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PATTERNS OF MOVEMENT OF DARK-RUMPED PETRELS AND NEWELL'S SHEARWATERS ON KAUAI[1]

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Abstract. We used ornithological radar and night-vision scopes to study movement patterns of Dark-rumped Petrels (*Pterodroma phaeopygia sandwichensis*) and Newell's Shearwaters (*Puffinus auricularis newelli*) on the island of Kauai, Hawaii, from 1992 to 1994. Movement rates on radar (targets/hr) for both species peaked for ~2 hr around sunset and sunrise and were low in the middle of the night. Dark-rumped Petrels generally moved during crepuscular periods, whereas Newell's Shearwaters were strongly nocturnal. Movement rates were much higher in fall 1993 than in fall 1992, probably because of effects of Hurricane Iniki in 1992, and were higher in summer than in fall, probably because of the presence of nonbreeding birds in summer. Movement rates increased through time in summer, probably because numbers of nonbreeding birds visiting colonies increased through time, but declined through time in fall because fewer adults returned to the colony as fledging progressed. Effects of the moon on movement rates appeared to be small. Movement rates varied geographically, generally being much higher on eastern and northern Kauai than on southern Kauai. Movements were predominantly inland in the evening, predominantly seaward in the morning, and both directions in the middle of the night. Birds flew between 8 and 800 m above ground level (agl) and averaged 142 m agl for all procellariid species combined. There was no relationship between elevation of a site and flight altitude of birds at that site. Flight altitudes at a site generally were highest during the evening peak of movement and lowest during the morning peak in summer but were not different among three periods of the night in fall. Dark-rumped Petrels flew at significantly higher altitudes than did Newell's Shearwaters in fall 1993 and summer 1994 but not in summer 1993.

Key words: Behavior; Dark-rumped Petrel; endangered species; Hawaii; Kauai; movements; Newell's Shearwater; radar; nocturnal; Pterodroma phaeopygia sandwichensis; Puffinus auricularis newelli.

INTRODUCTION

Races of both the Dark-rumped Petrel (*Pterodroma phaeopygia sandwichensis*) and the Townsend's Shearwater (*Puffinus auricularis newelli*; hereafter, Newell's Shearwater) are forms of tropical Pacific species that are endemic to the Hawaiian Islands (AOU 1983), where they are threatened with extinction. In 1984, 400–600 pairs of Dark-rumped Petrels were estimated to breed on Maui (Harrison et al. 1984), and recent records on Lanai and Hawaii suggest breeding (Conant 1980), as do records of juveniles on Kauai (Telfer et al. 1987). As of 1992, two colonies of unknown size were suspected to occur in the mountains of central and northwestern Kauai (Fig. 1; Gon 1988; T. C. Telfer, pers. comm.). Most Newell's Shearwaters are believed to breed on Kauai (Harrison et al. 1984, Harrison 1990). As of 1992, only 11 colonies representing perhaps 4,000–6,000 pairs were known there (Fig. 1; Harrison et al. 1984; Harrison 1990; Telfer, pers. comm.).

Populations of both species on the Hawaiian Islands formerly were substantially larger than they are now (USFWS 1983). Reasons for their declines are numerous: hunting by the early Hawaiians, trampling and predation of nesting colonies by introduced mammals, avian malaria and poxviruses, collisions with utility structures, and "fallout" mortality of fledging juveniles that are attracted to lights in the fall (Hadley 1961, Sincock and Swedberg 1969, Telfer 1979, Sincock 1981, USFWS 1983, Reed et al. 1985, Simons 1985, Telfer et al. 1987, Olson and James 1991). Hunting and predation by introduced mammals are thought to be the primary causes of declines of both species; today, predation is considered to be the major threat to surviving populations (USFWS 1983, Olson and James 1991).

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Although Dark-rumped Petrels and Newell's Shearwaters are endangered and threatened species, respectively, little information on many aspects of their biology is available (Simons 1984, 1985; Reed et al. 1985; Telfer et al. 1987). This paucity of information, even that on basic aspects of biology such as daily movements to and from nesting colonies, is largely due to the nocturnal habits of both species and the inaccessibility of their nesting colonies. Here, we describe the patterns of movement of these species on Kauai and compare those findings with what is known about these and similar species elsewhere.

METHODS

DATA COLLECTION

We monitored movements of Dark-rumped Petrels and Newell's Shearwaters on Kauai at 8 sites during 15–27 October (fall) 1992, at 13 sites during 1–25 June (summer) 1993, at 14 sites during 6–26 October (fall) 1993, and at 10 sites during 28 May–3 June (summer) 1994 (Fig. 1). We established monitoring sites at Waimea, Hanapepe, Wailua, Kealia, and Kalihiwai during all four seasons; at Kekaha, Kalaheo, Kalepa Ridge, Kapaa, Anahola Mountains, and Hanalei during three seasons; at Lihue Mall, Waiakalua Stream, and Princeville during two seasons; and at Kahili Mountain, Poipu, Nawiliwili, Lihue Airport, and Wainiha during one season each.

We used surveillance radar and night-vision scopes to monitor bird movements. The most extensive monitoring was done with surveillance radar; night-vision monitoring usually was conducted concurrently with radar sampling. During all monitoring sessions, we recorded weather conditions, light condition (daylight, crepuscular, or nocturnal; with or without precipitation), light level (in lux), and moon phase (quarterly phase and whether the moon was absent or present above the horizon). Hours of sampling in a night varied with weather, site, season, and type of monitoring.

Our mobile laboratory was equipped with a marine radar mounted on a truck camper. The surveillance radar scanned a circular zone around the lab and was used to measure movement rates, flight paths, and ground speeds of flying birds. It was an X-band radar transmitting at 9,410 MHz with peak power output of 10 kW. This radar laboratory and its capabilities are described in Cooper et al. (1991).

We monitored bird movements with radar for 3–13 hr/day during fall 1992 and summer and fall 1993. In summer, we generally sampled during the evening movement (19:00–21:59) and morning peak of movement (04:30–05:59). In fall, we generally sampled during the evening movement and the period when most juveniles were moving to sea (18:00–23:59). We also sampled during the entire night (18:00–06:00) in summer, 19:00–07:00 in fall) at Wailua and Kealia 1–3 times each season.

During each hour of sampling, we operated the surveillance radar at the 1.4-km range for two 25-min sessions. Information recorded on targets included time, direction of flight (to the nearest degree), flight behavior (e.g., straight, erratic), velocity (to the nearest 8 km/hr), species (if known), and number of birds (if known). To eliminate species other than those of interest, we recorded data only for targets flying ≥50 km/hr over land. We found that the two petrel species flew ≥50 km/hr but that almost all other species flew more slowly (see Results).

We used a 5 × Noctron-V night-vision scope to monitor species-specific timing of movements and flight altitudes for 2–6 hr/day during fall 1992, summer and fall 1993, and summer 1994. Although all data are referred to here as night-vision data, we used 10 × binoculars during short periods of daylight and crepuscular sampling. With few exceptions in 1992 and 1993 and all 1994 observations, night-vision data were collected concurrently with radar sampling. The night-vision scope's performance was enhanced greatly with lighting from street lights and an infrared spotlight that rendered the light invisible to the naked eye (thus not changing the birds' behavior). Information recorded on birds seen included time, species (lowest possible taxonomic unit), direction of flight (ordinal points), and flight altitude (meters above ground level [m agl]).

