SATELLITE TELEMETRY OF GREAT FRIGATEBIRDS *FREGATA MINOR* REARING CHICKS ON TERN ISLAND, NORTH CENTRAL PACIFIC OCEAN

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SUMMARY

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The Papahānaumokuākea Marine National Monument in the Northwestern Hawaiian Islands protects breeding habitat for many migratory animals. We used satellite telemetry to describe the areas in which a mobile top predator, the Great Frigatebird *Fregata minor*, traveled on foraging trips during the early chick-rearing period from a breeding colony on Tern Island, French Frigate Shoals. Identification of potential foraging events, indicated by a reduction in transit rate, allowed us to assess whether wide-ranging marine species such as Great Frigatebirds remain inside the protective boundaries of the Monument while brooding young chicks. Four of 11 foraging trips extended outside of the boundaries of the Monument. These movements may represent the shortest foraging distances that Great Frigatebirds travel from the colony because adults need to provision young chicks frequently. We also tracked one male that abandoned its nest on a journey to the southwest of Tern Island. This bird was tracked for 16 days before the transmitter's battery expired, and the last transmitted position was nearly 1100 km from Tern Island. These tracks, the first reports of frigatebird telemetry in the Pacific Ocean, provide information about the foraging behaviors of a top predator during a critical life-history stage—data that will complement tracking data of other species and aid in future conservation and management decisions concerning the Monument and surrounding waters of the Northwestern Hawaiian Islands.

Key words: Great Frigatebird, *Fregata minor*, Papahānaumokuākea Marine National Monument, Hawaii, satellite telemetry, habitat use

INTRODUCTION

Many animals have the capacity to move long distances. Migration is the most common example of large-scale movements, but animals also travel extensively to find food or mates. In the marine environment, many animals cannot remain in a single location for extended periods because environmental and anthropogenic factors drive fluctuations in resources such as prey availability. For example, fluctuations in sea surface temperature and salinity affect spawning, growth and development of fishes, influencing foraging movements of juvenile and adult fishes (Rijnsdorp *et al.* 2009). These movements in turn affect many aspects of marine ecology, including foraging opportunities for predators (Thompson & Ollason 2001; Schroeder *et al.* 2009), fish stocks and fisheries management (Huang *et al.* 2007). In sum, breeding and non-breeding movements of species in a marine environment are determined by a suite of factors that ultimately influence survival and breeding success.

Animal movements create difficulties for the conservation and management of mobile species, in part because the animals' ranges may transcend the jurisdictional boundaries of single agencies or countries (e.g. Serneels & Lambin 2001, Brindza *et al.* 2008, Egevang *et al.* 2010). Protective efforts for migratory and wide-ranging species are also limited by a dearth of information on breeding, non-breeding and foraging behaviors and habitats. One tool for conserving and managing mobile marine species is the establishment of reserves. Specifically, marine protected areas (MPAs) provide protection for species that reside in them during at least part of the year. Typically, a reserve protects terrestrial breeding habitat (for seabirds, sea turtles or pinnipeds) and might also protect important nearshore foraging areas. In the latter scenario, shallow-water foragers such as terns (Monticelli *et al.* 2006) might be effectively protected. However, because of differences in foraging behaviors, other species that need to travel far for food, such as albatrosses (Fernández *et al.* 2001), may not fully benefit from the protection the reserve offers. Thus, assessing the effectiveness of an MPA requires information about the movement and foraging behavior of species that use the area (e.g. Louzao *et al.* 2011). Additionally, the identification of foraging areas important to marine animals provides useful data about animals' relationships to fishing operations (Karpouzi *et al.* 2007), environmental variables (Wilson *et al.* 2002) and weather events (Schreiber & Schreiber 1984).

