

NOCTURNAL AND DIURNAL FORAGING ACTIVITY OF HAWAIIAN ALBATROSSES DETECTED WITH A NEW IMMERSION MONITOR¹

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Abstract. We used a new immersion monitor to study the foraging movements of two species of albatrosses that nest in the Hawaiian Islands. The monitors showed that breeding male Black-footed Albatrosses (*Phoebastria nigripes*) land on the water more frequently during the day than at night. Breeding male Laysan Albatross (*Phoebastria immutabilis*) behavior was more variable and also showed a diurnal bias. We found no evidence of a nocturnal foraging bias in either species; in particular, these species do not seem to be limited to live capture of nocturnally available squid. Such squid may, nonetheless, contribute to the diet as a result of scavenging.

Key words: activity monitor, Black-footed Albatross, diurnal foraging, Laysan Albatross, nocturnal foraging, *Phoebastria immutabilis*, *Phoebastria nigripes*.

INTRODUCTION

Significant gaps exist in our understanding of the foraging biology of albatrosses, especially regarding the question of scavenging. Albatrosses take most of their pelagic prey by surface seizing (Ashmole 1971) in remote locations that are difficult to observe. As a result, inferences regarding albatross foraging behavior come largely from proventriculus contents of birds in colonies (Harrison et al. 1983, Weimerskirch et al. 1986, Rodhouse and Prince 1993) and on-bird data-loggers (Prince and Francis 1984, Weimerskirch and Wilson 1992). Albatross diets appear to consist mostly of fish, fish eggs, fisheries offal, and especially squid (Warham 1990, Cherel and Klages 1997). Because some of the squid species found in the stomach contents of albatrosses are bioluminescent and migrate to the surface at night, it has been suggested that albatrosses generally feed at nighttime (Brooke and Prince 1991). However, pelagic squid are active, highly mobile animals with well-developed sensory systems (Cherel and Weimerskirch 1995), which would make live capture difficult. Croxall and Prince (1994) suggested that albatrosses seize dead squid from cetacean regurgitations, post-spawning die-off, and fishery waste, inert foods that can be obtained at any time of the 24-hr cycle.

Weimerskirch and co-workers (Weimerskirch

and Wilson 1992, Weimerskirch et al. 1994) used stomach temperature sensors to show that Wandering Albatrosses (*Diomedea exulans*) caught nocturnally migrating squid mainly during daytime hours, implicating a scavenging foraging mode. Moreover, not all albatross species rely heavily on squid. Harrison et al. (1983) showed that flying fish ova were the most important prey item by volume (44%) in the diet of Black-footed Albatrosses (*Phoebastria nigripes*). Black-footed Albatrosses are also known for their habit of following ships and feeding on discarded offal during the day (Gould and Hobbs 1993, Veit et al. 1996).

In this paper we address the question of nocturnal versus diurnal foraging in two sympatric albatrosses breeding in the Hawaiian Islands. Analysis of proventriculus contents indicates that one, the Laysan Albatross (*Phoebastria immutabilis*), depends much more heavily on squid than the other, the Black-footed Albatross (Harrison et al. 1983). This difference in diet has been attributed to differences in foraging strategies during the diel cycle. Circumstantial evidence (analyses of optical density units [D] of rhodopsin in the eyes) indicates that Laysan Albatrosses have better nocturnal vision than do Black-footed Albatrosses, the former having 16 D g⁻¹ and the latter 4 D g⁻¹. For comparison, Barn Owls (*Tyto alba*) have 20 D g⁻¹ (Harrison et al. 1983). Therefore, the higher proportion of squid in the diet of Laysan Albatrosses could be explained by nocturnal foraging on their part and diurnal foraging by Black-footed Albatross-

¹ Received 14 August 1999. Accepted 14 April 2000.

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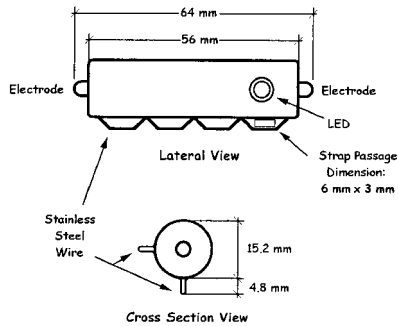


FIGURE 1. Schematic of immersion monitor.

es (Harrison et al. 1983). Direct evidence on this point would elucidate fundamental aspects of their foraging behavior, especially with regard to interactions with human fisheries in which albatrosses forage on hooked bait and become by-catch (Alexander et al. 1997, Olmos 1997).

