petrel burrows in and around Haleakala National Park, but I have determined through activity checks and monitoring that approximately 18% of the marked burrows have never been or are no longer active. Thus, I estimate that there are about 540 active nests. I estimate that there are no more than 35 active nests in the colony that have not yet been located, thus I assume the total breeding population on East Maui to be 575 pairs. Colony wide activity checks in years without significant predation indicate that 42% of all active burrows fledged chicks (Chapter 2). Reproductive data from years without significant predation indicate that 93% of the chicks that hatch, survive to fledge. This rate indicates that (42/.93) or 45% of the active burrows hatch chicks. Similarily, average hatching success is estimated at 71% indicating that (45/.71) or 64% of all active burrows have breeders in them each season. Since I have found that approximately 11% of all breeders do not attempt to breed in any one year (Chapter 2), it is estimated that 75% of all active burrows contain breeding adult birds. Thus it is estimated that there are approximately (575 x .75) = 431 pairs of breeding adult petrels, and that approximately 144 of the remaining active burrows are used by prebreeding birds. Since survival and fecundity estimates indicate adult birds make up 47.8% of the total population we can estimate the total breeding and nonbreeding population to be approximately (431/.478) = 901 pairs. Of these 901 pairs there will be approximately 470 pairs of prebreeding birds. These calculations suggest that about 30% (144/470) of these birds are establishing burrows in any year and that the remainder must either be visiting the colony but not establishing burrows, or must not yet have returned to the colony. This pattern resembles that exhibited by the Manx Shearwater (Harris 1966, Perrins et al. 1973, Brooke 1977). In most cases young birds do not return to the colony until mid-way through the prebreeding period, and burrows are not established until a year or two prior to the first breeding attempt.

These figures for breeding pairs can be translated directly into breeding females and used to construct the age distribution vector. Using the percentages given previously and the figures just derived, the vector can be approximated as follows.

Of 901 females:

52.2% or 470 would be juveniles
19.0% or 171 would be age six to eleven
12.3% or 111 would be age twelve to seventeen
7.9% or 72 would be age eighteen to twenty three
5.2% or 47 would be age twenty four to twenty nine
3.4% or 30 would be age thirty to thirty five

This vector will be used as the stable age distribution for the population in all of the calculations that follow. The population size at any point in the future can be found by calculating the final age vector as described previously and summing its elements. This value is equal to the number of females in the population at that point in time or the size of the total population expressed as pairs.

The matrix calculations are accomplished thorugh the use of a modified version of a FORTRAN program entitled MATRIX01 written by Dr. Chuck Fowler of the National Marine Mammal Laboratory, Seattle, Washington. The program allows the user to set up initial fecundity-survival matrices and age distribution vectors, and it then calculates the initial stable age distribution and population growth rate (Lambda). Changes in the population over time are determined in an iterative fashion, and the matrices can either be constant, as in this case, or they can be made functions of any number of variables to simulate competition or other influences. Simulations of the latter type are ignored in the present model because it is assumed that the current populations of Dark-rumped Petrels are not limited by these types of factors. There is ample evidence that all of the remaining seabird populations in Hawaii are presently smaller than their historic levels (Chapter 1). Given current population levels, it is unlikely that food resources for the Dark-rumped Petrel are limiting the population today. The high survival rate of nestlings over the last several years gives support to this assumption. In addition, although the primary nesting habitat for these birds is no longer suitable, due to a number of factors, there is no evidence that nesting habitat is in any sense limiting where the birds are nesting today. Therefore, no provisions for the influence of limiting resources on population growth rates have been incorporated into this model.

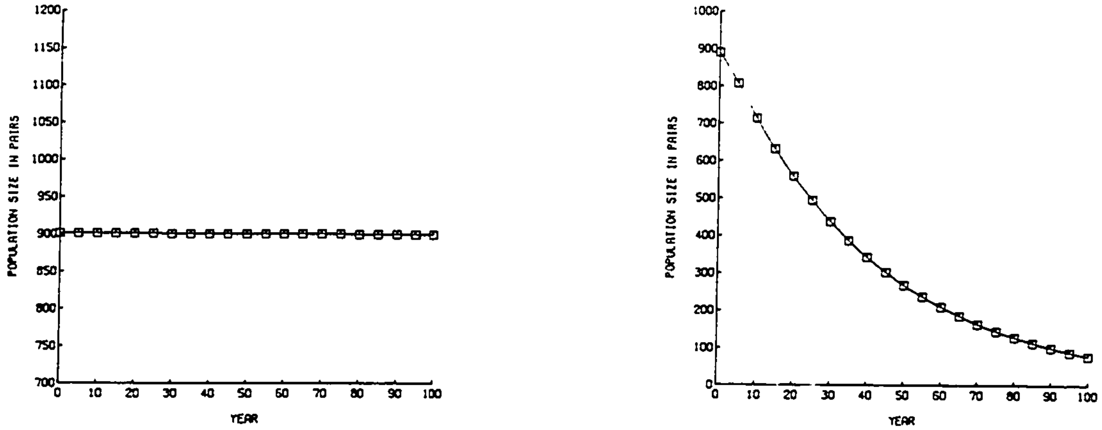
Simulations

The parameters used in the population model are listed in Table 29. The model assumes that birds begin breeding late in their sixth year, and it measures population size just after fledging. Egg loss and chick death, including light

Table 29. Parameters of the population model.

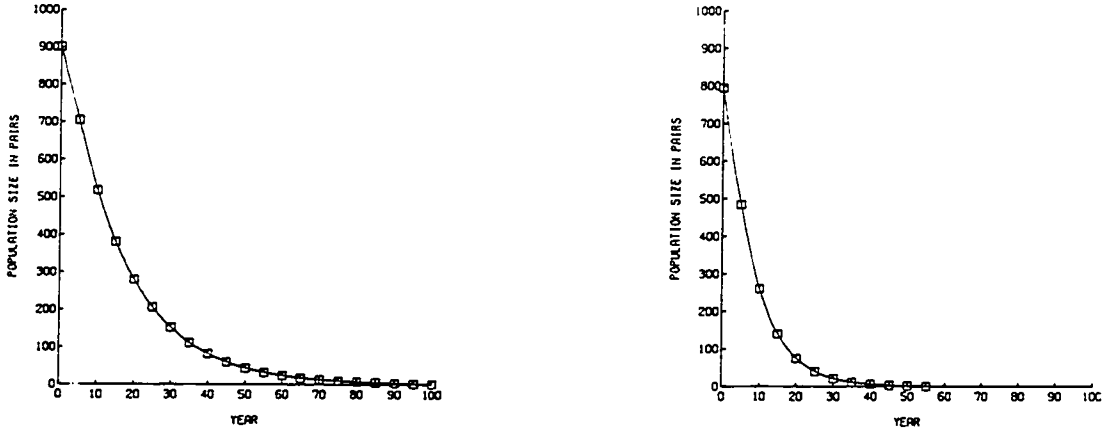
SIMULATION NUMBER	BREEDING FREQUENCY	ADULT YEARLY SURVIVAL	YEARLY FECUNDITY	REPRO. SUCCESS	JUVENILE YEARLY SURVIVAL	TOTAL JUVENILE SURVIVAL	LAMBDA (L)	"r"
1	.89	.93	0.294	.66	.8034	.2689	0.99998	.00002
2	.89	.90	0.267	.60	.8034	.2689	0.976	-.0243
3	.89	.85	0.245	.55	.8034	.2689	0.940	-.0619
4	.89	.80	0.156	.35	.8034	.2689	0.883	-.1244
5	.89	.93	0.267	.60	.8034	.2689	0.994	-.0060
6	.89	.93	0.245	.55	.8034	.2689	0.989	-.0111
7	.89	.93	0.156	.35	.8034	.2689	0.964	-.0366
8	.89	.90	0.294	.66	.8034	.2689	0.981	-.9192
9	.89	.85	0.294	.66	.8034	.2689	0.952	-.0492
10	.89	.80	0.294	.66	.8034	.2689	0.924	-.0790
11	.89	.93	0.320	.72	.8034	.2689	1.005	.0050
12	.89	.93	0.334	.75	.8034	.2689	1.008	.0080
13	.89	.93	0.231	.60	.8034	.2689	0.986	-.0141
14	.89	.93	0.173	.52	.8034	.2689	0.970	-.0305

related post-fledging mortality (Chapters 2 and 5), are incorporated in the yearly fecundity estimate. Fourteen simulations using fixed variables were run to determine the influence of various levels of survival and fecundity on population growth rates over a periods of up to 100 years. The initial population size used in these simulations was determined by combining the current estimate for the number of active nests on the colony with the appropriate age distribution. Thus, current estimates of population size vary from 901 pairs in a stable population to 725 pairs in a population that has been declining for a number of years. Simulations one through four depict the influence of increasing rates of predation, occurring throughout the nesting season (Figure 33). The first simulation represents a stable, undisturbed population achieving an average rate of reproductive success of 66%. The second simulation represents a case of mild predation in which less than ten percent of the nests experience predation in any year. These conditions resulted in a slight reduction in adult survival and reproductive success. The third simulation represents a more severe level of predation in which approx. 20% of the nests are affected in a season. The fourth simulation represents an extreme case, similar to 1979, when over 30% of the active nests received some predation.



Simulation #1

Simulation #2



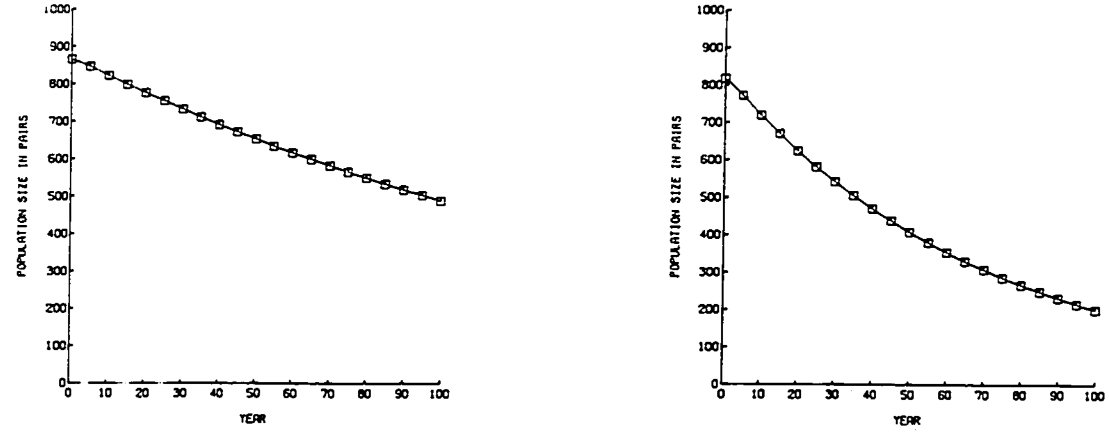
Simulation #3

Simulation #4

Figure 33. The impact of various levels of predation on Dark-rumped Petrel populations. Simulation 1 represents stable conditions; reproductive success = 66%, and adult survival = 93%. Simulation 2 represents a low level of predation in which reproductive success is reduced to 60% and adult survival to 90%. Simulation 3 represents a moderate level of predation in which reproductive success is reduced to 55% and adult survival to 85%. Simulation 4 represents a high level of predation similar to that observed in 1979 in which reproductive success was reduced to 35% and adult survival to 80%.

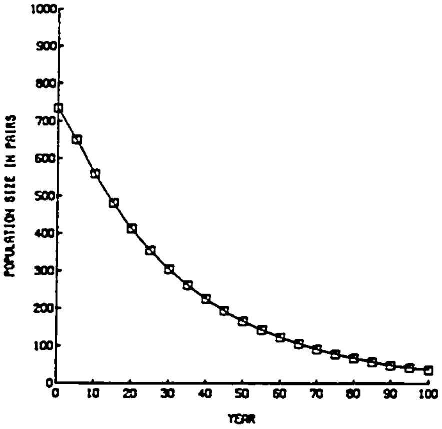
It is obvious from these projections that the Dark-rumped Petrel population is unable to withstand any level of predation for very long. Even the seemingly low levels of predation assumed in simulation two would reduce the population to less than half of its current size in less than 30 years. If predation similar to that experienced in 1979 continued unchecked, it could drive the present population close to extinction in less than 20 years. Obviously these are only estimates but they hold true for a wide range of initial assumptions. Within reasonable limits no matter what initial population parameters are chosen the impacts of consistent predation on the population are severe.

Simulations five through seven (Figure 34) and eight through ten (Figure 35) contrast the influence of decreasing reproductive success and decreasing adult survival. A reduction in either of these parameters will send the population into a steady decline, but the rate of decline is much more rapid if adult survival is reduced. The pattern resembles that in other "K" selected species such as African Elephants (Fowler and Smith 1973). For example, a 10% reduction in reproductive success will only reduce the population by a little over 0.9% each year while a 10% reduction in adult survival will result in a yearly population decline of over 5%. This relationship is a basic



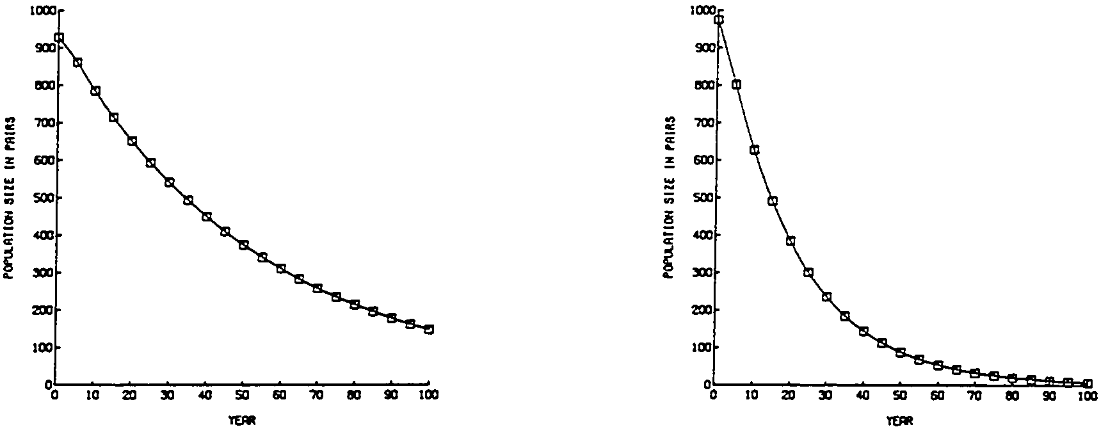
Simulation #5

Simulation #6



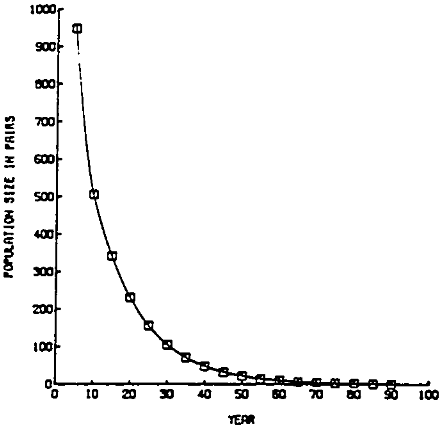
Simulation #7

Figure 34. The impact of declining reproductive success on Dark-rumped Petrel populations. Simulation 5 represents a reduction in reproductive success from 66% to 60%. Simulation 6 represents a reproductive success of 55% and simulation 7 represents a reproductive success of 35%.