The establishment of the 362 000 km² Papahānaumokuākea Marine National Monument in the Northwestern Hawaiian Islands (NWHI) in 2006 was a significant step toward the protection of many breeding marine animals. More than 90% of Hawaiian Green Sea Turtles *Chelonia mydas* nest on a single island within the Monument (Balazs & Chaloupka 2004), nearly all of the endangered Hawaiian Monk Seals *Monachus schauinslandi* birth pups within the Monument (Antonelis *et al.* 2006), and millions of seabirds also breed throughout the Monument each year. Some of these species are known to move continuously, foraging both within and outside the boundaries of the Monument (e.g. Hawaiian Monk Seals; Stewart *et al.* 2006), even when tied to land during the breeding season (e.g. Laysan *Phoebastria immutabilis* and Black-footed *P. nigripes* albatrosses; Kappes *et al.* 2010). However, we lack data on habitat use of many

species breeding within the Monument. Papahānaumokuākea is instrumental in protecting terrestrial breeding habitat, but more studies are needed on the use of waters within and outside the Monument by highly mobile animals.

The Great Frigatebird *Fregata minor* is a long-lived, top avian predator in the NWHI, whose at-sea worldwide distributions are not well known (Metz & Schreiber 2002). Outside the breeding season, these birds appear to range widely. Birds banded or tagged in French Frigate Shoals, NWHI, have been recovered or sighted up to 7 000 km away—on other Northwestern Hawaiian Islands and at Johnston Atoll, Wake Island, Papua New Guinea, the Philippines, and Japan (Dearborn *et al.* 2003; D.C. Dearborn & F. Juola, unpubl. data). Telemetry studies have also demonstrated wide-ranging movements of Great Frigatebirds during the postbreeding period in the Indian Ocean and of Magnificent Frigatebirds *Fregata magnificens* in the Atlantic Ocean. On postbreeding trips, these birds traveled up to 4 400 km and 1 400 km, respectively, away from their breeding colonies (Weimerskirch *et al.* 2006). Knowledge of foraging movements during the breeding season, however, is somewhat limited. Weimerskirch *et al.* (2004) tracked several Great Frigatebirds in the Mozambique Channel and found that brooding adults made short foraging trips within 150 km of the colony. Incubating birds took longer foraging trips that ranged up to 600 km from the colony. Additionally, breeding Great Frigatebirds tracked at Aldabra Atoll in the Indian Ocean exhibited longer foraging trips on average than those in the Mozambique Channel, presumably because of regional differences in oceanography (Weimerskirch *et al.* 2010). Wide-ranging movements of this species throughout the annual cycle, coupled with the longest period of parental care among birds (12–14 months; Dearborn & Anders 2006), recommend it as an informative species to study—successful breeders engage in central-place foraging throughout the entire year and must adjust to seasonal changes in prey availability to feed themselves and their chicks. Partly because we lack details of frigatebirds' movements, we know little about potential at-sea threats to the species. Great Frigatebirds associate with subsurface predators such as tuna when foraging (Au & Pitman 1986, Weimerskirch *et al.* 2004) but may not interact extensively with fishing vessels (Weimerskirch *et al.* 2010), unlike albatrosses, whose populations have declined as a result of bycatch (Véran *et al.* 2007). Great Frigatebirds also do not ingest plastic (Metz & Schreiber 2002). Further study of this species and its potential at-sea threats will aid in assessing the efficacy of MPAs for wide-ranging foragers.

In this study, we instrumented Great Frigatebirds with Argos satellite transmitters during chick brooding. This stage of the reproductive cycle places the greatest restrictions on forage-trip duration because adults must return to the nest frequently (every one to three days) to feed young, and these foraging trips likely represent the shortest distances that Great Frigatebird parents travel from the colony. Therefore, short trips during brooding allowed us to investigate whether the Monument provides minimal protection of the foraging habitat of Great Frigatebirds.

STUDY AREA AND METHODS

The study was conducted in May 2005 during the early chick-rearing period (mean chick age 5.5 days, range 4–12 days) on Tern Island (23°45'N, 166°17'W), French Frigate Shoals, in the Papahānaumokuākea Marine National Monument (Fig. 1). Tern Island supports several thousand breeding pairs of Great

Frigatebirds (Dearborn & Anders 2006). Tagged birds were part of a larger, ongoing study of the reproductive ecology of the species at Tern Island.

