

Habitat Affinities and At-Sea Ranging Behaviors among Main Hawaiian Island Seabirds: Breeding Seabird Telemetry, 2013–2016



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LANGUAGE NOTES

We have incorporated the Hawaiian language spellings of place names, including the use of the ‘okina and kahako, in the text, figure and table captions, and tables in this report. However, software limitations did not allow for inclusion of these diacritical markings in some figure labels.

ABOUT THE COVER

Cover photo: Red-tailed Tropicbird (Koa‘e‘ula, *Phaethon rubricauda*) off Mōkōlea Point, Kīlauea Point National Wildlife Refuge, Kaua‘i, in May 2016. Courtesy of Jonathan Felis (USGS).

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List of Abbreviations and Acronyms

BOEM	Bureau of Ocean Energy Management
BRBO	Brown Booby
CI	Confidence Interval
DLNR	Department of Land and Natural Resources (Hawai’i)
DOFAW	Department of Forestry and Wildlife
g	Gram
GPS	Global Positioning System
h	Hour
ha	Hectare
HILT	Hawaiian Islands Land Trust
IUCN	International Union for Conservation of Nature
km	Kilometer
KPNWR	Kīlauea Point National Wildlife Refuge
LAAL	Laysan Albatross
m	Meter
mamsl	Meters above mean sea level
MDR	Maximum-depth Recorder
MHI	Main Hawaiian Islands
min	Minute
MNSRP	Maui Nui Seabird Recovery Project
nm	Nautical miles

NPTZ	North Pacific Transition Zone
NWR	National Wildlife Refuge
OCS	Outer Continental Shelf
OWEI	Offshore Wind Energy Infrastructure
RFBO	Red-footed Booby
RST	Residence in Space and Time
RSZ	Rotor Sweep Zone
RTTR	Red-tailed Tropicbird
s	Second
SD	Standard deviation
TDR	Temperature-Depth Recorder
USGS-WERC	U.S. Geological Survey, Western Ecological Research Center
WTSH	Wedge-tailed Shearwater