We used standard field marks described in Harrison (1985) and occasional vocalizations to identify the two species during night-vision sampling. Dark-rumped Petrels were larger and had longer wings than did Newell's Shearwaters. Dark-rumped Petrels also had white foreheads (not always visible), flew with deeper wingbeats than did Newell's Shearwaters, and reminded us of flying Pomarine Jaegers (*Stercorarius pomarinus*) or nighthawks (*Chordeiles* spp.). In contrast, Newell's Shearwaters were considerably smaller than Dark-rumped Petrels and usually

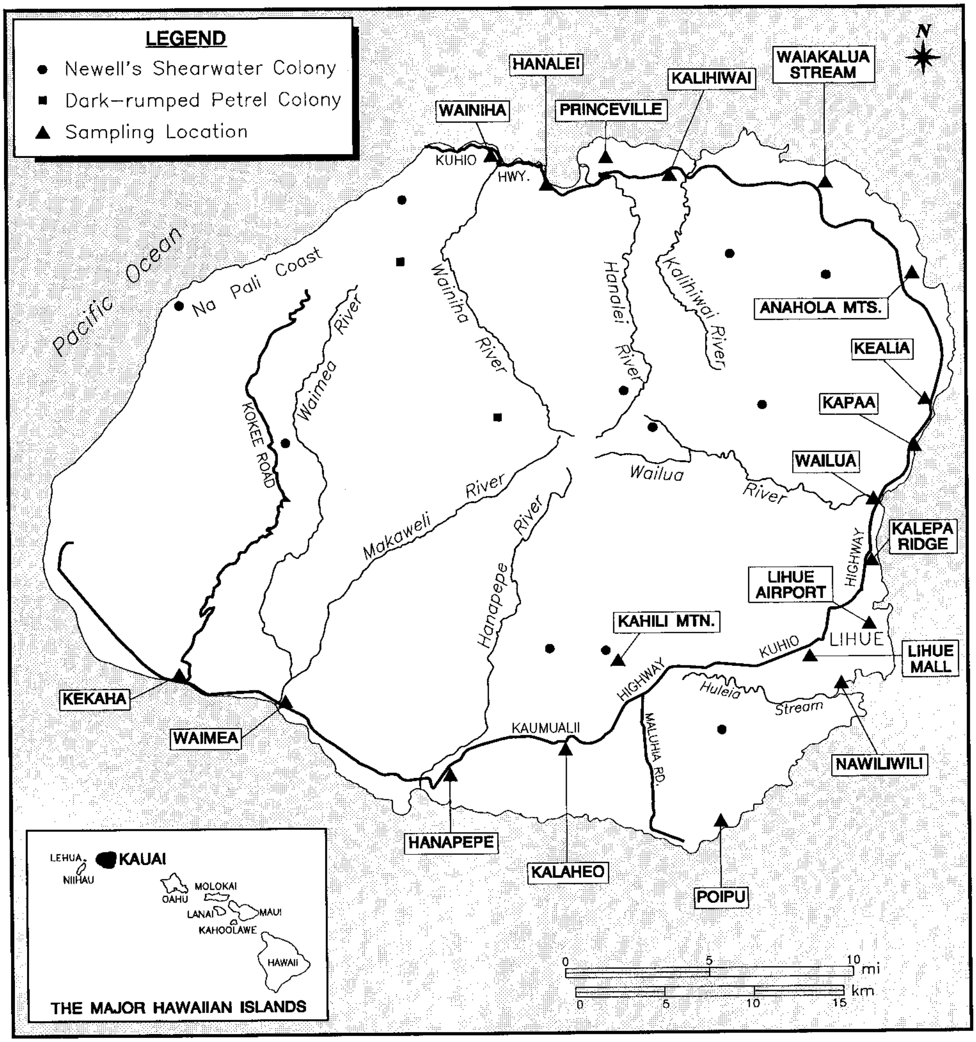

FIGURE 1. Locations of known or probable Dark-rumped Petrel (solid squares) and Newell's Shearwater (solid circles; Gon 1988; T. C. Telfer, Hawaii DLNR, pers. comm.) colonies and study sites for 1992–1994 radar and night-vision studies (solid triangles) on Kauai Island, Hawaii.

flew rapidly and with shallow, stiff wingbeats that reminded us of flying Spotted Sandpipers (*Actitis macularia*). The white sides to their rumps often were not visible because they flew at some distance above the ground. Many of these characters were seen quite clearly in the night-vision scope because the extensive background light (from nearby towns) greatly enhanced the image quality in the scope. Birds that were not seen clearly, however, were classified to lower taxonomic units, such as "unidentified shearwater or petrel."

DATA ANALYSIS

We examined data from the surveillance radar by movement rates and flight directions. In analyses involving movement rates, we first compiled data on the number of targets by 25-min sampling period, then converted them to estimates of numbers of targets/hr for each sampling period. We graphically examined variation in movement rates within a night during the evening peak of movement (18:00–20:59) the middle of the night (21:00–04:29) and the morning peak of movement (04:30–06:59) at the two sites (Wailua and Kealia) where we had collected data throughout the night. Other analyses on movement rates at all sites were standardized to the time period sampled at all sites and seasons ("evening movement", 18:00–21:59). After this temporal standardization, we examined variation in movement rates among nights at a site within the same season (graphically), between seasons in the same year (Wilcoxon matched-pairs signed-ranks test), between years at the same season (Wilcoxon matched-pairs signed-ranks test), among lunar phases within a season (graphically), and between geographic sections of the island (Mann-Whitney test). In all statistical tests reported here, we used an α of 0.05.

We compiled the data on flight direction of individual targets as frequencies of each ordinal direction (e.g., North [338–022°], Northeast [023–067°], East [068–112°]) at each site. We then standardized the directional data temporally by using only those from the inland peak of movement (18:00–20:59) and examined variation in flight direction among sites and seasons (no statistical analyses). We also examined variation in flight direction during all-night sampling at Wailua and Kealia by categorizing the direction of each target at each site as "inland" (i.e., in an inland direction from a line parallel to the overall coastline near that site), "seaward" (i.e., in a seaward direction from a line parallel to the overall coastline near that site), or "unknown" (parallel to the overall coastline near that site, circling, or flying erratically) and calculating frequencies of inland and seaward targets by time. The few observations of unknown direction were omitted from our summaries.

We compiled the data from the night-vision monitoring as numbers of birds of each species seen by minutes before or after civil sunset and sunrise (National Oceanographic and Atmospheric Administration, National Weather Service, Lihue, HI). We calculated mean flight altitudes for all procellariid species combined and each of the two species, for all times of the night, all seasons, and all sites combined. We used a Kruskal-Wallis test to examine whether flight altitudes of all procellariids combined differed by period of the night (as above) within each season at Wailua and Kealia. We calculated mean flight altitudes for each of the two species during the evening peak of movement (18:00–20:59), examined differences between seasons for a species (no statistical tests), and tested for differences between species within a season with Mann-Whitney tests. We used a Spearman rank correlation to determine whether there was a relationship between flight altitude of birds at a site and the elevation of that site above sea level.

RESULTS

SPECIES COMPOSITION

Dark-rumped Petrels were seen at nine of the 17 sampling sites: at three of six on the southern side of the island and at six of 11 on the eastern and northern sides. Because 36% of all tubenoses were unidentified to species, however, Dark-rumped Petrels probably occurred at more sites than we were able to confirm. Newell's Shearwaters were seen at 16 of the 17 sites, and we believe they also occurred at the seventeenth (Poipu). Newell's Shearwaters almost certainly represented a very high proportion of birds, primarily because most radar targets moved after the point of complete darkness, the time after which night-vision observations indicated that essentially only Newell's Shearwaters were moving (see below).

Other species were not common during periods of radar and night-vision monitoring. Wedge-tailed Shearwaters (*Puffinus pacificus*) occurred at only three coastal sites on the eastern shore, where they occasionally were pushed inland up to ~100 m by strong northeasterly winds; >1 bird was seen on only one night, however. Other species that also flew after dark or that sometimes flew at speeds >50 km/hr over land (and thus could have been classified on radar as petrels or shearwaters) were Black-crowned Night-Herons (*Nycticorax nycticorax*; generally <50 km/hr), Pacific Golden-Plovers (*Pluvialis fulva*), and occasionally tropicbirds (*Phaethon lepturus* and *P. rubricauda*; generally <50 km/hr). None of these species were abundant enough at any of the study sites to have caused extensive misclassification of targets on the radar, however, and none exhibited the nightly seaward-landward movements that the Dark-rumped Petrels and Newell's Shearwaters did.