To study the differences in foraging behavior during the 24-hr cycle, we developed an immersion activity monitor that detects entry and exit of a bird from the water. Because albatrosses must enter the water to obtain food, immersion frequency should be correlated with feeding effort. Together with satellite tracking data, these monitors provide detailed information on activity of the bird during foraging trips. In this paper we report data from monitors deployed on Hawaiian albatrosses and describe the performance of the immersion monitor.

METHODS

IMMERSION MONITOR COMPONENTS

The immersion monitor (Model A, Ferguson Manufacturing, Winston-Salem, North Carolina) was developed by us in conjunction with the manufacturer and is described here for the first time. It consists of a microcomputer, 32 KB RAM, two external electrodes which sense water contact, a visible light-emitting diode that signals status of the monitor, and a 3.6-volt lithium battery, all encased in a watertight enclosure (Fig. 1). The device's mass of 20.6 g represents < 1% of the mass of Laysan and Black-footed Albatrosses. The monitor can be linked to a standard PC via the PC's RS-232 serial port and an interface unit; power-up and data upload to the PC are mediated by the interface unit. Following power-up, at 0.5-sec intervals the microprocessor determines whether the circuit across the electrodes is closed (unit is immersed in wa-

ter) or open. If the circuit status changed since the previous check, then the duration of the immersion or emersion that just ended is written to RAM. The data thus consist of records of times of consecutive immersions and emersions. The number of wet-dry events recorded is limited by the battery life (3 years) and RAM. The capacity of the RAM will depend on the length of the character strings written to memory: if the monitor is immersed infrequently, then the average length of a given event's character string will be long and fewer events can be written to RAM. For the albatrosses that we studied, 3,500–5,000 events could be recorded. Our implementation of Model A ignored events with durations of 3 sec or less; this filter can be adjusted or disabled entirely.

TESTING THE IMMERSION MONITOR

We ground-truthed six monitors in laboratory trials by lowering them together into a water bath for a trial of six wet-dry periods (120, 60, 30, 10, 5, and 1 sec in duration). Each monitor was used in 10 such trials. We also tested five immersion monitors on Waved Albatrosses (*Phoebastria irrorata*) in the field on Isla Española, Galápagos, using the attachment technique described below. We held each bird alternately in and above ocean water for a series of wet trials (immersions of 2–20 sec separated by 20-sec dry periods) followed by a series of dry trials (emersions of 2–20 sec separated by 20-sec wet periods). For both laboratory and field trials, we compared the timing of wet and dry events detected by the monitor to the actual timing.

DEPLOYMENT ON HAWAIIAN ALBATROSSES

In January 1999, we attached 16 monitors to eight Black-footed Albatrosses and eight Laysan Albatrosses nesting on Tern Island, French Frigate Shoals (23°87'N, 166°28'W), in the Hawaiian archipelago, in conjunction with satellite-tracking studies of these species during the brooding period (hatching to chick age 18 days). Monitors were mounted on the ventral surface, just anterior to the brood patch, by creating a featherless space lined with two walls of adhesive tape and attaching the monitor to the tape within that space. A featherless space was required for successful operation of the monitor because wet feathers contacting the electrodes could close the circuit when the bird was out of

the water, incorrectly indicating that the bird was in the water. A sandwich of two strips of Tesa® tape formed each wall of the space; the two strips were attached adhesive side to adhesive side for a strong bond, and held 3–5 contour feathers between them. The second tape sandwich attached to 3–5 adjacent feathers; no feathers remained in the space between these parallel walls of tape. The monitor was seated between the two walls, and attached to the tape walls with Teflon ribbon that passed between eyelets on the monitor and holes punched in the tape wall. We then verified visually that the monitors were not in contact with any feathers. Similar studies mounted dataloggers on the leg (e.g., Weimerskirch et al. 1997); concerns from the permitting agency regulating our work that leg mounts could become tangled in fishing gear at sea prevented us from using this technique.