Simulation #8

Simulation #9

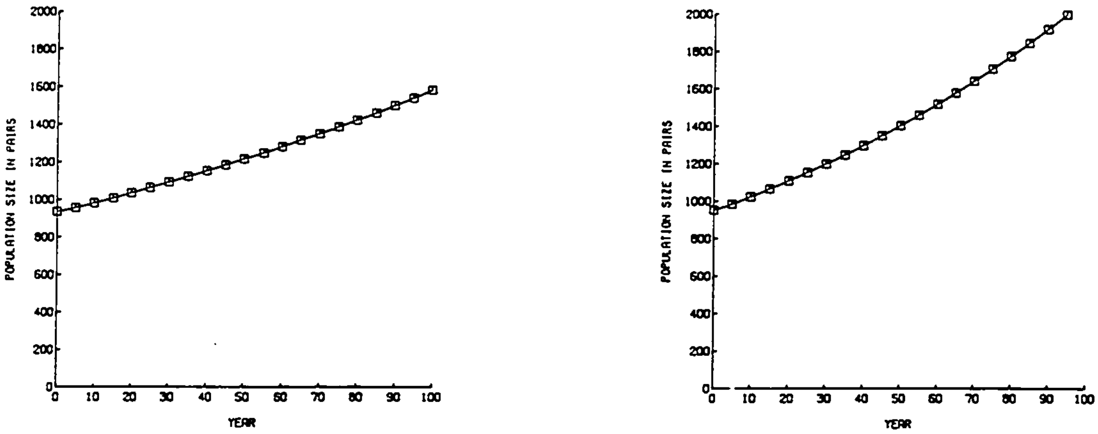


Simulation #10

Figure 35. The impact of declining adult survival on Dark-rumped Petrel populations. Simulation 8 represents a reduction in adult survival from 93% to 90%. Simulation 9 represents an adult survival of 85% and simulation 10 represents an adult survival of 80%.

principle of demography but is especially relevant in a species with a life history like that of the Dark-rumped Petrels. The management implications are clear; the highest priority should be given to protecting breeding adult birds. Predator control efforts should be most intense during the portion of the breeding season when adult birds are vulnerable (Chapter 5).

The next two simulations, numbers eleven and twelve, examine the the potential growth rates of an increasing population (Figure 36). Procellariiforms have little latitude to increase their fecundity because all species lay a one egg clutch. Lack (1954) and others have suggested that the clutch size in these birds is controlled by resource availability and that these resources never allow a doubling of reproductive output as would be required to increase the clutch size by a single egg. Adult birds could increase their fecundity by breeding more frequently but the estimate assumed in the model is one of the highest reported in the order, and it may represent a rate close to the maximum breeding frequency in this species. In an undisturbed population adult and juvenile survival are functions of the environment which, excluding predation, is assumed to be constant in the long term. Therefore, the parameter primarily responsible for alterations in the populations yearly growth rate is



Simulation #11

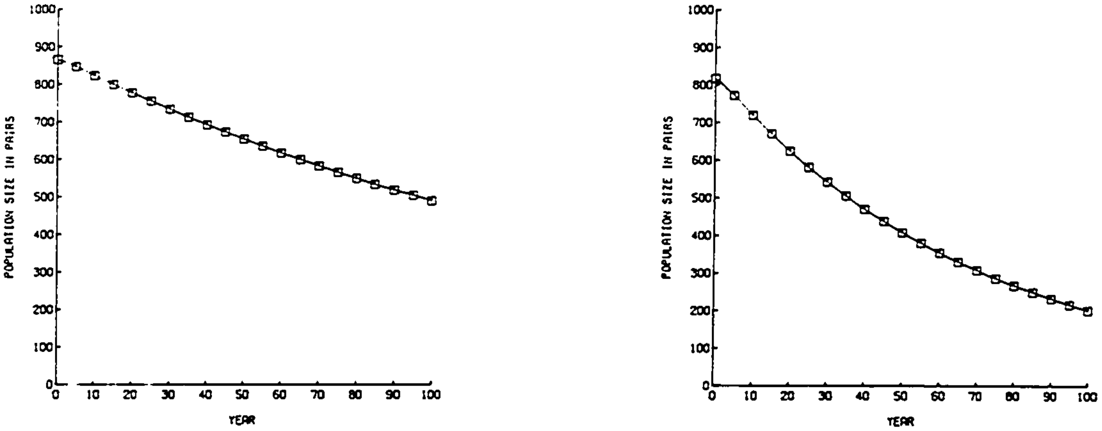
Simulation #12

Figure 36. Potential growth rates of Dark-rumped Petrel populations. Simulation 11 represents the response of the population to an average reproductive success of 72% and simulation 12 represents the response of the population to an average reproductive success of 75%.

reproductive success. On a yearly basis the model assumes that Dark-rumped Petrels average a reproductive success of 66%. Higher reproductive rates will cause the population to grow, while lower rates will cause it to decline. The maximum reproductive success recorded in the three years of the study was almost 72%, which as illustrated in simulation 11, yields an annual population growth rate of 0.5%. If the birds could achieve a success rate of 75%, about the maximum reported in similar species, we could expect their populations to grow at slightly over 0.67% per year. These two simulations serve to reinforce one of the most important aspects of the life history of these birds. Even under the best of conditions the intrinsic rate of increase of their populations is low, and the recovery of a population that has been severely reduced can be expected to be slow and erratic.

It is clear that even with the most optimistic assumptions the present petrel population would not be expected to double in size for over a century. If food and nesting resources are abundant as postulated, and if predation can be controlled, the population should be able to grow at a modest rate. Detection of this growth will require continued monitoring for decades.

The final two simulations (Figure 37) examine the impact of



Simulation #13

Simulation #14

Figure 37. The impact of light-related fledgling mortality on Dark-rumped Petrel populations. Simulation 13 represents an annual loss of 20 fledglings and simulation 14 represents an annual loss of 50 fledglings.

increased juvenile mortality resulting from the grounding of fledging chicks (Chapter 5). Up to 30 chicks have been recovered in past years and many of these died. With the increasing urbanization of Maui County it is likely that the problem will grow, and more fledging mortality will occur. Simulation 13 illustrates the impact of the loss of 20 fledglings out of an estimated average of 253 chicks fledged annually and simulation 14 illustrates a loss of 50 fledglings. A loss of 20 fledglings would lower reproductive success to 60 %, and in an otherwise stable population, cause an annual decline of 1.5%. A loss of 50 chicks would increase the rate of decline to 3%. This type of fledging mortality, although not desirable, is at its present level not a major threat to the remaining populations. Should the problem intensify it could contribute siginficantly to the decline of the remaining populations. At their current low levels these losses could be compensated for by increased reproductive success. This is not the case for other forms of mortality during the breeding season, such as predation on adult birds. For example, a loss of up to 20 fledglings per season could be compensated for by an average reproductive success of 71%. In contrast, a reduction of adult survival of only 2% would require a compensatory increase in reproductive success to over 80% which is clearly impossible for these birds. Light related fledgling mortality should be monitored closely in the future to prevent its becoming a significant mortality factor.

A serious concern with any endangered species or population is how natural variations in the population growth rate influence long term population stability (Miller and Botkin 1974, Miller 1978, Ehrlich and Ehrlich 1981). All populations fluctuate naturally from generation to generation in response to changing conditions, and in a well established population these fluctuations have no long term consequences. At some point though, as population levels decline, these natural fluctuations may push a population below the level from which it can recover. At low population levels all populations are threatened with extinction due to natural fluctuations, and in some cases, no level of protection can insure their survival once they have dropped below that point.

I have examined one aspect of the relationship between population size and natural variability in two additional simulations. I chose reproductive success for the analysis because it is a well documented aspect of Dark-rumped Petrel reproductive biology which shows natural variation from year to year. Unnatural sources of mortality, such as predation, have not been simulated since I have already demonstrated that even at low levels they will quickly drive the population to extinction. The parameters of the first simulation, a stable population, are assumed, but reproductive success is allowed to vary randomly from 55% to 76%. On average these rates yield a stable or slightly increasing population which fluctuates periodicallly between increasing and decreasing phases. From these simulations we can gain some insight into the response of the population to these random influences, and estimate at what population level these forces alone could drive the population to extinction.

The results of two typical simulations are presented in Figures 38 and 39. I assumed an initial population of 1000 pairs in the first simulation and 500 pairs in the second. In the first simulation the population fluctuated over a range of about 200 pairs, and in the second over a range of about 100 pairs. These results suggest that natural variations in reproductive success do not pose a threat to the population at its current levels. In fact, given these assumptions, this type of variability would not be cause for concern unless the population dropped to less than half of its present size. On the other hand, these simulations represent a very conservative estimate of the influence of random factors and yet they point out that natural variations can have a significant depressing affect on the populations growth rate, and that these factors could

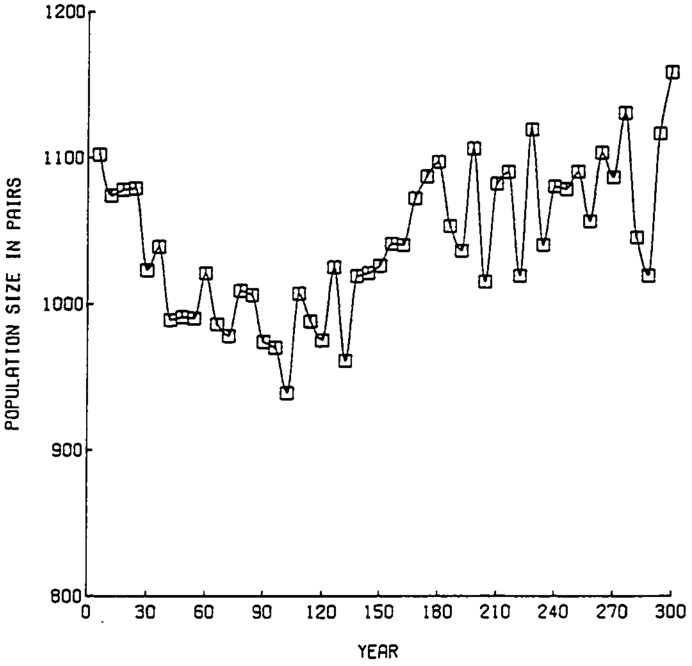


Figure 38. The impact of random variations in reproductive success on an initial Dark-rumped Petrel population of 1000 pairs. Reproductive success was allowed to vary randomly from 55% to 76%.

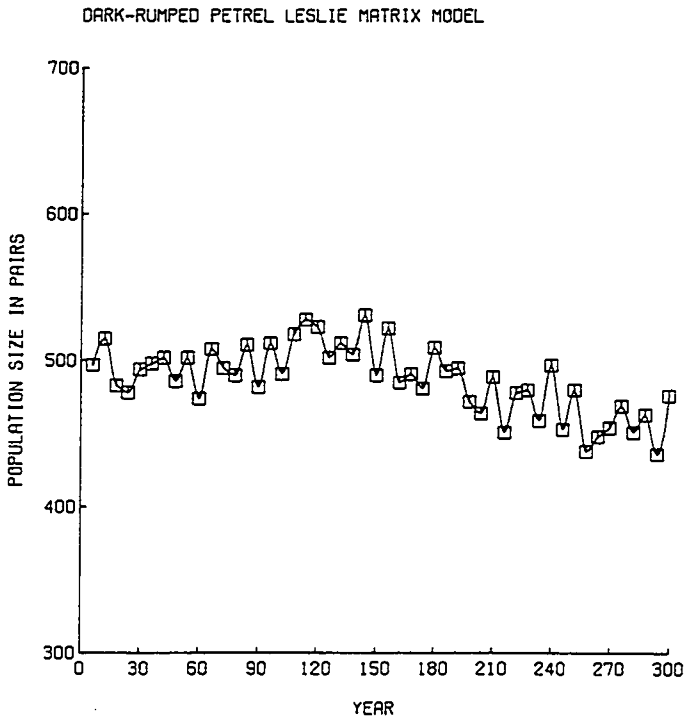


Figure 39. The impact of random variations in reproductive success on an initial Dark-rumped Petrel population of 500 pairs. Reproductive success was allowed to vary randomly from 55% to 76%.

combine to intensify other negative influences on the population such as predation. For example, in a worst case scenario, a season with high predation might be followed by a series of poor reproductive years. If this happened the population could be reduced dramatically in a short time.

These results have important management implications. First of all it is likely that the current population could fluctuate over the course of several decades by a hundred or more breeding pairs due simply to natural variations in reproductive success. Secondly, threats to the population such as predation should be evaluated with an awareness that they may be intensified by these random fluctuations.