TIMING OF MOVEMENTS

Both Dark-rumped Petrels and Newell's Shearwaters exhibited distinctive patterns of movement with respect to levels of ambient light. For

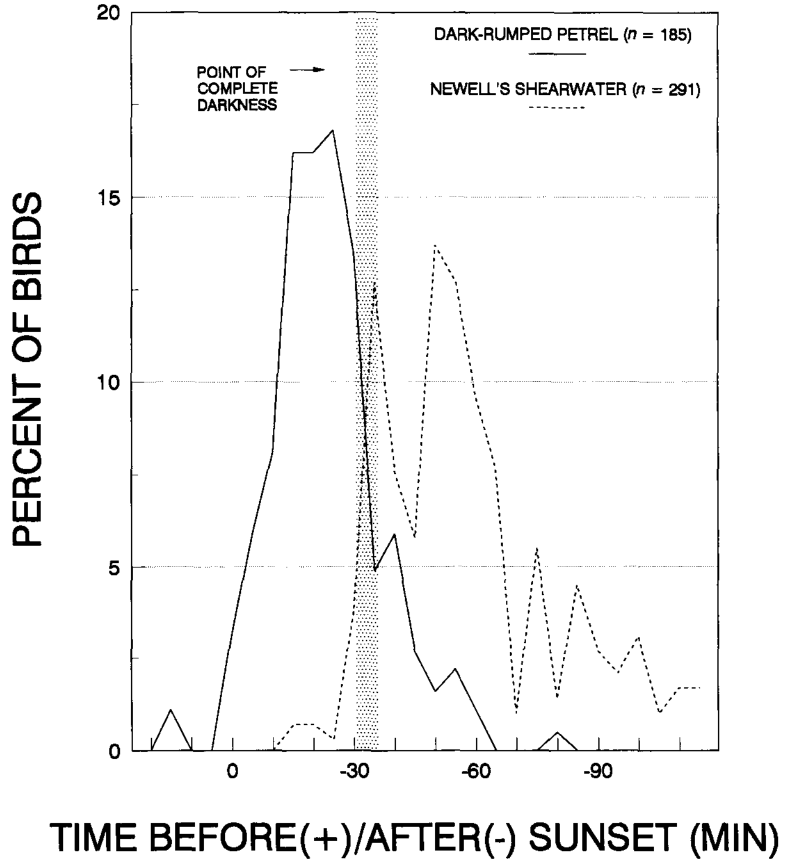

FIGURE 2. Evening patterns of movement of Dark-rumped Petrels and Newell's Shearwaters on Kauai during night-vision monitoring in summer 1993, fall 1993, and summer 1994, by time before and after sunset. Data for all seasons and sites were combined. The point of complete darkness occurred within the shaded zone on different nights, depending on the date and the amount of cloud cover.

each species, daily timing of movements with respect to light levels were similar among sites, years, and seasons, so all night-vision data sets were pooled for the following analyses.

In the evening, light levels fell rapidly between sunset and the point of complete darkness, which was that time when the light meter recorded an incident light level of 0 lux over most of the sky. At that time, however, a little light still could be seen in the western sky on a clear night for another ~20 min. Dark-rumped Petrels moved inland primarily between sunset and the point of complete darkness, with a small percentage of birds moving inland before sunset and after complete darkness (Fig. 2). In contract, Newell's Shearwaters exhibited almost no movement until after complete darkness, whereupon they moved inland in a wave that peaked for 30–40 min (Fig. 2). After that peak, the rate of movement decreased steadily until ~90 min after complete darkness, after which few birds were seen. The few night-vision data collected during the middle of the night (not presented here) indicated that low numbers of Newell's Shearwaters moved steadily throughout the night.

In the morning, the first light was seen in the eastern sky ~20–30 min before the end of complete darkness, which was that time after which the overall amount of incident light exceeded 0 lux and light in the eastern sky indicated that sunrise was not far off. After it was no longer completely dark (i.e., lux > 0), light levels increased rapidly and sunrise occurred ~30 min later. Dark-rumped Petrels first moved to sea while it was completely dark, and movement rates increased rapidly until they peaked just after the

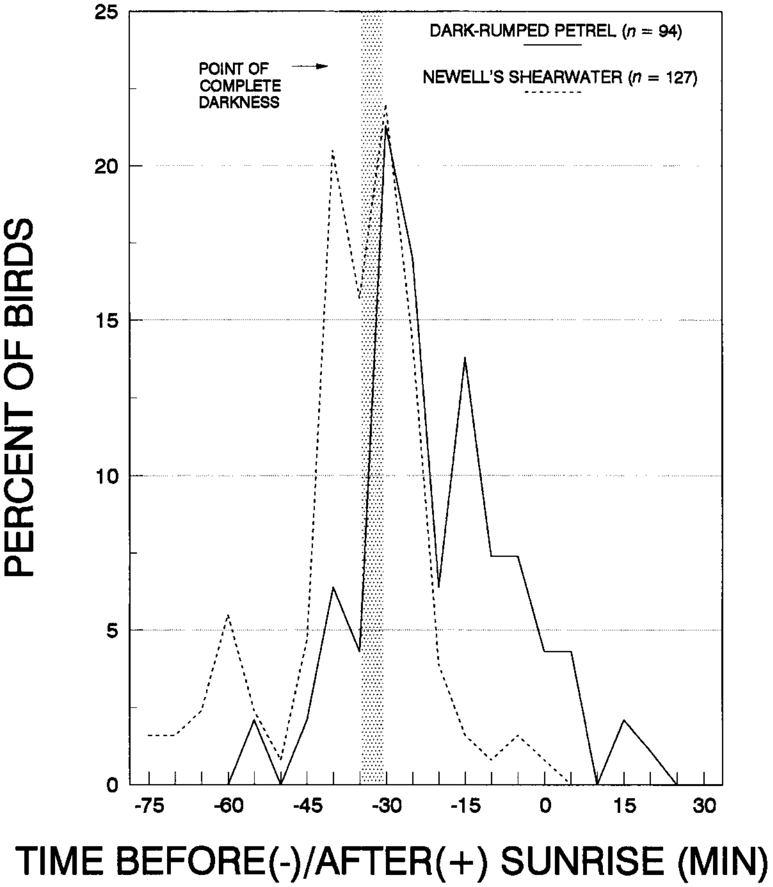

FIGURE 3. Morning patterns of movement of Dark-rumped Petrels and Newell's Shearwaters on Kauai during night-vision monitoring in summer 1993, fall 1993, and summer 1994, by time before and after sunrise. Data for all seasons and sites were combined. The point of complete darkness occurred within the shaded zone on different mornings, depending on the date and the amount of cloud cover.

point of complete darkness had been crossed (lux > 0; Fig. 3). This seaward movement continued at a decreasing rate until sunrise, and a few birds departed as late as 30 min after sunrise. Newell's Shearwaters moved all night but began moving to sea in numbers ~40 min before the first measurable light. Movement rates increased rapidly and peaked just after the point of complete darkness had been crossed (i.e., lux > 0), then essentially ceased within 15 min (Fig. 3). A few late-departing birds left as late as sunrise, however.

Patterns of movement rates of these species on radar during the entire night at Wailua and Kealia during 1992 and 1993 were similar to these patterns seen with the night-vision scope (Fig. 4). In all seasons, the greatest movement rates of radar targets occurred just after the point of complete darkness in the evening and around it in the morning, just as we saw in the night-vision monitoring. Few targets were seen on radar before sunset or >30 min after sunrise, and steady, but low-level, movements occurred during the rest of the night. This general pattern of movement varied little among sites or nights.

VARIATION IN MOVEMENT PATTERNS

The surveillance radar data set consisted of information on ~3,800 bird targets seen in fall 1992, ~30,500 targets in summer 1993, and ~20,300 targets in fall 1993. Sample sizes for the different analyses varied with the stratification or pooling that was employed.