Each bird received a dorsally mounted satellite transmitter (PTT100; Microwave Telemetry, Columbia, Maryland) to provide complementary location data (Fernández et al., unpubl. data). The data from the transmitter also were used to calculate trip distance, maximum range, and flight speed, excluding satellite data with a high degree of error (“Location Quality B”; Fernández et al., unpubl. data; methods available from David Anderson).

DATA ANALYSIS

To determine whether wet-dry events reported by the immersion monitors occurred during the day or night, we used Sinnott’s (1994) algorithm implementing the astronomical convention that sunrise and sunset occur when the sun’s center lies 50′ below the horizon, allowing 16′ for the radius of the solar disk and 34′ for atmospheric refraction to lift the upper limb of the sun to the horizon. Times of sunrise and sunset (UTC) vary with date, latitude, and longitude. We used the location information provided by each bird’s satellite transmitter to assign each event to day or night according to that algorithm. To test the hypothesis that the solar cycle influenced foraging activity, we compared the expected proportion of immersions during daytime vs. nighttime (based on the proportion of total daytime vs. total nighttime spent at sea) with the time reported by the immersion monitor. Statistical analyses were performed using Statistica v. 4.5.

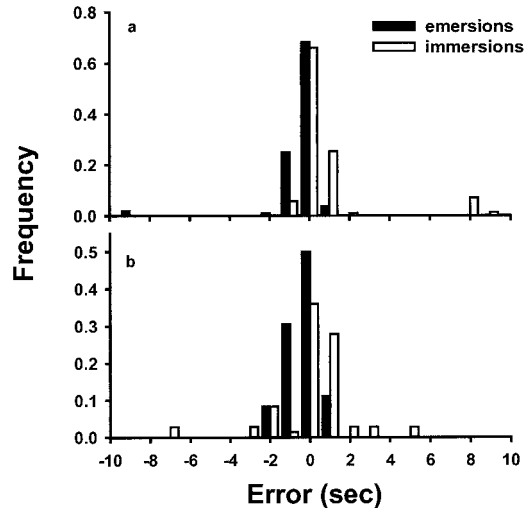


FIGURE 2. Frequency distribution of error in event duration during tests of immersion monitors in (a) water bath and (b) while on Waved Albatrosses.

RESULTS

GROUND-TRUTHING TRIALS

In laboratory trials, each of the six monitors recorded 100% of the immersions and emersions lasting 5 sec or more (100/100 total events for each monitor), and none of the events lasting 1 sec (0/20 total events for each monitor). The monitors thus performed as expected with a software filter that ignored events lasting 3 sec or less. Errors in immersion duration ranged from -1 sec (recording less wet time than real time) to +9 sec (Fig. 2a). This maximum error was measured in the same trial in all monitors and was undoubtedly due to human error by the investigator moving the monitors in and out of the water bath. Errors in duration of emersions varied from -9 sec to +1 sec (Fig. 2a). The actual duration of immersions and emersions and the duration reported by the immersion monitor were highly correlated (emersions: $r_s = 0.99$, $n = 300$, $P < 0.001$; immersions: $r_s = 0.99$, $n = 300$, $P < 0.001$).

The five monitors mounted on Waved Albatrosses detected 100% (45/45) of immersions, and 96% of emersions (43/45), of 4 sec or longer. None of the monitors detected events of 2 sec duration (0/10). The same monitor was responsible for the two undetected emersions (4 and 6 sec duration, respectively). Following that trial, we realized that the monitor’s attachment

TABLE 1. Day/night activity patterns of albatrosses at sea, January–February 1999. Larger values in day/night comparisons bolded.

Bird trip #	Proportion of time on water		Median immersions hr ⁻¹		Fraction of landings at night (total # landings)
	Day (total day hours)	Night (total night hours)	Day	Night	
Black-footed Albatrosses					
241 1	0.12 (73.8)	0.02 (92.5)	3.02	1.14	0.32 (271)
241 2	0.07 (65.0)	0.02 (90.8)	1.53	0.83	0.35 (157)
232 1	0.22 (45.0)	0.06 (62.5)	9.81	0.76	0.17 (553)
109 1	0.11 (34.8)	0.11 (46.0)	4.05	0.61	0.21 (307)
109 2	0.13 (16.0)	0.12 (13.0)	3.86	2.89	0.26 (146)
109 3	0.10 (27.7)	0.02 (39.1)	0.96	0.54	0.41 (44)
Laysan Albatrosses					
818 1	0.15 (33.0)	0.40 (26.8)	8.59	3.35	0.25 (305)
818 2	0.08 (62.0)	0.63 (14.4)	3.51	3.11	0.50 (489)
818 3	0.27 (12.4)	0.13 (12.6)	7.78	3.12	0.27 (140)
953 1	0.66 (25.5)	0.75 (32.0)	0.54	0.85	0.73 (52)
953 2	0.71 (164.3)	0.66 (215.0)	0.64	0.38	0.46 (257)
608 1	0.24 (24.2)	0.16 (26.2)	6.28	2.60	0.36 (197)
608 2	0.19 (50.5)	0.07 (53.0)	2.40	1.64	0.25 (243)