Abstract

Recent Hawai'i state clean energy policy mandates and federal interest in developing offshore renewable energy resources have prompted unsolicited lease requests for offshore wind energy infrastructure (OWEI) to be located in ocean waters off Hawai'i. This study describing at-sea ranging behaviors for five seabirds was intended to provide new information on Hawaiian breeding seabird distribution at sea, habitat utilization, and ranging behaviors within near-island waters and throughout outer continental shelf (OCS) waters surrounding the main Hawaiian Islands (MHI). We also estimate the percentage of time the five study species spent flying at altitudes equivalent to an expected rotor-swept-zone (RSZ; 30–194 m) for an offshore wind turbine and discuss potential collision risk from OWEI to the seabirds studied here. The MHI supports important seabird breeding populations and individual seabirds can now be equipped with a wide-variety of data loggers and location tracking devices that can provide complex, high-resolution information on movement patterns at sea. In this study, we used GPS loggers and temperature-depth-recorders (TDRs) to examine the at-sea distributions and ranging behaviors of five abundantly breeding species in the MHI: Red-tailed Tropicbird, Laysan Albatross, Wedge-tailed Shearwater, Brown Booby, and Red-footed Booby. We tracked these breeding seabirds from 14 different sites throughout the MHI; study colonies were located on the main islands of Maui, O'ahu, Kaua'i, and on associated islets. We used the Residence in Space and Time (RST) algorithm to classify behavior into resting, transiting, and searching/foraging (Torres et al. 2017). We used GPS altitude measurements to examine species-specific flight height and to estimate time spent flying in the RSZ. We mapped rediscritized tracking data for seabirds at each study colony according to behavioral class and trip type (when applicable) using kernel density estimates. During 2014–2016, we obtained GPS and TDR data from 59 and 34 Red-tailed Tropicbirds, respectively. Taken together, individuals revealed a bimodal (short- [~ 3 h, < 100 km range] and long- [> 3 d, > 800 km range]) trip foraging strategy. While ranging at sea, we estimated that Red-tailed Tropicbirds spend 70.6% (95% confidence interval [CI] 70.1–71.0%) of flight time in the RSZ. TDR data for tropicbirds was noisy and we could not reliably identify dives. During 2014 and 2016, we obtained GPS data from 35 Laysan Albatrosses nesting on Kaua'i and O'ahu. Individuals during the mid- to late-chick rearing period engaged in a bimodal short- (< 6 d, < 400 km range) and long- (> 6 d, $> 2,000$ km range) trip foraging strategy. While ranging at sea, we estimated that Laysan Albatrosses spend 2.57% (95% CI 2.50–2.64%) of flight time in the RSZ. During 2013–2015, we obtained GPS and TDR data from 313 and 55 Wedge-tailed Shearwaters, respectively. Considering all the data together, individuals revealed a multi-modal trip duration foraging strategy consisting of intra-day (< 24 h, < 100 km range), short (< 4 d, ~ 200 km range), and long (> 4 d, ~ 100 – 400 km range) trips. While ranging at sea, we estimated that Wedge-tailed Shearwaters spend 5.20% (95% CI 5.13–5.27%) of flight time in the RSZ. Wedge-tailed Shearwaters dove to a mean (\pm SD) depth of 1.78 ± 1.35 m (median = 1.38 m); the deepest dive recorded was to 10.06 m. The mean dive duration for Wedge-tailed Shearwaters was 3.12 ± 3.44 s (median = 1.80 s). During 2014–2015, we obtained GPS and TDR data from 42 and 37 Brown Boobies, respectively. Almost all foraging trips (97%) were single-day trips and we did not detect any bimodality in the distribution of single-day trip durations. Brown Boobies foraged relatively close to their colony (< 60 km range) and focused their at-sea use in nearshore, coastal waters off Kaua'i and Ni'ihau. While foraging at sea, we estimated that Brown Boobies spend 3.41% (95% CI 3.16–3.67%) of flight time in the RSZ. Brown Boobies dove to a mean depth of 1.42 ± 0.75 m (median = 1.25 m); the deepest dive recorded was to 8.19 m. During 2014–2016, we obtained GPS and TDR data from 164 and 108 Red-footed Boobies, respectively. Considering all the data together, individuals revealed generally a bimodal foraging trip strategy (short-duration trips lasted < 12 hrs and long-duration trips lasted 12–24 h); 53 individuals performed longer multiday trips. Short trips were < 70 km in range and long trips were < 130 km in range; the less frequent multi-day trips ranged ~ 120 – 250 km from the colony. While ranging at sea, we estimated that Red-footed Boobies spend 2.74% (95% CI 2.63–2.84%) of flight time in the RSZ. Red-footed Boobies dove to a mean depth of 1.12 ± 0.53 m (median = 1.00 m); the deepest dive recorded was to 7.57 m. This collaborative telemetry project contributed new information about the distribution at sea and ranging behaviors among several abundant, breeding seabird species throughout the MHI. More

studies would be required to fully evaluate variability in the at-sea behaviors among MHI seabirds associated with inter-annual environmental variability. These and additional telemetry data are unique and useful for future marine spatial planning; telemetry data provide for a more comprehensive assessment of the vulnerability at-sea of Hawaiian seabirds to potential offshore ocean energy infrastructure. Users should be aware of the biases and limitations associated with these data and take an informed, precautionary approach when conducting analyses and drawing conclusions. Ultimately, species-specific and colony-specific data for MHI seabirds will support better evaluations of risk and options for mitigation strategies, allowing diverse populations that characterize Hawaiian seabird avifauna to co-exist with a changing ocean environment.