Substantial among-night variation in evening movement rates (targets/hr) occurred at all study

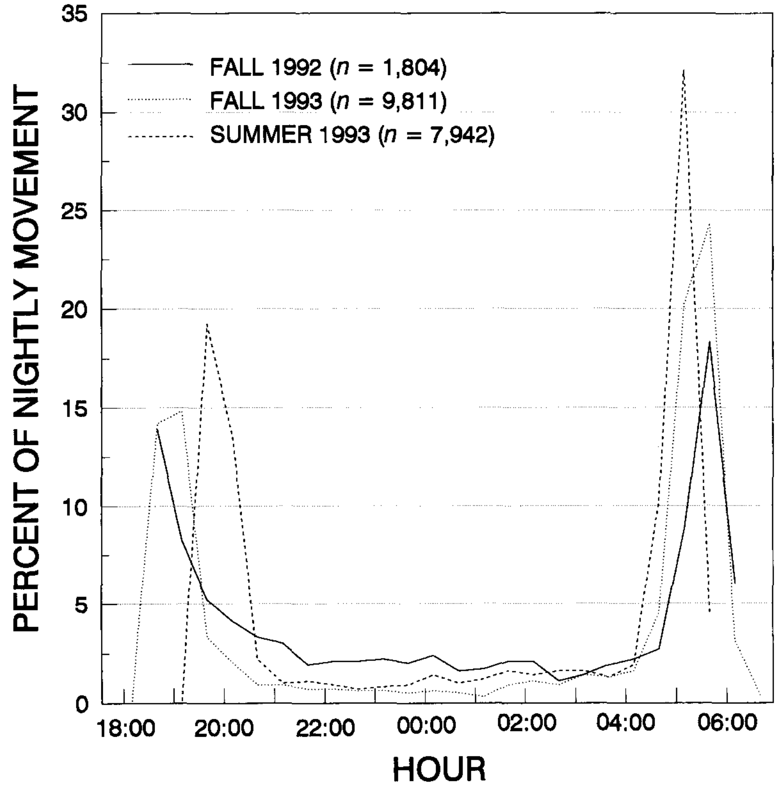

FIGURE 4. Nightly patterns of movement of targets on surveillance radar at the Wailua and Kealia study sites on Kauai, by hour of the night, fall 1992–fall 1993. Numbers in parentheses are total numbers of targets recorded on surveillance radar during that time period and season.

sites that we visited more than once in a season (Fig. 5). In summer 1993, rates at Wailua increased through time on all but one night, and those at Kealia increased steadily throughout that period. During both fall 1992 and fall 1993, evening movement rates at all sites declined after mid-October.

There also were substantial interannual and seasonal variations in evening movement rates, which were significantly larger in fall 1993 than in fall 1992 ($Z = -2.201$, $n = 6$, $P = 0.028$) and significantly larger in summer 1993 than in fall 1993 ($Z = -2.471$, $n = 12$, $P = 0.014$). On average, evening movement rates in fall 1993 were 4.0 ± 0.9 (±SD) times those in fall 1992, and rates in summer 1993 were 3.0 ± 2.8 times those in fall 1993. Only three sampling sites (Kekaha, Anahola Mountains, and Kalihiwai) had lower movements rates in summer than in fall.

Because each sampling period occurred during a period of less than one lunar phase, our data are inadequate to assess properly the effects of the moon on movement rates. Examination of movement rates at Kealia and Wailua over summer 1993 (Fig. 5), however, provides some insights into lunar effects, if we assume that the changes in movement rates were not affected by other factors (e.g., more nonbreeding adults and subadults visiting the colonies later in June; but see Discussion). Movement rates were >50% higher at Kealia during the new moon than during the full moon, but they were similar between the two lunar phases at Wailua. Thus, if moon phase did affect movement rates in summer, it appears that the effects were small and/or were being masked by other factors. Data from fall sampling periods were not suitable for such a comparison, because movements rates declined rapidly during the seasonal exodus of adults and juveniles from the colonies.

There was great geographic variability in evening movement rates, which generally were low at sites on the southern side of the island and high at sites on the eastern and northern sides of

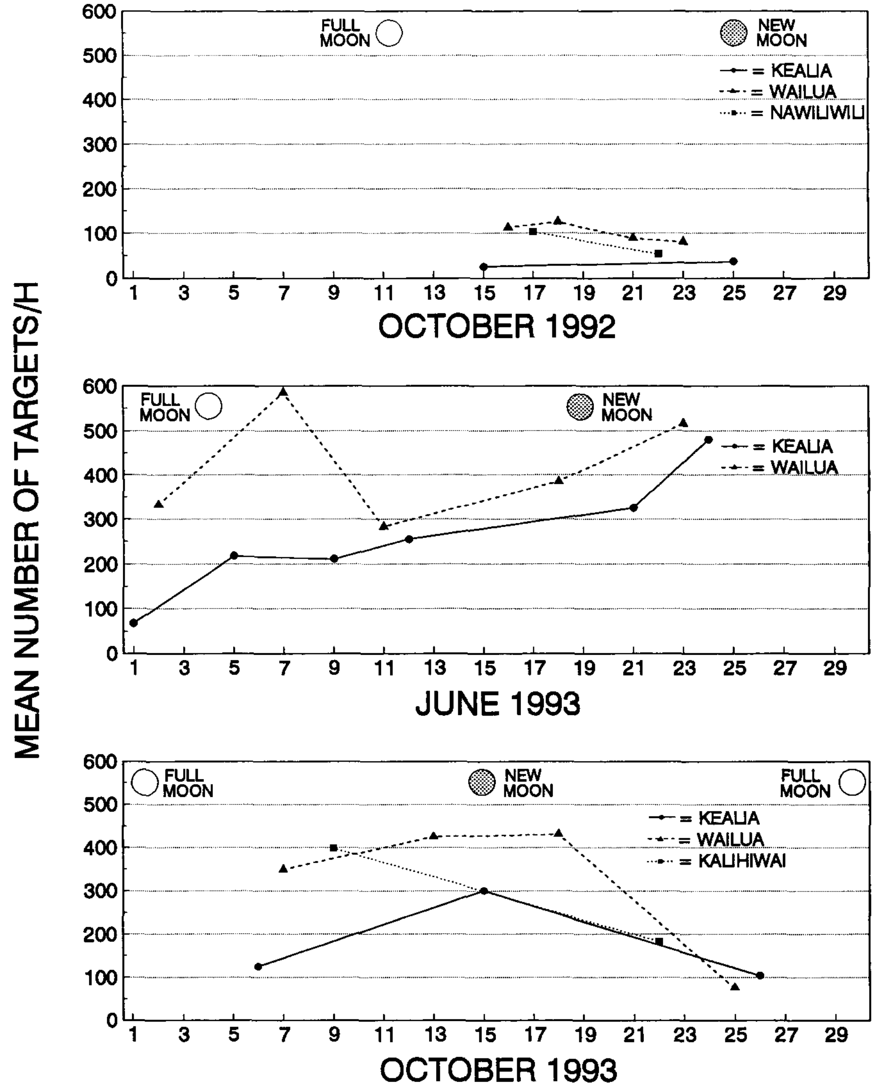

FIGURE 5. Among-night variation in mean movement rates (targets/hr) on surveillance radar at four study sites on Kauai, fall 1992–fall 1993. Data are standardized to the same time period sampled at all sites and seasons (18:00–21:59).

the island (Fig. 6). During fall 1992, mean movement rates were significantly smaller along the southern side of the island than along its eastern and northern sides ($U = 6.429$, $n = 13$, $P = 0.011$). During summer 1993, movement rates did not differ significantly between the two geographic areas ($U = 3.196$, $n = 22$, $P = 0.074$), although movement rates at the Kalaheo site (on the southern side) were unusually large during our one night of sampling (>3 times the average for the other three sites) and appear to have prevented this test from yielding a significant result. During fall 1993, movement rates again were significantly smaller on the southern side of the island than on its eastern and northern sides ($U = 8.214$, $n = 21$, $P = 0.004$).