had loosened during the test, allowing it to come in contact with wet feathers during periods out of the water. Errors in reported duration of immersion ranged from -7 sec to +5 sec and the median error was +1 sec. (Fig. 2b). Actual and reported durations of both immersions and emersions were highly correlated (both $r_s = 0.96$, $n = 36$, $P < 0.001$). Errors in duration of emersions ranged from -2 sec to +1 sec, and the median error was -1 sec.

ACTIVITY PATTERNS OF HAWAIIAN ALBATROSSES

Six monitors were recovered from the 16 that were mounted on Hawaiian albatrosses, from three Black-footed Albatrosses and three Laysan Albatrosses. We determined gender with the relative bill lengths of members of a pair (Fernández et al., unpubl. data). Five of these birds were males; the gender of the sixth, a Black-footed Albatross, could not be determined. We collected these six units during late incubation and the first 21 days of the brooding period, when these species perform short trips relatively close to the colony (within 1,500 km of Tern Island; Fernández et al., unpubl. data). The remaining 10 monitors either fell off the bird at sea (Black-footed Albatrosses) or were on birds that abandoned their nests (Laysan Albatrosses had a mass breeding failure at this time; Fernández et al., unpubl. data) and did not return to the breeding colony during our study.

We analyzed data from a total of 13 trips (6 trips by three Black-footed Albatrosses and 7 trips by three Laysan Albatrosses), which lasted from 1 to 15 days (median = 3.2 days). The distances covered by these two species were similar (Mann-Whitney U -test, $Z = 0.15$, $n_1 = 6$, $n_2 = 7$, $P = 0.89$); the median distance covered was 1,669 km (range 362–9,407 km; details of trips provided in Fernández et al., unpubl. data). Birds of both species traveled mostly to the north of Tern Island during this study.

During these trips, Black-footed Albatrosses spent an average of 90.8% of the time at sea flying (Table 1). One Laysan Albatross that performed unusually long trips for this stage of the reproductive cycle (Fernández et al., unpubl. data) spent most of its time on the water and only 31.8% of the period at sea flying. The other two Laysan Albatrosses spent on average 84.3% of the time at sea in flight. In both species, most immersions were short; for five of the six birds, less than one third of the immersions exceeded 100 sec in duration (Fig. 3). These short immersions are not likely to represent rest on the water because their duration is so brief; instead, they suggest surface foraging activity. To test the assumption that short immersions are associated with foraging activity, we compared the speed of movement between consecutive locations provided by the satellite transmitter with immersion frequency over the same interval; the

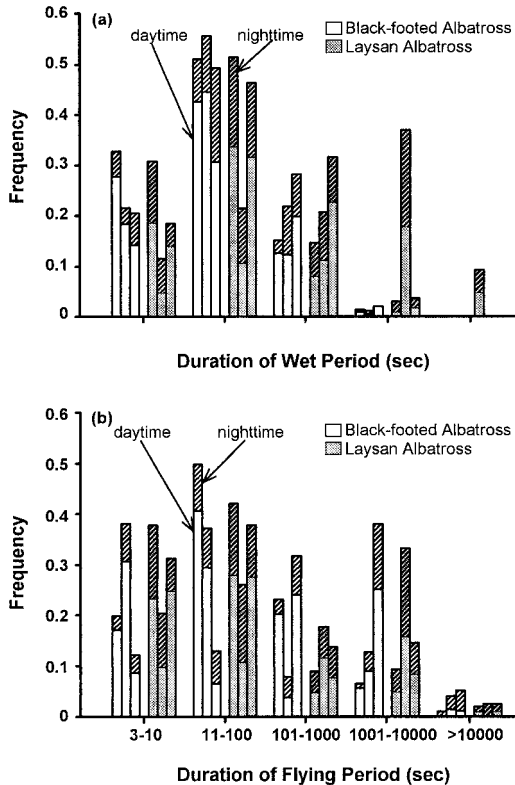


FIGURE 3. Distribution of period lengths while (a) on the water and (b) flying during daytime (bottom section of bar) and nighttime (top section of bar) for each of six Hawaiian albatrosses (all trips combined).