Another feature of the population dynamics of a "K" selected species like the Dark-rumped Petrel is an inherent lag time between a change in a life history parameter and its manifestation in the size or structure of the adult population. This lag is an inevitable consequence of the large juvenile component of the population and the the high survival rate of breeding adults. An example of this is illustrated in Figure 40. This simulation assumes a constant low reproductive success of 55%, as a result of predation or some other factor, which results in an annual population decline of about 1.1%. The figure contrasts the

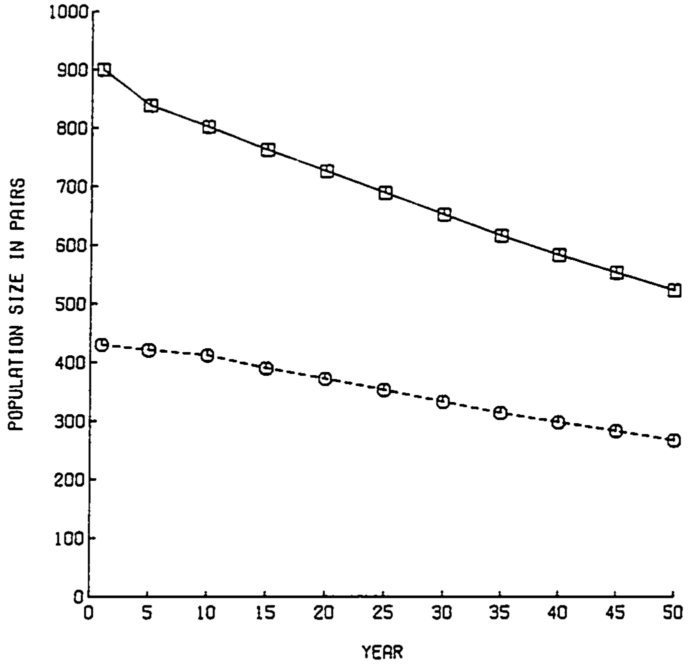


Figure 40. A comparison of the rate of decline of the total Dark-rumped Petrel population (solid line) with the rate of decline of the adult population (dashed line), given a constant reproductive success of 55%. Note that the adult population declines slower than the total population during the first 15 to 20 years and for this reason measurements of the total petrel population based solely on activity at breeding burrows may be misleading.

decline of the overall population with the decline of the breeding population, reflected in the number of active burrows at the colony. The importantance of this simulation is that the initial rate of decline of the adult population is considerably less than the rate of decline of the overall population. If the health of the petrel population were being assesed soley on the basis of the number of active burrows in the colony, as it has for most the past 15 years, there is a good chance that a steadily declining population would not be detected until the decline was well established. The simulation further emphasizes the need to monitor reproductive success directly at the colony on a yearly basis (Chapter 5).

Conclusions

This analysis has shown that population modeling can be used to assess the vulnerabilities of the Dark-rumped Petrel population, and it has made evident several unique features of this specie's population dynamics. One of the initial conclusions drawn from the model that was not intuitivly obvious was the size of the pre-breeding segment of the population. In species such as the Dark-rumped Petrel it is likely that up to 40% of the population is composed of birds that do not visit the breeding colony. This large juvenile cohort is an essential feature of birds with this type of breeding biology. In addition, it is likely that about 30% of the active burrows within the colony are occupied by pre-breeding birds. This substantial differance between the size of the breeding and nonbreeding segments of the population further emphasizes the importance of breeding adult birds in maintaining the integrity of the entire population.

The importance of breeding adult birds was dramatically emphasized by the response of the population to varying levels of predation. The model has demonstrated that almost no level of predation can be tolerated by the population for very long. The high rates of predation detected in 1979 could exterminate the population in less than a decade if they continued unchecked.

I have combined some of the information from the population simulations to examine the impact of isolated instances of predation, and the results were even more disturbing than the long term simulations. For example, I assumed that the current population experienced a level of predation similar to that portrayed in simulation #3 for a single season. In that case adult survival dropped to 85% and reproductive success to 55% for one year and then returned to normal. In the following years the population was allowed to increase at a moderately high rate assuming an average reproductive success of 70%. This level of predation is probably lower than that experienced by the population in 1979, and even allowing for an optimistic rate of recovery, the impact on the population was substantial. Following the year of predation the population declined for fifteen years to below 800 pairs, and did not recover to its former level for over 18 years. Even a modest level of predation, such as that portrayed in simulation #2 (10%) experienced for only a single season would require a recovery period of at least 7 years.

Obviously, predation on breeding adult birds is the most pressing threat to the survival of these birds. The highest priority should be given to protecting this segment of the population which is vulnerable from early March to mid July (Chapter 5). Trapping and other predator control efforts should be in full swing by February of each year and continue as long as is possible, at least through mid-July. Reproductive success has a less significant influence on population growth rates but it should be monitored continually if possible to determine its natural variability and to detect sources of reproductive failure such as poor hatching success, predation, and chick starvation.

Fledgling mortality due to light related groundings should be monitored and reasonable efforts made to minimize it. The problem can be expected to increase with urbanization in the future. The problem seems to be minor, but due to the small number of chicks fledged each season, the loss of even 15 or 20 chicks a season could tip the balance between a constant or increasing population and a declining one.

The model has also pointed out that random fluctuations in population size due to natural variations in reproductive success probably do not pose a threat to the population at its current size. Nevertheless they could result in substantial fluctuations in population levels and should be accounted for in future estimates of the affects of such factors as predation. In addition we should expect natural variations in the number of breeding burrows in the colony due to this factor alone.

Finally, the model strongly reinforces the view of these birds as an intensely "K" selected species (Macarthur and Wilson 1967). The resources upon which they depend require a conservative reproductive strategy marked by late maturity, low replacement rates, and long life. The bird's life history shows few of the compensatory attributes typical of more "r" selected species. They are unable to respond quickly to favorable conditions by increasing their fecundity, and even under optimum conditions are only capable of low rates of increase. Similarily, they are vulnerable to small changes in their adult mortality rates. All of the species in this order have evolved, some for millions of years, in a system in which mortality rates were governed primarily by the abundance of their food resources, or in some cases by the availability of nesting sites (Ashmole 1971). Their ability to avoid additional sources of mortality, such as predation, has allowed these birds to survive in the past, but mans activities have shifted the balance point. Due to their conservative life history strategies, species like the Dark-rumped Petrel are prime candidates for extinction in a world changing rapidly through human activity (Fowler and MacMahon 1982). If we can't insulate the remaining populations from these new sources of mortality, their populations will continue to decline.

CHAPTER 5

A MANAGEMENT PLAN FOR THE DARK-RUMPED PETREL

In this chapter I will discuss current threats to the remaining petrel populations and make suggestions on how management efforts can minimize those threats. By a population, I am referring to a geographically distinct assemblage of birds. Thus, the Haleakala colony is considered to be a population. In Appendix A I will outline a program of monitoring and conservation techniques intended to maintain the health of the remaining colonies. By controlling the factors that are currently reducing Dark-rumped Petrel populations, and maintaining the ability to detect changes in population levels, it is hoped that the current population can be preserved if not increased.

PREDATION AND DISTURBANCE BY INTRODUCED SPECIES

The most serious and immediate threat to the remaining Dark-rumped Petrel populations is predation by introduced mammalian predators. Mongooses are the most destructive of these predators and they were responsible for most of the predation observed during the course of this study. Of nine instances of predation in which the predator was identified, seven were attributed to mongooses and two to feral cats. It is important to keep in mind that in all of the incidents of predation I observed, it appeared that only a few indivivuals were responsible. In most cases no sign of predation or resident predators were detected until a rash of mortalities over the course of several days indicated the presence of a predator on the colony. Once it began, the mortality of adults and chicks usually continued until the predator was caught or left the area. On several occasions a single mongoose or pair of adults appeared suddenly in the colony, and once they discovered the nesting birds they systematically searched out and killed many of the petrels over a wide area. In most cases the birds that were killed were not eaten or even removed from their burrows. On the other hand, petrel eggs are a favorite with mongooses, and these were always eaten. It appeared that mongooses killed many of the birds while searching for eggs.

Mongooses

The presence of a mongoose on the colony is obvious by dead incubating adults and nestlings, the presence of predated eggs, or fresh scats. Dead adults and nestlings often show two characteristic puncture marks on the skull or the back of the neck (Figure 41). Eggs which have been eaten by a mongoose are usually found near the burrow entrance with their contents removed and a rather neat, 2-3 cm, hole in their sides (Figure 42). In inaccessible burrows, the sudden appearance of large numbers of flies around the burrow entrance in conjunction with the smell of the dead bird is also good evidence of predation.

I found no evidence of a resident population of mongooses at the summit of Haleakala. This was expected because the area is well above the normal range of these animals (Baldwin et al. 1952; Hinton and Dunn 1967; Tomich 1969a, 1969b). Mongooses had not been recorded at the summit prior to this study, and it appears that their arrival there is a recent development. It is likely that increased urbanization at lower elevations, increased visitation, and human activity within the park are encouraging the expansion of the mongoose's range. At present it seems that small numbers of mongooses are dispersing out of their normal range during the summer months. This movement results in some individuals finding their way into the petrel nesting areas. Because the trends that apparently led to this range expansion are continuing, it is likely that the influx of mongooses into Dark-rumped Petrel

Figure 41. Adult Petrel killed by a mongoose. Most birds are found in this condition with small puncture wounds about the neck and head.

Figure 42. Petrel egg eaten by a mongoose. Eggs are frequently found in the vicinity of burrows, often with a small hole chewed in the side and the contents licked out.

nesting areas may increase.

Although mongooses are reportedly easy to trap at lower elevations (Pank 1980), this was not the case with the individuals that visited the summit of Haleakala. Perhaps it was the abundant food available within the colony or perhaps it was due to the unfamiliar environment. Whatever the reason, the mongooses inhabiting the summit proved to be very difficult to trap. Some mongooses clearly ignored the traps that they encountered as they roamed about the colony. In 1979 at least three birds were killed in the main colony following the establishment of the trapping program. Trapping was initially done with medium sized Havahart traps, but due to their limited effectiveness a number of wooden tunnel-type traps were eventually added (Figure 43). These traps were highly recommended by several local Maui trappers but they did not prove to be significantly better than the Havahart traps.

Six captive mongooses were observed in an outdoor cage during the study to determine their food preferences and general behavior. A number of chemical attractant scents were tested as baits, but none proved attractive to mongooses. In addition, a variety of other baits were tested including beef, dog food, cat food, cheese, coconut, peanut butter, fresh fish, dried fish, smoked fish, eggs,

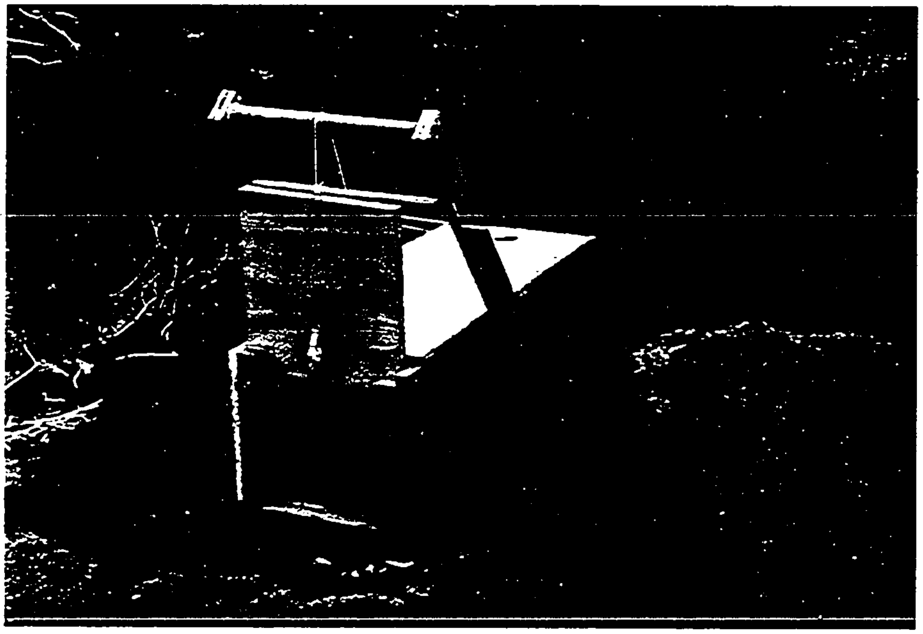


Figure 43. A wooden tunnel-type mongoose trap.

pork and pork fat. Dog food, cat food, and eggs were all effective baits, but surprisingly pork fat proved to be the most irrestible bait tested. The captive mongooses went to great lengths to get to a piece of pork fat, and it proved to be an excellent bait due to its ability to remain soft, moist and odorous in spite of the very dry conditions at the summit. Drying was a major problem with most other baits. The captive animal observations also pointed out several aspects of mongoose behavior that are not generally well known.

First of all, the mongooses I observed proved to be very adept climbers. They could scale the hardware cloth sides of their cage with ease, and were even able to traverse the roof of the cage by hanging upside down. Individuals were also observed climbing posts and tree limbs that were placed in the cage. Mongooses are not thought to be good climbers, and some efforts to control them have included fencing (Telfer 1981). My observations suggest that fencing may not be an effective method of excluding mongoose from an area, and also imply that forest birds may be at greater risk of mongoose predation than is generally appreciated. I determined that mongooses were capable of entering a hole less than 5 cm in diameter, an ability which makes all Dark-rumped Petrel burrows accessible to them. Therefore, it would be impossible to exclude mongooses from petrel burrows by using baffles, a technique which has been successfully employed to protect endangered Bermuda Petrels from their major predators, Tropic Birds (Wingate 1977).

Feral Cats

Feral cats also pose a significant threat to nesting petrels, and cat predation was responsible for some of the mortality observed during the study. As with mongooses it appeared that at present only a small number of individuals were responsible for the predation within the colony (Chapter 2). Cats and cat sign have been observed throughout the upper elevations of Haleakala both within and outside the park. Like mongooses, cats appear to enter the nesting areas from all directions, particularly via Kaupo and Koolau gaps. Due to the large feral cat populations at lower elevations, it is likely that the movement of vagrant individuals into the petrel nesting areas, especially during the nesting season, will be a continual problem. The presence of cats in the nesting areas is further aggravated by park visitors that occasionally abandon unwanted cats at the summit. This problem could be reduced by a public information campaign aimed at informing visitors of the threat that feral pets, especially cats, pose to native wildlife. A program directed at a similar problem in New Zealand has used this approach with some success (New Zealand Wildlife Service 1979).

Most cats and cat sign were observed in close association with areas of human activity, particulary the summit of Haleakala, parking areas and overlooks, and the cabins inside the crater. This is most likely the result of the concentration of food in these areas, including rats, mice, and garbage. Control efforts, particulary trapping, should be concentrated in these areas as well as along the primary access routes to the summit, the park road, skyline drive, and Kaupo Gap. Mid-sized and large Havahart traps were used successfully to control cats during the study. Cats appear to be less trap shy than mongooses and were readily attracted to cat food or dog food bait.