FLIGHT DIRECTION

Flight directions of radar targets during 18:00–20:59 (the evening peak of movement) were predominantly inland at all sites except Kekaha, Nawiliwili, and Lihue Mall (Fig. 7). At Kalaheo,

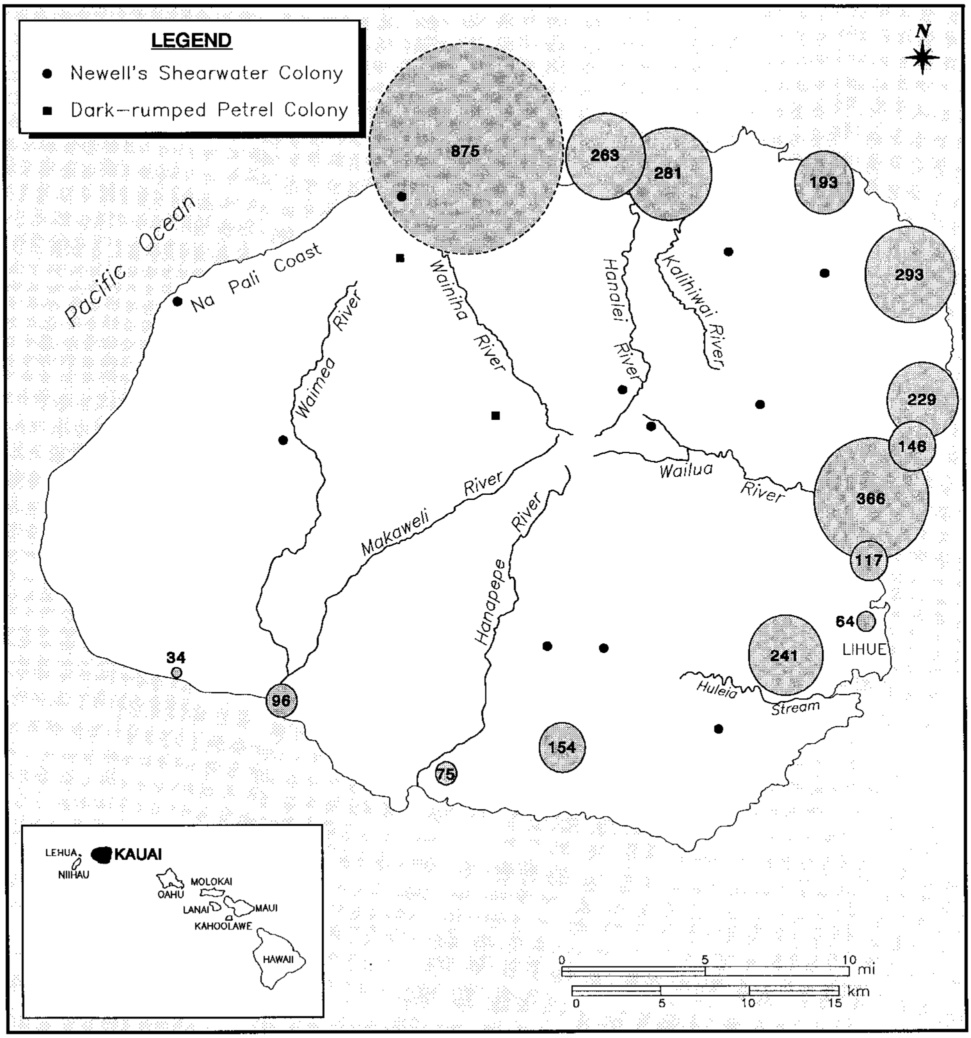

FIGURE 6. Geographic variation in mean movement rates (targets/hr) on surveillance radar around Kauai, summer 1993. Data are standardized to the same time period sampled at all sites and seasons (18:00–21:59). Sizes of shaded circles are proportional to the rate of movement; the circle for Hanalei is dashed because it is out of scale.

Poipu, Wailua, Kapaa, Kealia, Anahola Mountains, Waiakalua Stream, and Kalihiwai, most of the targets were headed toward known nesting colonies of either species. At other sites, most targets were headed toward areas that contained nesting habitat, even though there are no known nesting colonies in the vicinity of these sites at this time. Locations of most nesting colonies of these species on Kauai are largely unknown, however.

Variation in flight direction was low between years and between seasons at all sites except Waimea and Hanapepe. The mean difference at sites other than these two was 20 ± 13° ($n = 11$ comparisons of most extreme differences in mean directions at a site between seasons), and the median was 17°. In contrast, mean flight directions varied among seasons over 94° at Waimea and over 104° at Hanapepe.

For all-night data from both Wailua and Kealia combined and in both seasons, most of the targets observed during the evening peak of movement were headed inland, most of the targets observed during the morning peak were

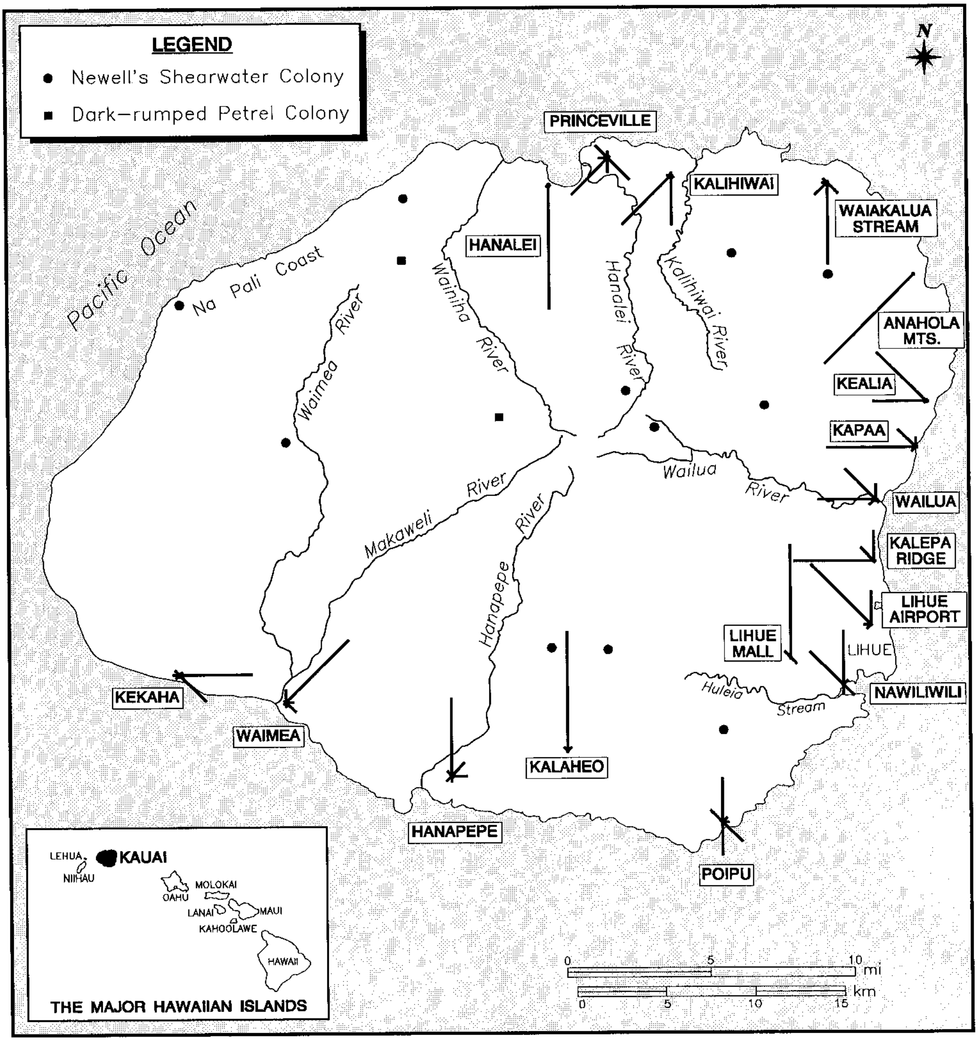

FIGURE 7. Flight directions of targets on surveillance radar during the evening peak of movement (18:00–20:59) on Kauai, fall 1992–fall 1993. Lengths of spokes on the compass rosettes are proportional to the percentages of targets flying in the directions indicated.

headed seaward, and similar percentages of targets were headed in both directions during the middle of the night (Fig. 8). Because nights were shorter in summer than in fall, there was a slight difference in timing between seasons. Inland movements in summer peaked during 19:00–19:59 and in fall peaked during 18:30–19:29 during both years. Seaward movements peaked during 04:30–05:29 in both seasons.