two parameters were negatively correlated ($P < 0.05$) for five of the six birds (Spearman r_s ranged from -0.40 to -0.61). We have shown elsewhere (Fernández et al., unpubl. data) that speed also is negatively correlated with turning angle. These data suggest that birds in a foraging mode engage in area-restricted searches for prey (Curio 1976), presumably after encountering a concentration of prey, and during this search they cover short distances, turn frequently to remain in the area, and alight on the water frequently for short intervals.

DIURNAL AND NOCTURNAL FORAGING

In the six trips of Black-footed Albatrosses, daytime immersions occurred at a higher frequency than expected from the proportion of time spent during daytime ($\chi^2_1 = 6.0$, $P < 0.05$). The seven trips of Laysan Albatrosses did not show any detectable bias ($\chi^2_1 = 1.3$, $P > 0.20$). However, one of these trips had a small expected number

of landings (Table 1: bird 953, trip 1), limiting resolution, and another was unusual in the length of landings (Table 1: bird 818, trip 2); excluding these two trips, all five Laysan Albatross trips showed a bias toward daytime immersions ($\chi^2_1 = 5.0$, $P < 0.05$). We observed no difference in duration of daytime and nighttime immersions in either Black-footed (Mann-Whitney U -test, $Z = 0$, $n_1 = n_2 = 7$, $P = 1.0$) or Laysan Albatrosses (Fig. 3; Mann-Whitney U -test, $Z = 0$, $n_1 = n_2 = 6$, $P = 1.00$). Note that some birds contributed more than one trip to these analyses.

The immersion rate per hour varied from 0–61 for Black-footed Albatrosses and from 0–57 for Laysan Albatrosses. The immersion rate during the daytime was higher than during nighttime for all six Black-footed Albatross trips (Sign Test, $P = 0.04$), by factors of 0.33–12.91 (Table 1). For Laysan Albatrosses, daytime rate exceeded nighttime rate in six of seven trips (Sign Test, $P = 0.13$), with daytime rates generally 1.5–2.5 times higher than nighttime. The peak immersion rate occurred during daytime in all six Black-footed Albatross trips (Sign Test, $P = 0.04$), but in only four of seven Laysan Albatross trips (Sign Test, $P = 1.00$).

During a trip, a bird may pass through areas of abundant food and areas of little food, and this variation should be reflected in immersion rate. To control the spatial contribution to variation in immersion rate, we compared the rate during a given daytime period with the rate in the subsequent nighttime period, reasoning that the bird was in the same general area, with the same food abundance, during both periods. Daytime and subsequent nighttime immersion rates were similar for both species when the daytime rate was less than 4 hr^{-1} (Fig. 4; Black-footed Albatross, higher daytime rate in 20/31 cases, Sign Test, $P = 0.15$; Laysan Albatross, higher daytime rate in 4/6 cases, Sign Test, $P = 0.68$). However, daytime immersion rate exceeded nighttime rates in both species when daytime immersion rate exceeded 4 hr^{-1} (Black-footed Albatross, higher daytime rate in 9/9 cases, Sign Test, $P = 0.008$; Laysan Albatross, higher daytime rate in 8/9 cases, Sign Test, $P = 0.046$).

Combining all satellite data across birds, for Black-footed Albatrosses the speed of movement between consecutive locations did not differ between day (median = 21.4 km hr^{-1}) and night (median = 19.9 km hr^{-1} ; Mann-Whitney U -test, $Z = 0.34$, $n_1 = 18$, $n_2 = 23$, $P = 0.73$).