Rats

All three species of rats found in Hawaii, the Black Rat Rattus rattus, the Norway Rat Rattus norvegicus, and the Polynesian Rat Rattus exulans, are suspected predators of Dark-rumped Petrels (Larson 1967, King 1971). All have been trapped within the park and at least two species, the Black Rat and the Polynesian Rat, have been trapped within the petrel nesting area. Kepler (1967) has shown that Polynesian Rats can be serious predators on the eggs, nestlings, and even adults of Laysan Albatrosses and other Pacific seabirds. Perhaps for this reason much of the predation detected in earlier studies was attributed to rats. Rats were clearly the most abundant predator in the petrel nesting areas when this study began, but I was unable to obtain any direct evidence that they were responsible for the predation I observed. I found some evidence that rats had scavanged carcasses left by cats or mongooses, but I found no cases of predation that were caused solely by rats. In fact, although rats have been previously thought to be serious petrel egg predators, I found strong evidence to the contrary within Haleakala National Park. Chicken eggs, which are smaller and presumably easier to eat than petrel eggs, were used as mongoose bait in many of the traps that also caught rats. In no instances did the trapped rats eat the eggs, and in some cases the rats died in these traps, apparently of starvation or exposure.

Rats were relatively easy to control within the petrel nesting areas, and the catch data indicate that intensive trapping was successful in eliminating most of the resident rat population (Chapter 2). Rats are easily trapped using Havahart traps baited with peanut butter or fresh coconut. Trapping efforts should be concentrated in areas of human activity, especially the summit, the crater cabins, the park road, and headquarters area. The rat population can be expected to vary in proportion to the amount of waste food that is generated by park visitors and residents. Therefore, from the perspective of Dark-rumped Petrel management, food concessions within the park would be highly undesirable. Picnicing outside of Hosmer Grove and the crater cabins should be discouraged, and cooperative efforts to control waste food sources in the Science City complex should be initiated. Although rats were not identified as major predators of petrels in this study, this does not rule out the possibility, especially if their population levels increase. In addition, it is likely that rat populations could contribute indirectly to the loss of petrels by acting as a food resource for cats and mongooses. Any efforts to reduce rat populations will also contribute to the reduction of these other predators within the petrel nesting areas.

Feral Goats

Goats are not petrel predators, but some evidence collected during the study indicates that they may be having a negative impact on nesting petrels in some areas. Goats often choose as bedding sites the same cliff ledges and outcrops that make ideal locations for petrel burrows. I found a number of cases, primarily in areas with large goat populations, in which goat bedding sites had become established in front of former petrel burrows. Most of those burrows were no longer active, and although it was impossible to determine if the goats were responsible, it was clear that the goats would have substantially interfered with any birds trying to use those burrows (Figure 44). A number of cases were also found in which goat bedding activity resulted in the collapse of an adjacent petrel burrow. Thus, although goats do not at this time pose a serious threat to the remaining petrel populations, their activity within a petrel breeding area may reduce the amount of available nesting habitat. Control efforts currently in effect to reduce goat populations in Halealala National Park should have a beneficial impact on the petrel populations.

Feral Pigs

Feral pigs have been implicated as serious predators of Dark-rumped Petrels in the Galapagos (Harris 1970, Tomkins 1980). Pig rooting destroys petrel burrows, and pigs are also known to dig up, kill, and eat petrel adults, eggs, and nestlings. Some authors have even reported cases in which the flesh of a pig killed by hunters was strongly tainted with the taste of petrels, due to the large number of birds the pig had eaten (Harris 1970). It may well be

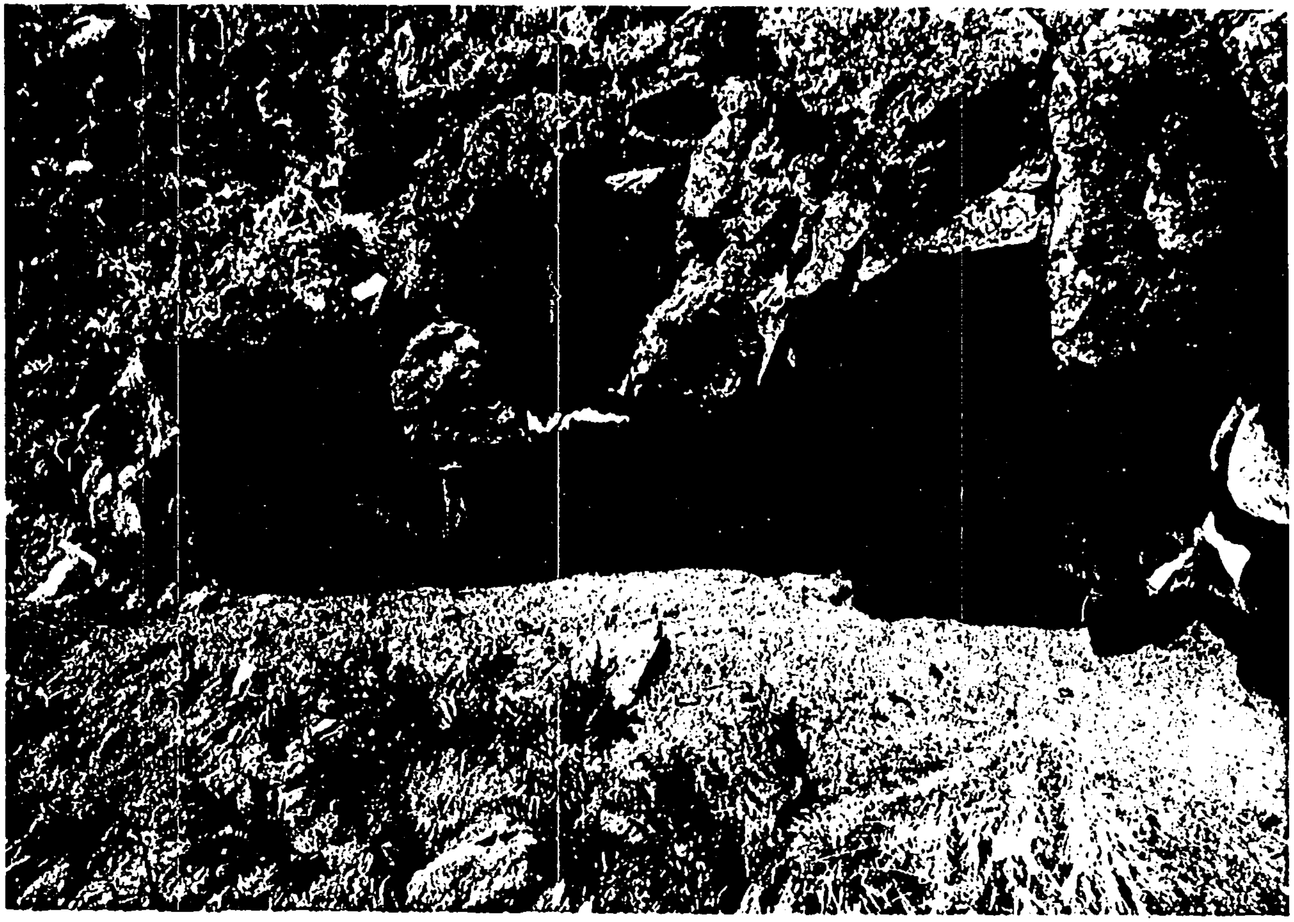


Figure 44. Feral goat activity at a Dark-rumped Petrel nest site. Goats often make bedding sites on the ledges that are used by petrels for landing areas and burrows. Bedding activity may result in the collapse of adjacent burrows.

that pigs contributed to the elimintaion of the large petrel colonies that existed at lower elevations in Hawaii in the recent past. Pigs do not appear to pose a direct threat to the remaining Dark-rumped Petrel populations because most birds nest well above the pig's normal range. In locations where the ranges of pigs and petrels overlap, such as Hana Mountain, and above Holua Cabin on Maui, pig control could benefit nesting petrels. An expansion of pig activity into petrel nesting areas could have negative consequences, and strong efforts should be made to prevent this possibility.

Short-eared Owls

Another potential predator of Dark-rumped Petrels in Hawaii is the Short-eared Owl. These owls are important predators of Dark-rumped Petrels in the Galapagos and there is some evidence that they also prey on Hawaiian birds. I found two petrel carcasses that appeared to be the remains of owl kills (Chapter 2). Short-eared owls are common below about 2000 m on East Maui, and their range does not overlap significantly with the nesting range of the Dark-rumped Petrel. Therefore, owls are not currently considered to be serious predators of Dark-rumped Petrels, but this possibility should not be ruled out if owl populations increase.

Predator Control

Protecting the remaining Dark-rumped Petrel populations from predators will be a substantial and continual task. These birds nest in rugged terrain and they are dispersed over more than 100 km^2. Due to current restrictions governing the use of poisons on federal land, and the vulnerability of petrels to lethal trapping methods, current control efforts must rely primarily on livetrapping. This is an expensive, time-consuming method of predator control, and in some cases it is only partially effective. Nevertheless, it is the best method currently available, and it should be carried out to the maximum extent possible. The following recommendations are made to insure the greatest success of the trapping program.

1. Traplines in areas of petrel or predator concentrations should be established, (where they do not already exist) and maintained on a regular basis. These areas include; the main west rim petrel colony, the summit area, the park road, overlooks, the headquarters area, Hosmer's grove, the crater cabins and, if possible, the Waikau area and upper Kaupo gap.

2. Traplines should be checked and rebaited at least twice

a month. During these checks the traps should be physically checked to insure that they are in working order. Baits should include cat or dog food, pork fat, and peanut butter or coconut to insure that all three of the major predators will be attracted.

3. Both large and medium sized live traps should be used to insure that large cats will be caught.

4. Traps within petrel nesting areas should be protected with barriers or placed in locations which will minimize the likelihood that they will inadvertently catch wandering petrels. No traps should be placed within 10 meters of an active petrel burrow.

5. Records should be kept indicating the frequency with which the traplines are checked. These records should indicate the number, species, and location of the animals caught and if possible the specimens age and breeding status. The results should be summarized and tabulated at least once a year so that trends in the predator populations can be identified.

In addition to the trapping program, attention should be given to the following aspects of the predation problem. First of all, control efforts aimed at goat and pig populations should be carried out to minimize the attraction of predators into petrel nesting areas. Rats, cats, and mongooses are all known to scavange extensively. The shooting of goats and pigs within petrel nesting areas, particularly during the breeding season, could attract predators into the colony.

Secondly, new approaches to solving the predation problem should be pursued. The process of obtaining an exemption of executive order #11643 and permission to use chemical control agents should be investigated. If, as expected, predator populations increase in the future, the current predator control methods are unlikely to provide permanent protection for the nesting Dark-rumped Petrels. Livetrapping is an expensive and time consuming solution to the problem. With adaquate research it is likely that a chemical control program could be developed that would target specific predators and pose little threat of secondary effects. The New Zealand Wildlife Service has had considerable success in developing chemical control programs aimed at a variety of introduced mammalian predators (Rammell and Fleming 1979). Peter Conally of the Hawaii State Game Department has established contacts with several members of the New Zealand Wildlife Service on this topic, and has found them to be very helpful in providing suggestions on possible methods of controlling introduced predators in Hawaii. In addition, Dr. Jim Keith of the Denver Wildlife Research Center has indicated that the center is interested in sharing its considerable experience in chemical control methods. Dr. Keith has recently visited the Galapagos as a consultant to help develop control methods for the black rat, a serious predator of the Galapagos Dark-rumped Petrel. The center has primarily been interested in agricultural pests in the past, but they are beginning to expand their work to include predation problems involving endangered species, especially in tropical areas. Dr. Keith has indicated to me that all that is required to to get the necessary research going is for the interested organizations in Hawaii to express their specific needs to the Denver Wildlife Research Center. Both of these avenues of assistance should be pursued while there is still time to develop a carefully researched, predator-specific, control program.

Pank (1980) has already outlined the steps that would be necessary for the development of a new control program. Controlled studies need to be initiated to determine the relative effectiveness of non-chemical control methods, such as physical barriers, traps and their associated baiting methods, and biological agents. In addition, a toxicant development and registration program should also be initiated. This study would include the laboratory development of baits and toxicants and determine effective concentrations and application methods. An assesment of non-target hazards would be required as would field studies to determine application rates, non-target impacts, and overall effectiveness.

In conjunction with the research just discussed I would recommend that a comprehensive investigation of the behavior and general biology of feral cats and mongooses in Hawaii be initiated. An applied study of these animals focusing on their role as predators of native wildlife would make a substantial contibution to our understanding of these predators and our ability to control them. It would be particularly useful to know something about the distribution, movement, and dispersal patterns of these animals, their food habits, and social structure.

Other Sources of Disturbance and Mortality

Although predation is the major threat to the remaining petrel populations at present, several other factors are also contributing to their decline. These include man-made obstacles, light-related mortality, and the disturbance of breeding birds by human activities. The most serious of these is light-related mortality and the problem is similar to that described for the Newell's Shearwater on Kauai

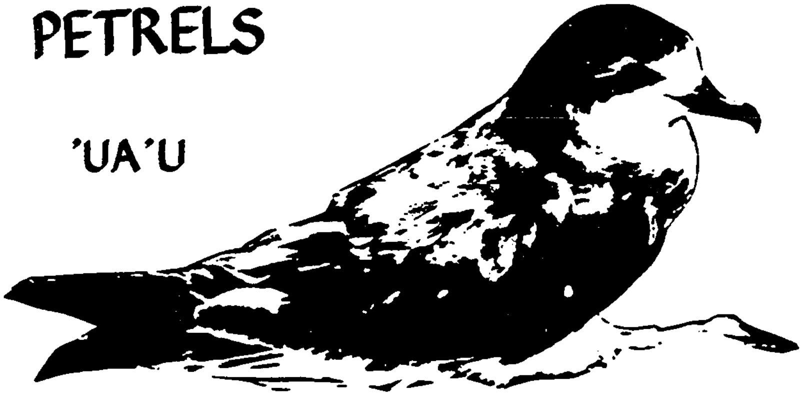
(Sincock and Swedberg 1969, Telfer 1979). Both adult and fledgling Dark-rumped Petrels are attracted to lights, although the problem is most serious in fledgling birds. The birds are attracted to lights, and they often fly into them injuring themselves and crashing to the ground. Uninjured birds often fall to the ground in a disoriented state and are unable to take off. The victims of these accidents suffer a high rate of mortality unless they recieve some sort of assistance. A recovery program on Kauai has been very successful in rescuing most of these downed birds. Between 1978 and 1980 over 4000 birds were collected and most were successfully released. A publicity campaign has informed the public of the problem and encouraged people to collect any downed Newell's Shearwaters and bring them to an aid station.