We first fitted two birds with dummy transmitters to ensure that the instrumentation did not inhibit flight or other behaviors. Next, we deployed satellite transmitters (Microwave Telemetry PTT-100), attaching them with Tesa tape #4651 (Fernández *et al.* 2001) to six Great Frigatebirds. The package weight was 23 g, and typical body mass in this population is 1.5 kg for females and 1.3 kg for males—thus, instruments constituted 1.5–1.8% of body mass. Birds were captured by hand at the nest during the day. Transmitters were attached by laying strips of tape beneath a cluster of contour feathers in the center of the back, then wrapping the tape around the feathers and the transmitter. We also attached yellow vinyl patagial tags bearing unique alpha-numeric codes to the birds for non-invasive identification and monitoring at the colony. During incubation and early chick-rearing, Great Frigatebirds immediately leave the breeding colony upon the return of their mate (Dearborn 2001; Weimerskirch *et al.* 2004). Thus, once instrumented, our tagged birds left the island to undertake a foraging trip when their mates relieved them at the nest. After one to three days, tagged birds returned from the foraging trip to relieve their mates, and when the mates returned, tagged birds left the island to undertake a second foraging trip. Upon their return from this second trip, we removed the transmitter.

Argos locations were recorded during the entire time a bird carried a transmitter. We included all location classes returned by Argos and then used movement-based criteria to filter out unrealistic movements (e.g. Shaffer *et al.* 2005, Adams and Flora 2010, Kappes *et al.* 2010). Specifically, we applied a speed filter (Tremblay *et al.* 2006) in MatLab (The MathWorks, Natick, MA), retaining only locations in which the transit rate between two successive locations did not exceed 65 km/h (Weimerskirch *et al.* 2003). The resulting tracks retained 92.2% (n = 664) of all returned locations.

The rate at which Argos-equipped satellites pass over a given location is not constant; therefore, animal movements are not sampled at regular intervals (Wilson *et al.* 2002). Interpolation resamples the data at evenly spaced intervals (e.g. one location per hour in this study) and allows for more fluid, realistic representations of the movements
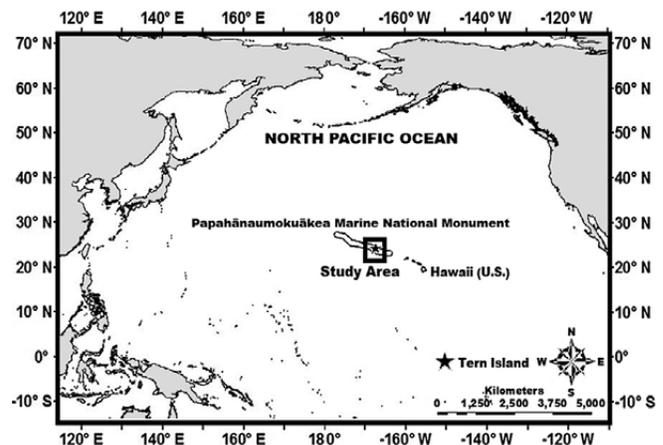

Fig. 1. Study area (Tern Island, Northwestern Hawaiian Islands) and surrounding features, including Papahānaumokuākea Marine National Monument.

of marine animals. We interpolated the filtered tracks using a Bézier curve (μ = 0.3; Tremblay *et al.* 2006). We then calculated transit rates and distances traveled using the interpolated tracks.

Although an altimeter offers a direct approach for identifying potential foraging events, it cannot be used in conjunction with satellite transmitters because the combined mass of the two instruments is too great for frigatebirds to carry (Weimerskirch *et al.* 2004, 2010). Therefore, we used an indirect approach. We manually examined the telemetry tracks to identify "potential foraging events," which were indicated by a reduction in transit rate (Hyrenbach *et al.* 2002). Specifically, we followed a modified method for Great Frigatebirds (Weimerskirch *et al.* 2004) that identifies a potential foraging event by, for instance, three or more successive points less than 10 km apart and separated by at least 30 minutes. We further modified this method for our processed data set, which was interpolated to one location every 60 minutes: potential foraging events comprised three or more successive points <10 km apart and separated by 60 minutes.

We used a mixed-model ANOVA to test whether frigatebirds exhibited different transit rates during night and day. The data points were estimates of transit rate from each day or night period of flight from every bird. Time (day vs. night) was used as a fixed factor, and the identity of the bird was incorporated as a random factor via Restricted Maximum Likelihood (REML). Unless otherwise noted, means ± SD are reported.