1 Introduction

Recent interest has increased related to developing sources of renewable energy to reduce dependence on oil. Some of those sources will include construction and maintenance of power generation infrastructure located within U.S. continental shelf waters, and potentially within deeper waters off the U.S. Pacific coast and beyond state waters (i.e., outside three nautical miles [nm]). As of January 2017, Hawai'i state clean energy policy mandates and federal interest in developing offshore renewable energy resources have prompted three unsolicited lease requests for offshore wind energy infrastructure (OWEI): AW Hawai'i Wind's O'ahu Northwest and South Projects and Progression Hawai'i Offshore Wind's South Coast of O'ahu Project. Each project proposes OWEI with a capacity to generate approximately 400 megawatts of renewable energy by installing about 50 floating, 8–10-megawatt wind turbines. On June 24, 2016, BOEM published a “Call for Information and Nominations” (Call) to seek additional nominations from companies interested in commercial wind energy leases within two Call areas offshore Hawaii that encompassed the areas proposed in the unsolicited lease requests. The most recent information on BOEM's activities in Hawaii can be found at <https://www.boem.gov/Hawaii/>. The industry's intent and capacity to develop these resources in the future highlights the need for additional ocean- and island-based environmental assessments to inform planning. This study describing at-sea ranging behaviors among seabirds is intended to provide new information on Hawaiian breeding seabird distribution at sea, habitat utilization, and ranging behaviors within near-island waters and throughout outer continental shelf (OCS) waters surrounding the main Hawaiian Islands (MHI). The MHI supports important seabird breeding populations, but comprehensive, vessel-based surveys (concentrated in August–November) are few (Winship et al. 2016) and until now, telemetry studies targeting seabirds nesting in the MHI were restricted to two species (Hawaiian Petrel, *Pterodroma sandwichensis*, 'Ua'u, J. Adams unpublished data; Laysan Albatross, *Phoebastria immutabilis*, Mōli, Young 2009).

Understanding seabird movements at sea is a complex problem because most seabirds tend to be far-ranging and cover long distances during foraging trips. Traditional methods quantifying distributions and abundances at sea among seabirds involve environmentally- and diurnally-constrained ship-, aircraft-, or land-based visual surveys. Since the late 1970s, technology-aided observations of seabirds have increased rapidly. Miniaturization and technological improvements now allow even the smallest seabirds (<200 g) to be tracked at sea (Adams et al. 2008, Soanes et al. 2015, Maxwell et al. 2016). Individual seabirds can now be equipped with a wide-range of data loggers and location tracking devices to provide much more detailed information not only on movement patterns, but also various environmental conditions that influence movements and habitat use (Wilson et al. 2002, Burger and Shaffer 2008). Telemetry allows unique insight into oceanographic features (e.g., fronts, shelves, seamounts, water masses, etc.) that seabirds utilize as well as various flight and foraging patterns (Baduini and Hyrenbach 2003, Burger and Shaffer 2008, Wakefield et al. 2009, Dean et al. 2012). Telemetry coupled with geographic information systems also allows for time-integrated spatial assessments of utilization by seabirds of designated marine zones (Adams et al. 2012, Maxwell et al. 2016, Louzao et al. 2012), areas associated with risks (e.g., by-catch; Guy et al. 2013), or areas proposed for offshore energy development (Soanes et al. 2013, Cleasby et al. 2015). In this study, we used a variety of bio-telemetry devices to examine the at-sea distributions and ranging behaviors for five species of seabirds breeding throughout the MHI: Red-tailed Tropicbird (*Phaethon rubricauda*), Laysan Albatross (*Phoebastria immutabilis*), Wedge-tailed Shearwater (*Ardenna pacifica*), Brown Booby (*Sula leucogaster*), and Red-footed Booby (*S. sula*).

Our study objectives were: (1) synthesize previously-existing bio-logging and other relevant data for the five study species, (2) conduct multi-species and multi-scale quantifications of at-sea habitat utilization, (3) evaluate at-sea ranging behaviors and flight heights in relation to potential OWEI, and (4) quantify and map species-specific and multi-species hotspot areas at sea off MHI. Data generated are intended to inform resource managers concerned with evaluation of proposed renewable energy sites and environmental review of specific renewable energy project proposals received by BOEM. In addition,

new data regarding colony-based seabird ranging distributions at sea throughout the MHI will enhance incipient efforts to apply predictive modeling for species distributions (Grecian et al. 2012, Czapanskiy et al. 2018a,b) and applied vulnerability evaluations for MHI seabirds that could overlap with offshore renewable energy infrastructure (Kelsey et al. 2018).