The problem with the Dark-rumped Petrel is of a much smaller scale but its implications for the health of the remaining populations are serious (Chapter 4). Small numbers of grounded petrels have been reported over the last 15 years. Most birds are fledglings found in the fall. The groundings occured sporadically, and in many years no birds were reported. A large grounding occurred in the early 1970's when 20 - 30 birds were grounded in Lahaina (C.B. Kepler pers. com.) No data are available on those birds, and the first documented groundings occurred in 1976 when eight birds were recovered. Three of those birds died, and the remaining five were banded and released. No grounded birds were recovered during the first year of this study, and to assess the severity of the problem an intensive publicity campaign and recovery program was initiated in 1980. Leaflets describing the birds and the problem were distributed throughout Maui and Lanai, and posted in businesses and public schools (Figure 45). Several newspaper articles and radio spots describing the problem were also arranged. Petrel aid stations were set up and checked daily at three locations on Maui as collection points for grounded birds. No birds were recovered in 1980 indicating that few if any birds were grounded that year. The campaign was successful in educating the public on the problem, and it was continued in 1981. In that year the publicity campaign was similar to the year before but the number of aid stations was reduced to one. Three birds were recovered in 1981 and two survived and were released. Again public interest appeared high, and it is thought that most of the grounded birds were recovered. It is recommended that the recovery program be continued on a regular basis in the future. This will allow the continued assessment of the problem, and it can be accomplished with a small amount of effort. The publicity campaign should be started in early October, and the aid station set up and monitored from mid-October to mid-November. It is likely

WANTED

DARK RUMPED PETRELS

OR 'UA'U



DARK-RUMPED PETRELS ARE MEDIUM SIZED BLACK AND WHITE SEABIRDS WITH A WING SPAN OF APPROXIMATELY THREE FEET. THESE BIRDS ARE NATIVE TO HAWAII AND ARE THREATENED WITH EXTINCTION. THEY NEST IN HALEAKALA CRATER AND YOUNG BIRDS OCCASIONALLY BECOME GROUNDED IN OCTOBER AND NOVEMBER AFTER FLYING INTO LIGHTS IN URBAN AREAS.

IF YOU FIND A PETREL NOTE YOUR LOCATION, PLACE IT IN A BOX AND BRING IT TO THE PETREL AID STATION AT THE MAUI ZOO IN WAILUKU. FOR ADDITIONAL ASSISTANCE CONTACT HALEAKALA NATIONAL PARK AT 572-9306. PLEASE DO NOT RELEASE THE BIRDS YOURSELF BUT BRING THEM TO THE AID STATION WHERE THEY WILL BE CARED FOR, INSPECTED FOR INJURIES, BANDED, AND SAFELY RELEASED. YOUR HELP WILL BE GREATLY APPRECIATED.

HALEAKALA NATIONAL PARK
U.S. FISH AND WILDLIFE SERVICE
DIVISION OF FISH AND GAME, DLNR

Figure 45. Petrel wanted poster. This poster is distributed each fall to alert local residents to be on the lookout for grounded petrels.

that light-related groundings will increase as urbanization outside of the petrel nesting areas increases. Continuation of the program will maintain public awareness, which is necessary for the success of the program, and it will allow the detection of any increases in the problem in time to take remedial action.

Lights in the vicinity of the nesting colony are also a threat to Dark-rumped Petrels. Haleakala National Park records indicate that over the past 15 years approximately six adult petrels have been killed in collisions with vehicles on the park road. If human activity and traffic at the summit increase, this form of mortality can be expected to increase as well. Birds are also attracted to lights on buildings, and although no mortality related to these lights has been documented they may be a source of disturbance to breeding birds and a potential source of mortality. Park policy should discourage lights on the summit, and cooperation should be sought from Science City residents to minimize the problem. Park personnel should keep careful records of light-related mortality. This will allow them to detect any increases in the problem, and the information will be useful if restrictions on lights at the summit need to be pursued at some future time.

A number of petrels have also been killed on Haleakala after of colliding with man-made obstacles. Wires, poles and towers are apparently not visible to night flying petrels, and these obstacles should be kept as far from known petrel nesting sites as possible. Currently, most of these obstacles are located within the Science City complex. The complex is outside of the major flight paths of petrels, and it does not appear that it has been an important factor in this problem. Future developments at the summit of Haleakala should be planned so as not to increase this source of mortality.

Two adult birds have been killed over the past several years as a result of collisions with wire fences within the park (Figure 46). With the expansion of the fencing program this problem will probably increase. It may be necessary to make portions of the fence that pass near active petrel burrows more visible by some means, such as attaching reflective material to the top strand of wire.

Another potential threat to the remaining Dark-rumped Petrel populations is disturbance related to human activities, vehicle traffic, and aircraft. As nocturnal burrow-nesting birds, Dark-rumped Petrels are not usually in direct contact with humans. In addition, having evolved in a predator-free system, these birds do not respond readily to forms of disturbance that many other species find

Figure 46. Adult petrel impaled on barbed wire. Fencing and other obstacles in the vicinity of petrel nests can pose a threat to flying birds.

intolerable. This behavior is one of the factors that makes them so vulnerable to predators, but it also makes them more likely to be able to survive in an area such as Haleakala National Park where some level of human activity will always be present.

In general, Dark-rumped Petrels are quite tolerant of human activity in and around their nesting colony as long as birds are not directly disturbed within their burrows. For example, some birds have nested successfully for several years in locations receiving considerable human activity. These include sites just below the Haleakala visitor center, along sliding sands trail, and within 10 m of a busy corner on the park road. As in any species, individual birds show differant tolerances to disturbance, and these examples probably represent one extreme. I found that some adult birds were tolerant of a high degree of disturbance while they were on the nest whereas other birds readily deserted their nests in response to any form of burrow disturbance. I found no evidence that my activity around the nest site caused breeding failures, and the several cases of disturbance that I was responsible for all resulted from my unintentional disruption of incubating birds on the nest. The birds are most sensitive to disturbance from early March until the beginning of the nestling period in July. Human activity within (or adjacent to) the colony should be minimized during this period and the monitoring of birds within their burrows should only be done with great care by experienced personnel. Only chicks remain on the colony during the day from July to November and they are quite tolerant of most types of human activity. I weighed and measured nestlings regularly throughout the study and found no evidence of a reduction in reproductive success as a result of my activities. In general, disturbance of nesting birds should be minimized as much as possible especially during the incubation period. The presence of a small number of informed people in and around the nesting colony at any time of the year should not pose a threat to breeding birds as long as the birds are not disturbed within their nesting burrows.

At its present level vehicle traffic in the vicinity of petrel burrows does not appear to disturb nesting birds. A greater threat is posed by the potential for collisions between night-flying petrels and vehicles as discussed in the previous section. Helicopter traffic in and around Haleakala National Park has increased in recent years, and it represents another source of disturbance for nesting birds. Helicopters are a notorious source of disturbance for many surface nesting seabirds (A. Sowls pers. comm.) but their effects on burrow nesting species are poorly understood. As a precaution, helicopter traffic in and around petrel nesting areas should be minimized throughout the breeding season, and if possible, eliminated during the incubation period.

Human activity per se does not pose a serious threat to the remaining petrel populations. It is the factors associated with human acivity, such as increased refuse and the predators it attracts, or additional outdoor light sources that cause the majority of problems for the remaining birds. Simply insulating the birds from obvious forms of disturbance such as park visitors will in no way insure their survival.

AN ECOSYSTEM APPROACH TO DARK-RUMPED PETREL MANAGEMENT

As a conclusion to the Dark-rumped Petrel management plan I would like to discuss the need for an integrated approach to the management of all threatened resources. It is tempting to narrow one's viewpoint when working with endangered species and often management plans are formulated from this limited perspective. In Hawaii where so many species of plants and animals are endangered it is much easier to see why attempting to manage natural resources from the perspective of a single species cannot succeed. As management efforts for one species are put into effect their unintended impact on other species often become clear. It is only after noting these unanticipated connections that the need for an ecosystem approach becomes evident. As an example of this process, I will give some examples of how my work on the Dark-rumped Petrel has shown me the problems caused by single species approaches to natural resource management.

Many of the problems in Hawaiian ecosystems stem from introduced plants and animals. Within Haleakala National Park, feral goats and pigs are destroying vast areas of native vegetation and its associated fauna. The removal of these animals from the park has justifiably become a top resource management priority but it cannot be viewed in isolation. For example, when viewed from the perspective of the Dark-rumped Petrels, the removal of goats and pigs may have both and costs and benefits. Goats in some areas appear to have taken over many of the ledges that make prime petrel nest sites and their bedding behavior may occasionally collapse or destroy petrel burrows. Also, the carcasses and other debris associated with the hunting of goats within the park may attract predators into areas where petrels are nesting. In this sense the removal of goats will probably benefit the petrels. On the other hand, the goats, by reducing the vegetative cover on the petrel colony, may be limiting the food and cover required by some predators, and thus their presence may benefit the petrels. Also, the fences being built to control goats may, as already discussed, pose a threat to nesting petrels if they are built too close to the bird's burrows. Viewed from this perspective, the removal of goats could result in new threats to the remaining petrels.

Another example involves exotic game birds, such as chukar and pheasants. These birds are popular with bird hunters in Hawaii and politically it would be very difficult to remove them. Aside from this consideration they remain the source of a resource management dilema due to their ambiguous role in native ecosystems. The birds are common within Haleakala National Park and some concern has been expressed over their role as competitors with endangered native birds, such as Nene, for food resources (Paul Banko pers. com.). Other researchers have voiced concern that these birds may be responsible in part for the lack of regeneration of native flora within the park (Jacobi 1980). On the other hand, these birds are now an integrated part of these ecosystems, and we cannot expect to remove them without some repercussions. The effects may not always be beneficial. If these exotic birds are acting as a buffer by drawing predation pressure away from native species, such as the Dark-rumped Petrel, then removing them without simultaneously controlling the predator population could have serious consequences.

A related example involves the control of predators. If, for example, the removal of predators to aid the petrel population caused a dramatic increase in the game bird population the result may be an unanticipated negative effect on Nene populations or native flora. Obviously the scenerios are endless and much of this speculation is based on little or no data. The purpose of this discussion is to point out that management decisions need to be made in the context of the entire ecosystem. We are beginning to understand that as resource managers we cannot formulate our management plans based on myopic species-specific approaches to management problems. Simplistic dichotomies such as exotic versus native become meaningless as we begin to understand the interconnected nature of the systems with which we are dealing. The more we understand these interrelationships the more likely we will be to anticipate and detect these secondary effects in time to modify our management strategies accordingly.

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APPENDIX A

A MONITORING PROGRAM AND CONSERVATION TECHNIQUES

A major component of the management plan for the Dark-rumped Petrel is a monitoring program. The purpose of the program is to provide an indication of the health of the remaining populations and to allow the detection of both long and short term changes in population levels. The program consists of four main components, colony wide surveys, activity checks of the White Hill sub-colony, monitoring of accessible burrows, and a banding program.

Colony Wide Surveys

The nesting colonies of Hawaiian Dark-rumped Petrels were rediscovered on the island of Maui in 1954 (Richardson and Woodside 1954). Efforts to determine the size and range of the remaining breeding colonies have continued since the discovery, and to date over 600 burrows have been identified and mapped in and around Haleakala National Park. The yearly petrel surveys conducted over the last fifteen years, primarily by Jitsumi Kunioki of the National Park

Service, have provided base line information on the distribution of petrel burrows throughout the park, and the number of active burrows in the colony each season. It is essential that these surveys be continued in the future in order to detect changes in the size of the petrel population, and changes in the reproductive success of breeding birds.

Census and activity data since 1967 have been summarized in a petrel burrow activity index on file at Haleakala National Park. The file should be used with the burrow location index. Together the two provide a record of the location and activity data of all the known petrel burrows. The activity index has been divided into nine sections by area. The areas correspond to the primary sub-colonies within the Haleakala population (Figure 3). The burrows within each area are listed in numerical order. Data are summarized on a yearly basis for each burrow indicating if the burrow was checked, and the status of the burrow that year. Within each sub-colony burrows are located with the burrow location index. The location index is comprised of burrow location maps, and in most cases corresponding photographs of the sections of the colony covered by the maps (Figures A1 and A2). Burrows are located within the sub-colonies by combining the information from the photographs and the maps, and are identified by painted

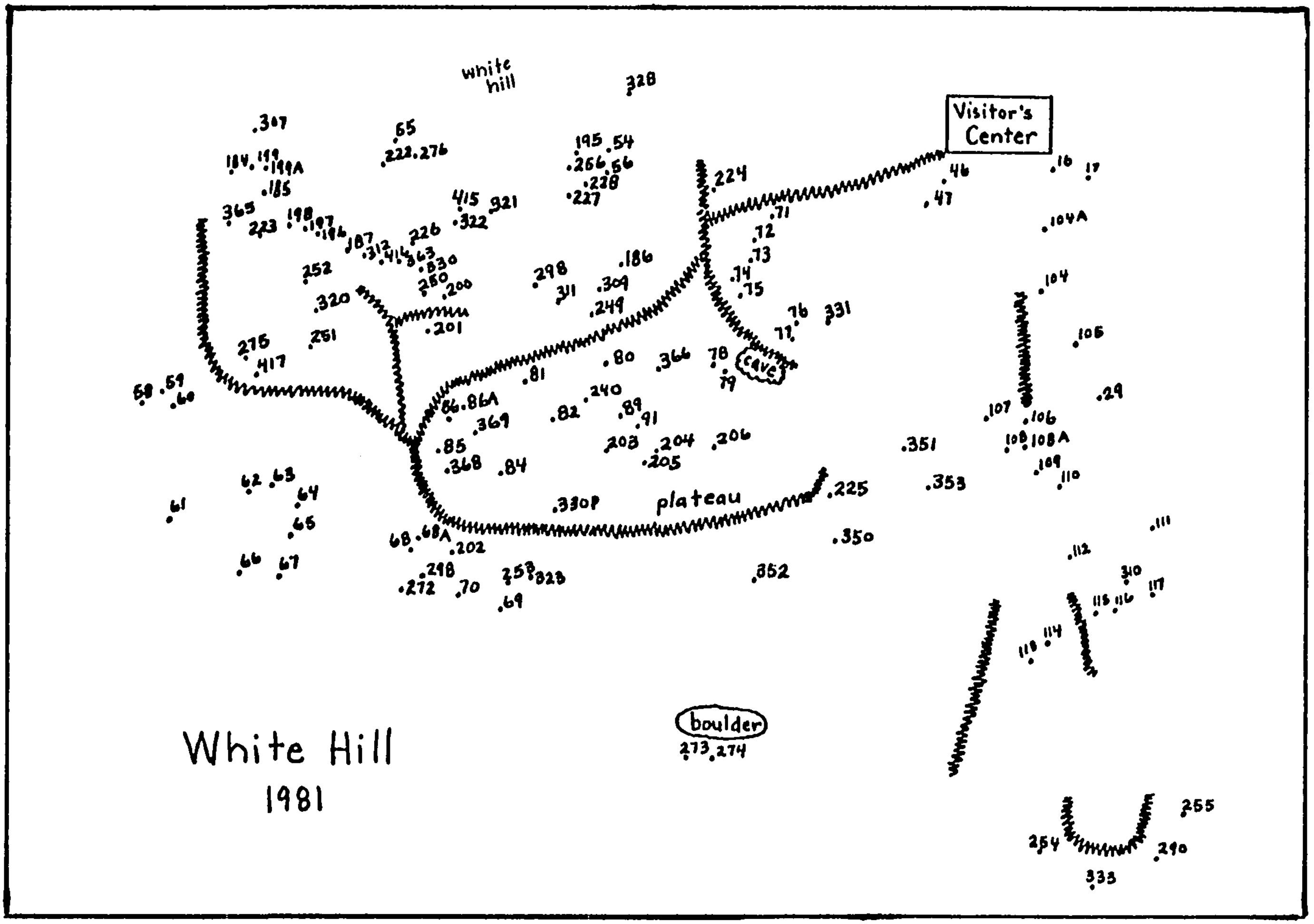

Figure A1. Petrel burrow map. Hand drawn maps of this type have been made for each of the major petrel nesting areas. Burrow numbers coincide with data in the petrel burrow index and burrow location photos.