RESULTS

We placed transmitters on six Great Frigatebirds caring for chicks that were 4 to 12 days old at the beginning of the study (Table 1, Fig. 2). There were 720 locations returned for all birds, encompassing eleven roundtrip foraging bouts, and one incomplete trip (L80). Parents' trips lasted 1–3 days and covered 399 ± 189 km (mean ± SD) on average (range 73–732 km, n = 11 completed trips). Four birds (not including the extended second trip of L80) traveled beyond the boundaries of the Papahānaumokuākea Marine National Monument before returning to feed their nestlings (Fig. 2, Table 2).

There were 19.8 ± 1.9 Argos locations returned per bird per day. The quality of locations was most commonly (64.4%) of class "0" (expected to fall within 1.5 km of true location). Visual examination of all 12 foraging tracks (two trips by each of six birds) revealed that four birds took their second foraging trip in a direction roughly opposite to the first trip (Fig. 2). The incomplete data on the second trip of male L80 (Fig. 3) were due to a dead battery or loss of the instrument. This bird did not return to the colony in typical fashion from its second foraging trip, but instead flew in a southeasterly direction for 16 days, until the transmitter ceased transmitting, 1 088 km from Tern Island. The bird's mate abandoned the nest when L80 had been gone for 10 days, and the nest failed. L80 returned to the colony approximately one month later, but without the transmitter.

Based on 75 estimates of transit rates, birds flew more slowly at night (20:00–06:00; 8.4 ± 3.7 km/h (± SE) at night versus 10.5 ± 4.1 km/h during the day; $F = 5.01$, $P = 0.0285$). Differences among birds accounted for 14.4% of the variance in estimated transit rates. We tracked birds during all phases of the lunar cycle (new, half, and full moon), and birds exhibited a mix of straight and looping tracks during each of those phases.

Based on the criterion of a short-term reduction of transit rates during the daytime (06:00–20:00), we identified 28 potential foraging events during the 12 trips. Fifteen of those events occurred during the extended second trip of L80 (Fig. 3). The transit rates of the outbound and return portions of the trips that contained potential foraging events did not differ significantly ($t = –0.13$, $P = 0.898$; Table 3).

DISCUSSION

Papahānaumokuākea Marine National Monument appears to provide only partial protection of Great Frigatebird foraging habitat during the chick-brooding period. Our Argos tracks indicated that

TABLE 1
Transit rates, distances and durations of foraging trips from Tern Island by Great Frigatebirds during early chick-rearing

Individual	Sex	Trip	Transit rate (km/h)	Distance (km)	Farthest distance from Tern Island (km)	Time (h)	Inferred foraging events
L77	Male	Trip 1	10.4	227.9	83.3	22	1
		Trip 2	11.4	732.2	249.9	64	3
L78	Female	Trip 1	3.3	73.5	22.7	22	0
		Trip 2	9.5	262.2	54.7	29	2
L79	Female	Trip 1	11.2	392.5	131.0	37	2
		Trip 2	11.1	431.5	153.8	39	0
L80	Male	Trip 1	6.9	436.7	132.5	63	1
		Trip 2	8.4	3070.8	1087.9	367	15
L82	Female	Trip 1	12.7	519.7	190.8	41	1
		Trip 2	10.4	575.8	209.0	56	2
L83	Male	Trip 1	13.5	514.7	181.5	38	1
		Trip 2	10.1	222.3	49.9	22	0

frigatebirds foraged both inside and outside of the boundaries of the Monument during this part of the breeding season (Figs. 1 & 2; Table 2). This brooding period puts the greatest constraint on the birds' foraging time, and frigatebirds are expected to forage nearer the colony than they would during incubation and post-brooding. However, our tracking data demonstrate that even the shortest trips (22 h) ranged up to 228 km. Four of the six birds traveled outside the boundaries of the Monument at least once while foraging (Table 2). As chicks age, Great Frigatebird parents spend longer periods away from the nest, and may travel farther to forage. The Monument effectively protects nesting habitat and some portion of the foraging area of Great Frigatebirds, but it does not protect all of the foraging areas used by breeding birds.