In many cases, topography often influenced flight patterns at a site and suggested that many, but not all, birds used "flight corridors" for commuting between the sea and inland nesting colonies. Movement rates on the northern half of the Kalepa Ridge site, which was on the southern edge of the Wailua River valley, were much higher (4–7 times as many targets) than they were on the southern half of the site, which was considerably farther from that valley. Further, targets on the northern half of the site flew into the Wailua valley, whereas most targets on the southern half of the site flew parallel to (i.e., northwesterly) and either east or west of the Kalepa Ridge, which was a 200-m-high ridge run-

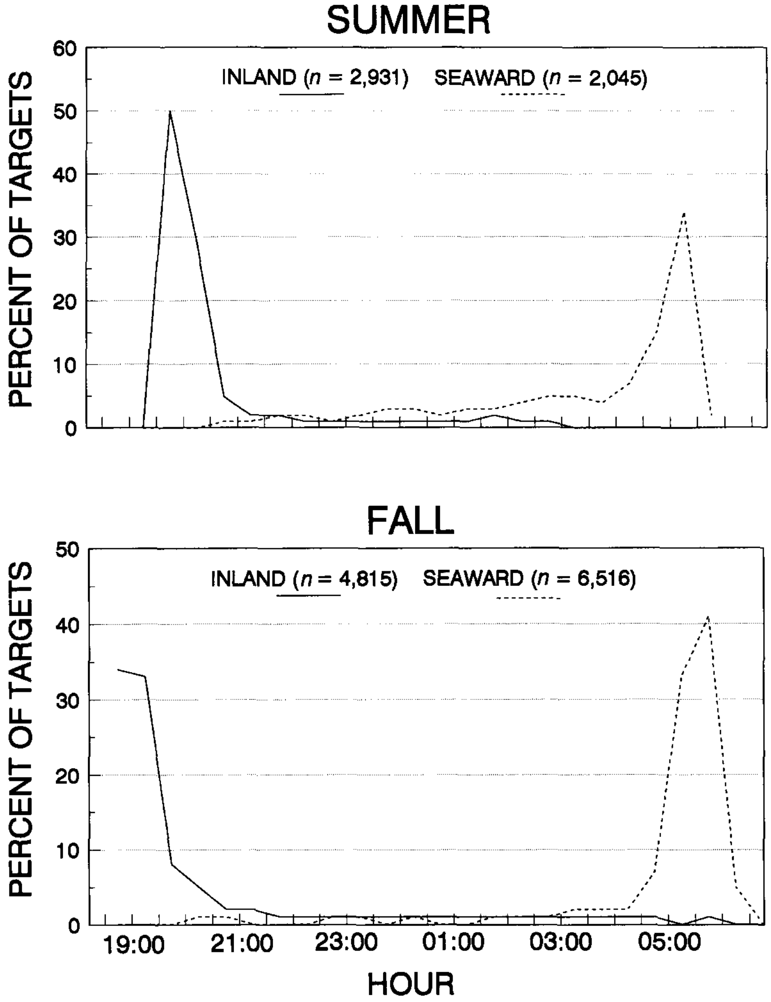

FIGURE 8. Nightly patterns of movement of targets on surveillance radar at the Wailua and Kealia study sites on Kauai, by direction and by hour of the night, fall 1992–fall 1993.

ning slightly obliquely to the coast. We saw similar patterns in southern Kauai, where most birds flew eastward past the Kekaha site to funnel inland up the Waimea River valley at the Waimea site, and in northern Kauai, where birds entered the Hanalei River valley over a broad front, from east of the Kalihiwai River to west of the Wainiha site.

FLIGHT ALTITUDE

When data from all procellariid species, times, seasons, and sites were pooled, flight altitudes ranged between 8 and 800 m agl and averaged 142 m agl (SD = 122 m, $n = 1,413$). Similar data for Dark-rumped Petrels ranged between 10 and 700 m agl and averaged 192 m agl (SD = 154 m, $n = 279$) and for Newell's Shearwaters ranged between 8 and 750 m and averaged 125 m agl (SD = 97 m, $n = 564$). There was no relationship between elevation of a site (m above sea level) and flight altitudes of all procellariids combined during night-vision sampling at that site during either the evening ($r = -0.2841$, $n = 32$, $P = 0.115$) or the morning ($r = 0.5941$, $n = 9$, $P = 0.092$) peak of movement.

Flight altitudes of all procellariids combined were significantly higher in the evening than in the morning during both summers at Kealia and during summer 1993 at Wailua (Table 1). Altitudes generally were not significantly different

TABLE 1. Mean flight altitudes (m agl) of all procellariids during night-vision monitoring at Wailua and Kealia sampling sites, Kauai, by site, season, and time period, fall 1992–summer 1994.

Site/season	Time period: Evening peak[1] $\bar{x} \pm$ SD	n	Middle of night[1] $\bar{x} \pm$ SD	n	Morning peak[1] $\bar{x} \pm$ SD	n	Kruskal-Wallis H'	df	P[2]	Conclusion from multiple comparisons[1]
Wailua										
Summer 1993	159 ± 95	60	124 ± 38	7	43 ± 28	175	98.562	2	<0.001***	EV = MI > MO
Fall 1993	181 ± 123	85	105 ± 102	20	164 ± 95	16	12.804	2	0.002**	EV = MO > MI
Summer 1994	168 ± 90	30	35 ± —	1	162 ± 53	2	2.543	2	0.280	EV = MI = MO
Kealia										
Summer 1993	93 ± 64	36	25 ± 0	2	37 ± 18	124	43.732	2	<0.001***	EV > MI = MO
Fall 1993	114 ± 91	14	113 ± 84	9	— ± —	0	0.001	1	0.751	EV = MI
Summer 1994	155 ± 33	3	— ± —	0	46 ± 18	58	8.465	1	0.004**	EV > MO

[1] EV = evening peak (18:00–20:59); MI = middle of night (21:00–04:29); MO = morning peak (04:30–06:59).

[2] *, **, and *** = test statistic is significant at $\alpha = 0.05$, 0.01, and 0.001, respectively.

TABLE 2. Mean flight altitudes (m agl) of Dark-rumped Petrels and Newell's Shearwaters on night-vision monitoring during the evening peak of movement (18:00–20:59) on Kauai, by season, summer 1993–summer 1994.

Species/season	$\bar{x}$	SD	n
Dark-rumped petrel			
Summer 1993	216	113	19
Fall 1993	190	123	22
Summer 1994	274	149	140
Newell's Shearwater			
Summer 1993	191	129	63
Fall 1993	133	93	170
Summer 1994	141	97	70

between evening and morning at both sites during fall, although they were significantly lower in the middle of the night at Wailua in fall 1993. The pattern probably was not significantly different at Wailua in summer 1994 because of unusually high flight altitudes of the few birds seen there in the morning.