Herein, U.S. Geological Survey, Western Ecological Research Center (USGS-WERC) reports results from our four study objectives. This study entailed tracking and mapping species-specific distributions at sea from multiple breeding colony locations throughout the MHI. Fieldwork throughout the MHI would not have been possible without a strong network of collaborators that shared enthusiasm for contributing hard work to increase knowledge about the ranging behaviors of Hawaiian seabirds at sea. With support from USGS, Oikonos Ecosystem knowledge (Waimanalo, O'ahu), worked closely with Pacific Rim Conservation (Honolulu, O'ahu) to coordinate tracking of Wedge-tailed Shearwaters and Laysan Albatross at Ka'ena Point, O'ahu. Both groups have extensive local knowledge about seabirds in Hawai'i and were able to work successfully with the confidence and support of the State of Hawai'i Department of Land and Natural Resources-Division of Forestry and Wildlife (DLNR-DOFAW), Marine Corps at Marine Corps Base Hawai'i, and private land managers (Na 'Aina Kai, Kaua'i). Maui Nui Seabird Recovery Project (University of Hawai'i, Pacific Cooperative Studies Unit) personnel fulfilled a similar roll and greatly aided in the collection of Wedge-tailed Shearwater tracking data from Maui. Cooperation with Kilauea Point National Wildlife Refuge (KPNWR) staff enabled mutual programmatic benefits toward enhancing seabird conservation science at the refuge. The Hawai'i State DLNR-DOFAW seabird biologists and branch chiefs were also instrumental for achieving results and provided much useful information and oversight. Without the help of these groups and others (see Acknowledgments), we would have been less successful in achieving the results presented herein.

These data contribute to a growing amount of seabird telemetry data (mostly Laysan Albatross) from the northwestern Hawaiian Islands (Fernández and Andersen 2000, Fernández et al. 2001, Hyrenbach et al. 2002, Shaffer et al. 2005, Young et al. 2009, Gilmour et al. 2012, Hyrenbach et al. 2010, Kappas et al. 2010, Connors et al. 2015, Thorne et al. 2016) and provide more recent information regarding the variability in the distribution, habitats, and behaviors at sea among the seabird community that exists within the central and northeastern subtropical Pacific Ocean.

2 Methods

2.1 Study Sites and Species

We tracked breeding seabirds from 14 different sites throughout the MHI (Figure 1, Table 1). Specifically, this project focused on five species: Red-tailed Tropicbird, Laysan Albatross, Wedge-tailed Shearwater, Brown Booby, and Red-footed Booby (Table 1). Study colonies were located on the main islands of Maui, O'ahu, Kaua'i, and on associated islets (Figure 1).

2.1.1 Maui Nui

The islands of Maui, Lana'i, Kaho'olaw and Moloka'i together comprise Maui Nui. Important nesting colonies for Wedge-tailed Shearwater occur throughout coastal Maui Nui. Several offshore rocks have not been as well-surveyed, although some have habitat that supports Wedge-tailed Shearwaters and perhaps other cryptic nocturnal species (e.g., Bulwer's Petrel, *Bulweria bulwerii*, 'Ou). High-elevation (>2500 m) montane areas on Haleakala support relatively large remaining populations of Hawaiian Petrel. The presence of Newell's Shearwaters (*Puffinus newelli*, 'A'o) in remote cloud forests on Maui is not well known, but there is a well-documented colony on Lanai (VanZandt et al. 2014). We focused tagging efforts on Wedge-tailed Shearwaters at three sites on Maui: Hāwea Point, Ho'okipa, and Kama'ole.

Hāwea Point, Kapalua, Maui — Hāwea Point was gifted to the Maui Open Space Trust in 2004 and is managed as a conservation easement by the Hawaiian Islands Land Trust (HILT, Honolulu, O‘ahu). Located along the northwest coast of west Maui, this 0.8-ha colony is located on exposed coastal bluffs mostly vegetated with introduced kykuyu grass (*Pennisetum clandestinum*) and supports a growing population of about 400 nesting Wedge-tailed Shearwaters (HILT, unpublished data, <http://www.hilt.org/>; Figure 1 and Figure 2). The colony, adjacent to the Montage Kapalua Bay Resort, has public access. Preservation of this colony can be attributed to local resident, Isao Nakagawa, who provided stewardship. The Maui Nui Seabird Restoration Project (MNSRP, Makawao, HI) now works with HILT and Hawai‘i DLNR-DOFAW to monitor shearwaters here.