We used a reduction in transit rate as an indicator of potential foraging events, an indirect approach that could err in either direction—either missing true foraging events or inferring events that did not occur.
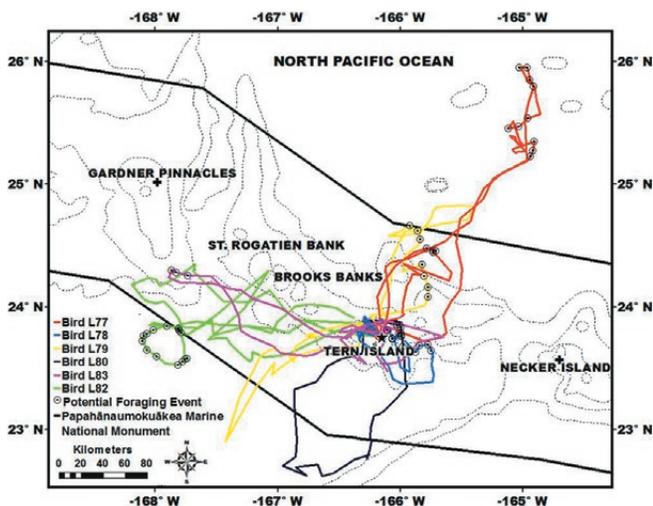

Fig. 2. Foraging tracks of six Great Frigatebirds (two foraging trips per bird, except one foraging trip for L80) during early chick-rearing from Tern Island, French Frigate Shoals. Black circles within bird tracks indicate slower flight periods thought to correspond to foraging events. Dotted lines delineate bathymetry.

TABLE 2
Residence times, inferred foraging events and percentage of total foraging events within the boundaries of Papahānaumokuākea Marine National Monument by six Great Frigatebirds rearing young chicks on Tern Island

Individual	Hours tracked	% time inside monument boundaries	Inferred foraging events	% inferred foraging events inside monument boundaries
L77	88	52	4	25
L78	51	100	2	100
L79	76	84	2	50
L80	430	21	16	6
L82	97	79	3	0
L83	60	100	1	100

The horizontal transit rates of frigatebirds are reduced during some portions of flight because frigatebirds continuously change altitude while climbing thermals and descending; more time may be spent gaining or descending altitudes of several hundred meters than is spent moving horizontally (Weimerskirch *et al.* 2003). Slower horizontal movement causes satellite tracks to appear stationary. Slow transit rates and the resulting static tracks therefore present difficulties in interpretation of Great Frigatebird movements that are based on changes in transit rate. It is possible that the "foraging events" we inferred simply reflected birds riding in a thermal or resting on the wing (Weimerskirch *et al.* 2010). In our data, potential foraging events were infrequent (not all birds exhibited the slow transit rates of inferred foraging activity on all days they were tracked; Table 1). Inferred foraging occurred throughout the day, but some birds flew for up to 27 h before a potential foraging event occurred (L82), and three birds (L78, L79, L83) did not exhibit any potential foraging activity during one of their foraging trips (Table 1). There were also several Argos locations that indicated that the birds were moving very slowly within French Frigate Shoals. Great Frigatebirds immediately vacate the nest when they are relieved by their mate (Dearborn 2001; Weimerskirch *et al.* 2004), and we did not observe tagged birds in the colony except when they were on their nests. Furthermore, adult Great Frigatebirds from this colony have not been observed to forage within the atoll. Therefore, the slow, local flight we observed likely involved birds flying in thermals above the island, which is common (M.E. Gilmour, pers. obs.). Conversely, although a reduction of transit rate may be a useful indicator of potential foraging activities of pelagic seabirds traveling great distances, this method may fail to detect foraging events. Great Frigatebirds at times approach the sea surface, catch a fish, and continue flying (E.A. Schreiber, pers. obs.). Without altimeter data, telemetry studies would not be able to capture such behavior.