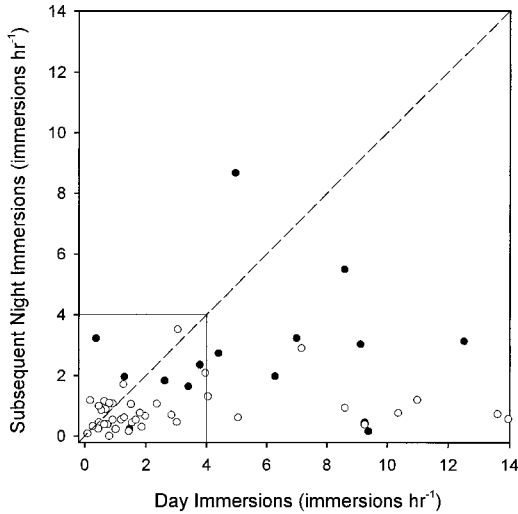


FIGURE 4. Immersion frequency during daytime hours by immersion frequency during the subsequent nighttime period. Open circles: Black-footed Albatrosses; closed circles: Laysan Albatrosses.

The same was true for Laysan Albatrosses (day median = 29.6 km hr⁻¹; night median = 26.2 km hr⁻¹; Mann-Whitney *U*-test, $Z = 0.29$, $n_1 = 55$, $n_2 = 72$, $P = 0.77$).

DISCUSSION

IMMERSION MONITOR PERFORMANCE

We have demonstrated the utility of a new miniature monitor, which records 100% of wet-dry events that lasted over 3 sec in controlled trials both in laboratory and field conditions and fails to record events of shorter duration (this detection threshold is adjustable). When error exists, it is typically slight. The immersion monitor is more likely to record slightly longer wet periods (median = +1 sec) and slightly shorter dry periods (median = -1 sec) than the actual ones. Nonetheless, the size of the unit and the quality of the information retrieved make this immersion monitor a useful device that can be employed in studies of foraging behavior of species that move between water and air. Compared with other such monitors (Prince and Francis 1984, Afanasyev and Prince 1993, Weimerskirch et al. 1997), this unit is smaller, is able to produce times and durations of events (not simply total elapsed time in water [Cairns et al. 1987]), and is dramatically less expensive (\$150) than other commercially available activity loggers. It has substantially less memory than larger units;

however, in our implementation, less than 10% of available memory was used.

ACTIVITY PATTERN OF HAWAIIAN ALBATROSSES

This is the first study to provide data on Hawaiian albatross foraging behavior during the breeding season using information from satellite telemetry and an immersion monitor. We characterized the foraging patterns of Laysan and Black-footed Albatrosses during the incubation and chick-brooding stages of the breeding cycle. It is important to note that we retrieved monitors only from males and therefore the behavior described cannot be assumed to be typical of both genders and of all parts of the breeding cycle.

During our study, short trips were performed in which a high percentage of the total time was spent flying over the ocean, in an apparent searching mode of continuous, relatively straight flight. Weimerskirch (1997) suggested that this behavior is an adaptation to locate unpredictable prey. The foraging trips of these two species matched this description, given that during the short trips that we monitored they fed in the relatively unproductive waters around Hawaii (SeaWiFS 1999). Therefore, it is probable that during these foraging trips the birds spent most of the time searching for scarce prey. During these short trips, immersion frequency was negatively correlated with speed, indicating transitions in locomotor behavior from patch location to patch exploitation. Both species often landed on the water for short periods, presumably when they located potential prey. This behavior also was found in Wandering Albatrosses nesting on the Crozet Islands where the number of landings during searching days was higher than during moving days (Weimerskirch et al. 1997).

Our data on immersion frequency and duration, flight speeds, and time spent on the water are inconsistent with a bias toward nocturnal foraging. Although our data are limited (possible non-independence of trips performed by the same individual, two Laysan Albatross trips had atypical aspects), they suggest that birds of both species split their foraging time between nocturnal and diurnal foraging. The results for immersions per hour (Table 1) indicate that over an entire trip, daytime rates exceed nighttime rates, often dramatically. This bias is driven by much higher daytime immersion rates in areas where overall immersion rate was high (Fig. 4), per-

haps indicating high feeding activity. When overall immersion rate was low (perhaps indicating low food abundance), we detected no bias toward either daytime or nighttime. There appears to be a constant baseline level of nighttime immersions, even when the birds had recently (during the previous daytime) immersed themselves frequently (Fig. 4). Daytime foraging appears to be more important for these two albatross species, and especially for Laysan Albatrosses, than has been previously recognized.