The night-vision observations provided us with species-specific estimates of flight altitude during the evening peak. During most seasons, Dark-rumped Petrels flew at ~200–250 m agl during the evening peak, whereas Newell's Shearwaters flew at ~150 m agl (Table 2). Flight altitudes of Dark-rumped Petrels during the evening peak were not significantly different from those of Newell's Shearwaters in summer 1993 ($U = 0.767$, $n = 82$, $P = 0.381$) but were significantly higher in both fall 1993 ($U = 3.966$, $n = 192$, $P = 0.046$) and summer 1994 ($U = 43.999$, $n = 210$, $P < 0.001$).

There was considerable among-site variation in flight altitudes. To some extent, this variation reflected differences in local topography, in that birds that had to ascend over or into mountains near the coast (e.g., Wailua, Hanalei) had to climb more as they headed inland than did birds at sites with mountains farther from the coast (e.g., Kapaa, Kealia). Evening flight behavior at some sites reflected this pattern, in which birds that were sitting in a flock on the water took off, circled upward in a corkscrew-shaped motion over the water to gain altitude, and then headed inland. This behavior was particularly common in Hanalei, where cliffs >300 m high occur adjacent to the coast and the topography climbs rapidly to >1,000 m. In another evening behavior, the birds gained some of the needed altitude off-shore, then climbed rapidly as they headed inland; this behavior was seen often at Wailua. In contrast, flight in the morning consisted of heading to sea while rapidly losing altitude.

DISCUSSION

SPECIES COMPOSITION AND TIMING OF MOVEMENT

Dark-rumped Petrels appeared to be uncommon but fairly widespread on Kauai. They probably are not very numerous, as indicated by their movement to and from colonies within a fairly small window of time and light and by the few targets recorded on radar at that time. We believe that they occurred in low numbers (low tens of birds) at most sites on the southern side of the island and in moderate-high numbers (tens–low hundreds) at most or all sites on the eastern and northern sides of the island, with high numbers from Wailua to Kealia and very high numbers (many hundreds) at Hanalei and probably westward. Indeed, most of the few Dark-rumped Petrels that have been recovered by the Save Our Shearwaters (SOS) Program, which rescues downed birds during the fall, have been found in the Hanalei-Princeville area, near the Na Pali coast (Telfer et al. 1987; Telfer, unpubl. data).

Newell's Shearwaters were widespread on Kauai, and we observed them at essentially all sampling sites. They represented a great majority of the targets recorded on radar during the hours of complete darkness. At some sites, we recorded >1,000 targets moving inland after complete darkness, suggesting that large numbers of these birds occur over the island as a whole. We believe that they occurred in low-moderate numbers (high tens–low hundreds of birds) at sites on the southern side of the island, with moderate numbers at Hanapepe and Kalaheo, and in moderate-high numbers (low hundreds–low thousands) at most sites on the eastern and northern sides of the island, with high numbers from Wailua to Kealia and high–very high numbers (thousands) at Hanalei. This pattern of both abundance and widespread distribution is reflected in the fact that >99% of the birds recovered by the SOS Program around Kauai are Newell's Shearwaters (Telfer et al. 1987; Telfer, unpubl. data).

We were unable to use the night-vision data to estimate the relative abundance of the two species, because the petrels tended to fly under conditions of greater ambient light and higher altitudes than the shearwaters did, thus increasing the probability of our sighting petrels before dark and shearwaters after dark. We suggest that perhaps 2–10% of the total population of inland-nesting procellariids on Kauai are Dark-rumped Petrels, with the remainder being Newell's Shearwaters. Data collected by the SOS Program suggest that Dark-rumped Petrels constitute a small fraction of all birds that are recovered (Telfer at al. 1987; Telfer, unpubl. data), but the data probably are biased by the low recovery of either species along the Na Pali coast, where the largest numbers of Dark-rumped Petrels probably occur, and by the possibility that Dark-rumped Petrels may be attracted to lights less strongly than are Newell's Shearwaters. Interspecific differences in attraction of other procellariiform species to lights have been noted by Swales (1965).

The differences in the timing of movement that we observed between these two species simply may be related to intergeneric differences in behavior. Although almost all *Puffinus* shearwaters are nocturnal around breeding colonies, several *Pterodroma* petrels are crepuscular or even diurnal (Warham 1990, Zimmer 1992). Beyond intergeneric differences in degree of nocturnality, Dark-rumped Petrels exhibit variation in the timing of arrival at different colonies in the Galapagos Islands (Tomkins and Milne 1991).

GEOGRAPHIC AND TOPOGRAPHIC VARIATION IN MOVEMENT RATES

Movement rates on radar generally were largest in eastern and northern Kauai and smallest in southern Kauai, although there was great among-site variation in movement rates within each of these regions. This geographic variation in movement rates probably is related to the proximity and amount of nesting habitat and generally matches patterns of fallout that have been described by the SOS Program, in that few (<25%) birds fall out on the southern side of the island and most fall out on the eastern and northern sides (Telfer et al. 1987). It also is possible that movement rates are lower on the southern side of the island because the southern colonies are more depleted by predators than are colonies elsewhere on the island. The SOS data also indicate that fallout is heaviest near brightly lit, coastal urban areas and near river mouths. We found, however, that movement rates also may be large in areas other than brightly lit places or river mouths. For example, the Anahola Mountains and Waiakalua Stream sites were neither brightly lit nor near a river mouth, yet movement rates on radar at both sites were substantial in both summer and fall 1993.

Our impression is that valleys sometimes, but not always, focused movements of the two species into flight corridors and that colony locations and the presence of topographic barriers affected the position and width of corridors. Valleys may be important in navigation during periods of limited visibility (e.g., when no moon is visible, during inclement weather), although we were unable to evaluate this proposition. Given the high flight altitudes at many sites, it was not surprising that some birds flew without regard to the presence of topographic barriers, as has been seen for Greater Shearwaters (*Puffinus gravis*; Swales 1965).

At this time, it is unclear how consistently birds use specific flight corridors when flying to and from colonies. During all-night radar sessions, total numbers of birds flying inland and seaward were highly similar on some nights but differed on others, suggesting that specific flight corridors were not always used within a night or that nonbreeders were exhibiting irregular patterns of colony attendance. Little is known about specificity of flyway use by either petrels or shearwaters, but Hutton's Shearwaters (*Puffinus huttoni*) in New Zealand are believed to use well-defined and narrow flyways when going to and from their mountainous, inland colonies (Harrow 1976).

DIEL VARIATION IN MOVEMENT RATES

The movement of birds inland peaked just after sunset and was followed by steady, low-level movements in both directions during the middle of the night and by a large, seaward exodus just before dawn. This inland-seaward pattern of movement has been recorded for a large suite of nocturnal tubenoses (Murphy 1936; Warham 1958; Swales 1965; Harris 1970; Harrow 1976; Harper 1983; Simons 1981, 1985; Watanuki 1986; Cruz and Cruz 1990; Klomp and Furness 1992).

Based on what is known about the behavior of tubenoses (Warham 1990), the early-evening inland pulse in summer consisted of breeding adults and nonbreeding adults and subadults. In fall, the inland pulse consisted of breeding adults returning to the colony to feed young; nonbreeders are not present on the colonies this time of the year (Harper 1983, James 1985, Simons 1985, Cruz and Cruz 1990, Podolsky and Kress 1992). Movements during the middle of the night were those of adults and nonbreeders (summer and fall) or of adults and fledglings (fall). Most Newell's Shearwaters fledge 1–4 hr after sunset (Telfer et al. 1987), and most fallout of fledgling shearwaters on Kauai occurs during that same period (Reed et al. 1985). The number of birds detected on radar after this period in fall did not decline, however, which would occur if adults carrying food were arriving from successively greater distances from the colony (Imber 1975), if juveniles represented a small proportion of the total number of birds moving in a single night, or if differences in wind direction and speed caused nightly differences in the timing of return of birds to a colony (Harper 1983). In our study, peak arrival times varied by up to 15 min among nights within a season, and we speculate that they reflected among-night differences in environmental conditions or foraging distances. Peak arrival times also differed between seasons, probably because of differences in the timing of sunset and sunrise. Such a seasonal difference in arrival times of Dark-rumped Petrels also has been seen at Maui (Simons 1985).