From previous work on diet or at-sea observations of frigatebirds, three environmental factors seem important in determining foraging locations. First, Great Frigatebirds may use physical cues to locate areas of available prey. Potential prey are known to congregate at upwellings and around eddies (Tew Kai *et al.* 2009). Tagged birds
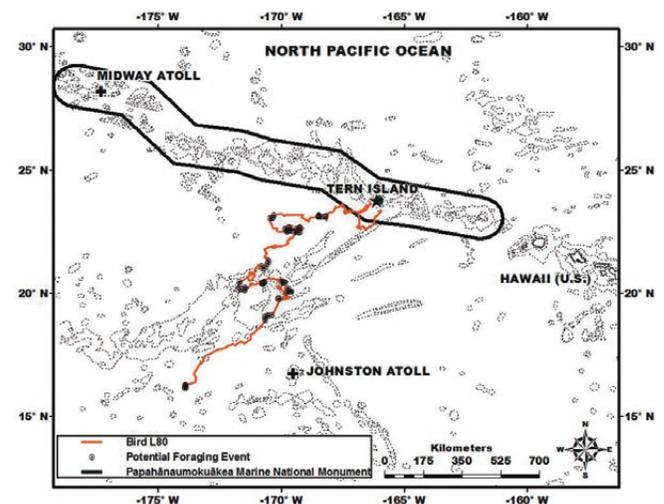

Fig. 3. Foraging tracks of L80 from Tern Island. The second trip was transmitted for 16 days until the transmitter battery expired. Black circles within track indicate slower flight periods thought to correspond to foraging events. Dotted lines delineate bathymetry.

traveled along the edges of shallow areas to the west (L82 and L83; Fig. 2) and to the southwest (L80; Fig. 3) of Tern Island, and one bird (L77) visited an area containing small seamounts to the north of Tern Island (4 500 m approximate depth; Fig. 2). Those areas may exhibit some upwelling activity. In the ocean surrounding the NWHI, northeasterly trade winds, in combination with the Hawaiian Lee Current and the North Hawaiian Ridge Current, influence water movement and nutrient exchange (Calil *et al.* 2008), creating potentially important areas of local prey aggregation. Notably, however, strong currents occur in an area 500 km southeast of Tern Island, and to a lesser extent 300 km to the northeast (Calil *et al.* 2008; Yoshida *et al.* 2010)—areas to which our tagged Great Frigatebirds did not travel (Fig. 2).

Second, frigatebirds are reported to associate with predators such as dolphins (Au & Pitman 1986) and tuna (Weimerskirch *et al.* 2004) that drive schools of fish to the surface. These subsurface predators are found in pelagic waters throughout the Pacific Ocean (Scott & Cattanach 1998; Bertrand *et al.* 2002), and Great Frigatebirds may travel to deeper waters on both sides of the Monument's boundaries in search of feeding opportunities associated with them. Indeed, most of the potential foraging events we identified occurred over deeper waters (4 500–5 100 m) where chlorophyll levels were low (0.35 mg/m^2; NOAA CoastWatch Program, NASA Goddard Space Flight Center & GeoEye, accessed 23 January 2011; http://las.pfeg.noaa.gov/oceanWatch/oceanwatch.php#). In those situations, there was an absence of upwelling or other obvious physical features that could aid frigatebirds in finding food.

Third, some of the frigatebirds' preferred prey exhibit high temporal and spatial variability. Important prey include flying fish and squid, which are consumed throughout the year (Harrison *et al.* 1983; Metz & Schreiber 2002; M.E. Gilmour and D.C. Dearborn, pers. obs.), but other prey such as scad (Carangidae) and halfbeaks (Hemiramphidae) appear to be locally and seasonally important (Harrison *et al.* 1983). Changes in sea temperatures and productivity affect the movements of adult and juvenile fish and squid (Pierce *et al.* 2008), potentially shifting foraging areas of Great Frigatebirds throughout the breeding season.