Devices to record the timing of influx of cold material during foraging trips have shown that Wandering Albatrosses of the Crozet Islands ingest larger amounts during the day than at night (Weimerskirch and Wilson 1992). Given their squid-based diet and the nocturnal migrations of squid to the surface, these activity patterns indicate that much of their food acquisition was through scavenging. We did not sample the gut contents of the birds in our study because we continued to satellite-track them after removing their immersion monitors and we wanted to minimize disturbance.

Studies of Hawaiian species caught in drift-net fisheries (Gould and Hobbs 1993) have shown that the ratio of Laysan to Black-footed Albatrosses caught in high seas driftnets (3.7:1) is much lower than the ratio of the total population (12.8:1). This suggests that Black-footed Albatrosses more often supplement their natural diet by scavenging offal. Moreover, studies of isotope concentrations in the breast tissue of Hawaiian albatrosses indicated that Laysan Albatrosses fed at a trophic level one-third to one full step lower than did Black-footed Albatrosses (Gould et al. 1997), indicating that Black-footed Albatrosses rely heavily on high trophic level food that would be difficult to obtain except by scavenging. Bias toward feeding activity during daytime (this study), boat-following behavior (Whittow 1993, Veit et al. 1996), and chunks of scavenged birds (Harrison et al. 1983), mammal tissue, and monofilament line (Gould et al. 1997) in the digestive tract of Black-footed Albatrosses support the idea that this species scavenges frequently. The new data provided by our study highlight the importance of daytime foraging for Laysan Albatrosses also. We do not know whether Laysan Albatrosses that we studied took live or dead prey during the day; they may have scavenged, or may have taken diurnally-active live prey. Data from females, breed-

ers during other parts of the reproductive period, and nonbreeders, plus food samples, will be required to fully characterize the relative importance of diurnal vs. nocturnal foraging in Hawaiian albatross species.

ADAPTATIONS FOR NOCTURNAL FEEDING

The contrast between these two species in rhodopsin content of the eyes has been used as circumstantial evidence of more nocturnal foraging by Laysan (whose rhodopsin content approaches that of Barn Owls) than by Black-footed Albatrosses (Harrison et al. 1983). Our data show higher immersion frequencies in daytime by both species, and we assume that immersion frequency is an indicator of feeding activity. We found that breeding male Laysan Albatrosses foraged far to the north of Tern Island during most of the chick-rearing period in 1998, in contrast to the brief chick-brooding period during which we conducted our study (Fernández et al., unpubl. data). Laysan Albatrosses foraging at high latitude during the chick-rearing period (February–May), when day lengths there are short, might experience stronger selection than would Black-footed Albatrosses for effective night foraging even if they feed at higher rates during the day and/or prefer to feed at that time, simply because the day length is short. Chick-rearing trips in 1998 often were directed at the Aleutian Islands and Gulf of Alaska. At this latitude (50°N), Sinnott's (1994) algorithm indicates that daylength is 11.0 hr on March 1. For comparison, Black-footed Albatrosses foraged at lower latitudes in 1998, generally off the west coasts of California, Oregon, and Washington, at latitudes 30–45°N. However the difference in length of daylight is slight: on March 1 at latitude 40°N, daylength is 11.3 hr. These considerations indicate that daylength does not constrain daytime foraging differently in these two species to an important degree. Instead, Laysan Albatrosses at high latitude may forage at higher hourly rates at night than is indicated by our data from lower latitudes. A test of this hypothesis will require additional use of satellite tracking and immersion or other activity monitors deployed later in the breeding cycle.

ACKNOWLEDGMENTS

We thank Jake Anderson, Laura Carsten, Ken Feeley, Franz Juola, Conor McGowan, Elaine Porter, Carl Safina, Tammy Steeves, and Shihway Wang for field assis-

tance, and H. Weimerskirch, J. Ludwig, W. Koenig, L. Clifford, H. Townsend, and an anonymous reviewer for comments on drafts of the manuscript. The U.S. Fish and Wildlife Service, Honolulu, Hawaii and the Charles Darwin Foundation provided logistic support. Funding was provided by National Science Foundation grant DEB 9629539 to DJA, the U.S. Fish and Wildlife Service, and Wake Forest University.

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