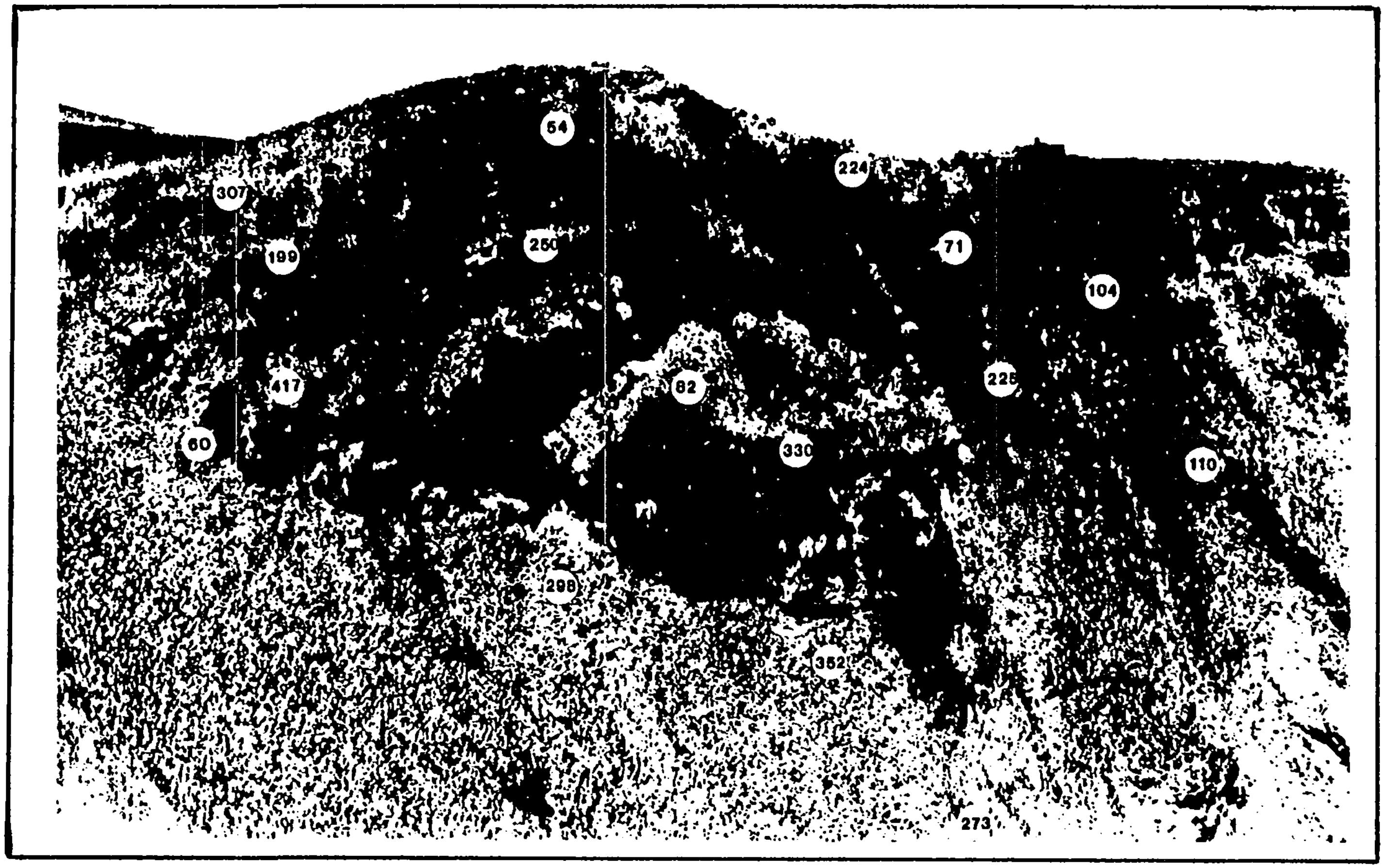

Figure A2. Burrow location photo. Photos of this type have been made of each of the major petrel nesting areas for use with the burrow location maps. Only a portion of the existing burrows are labled. These burrows are used as reference points for locating other burrows in the area.

numbers in the vicinity of the burrow entrance. Due to the variations in effort and personnel on the surveys over the years, the numbering scheme is somewhat erratic, and in many cases two or more burrows in different areas share the same number. Within a sub-colony all of the burrows have different numbers, and as long as this system is maintained confusion over burrow numbers should not be difficult to resolve. The burrow indexes have proved to be very useful tools for organizing yearly colony census data. I recommend that they be retained and expanded in the future. Several improvements to the system could be implemented in the future. The peripheral nesting areas including the south rim, Hana Mountain, and the west slope remain to be photographed, and all of the burrow maps could benefit from periodic updating. In addition, the method of numbering is not entirely satisfactory. The painted numbers at burrow entrances are unsightly, often difficult to read, and they require periodic repainting. Also, it is impossible to remove the numbers if burrows are judged to be inactive. The primary benefit of the painted numbers is that they are easy to see from a distance, making the task of locating burrows on the ground much simpler. I suggest that in the future burrows be numbered with permanent metal tags and that removable painted markers such as rocks or cairns be used to help locate burrows. In this way the markers or burrow numbers can be removed when they are no longer needed, but burrows will still be easy to locate.

Colony-wide surveys should be conducted at the same time each season. The best assesment of the colony will be obtained if the surveys start in early July, and they should be completed by the end of August. Individuals participating in the surveys should be experienced or trained so that they are able to identify the signs of a petrel burrow, bird activity, and predation. Field workers should be able to distinguish between cat, mongoose, and rat tracks and droppings, and they should be aware of the sign of other birds that visit the colony including Chuckar (*Alectoris chukar*) and Nene (*Branta sandvicensis*). Beginning with the White Hill sub-colony, the surveys should cover as much of the known nesting area as possible each season. At least 50% of the known burrows should be checked each year. Field workers should score burrows as active or inactive, and record all signs of activity including tracks, droppings, nest material, egg shells or feathers. The burrow should be visually inspected with a flashlight in an attempt to locate the nest chamber or evidence of other activity within the burrow. Any evidence of predation should be carefully noted including predator droppings, or the remains of eggs, nestlings or adults. Any evidence of a breeding attempt such as an incubating adult, a nestling or an egg should also be recorded. Finally all evidence of activity at the burrow should be removed so that it is not recorded in future surveys. Any new burrows located should be marked and mapped. If a new burrow shows signs of activity for several years in succession it should be given a permanent number. It is important that new burrows be given this observation period because in many cases they will be found to be temporary burrows, often the work of prospecting pre-breeding birds. The data from the surveys should be entered into the the burrow activity index and summarized on a yearly basis. Yearly tabulations should include the number of burrows surveyed, the percentage of active burrows, the percentage of burrows showing signs of predation, and other relevant information such as the number of new burrows located and the status of accesible burrows. In this way long term trends in the petrel's reproductive success and population size can be monitored.

It is likely that most of the existing Dark-rumped Petrel nest sites have been located, but several potential nesting areas should still be thoroughly surveyed. The most promising of these areas is the portion of the west rim of Haleakala between Holua Cabin and the adze quarry. Over 80 new burrows were located and mapped in this area in 1980, but much of the area remains to be checked. The west slope of Haleakala has also received limited coverage, and it is possible that this area may contain more petrel burrows than are currently known. Both areas should be systematically searched as part of future census efforts. Possible nesting areas outside of east Maui have been reported on Molokai, Hawaii, and Lanai but only Lanai appears to hold the potential for a viable nesting colony. Several visits to the upper ridges of Lanai during the course of this study confirmed a considerable amount of Dark-rumped Petrel activity in the form of flying and calling birds, but no active burrows were located. It is important to determine if a breeding colony exists on Lanai. The petrel activity is concentrated in the vicinity of Kumoa Gulch but the steep terrain and dense vegetation (Figure A3) make searching for burrows almost impossible. The use of a trained dog may be useful in locating burrows. The strong scent associated with petrel burrows should make this a relatively simple matter.

Activity Checks at the White Hill Sub-colony

As a complement to the colony wide surveys, I recommend that the periodic activity checks of burrows in the White Hill sub-colony (Chapter 2) be continued as part of the monitoring program. These checks provide a good estimate of attendance patterns at the colony, breeding chronology, and reproductive success. Approximately 105 burrows were

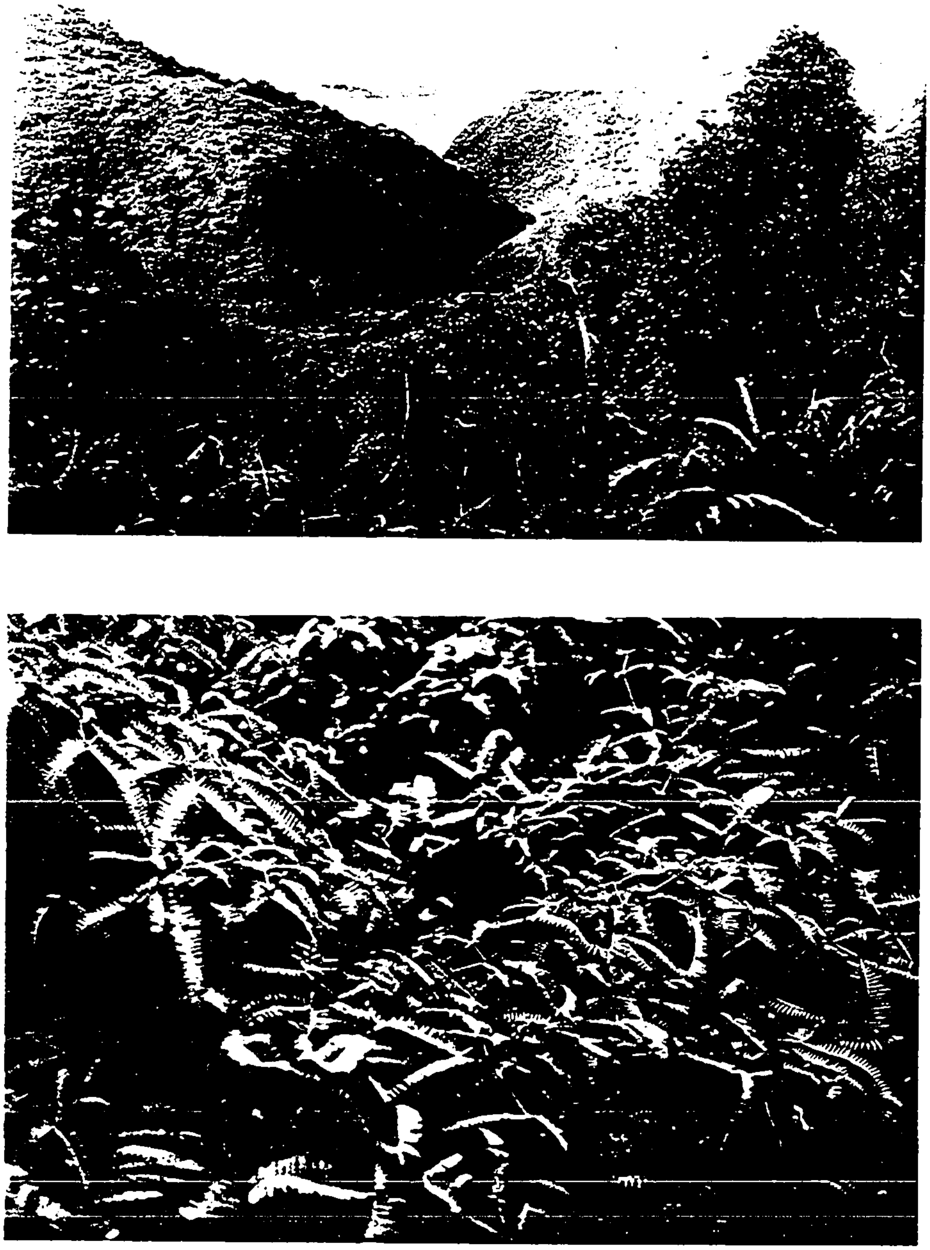

Figure A3. Dark-rumped Petrel habitat on the island of Lanai. Petrels may nest in the dense vegetation along the steep canyon walls at the top of the island (upper photo). A dense mat of false staghorn fern (up to 2 m thick) makes locating burrows in this habitat difficult.

monitored during the study by placing toothpick barriers at their entrances at regular intervals. The burrows were checked every ten days and those that were visited during the interval were recorded. From this data it is possible to determine the percentage of successful breeders in the sub-colony since failed breeders and prebreeding birds appear to stop returning to the colony by late August. Of the remaining burrows, those fledging chicks can be determined by noting which burrows continue to be visited by adult birds late in the season, and which burrows show signs of fledgling down at their entrances in October. In addition, the periodic checking of a reasonably large sample of burrows increases the possibility that evidence of predators on the colony will be detected quickly. Also, a number a accessible burrows are located within the White Hill sub-colony, and the monitoring of these burrows in conjunction with the activity checks will provide valuable information on the health of the population throughout the breeding season.