In our study, all tagged birds were feeding chicks of similar age (4–12 days old) but foraged in very different areas surrounding French Frigate Shoals. Birds traveled 74–732 km on foraging trips lasting one to three days (Table 1). None of the six birds returned to the same area on the second of two foraging trips, and four birds made consecutive trips that were essentially in opposite directions (Fig. 2). Additionally, although transit rates from Tern Island to each bird's first potential foraging event (8.9–16.6 km/h) were similar to the return transit rates (8.9–17.4 km/h; Table 3), there was variation among birds in both transit rates and linearity of flight paths on both the outbound and return portions of foraging trips. For example, Great Frigatebirds exhibited both looping and straight courses (Fig. 2) while flying at various transit rates (Table 1). A combination of slower transit rates and looping courses suggests a bird continuously searching for prey, whereas faster transit rates coupled with straight tracks may indicate a bird quickly flying to known feeding areas. Experience in both breeding and local foraging likely varied among our tracked Great Frigatebirds. Foraging strategies incorporating experience have been demonstrated in northern seabirds such as Black-legged Kittiwakes *Rissa tridactyla* (Irons 1998) and Thick-billed Murres *Uria lomvia* (Woo *et al.* 2008).

Weimerskirch (2007) concluded that looping foraging courses are more common in tropical seabirds than in seabirds foraging in temperate or polar regions, and our tracked Great Frigatebird movements contrast with tracking studies that found seabirds flying directly to foraging grounds (Freeman *et al.* 2010) and/or making straight-line return trips (Pettex *et al.* 2010). Tropical seabirds may use varying foraging strategies because productive foraging areas in subtropical, pelagic waters are patchy (Longhurst & Pauly 1987). In the absence of any one especially productive foraging area, Great Frigatebird parents appear to explore a variety of areas around Tern Island and the Monument.

We identified several potential foraging events at night (not depicted in figures). While Weimerskirch *et al.* (2010) also observed a larger number of periods of reduced flight at night than during the daytime, Weimerskirch *et al.* (2004) used altimeter data to

TABLE 3
Time spent foraging and characteristics of outbound and return flights
of six Great Frigatebirds during early chick-rearing at Tern Island[a]

Individual	Outbound distance to first foraging event (km)	Time outbound (h)	Transit rate (km/h)	Time spent foraging (h)	Return distance from last foraging event (km)	Time inbound (h)	Transit rate (km/h)
L77	149.6	14	10.7	3	59.5	4	14.9
	213.4	18	11.9	2	313.6	18	17.4
L78	116.0	13	8.9	3	32.3	3	10.8
L79	53.2	4	13.3	3	240.4	23	10.5
L80	18.4	2	9.2	6	374.9	42	8.9
L82	315.3	19	16.6	3	185.1	18	10.3
	319.9	27	11.9	3	191.6	18	10.7
L83	243.0	18	13.5	2	251.2	18	14.0

[a]   Twenty-eight foraging events were inferred among all tagged birds, but only two birds (L77 and L82) exhibited likely foraging events during both tracked foraging trips. Because L80 did not return to Tern Island during the second foraging trip, only the first foraging trip is included in the table.

show that frigatebirds do not approach the surface after dark and concluded that frigatebirds do not feed at night. It is possible that frigatebirds do not feed at night for lack of visibility, although we tracked birds during all parts of the lunar cycle (new, half, and full moon) and observed looping tracks and reduced transit rates (suggesting feeding) during each lunar phase, as well as during the day. Additionally, birds flew within the colony on moonlit nights, suggesting that there is enough light for them to see. It is possible that, during nights with sufficient moonlight, frigatebirds forage on prey such as nocturnal, vertically migrating squid. Diet alone cannot resolve the question—Black-footed and Laysan albatrosses from Tern Island are thought to scavenge dead squid from the sea surface during the day (Fernández & Anderson 2000), and it is possible that Great Frigatebirds do the same.

CONCLUSION

Papahānaumokuākea is a protected area for many endemic and migratory terrestrial and marine species. The protection and preservation of the NWHI provides habitat for many species that use the land and waters within the Monument for breeding. However, because species such as Great Frigatebirds and other pelagic foragers (e.g. Black-footed and Laysan albatrosses, Kappes *et al.* 2010; Red-footed Boobies *Sula sula*, Young *et al.* 2010) travel long distances to feed, the Monument only partially protects their food resources. Knowledge of large-scale movements, feeding areas and wintering areas are essential for developing management plans and protected areas that safeguard the resources needed by these species.

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