SEASONAL VARIATION IN MOVEMENT RATES

The summer increase in movement rates resulted from increasing numbers of breeders returning to lay eggs or, more likely, from increasing numbers of nonbreeding birds visiting the colonies. The general pattern for tubenoses is that older breeders return to the colony sooner after the pre-laying exodus than do younger breeders (Warham 1990) and that nonbreeders arrive later than do old breeders and in a specific sequence according to age (Serventy 1967, Fisher and Fisher 1969). The fall decline in movement rates resulted from the pre-fledging exodus of breeding adults (Serventy et al. 1971, Warham 1990) and the exodus of fledged juveniles from the island. Although both phenomena were occurring fairly contemporaneously, the fact that there were two adults (which may have visited the colony one or more times each/night) for every juvenile (which presumably made only one trip from the colony) suggests that the seasonal abandonment of colonies by adults probably had a greater effect on this decline.

There still were considerable numbers of radar targets flying inland on our last sampling nights in late October 1992 and 1993. Most adults Newell's Shearwaters should have abandoned the colonies by that time, although a few may not have left until the end of November (Telfer et al. 1987). One possible explanation for this late movement is that a large proportion of the birds still flying inland in late October were Dark-rumped Petrels, which fledge later (15 October–20 November on Maui; Simons 1985) than do Newell's Shearwaters (10 October–10 November; Telfer et al. 1987).

The decline in movement rates from summer to fall was expected, for attendance at colonies by nonbreeders and failed breeders declines as chick-rearing progresses (Serventy et al. 1971, Warham 1990). Three sites exhibited much larger inter-seasonal declines (~90%) than occurred at the other sites, however. The large decline at Kalaheo could have been caused by breeding failures at Newell's Shearwater colonies in those areas, as suggested by the low reproductive success of a colony near Kalaheo (D. G. Ainley and R. Podolsky, pers. comm.). The large decline at Kapaa could have been caused by the continued closure of several resorts whose lights formerly attracted shearwaters (Reed et al. 1985) in the Kapaa area after Hurricane Iniki. The large decline at Hanalei reflected the fact that it was sampled after most adults and juveniles adults already had left the island. Many Newell's Shearwater juveniles were retrieved by the SOS Program in the Hanalei-Princeville area in 1993 (Telfer, unpubl. data), suggesting that productivity in that region was not low.

Because each sampling period occurred during a period of less than one lunar cycle, our data are inadequate to assess properly the effects of moon phase on movement rates. The observed patterns, however, suggest that the effects were small or were masked by other factors. Other studies suggest that return rates of breeding adults are not affected by lunar phase (Warham 1960, cited in Harris 1966; Harris 1966; Harrow 1976; Brooke 1990) but that attendance by nonbreeders is depressed during first-quarter and full moons (Warham 1960, cited in Harris 1966; Harris 1966; Imber 1975; Harrow 1976; James 1985; Brooke 1990; Warham 1990; Klomp and Furness 1992).

INTERANNUAL VARIATION IN MOVEMENT RATES

On average, movement rates in fall 1993 were about four times those in fall 1992, probably because of effects of Hurricane Iniki in September 1992. If the hurricane and its resultant effects killed large numbers of juveniles or blocked entrances to burrows, many adults would have abandoned the colony before our October 1992 study began. Hurricane-induced loss of Wedge-tailed Shearwater chicks at Kilauea Point was 30–40% (K.J.F. Viernes, pers. comm.), indicating a substantial effect on at least that species. Aerial surveys on Kauai after the hurricane found massive wind-caused damage to vegetation and landslides at Newell's Shearwater colonies (Telfer, pers. comm.). Further, the number of birds recovered by the SOS Program in fall 1992 (just after the hurricane) was about 70% of the mean recovery rate during 1978–1991 (Telfer, unpubl. data). All of these observations suggest that numbers of petrels and shearwaters on Kauai were depressed in fall 1992 because of the hurricane (and probably fewer lights to attract juveniles) but rebounded in 1993. It also is possible that the differences we observed on radar simply reflected annual variability.

Because numbers of targets seen on radar in fall 1993 were about four times those seen in fall 1992, we expected SOS numbers to return to normal levels in 1993. Surprisingly, SOS figures indicate that the number of birds recovered in 1993 was only slightly higher than that in 1992 (Telfer, unpubl. data). It is possible that SOS recovery data are not good indicators of reproductive performance; however, we are unable to evaluate this possibility. Alternatively, SOS data are useful indicators, but interannual variability in colony attendance, the loss of a few key SOS volunteers, and the continued closure of several large resorts around the island whose lights formerly attracted shearwaters (Reed et al. 1985) resulted in the lower numbers recovered in 1993. Although we are unable to evaluate any of these propositions, the great difference seen in movement rates on radar between 1992 and 1993 indicates that there was a dramatic difference in the number of birds visiting Kauai at those times.

FLIGHT DIRECTION

Flight directions on both radar and the night-vision scopes indicated that most of the birds during the evening peak of movement were heading inland toward known nesting colonies or toward areas that contained suitable nesting habitat (much of the high interior of the island). Enormous effort would be required to locate all nesting colonies of these two species on Kauai.

Flight directions also suggested that many, but not all, birds used something resembling flight corridors when commuting to and from nesting colonies. Some birds flew a substantial distance parallel to the coastline to enter large river valleys that originated in the interior of the island, suggesting that these large valleys somehow are used in orientation while commuting inland at night. On the other hand, a substantial percentage of birds did not seem to orient to river valleys but instead simply flew directly inland from the sea. All birds at some sites (e.g., Waiakalua Stream) did not orient to river valleys at all. These results suggest that river valleys may constitute flight corridors for many, but not all, birds.

FLIGHT ALTITUDE

Prior to this study, biologists studying these birds on Kauai were limited to observing birds only visually in street lights; consequently, they concluded that flight altitudes of Newell's Shearwaters were quite low (Telfer, pers. comm.). Although we saw a few birds flying at low altitudes around lights, the night-vision data clearly indicated that most birds flew at much higher altitudes than previously was believed.

Among-site variation in flight altitudes probably resulted from several factors, including proximity of the sampling site to the ocean and to lights, distance to and elevation of the colony where the birds were headed, presence or absence of mountains or topographic barriers adjacent to the ocean, and probably weather conditions. The only available information on flight altitudes of other petrels and shearwaters is for Dark-rumped Petrels, which fly inland at dusk at 70–100 m agl in the Galapagos (Harris 1970), and of Greater Shearwaters, which fly inland "at heights varying from a few feet to a thousand feet above sea level" in Tristan da Cunha (Rowan 1952).

Flight altitudes of Dark-rumped Petrels and Newell's Shearwaters during summer 1993 were substantially and significantly lower during the morning exodus peak than during the evening peak. In the evening, most birds gained altitude over the ocean before heading inland but in the morning descended from the high-elevation colonies and rapidly descended as they approached the island's shoreline. This diel difference in behavior explains why most collisions with powerline wires along the perimeter road of Kauai occur at coastal sites in the morning during summer (Day and Cooper, unpubl. data). Although it is possible that this morning decline in flight altitude reflects a response to meeting headwinds at some sites, we believe that it more strongly reflects proximity to the shoreline. For example, birds at Wailua and Kealia during mornings in 1994 flew at much higher altitudes ~1,000 m inland ($\bar{x} = 163$ m and $n = 30$ for all birds at both sites combined) than they did while crossing the coastline a few seconds later ($\bar{x} = 62$ m and $n = 16$ for both sites combined), even though they were facing the same wind direction and speed in both locations (Day and Cooper, unpubl. data). Further, both species forage by flying near the sea's surface, so there is no reason for these birds to maintain the inland altitudes of their nesting colonies after they go to sea.

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