Data from these checks should be tabulated for individual burrows, and for the entire subcolony. Based on these findings an estimate of the percentage of active burrows fledging chicks each season should be made and compared to past years. A summary of recent activity at these burrows is presented in Table A1.

Table A1. Activity monitoring burrows in the White Hill sub-colony.

Burrow Number	Location	Current Status	Estimated # Chicks Fledged 1979-1981	Comments
224	U	I	0	
54	U	A	0	
195	U	A	0	
256	U	A	0	Event recorder, chick killed 1979
228	U	A	0	
56	U	A	0	
55	U	A	0	
276	U	A	0	
222	U	A	0	
322	U	A	1	
321	U	A	1	
321A	U	A	0	New burrow in 1979
227	U	A	0	
186	U	A	0	
309	U	I	0	
311	U	A	1	
249	U	A	0	Event recorder, chick killed 1979
298	U	A	0	
330	U	A	0	Event recorder, chick killed 1979
200	U	A	2	Event recorder, chick killed 1979
250	U	A	1	Event recorder, chick killed 1979
201	U	A	0	
226	U	A	1	
363	U	A	0	
312	U	A	2	
187	U	A	0	
196	U	A	1	
197	U	I	0	
198	U	A	2	
184	U	A	3	
185	U	I	0	
199	U	A	0	
199A	U	A	1	
307	U	A	1	
365	U	A	1	
223	U	A	1	
252	U	A	0	
320	U	A	0	
251	U	A	3	
275	U	I	0	
417	U	A	1	
60	L	I	0	
58	L	I	0	
59	L	A	0	
61	L	A	0	

Table A1 continued. Activity monitoring burrows in the White Hill sub-colony.

Burrow Number	Location	Current Status	Estimated # Chicks Fledged 1979-1981	Comments
62-63	L	A	0	Adult killed 1979
64	L	I	0	
65	L	A	1	
66	L	A	0	
67	L	I	0	
68	L	I	0	
68A	L	I	0	
298	L	A	0	
202	L	A	1	Adult killed 1979
272	L	A	3	
70	L	A	1	
253	L	A	0	
69	L	A	0	
323	L	A	0	
352	L	A	0	
366	P	A	1	
240	P	A	0	
80	P	I	0	
80A	P	A	1	Event recorder, artificial burrow.
79	P	A	2	
78	P	A	0	
89	P	I	0	
91	P	I	0	
86A	P	A	2	Event recorder
86	P	I	0	
85	P	A	1	
84	P	A	0	
82	P	A	2	Event recorder
81	P	A	0	
368	P	A	1	
369	P	A	3	
330P	P	A	3	Event recorder
206	P	A	1	
205	P	A	3	
204	P	A	1	
203	P	A	2	
350	V	A	0	
353	V	A	2	
225	V	A	0	
351	V	A	1	
110	V	A	1	
109	V	A	1	
108	V	A	3	
29	V	A	3	

Table A1 continued. Activity monitoring burrows in the White Hill sub-colony.

Burrow Number	Location	Current Status	Estimated # Chicks Fledged 1979-1981	Comments
104	V	A	2	
105	V	A	1	
104A	V	A	2	
106	V	A	2	
107	V	I	0	
77	V	A	3	
76	V	A	1	
331	V	A	0	
75	V	A	3	
74	V	A	0	
73	V	A	3	
72	V	A	2	
71	V	A	2	

Location codes: U = upper white hill, L = lower white hill, P = plateau area, V = below visitor center

Status codes: A = active, I = inactive

An event recorder was used to continuously monitor the activity at ten burrows during the study, and the recorder has been kept in operation since that time. The recorder has been incorporated into a display in the summit visitor center at Haleakala National Park which describes the purpose of the recorder and the biology and conservation needs of the Dark-rumped Petrel. The event recorder provides interesting information on the attendance patterns of the birds including the return of birds each spring, the incubation and feeding patterns of adults, and the fledging dates of nestlings. This data is not directly necessary for the conservation of these birds, but it does provide a long term record of the variability of of these aspects of the birds biology for a small amount of effort. The continued operation of the event recorder will be left to the discretion of park personnel. The recorder requires the following maintenance. All of the switches should be tested twice each season and any faulty switches repaired. The elastic centering threads in the switches should be replaced at the beginning of each season. The switches should also be removed every two to three years and overhauled. At this time the connecting wires and contact points should be replaced and new emery cloth glued to the floor of the tube. The charts in the recorder should be replaced once every two months, and the recorder wound once a week. Each time the recorder is wound the date and time should be written on the chart and the chart should be reset to the correct time if necessary. Finally, the ink in the recorder needs to be re-filled twice a year and at those times all of the pens should be removed and cleaned with water. The data charts from the recorder should be carefully dated, labled, and saved for future use.

Monitoring Accessible Burrows

Without access to the nest chamber of an active burrow it is difficult to know with certainty the status and fate of that burrow during the breeding season. Due to the small number of petrel burrows in which the nest chamber is accessible, indirect monitoring methods such as surveys, activity checks, and event recorders are needed, but these methods only provide an approximation of yearly reproductive success. The best method of determining the yearly reproductive success of breeding petrels, and of locating evidence of predators on the colony, is to monitor accessible burrows throughout the season. At the beginning of this study only two petrel burrows in which the nest chamber was accessible were known. Currently, over 40 active accessible burrows have been located, and many of these have been used by breeding birds in the past three years. Some burrows have been accessed by excavating a hole over the nest chamber, and installing a removable cover, while in others the nest was visible from the burrow entrance. A list and map of these accessible burrows has been provided to the resource management division of Haleakala National Park. They will not be published here due to their importance in future monitoring programs and the vulnerability of the birds to disturbance. The validity of the monitoring program will largely depend on the existence of an adequate sample of accessible nests (25 or more). Therefore, known nests should be carefully protected.

As many accessible nests as possible should be checked a minimum of four times a year. The first check should be done in the middle of April at which time the surveyor should aquaint him/herself with the layout of the burrow, and note any signs of pre-breeding activity such as droppings, digging, or nest material. The nest chamber should be located at that time so that during the next check the burrow can be examined without disturbing the incubating bird. The next check should occur after egg laying has been completed in the middle of June. At that time the burrows should be checked for the presence of an incubating adult. Extreme care should be taken to avoid disturbing incubating birds. In general, if one is quiet around the nest it is possible to examine the nest chamber with a flashlight without rousing the incubating adult. In some cases it may be necessary to reach carefully into an excavated burrow to determine if an adult bird is present on the nest. The third check should take place in late July to determine the number of burrows with nestlings or unhatched eggs. Any previously active burrows that are empty at this time should be carefully searched for evidence of unhatched eggs or predation. A final check should be done in early October to determine the number of chicks that have survived to fledging. From these observations the percentage of active burrows containing breeding birds can be calculated as well as the seasons hatching and fledging success. Overall reproductive success can also be estimated as the percentage of eggs laid that produced fledglings. These data are the most valuable for determining the general health of the breeding population, especially in combination with the census data discussed previously.

Banding Study

A banding study of the Dark-rumped Petrel was initiated in 1980, and since then over 80 birds have been banded including 43 breeding adults (Table A2). This data has

Table A2. Dark-rumped Petrel banding data.

Band Number	Date	Location	Age	Comments
554-50501	1964	Holua cabin	A	
554-50502	"	"	N	
554-50503	"	"	A	
554-45004	1965	# 3	A	
554-45005	"	"	A	
554-28201	1966	# 6	A	
554-28202	"	"	A	
554-28203	"	"	N	
554-28204	"	# 5	A	
554-28205	"	# 3	N	
554-28206	"	# 4	A	
554-28207	1968	# 6	N	
554-28208	1969	# 6	N	
554-28209	1970	# 15	A	
554-28210	"	# 11	A	
554-28211	"	# 10	A	
554-28212	"	# 142	A	
554-28213	"	# 6	A	Formerly #554-28202
554-28214	"	"	A	Formerly #554-28201
554-28215	"	# 4	N	
554-28216	"	# 5	N	
554-28217	1971	# 6	N	
554-28218	1972	# 71	A	
554-28219	1974	# 6	N	
554-28224	"	Summit	A	Grounded bird, released.
554-28220	1975	"	"	Grounded bird, released.
554-28222	"	# 82	A	
554-28223	"	# 250	A	
554-28234	1976	Kahului	F	Grounded bird, released.
554-28235	"	"	F	"
554-28237	"	"	F	"
554-28238	"	"	F	"
554-28239	"	"	F	"
554-28241	"	"	F	"
584-14602	1979	# 1	N	
584-14603	"	# 308	N	
584-14604	"	# 163	N	
584-14605	"	# 170	N	
584-14606	"	# 171	N	
584-14607	"	# 19 CC	N	
584-14608	"	# 330P	N	
584-14609	"	# 86A	N	
584-14610	"	# 82	N	
584-14611	"	# 6	N	
584-14612	"	# 410	N	
584-14613	"	# 414	N	
584-14614	"	# SC25	N	

Table A2 continued. Dark-rumped Petrel banding data.

Band Number	Date	Location	Age	Comments
584-14801	1980	Summit	A	Grounded bird, released.
584-14802	"	# SC25	A	Male
584-14803	"	"	A	Female
584-14804	"	# 330	A	
584-14805	"	# 82	A	
584-14806	"	# 202	A	
584-14807	"	# 249	A	
584-14808	"	# 249	A	
584-14809	"	# 6 South rim	A	
584-14810	"	Puu Maile # 1	A	
584-14812	"	Puu Maile # 2	A	
584-14813	"	# 200	A	
584-14814	"	# 82	A	
584-14815	"	# 202	A	
584-14816	"	# 298	A	
584-14817	"	# 312	A	
584-14818	"	# 196	A	
584-14819	"	# 298	A	
584-14820	"	# 252	A	
584-14821	"	# 73	A	
584-14822	"	# 186	A	
584-14823	"	# 251	A	
584-14824	"	# 104A	A	
584-14825	"	# 200	A	
584-14826	"	# 251	A	
584-14827	"	# 307	A	
584-14828	"	# 73	A	
584-14829	"	# 322	A	
584-14830	"	# 106	A	
584-14831	"	# 312	A	
584-14832	"	# 75	A	
584-14833	"	# 106	A	
584-14834	"	# 19 CC	N	
584-14835	"	Puu Maile # 1	N	
584-14836	"	Puu Maile # 2	N	
584-14837	"	# 6	N	
584-14838	"	# 44	N	
584-14839	"	# 82	N	
584-14840	"	# 200	N	
584-14841	"	# 163	N	
584-14842	"	# 71	N	

Table A2 continued. Dark-rumped Petrel banding data.

Band Number	Date	Location	Age	Comments
584-14843	1981	Kalahaku	A	Injured bird, released.
584-14844	"	# 16	A	
584-14845	"	# 61	A	
584-14846	"	White Hill	A	Caught on ground, released.
584-14847	"	# 77	A	
584-14848	"	# 77	A	
584-14849	"	# 29	A	
584-14850	"	# 226	A	
584-14851	"	White Hill	A	Caught on ground, released.
584-14852	"	# 108	A	
584-14853	"	# 104	A	
584-14854	"	# 104A	A	
584-14855	"	# 311	A	
584-14856	"	# 72	A	
584-14857	"	# 109	A	
584-14858	"	# 250	A	Formerly # 554-28222
584-14859	"	# 6	N	
584-14860	"	# 196	A	
584-14861	"	# 184	A	
584-14863	"	# 16	A	
584-14864	"	# 184	A	
584-14865	"	# 75	A	
584-14866	"	# 250	N	
584-14867	"	# 200	N	
584-14868	"	# SC25	N	
584-14869	"	# SC21	N	
584-14870	"	# 321	A	
584-14871	"	# 321	A	
584-14872	"	# 104	A	
584-14873	"	# 330P	N	
584-14874	"	Puu Maile # 1	N	
584-14875	"	Puu Maile # 2	N	
584-14876	"	# 71	N	
584-14877	"	# 170	N	
584-14878	"	# 196	N	
584-14879	"	# 202	N	Hand raised chick.
584-14880	"	Kahului	F	Grounded bird, released.

Age code: A = adult, N = nestling, F = fledgling been incorporated into a model of the population biology of the birds (Chapter 4), but the effort will have to be continued for many years before reliable estimates of some life history parameters can be made. Without the banding data necessary for making good estimates of survival rates in these birds, we will never be able to determine the actual age structure of the population, and the vulnerability of the population to reductions in survival and reproductive success caused by predation and other factors. The banding study is not essential to the conservation of the birds and deserves the lowest priority of all of the topics thus far discussed. Nevertheless, it will substantially improve our understanding of the biology of these birds and should be continued as management resources permit.

The most efficient method for banding large numbers of petrels is to trap adult birds as they return to their burrows on feeding visits during the nestling period. Adult birds have a strong attachment to their chicks at this time, and they will not desert if they are handled carefully. Beginning in late July Havahart traps should be placed at the entrance to burrows in such a way that the birds will be forced to walk through them to get to their nests (Figure A4). In some cases rock barricades will have to be built around the traps to prevent the birds from

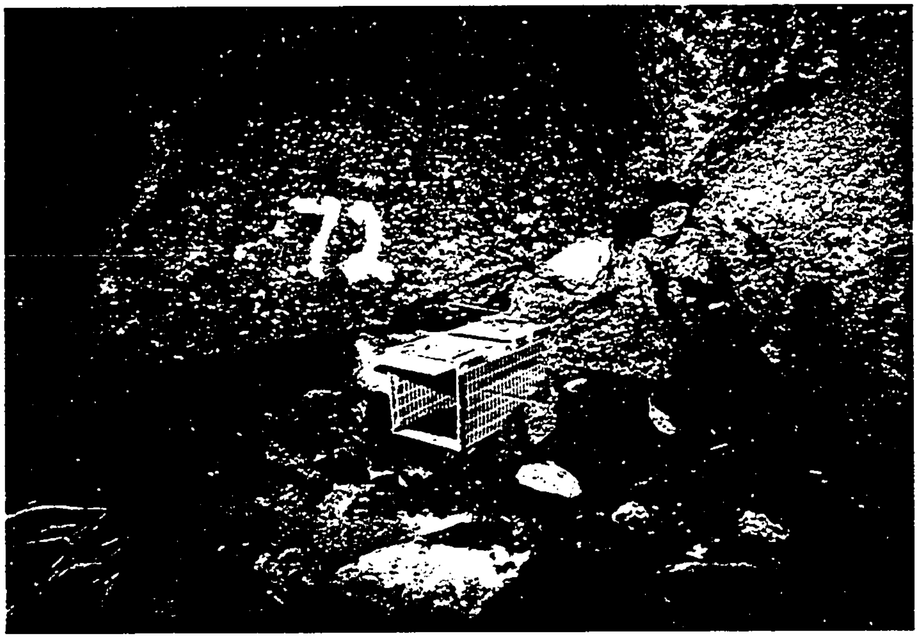

Figure A4. A havahart trap set at a petrel burrow for capturing adult birds. It is essential that traps be set in such a way as not to inhibit adult birds from entering their burrows normally.

bypassing the trap entrance. To minimize the disturbance to the birds, it is essential to place the traps with considerable care. Not all burrows will be suitable for trapping and in others a good deal of effort may be required to install a trap properly. Traps must be installed so that adult birds can follow a natural approach to the burrow as they attempt to enter it. The trap must trip easily and the external trip mechanism must be protected so that it is not tripped accidentally by a bird probing around the outside of the burrow. The primary consideration should be that a bird has a high likelihood of being caught as it attempts to enter its burrow in a normal fashion. It is important that birds are not frustrated in their attempts to enter their burrows, a situation which may lead to desertion.

The traps should be set before dark each day and checked every two to three hours during the night. Trapped birds should be removed and have their bills wired shut with a sandwich bag twist-tie (Figure A5). The twist-tie will discourage the birds from regurgitating the food they have brought for their chicks, and allow them to be easily handled and banded. After removing the twist tie, the birds should be released into their burrows to feed their chicks. Careful records of the banding effort should be kept at all times. A reasonable goal for the banding

Figure A5. Removing a trapped petrel from the trap. Note the twist tie on the bill.

program would be the banding of 50 to 100 pairs of breeding adults within the White Hill colony and as many fledglings as possible. Following this, a regular re-trapping program will allow an estimation of of the mortality rates of adult birds and the recruitment rate of new breeders into the population.

Observations made during the study indicate that nestlings begin to venture from their burrows several weeks before fledging and this behavior may make it easy to band most of the fledgling population each season. Although the method has not been tested, it should be possible to trap fledglings as they leave their burrows in the evening beginning in mid-October. If successful, this technique would be a valuable addition to the banding program, because nestlings are currently the most difficult component of the population to band.

Finally, I will discuss two additional topics that relate to the conservation of the Dark-rumped Petrel. The first deals with methods developed for hand-feeding injured or orphaned petrels, and the second with the potential for transplanting Dark-rumped Petrels to predator-free habitats.

Feeding Captive Birds

Procellariiformes are notoriously difficult to sustain on an artificial diet but circumstances involving injured or orphaned birds often require it nonetheless (Wingate 1972, Robertson and Wright 1973). In an endangered species like the Dark-rumped Petrel it is useful to be able to nourish sick or injured birds because even a small reduction in mortality rates can have important consequences for the entire population. I had the opportunity to hand raise a Dark-rump Petrel chick in 1981, and through the experience developed a successful method for sustaining petrels on an artificial diet. The method has also proven valuable for nursing injured petrels back to health. Two birds involved in collisions with vehicles on the park road, and several exhausted fledglings that became grounded after colliding with lights in urban areas were also revitalized with these techniques.

The diet is based on a formula developed by John Sincock of the U.S. Fish and Wildlife Kauai Field Station. He has used it for number of years to sustain grounded Newell's Shearwaters prior to their release. The formula I used contains a number of additional ingredients, including frozen euphausids, brine shrimp and trace minerals (Table A3). It must meet most of the birds dietary requirements **because** it was the only food consumed by a totally

Table A3. Recipe for Dark-rumped Petrel puree.

1/8 Cup Instant Ocean

3 Drops Trace Minerals

2 Hard Boiled Egg Yolks

1 Tbs. Corn Syrup

2 Tbs. Corn Oil

8 Oz. Fresh Frozen Euphausids

16 Oz. Fresh Frozen Brine Shrimp

16 Oz. Fresh Frozen Squid

8 Oz. Fresh Frozen Whole Fish

Ringers Solution

Make sure ingredients are fresh and that work area, utensils, and containers are sanitary. Mix ingredients in a blender adding Ringers Solution as needed to make a thick paste. Divide mixture into portion sized containers and freeze immediately. Note: most ingredients are available through pet stores that specialize in tropical fish.

hand-raised chick that fledged successfully in 1981. The most important consideration in preparing the food is to use very fresh, or preferably, fresh frozen ingredients, and to maintain sanitary conditions throughout. Procellariiformes are apparently very susceptible to bacterial contamination of their food (Wingate 1972).

After the food is prepared, it should be stored in individual portions of approximately 50 ml and frozen immediately. In this way freshly thawed food can be used for each feeding. Birds are fed with a large syringe and tube, and the food is injected directly into their stomachs (Figure A6). The tube should be approx. 10 cm in length, tapered at the tip, and smoothed by lightly passing any rough edges over a flame. A smaller, 0.5 cm outer diameter tube is used for young chicks, and a large, 1.0 cm outer diameter tube is used for larger chicks and adult birds. The syringe and feeding tube should boiled for several minutes before each feeding. To feed the birds, first fill the syringe with the desired amount of food. Young chicks can eat 10 to 50 cc's at a feeding while large chicks and adults will eat 50 to 150 cc's. Remove any air from the syringe and feeding tube. Lightly coat the outside of the feeding tube with vegetable oil. Then, wrap the bird in a towel, open its bill and carefully work the feeding tube into the bird's stomach. Many birds will voluntarily

Figure A6. Feeding petrels prepared food with a syringe. New birds may require two people and should be wrapped in a towel (upper photo). Birds accustomed to the proceedure often swallow the feeding tube willingly (lower photo).

swallow the tube after it has started down their throat. Next, slowly inject the food into the bird's stomach and remove the tube. Allow the bird to rest quietly for several minutes before moving it. Carefully wash all utensils, the syringe and feeding tube in hot soapy water and rinse thoroughly.

Captive birds should be kept in a box approximately 50 cm square and 25 cm high that contains an entrance hole on one side and a removable lid. The box should be filled to a depth of approximately 8 cm with cinders or other porous material, and placed in a predator-proof holding pen. Birds should occasionally be placed in a tub of luke-warm water before returning them to their pen as this seems to stimulate preening and help the birds maintain their plumage. Chicks or adult birds with severely fouled plumage should be washed carefully in warm soapy water, rinsed, and dried with a hair dryer. The activity of injured birds will indicate when they are ready to be released. Birds that venture from their burrows frequently at night and are capable of flapping their wings strongly when held by their feet are probably ready to be set free. It is best to release birds in an area where they can be recovered easily should they be unable to fly.

The Feasibility of Transplanting Dark-rumped Petrels

The technique of transplanting or attracting seabirds to new nesting locations has shown promise in a number of species and it has been suggested as a potential solution to the problems faced by the remaining Dark-rumped Petrel populations (Telfer 1981). Atlantic Puffins (*Fratercula arctica*) have been successfully reintroduced to their former breeding grounds in Maine, and the techniques of that study have been applied with some success to other species including Leach's Storm Petrels, and Common Terns (Kress 1982). Based on this work, an experimental cross-fostering transplant study involving the threatened Newell's Shearwater and Wedge-tailed Shearwaters was initiated by the U.S. Fish and Wildlife Service on Kauai in 1978. The program has shown some promise and of the 91 Newell's Shearwater eggs fostered by Wedge-tailed Shearwaters in recent years, 67 chicks were fledged (Telfer 1981). It is hoped that the fledglings will return to their foster nesting location, which can be protected from predators, and establish a new nesting colony. Depending on the success of this study it has been suggested that a similar program may benefit the Dark-rumped Petrel.

With this possibility in mind I participated in a number of surveys of potential offshore island transplant sites in 1981 (Simons et al. 1983, Kepler et al. 1983a, 1983b).

There are only a few small offshore islands in the vicinity of the Haleakala petrel population and they represent the only predator-free nesting habitat that remains today. The surveys of these islands revealed that they would be unlikely candidates for a transplant program for a number of reasons. First of all, most of the islands have been used as bombing targets at some time in the past, and in many cases much of their already limited habitat for burrowing birds has been destroyed. Secondly, the islands appear to be saturated with other nesting seabirds, primarily Wedge-tailed Shearwaters. This suggests that any transplanted birds would face a considerable amount of competition if they attempted to breed there. Finally, even if these problems could be overcome the total amount of nesting area would still be quite limited and thus the size of the transplanted population would always be small.

Several other considerations also suggest that a transplant program would be inadvisable at this time. The populations of an endangered species like the Dark-rumped Petrel are fundamentally different from those of an abundant species like the Atlantic Puffin or Common Tern. It appears that in a healthy seabird population a significant portion of each years fledglings disperse to new breeding areas. This has been demonstrated in Manx Shearwaters (Harris 1972), Herring Gulls (Larus argentatus) (Chabrzyk and Coulson

1976), Fulmars (Dunnet et al. 1979), and Puffins (Harris 1983). The possibility of attracting individuals from these populations into unoccupied habitat on the fringes of their breeding range would appear to be much more likely than in a dwindling population like the Dark-rumped Petrel's. I would expect, in a declining population, that the number of dispersing individuals would be reduced, and thus lessen the chances of a new colony becoming established. Also, in the previous successful transplant studies, competition with other species has not been a factor. It would be impossible to eliminate this factor in a transplant program involving Dark-rumped Petrels. The cross-fostering aspect of the program is not a proven technique in seabirds, and it should be tested on a similar but common species before being attempted on an endangered population. Finally, there is no evidence that the habitats available as transplant sites for Dark-rumped Petrels have ever been utilized by these birds. Since most species of marine birds have rather specific habitat requirements it would seem unlikely that they would be easily attracted into novel breeding habitats (Buckley and Buckley 1980). Dark-rumped Petrels are primarily upland nesters and most of the known breeding sites, past and present, have been at elevations above 800 meters (Bryan 1908, Richardson and Woodside 1954, Hirai 1978, Conant 1980, Simons 1980,1981). For these reasons, the possibility of luring petrels to sea level nesting sites on offshore islands seems unlikely.

Due to these difficulties, I recommend that a transplant program involving Dark-rumped Petrels not be attempted. The birds that remain today appear to have abundant nesting habitat available to them where they currently breed, and should be able to flourish if they can be protected from predators. Management efforts should be focused on protecting the established populations of these birds from the factors that threaten their survival. Figure A7 outlines a calendar of monitoring activities suggested for the Haleakala Dark-rumped Petrel population.

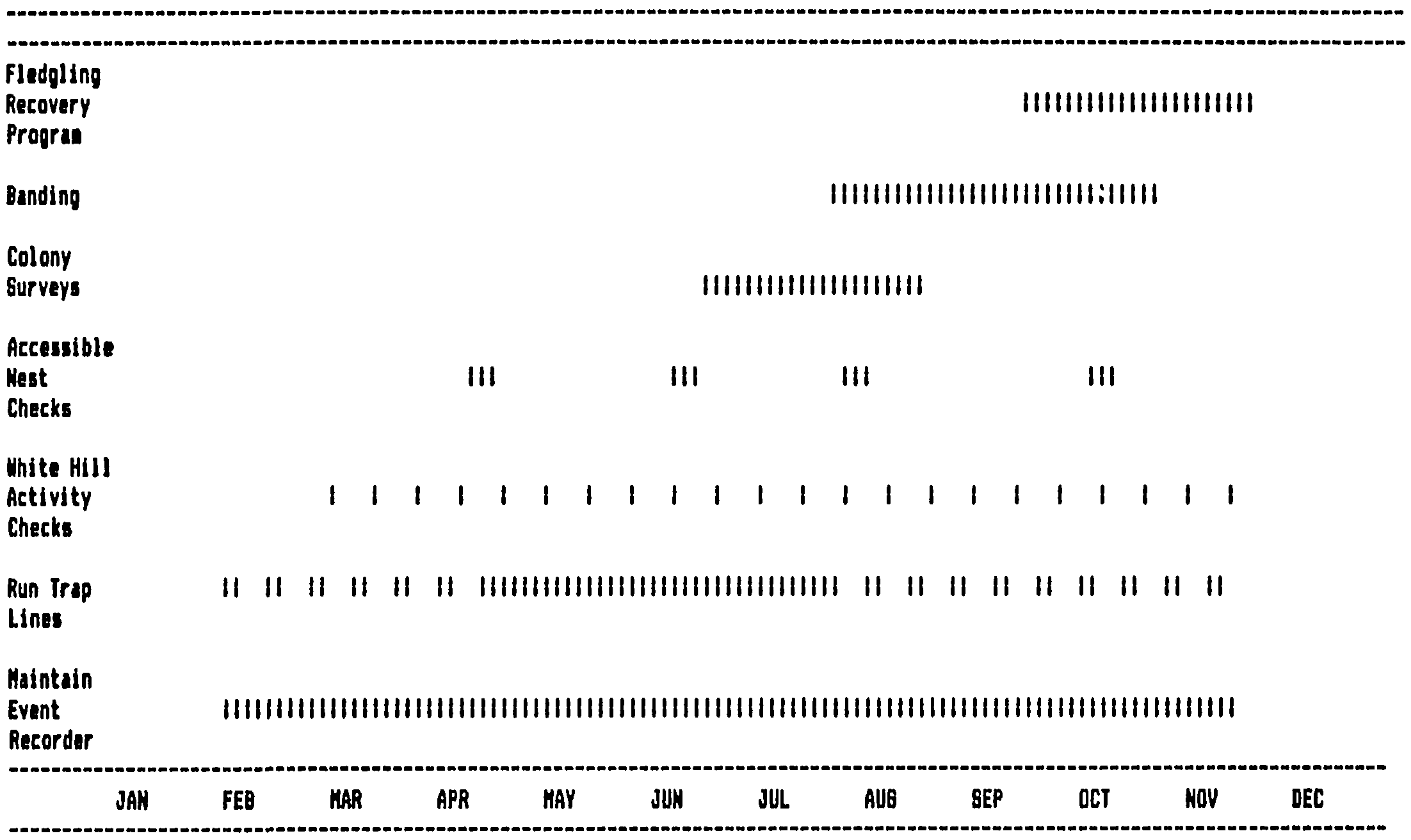

Figure A7. A calender of monitoring activities related to the conservation of the Dark-rumped Petrel.

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"Development of a management plan for the Dark-rumped Petrel in Haleakala National Park, Hawaii Forestry and Wildlife Conference, Honolulu, Hawaii, 2 - 4 October 1980

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