Ho‘okipa, Pā‘ia, Maui — The Ho‘okipa Wedge-tailed Shearwater colony (0.2 ha) is located on the north shore of Maui between Pā‘ia and Haiku, adjacent to the Hana Highway and Ho‘okipa Beach Park (Figure 1 and Figure 3). The surrounding lands are agricultural (formerly sugar cane) and the colony site, owned and managed by Maui Land and Pineapple Company, Inc. (MLandP, Maui), was actively grazed by cattle but was fenced in 2017 to protect it and native plant restoration efforts from grazing. The Ho‘okipa colony, which supports about 50 breeding pairs of Wedge-tailed Shearwaters (J. Penniman, unpublished data), is vegetated with introduced grasses and is located along a wind-swept bluff crest adjacent to the rocky shoreline. MNSRP now works with MLandP and Hawai‘i DLNR-DOFAW to monitor shearwaters here.

Kama‘ole III, Kīhei, Maui — This colony is located within a 2.4-ha County Beach Park located along South Kīhei Road between Kīhei and Wailea (Figure 1 and Figure 4). Approximately 50–100 breeding pairs of Wedge-tailed Shearwater nest in a scrubby area adjacent to a grass lawn area (J. Penniman, MNSRP unpublished data); the colony is publicly accessible and bisected by trails that access the coast. MNSRP now works with Hawai‘i DLNR-DOFAW to monitor shearwaters here.

2.1.2 O‘ahu

O‘ahu supports the largest number of breeding seabirds in the MHI (mostly Wedge-tailed Shearwaters throughout and Sooty Terns [*Onychoprion fuscatus*, ‘Ewa‘Ewa on Manana Islet); most seabirds are associated with several substantial colonies located on windward offshore islets (Harrison 1990, Pyle and Pyle 2017). In addition, Marine Corps Base Hawai‘i supports nesting Wedge-tailed Shearwaters and Red-footed Boobies and two sites (Ka‘ena Point and Kuaokala) support small populations of nesting Laysan Albatross (Young et al. 2009a).

Black Point, O‘ahu — Black Point is the site of the Freeman Seabird Reserve. In 2007, the Hawai‘i Audubon Society (Honolulu, O‘ahu) was gifted this 0.4-ha coastal property located on the southern coast of O‘ahu (Figure 1 and Figure 5). The colony is surrounded by suburban development and is the only suitable habitat for nesting shearwaters remaining on O‘ahu’s south shore. In 2014, this colony supported approximately 215 breeding pairs of Wedge-tailed Shearwaters (Hyrenbach and Johnson 2014). Annual monitoring of shearwaters here has been conducted since 2009 by Dr. David Hyrenbach, Professor of Oceanography, and students at Hawai‘i Pacific University (Hyrenbach and Johnson 2014).

Hālonā Point, Hawai‘i Kai, O‘ahu — This ~1.0-ha colony is located on the southeastern Ka‘iwi coast of O‘ahu and consists of a ~500-m length of steep and rocky slopes and coastal cliffs that are mostly barren (Figure 1 and Figure 6). The site is publicly-accessible and narrowly-constrained (~30 m) between the ocean and the Kalaniana‘ōle Highway. Approximately 45 pairs of Red-tailed Tropicbirds nested here in 2012; numbers of breeding tropicbirds have increased here since 2005 after initiating trapping targeting mongoose and feral cats near nesting sites (VanderWerf and Young 2014).

Ka‘ena Point Natural Area Reserve, O‘ahu — This Hawai‘i State Natural Area Reserve is located on the northwestern tip of O‘ahu (Figure 1 and Figure 7). The wind-swept coastal environment supports unique,

dry coastal shrublands and rare coastal plants, including three species of endangered plants (VanderWerf et al. 2014). Predator control initiated in 2000 and the installation of a predator-proof fence in 2011 has added substantial protection to the 20-ha portion of the reserve that supports nesting seabirds. The number of nesting Wedge-tailed Shearwaters increased from <20 pairs in 1993 to >5,000 pairs in 2013 (VanderWerf et al. 2014). During 2005–2008, O‘ahu supported ~365 Laysan Albatross (of which 47% are nesting adults), with ~50 nests at Ka‘ena Point (Young et al. 2009b).

Mokū‘auia Island, Lā‘ie, O‘ahu — One of five islets visible from Lā‘ie Point, Mokū‘auia (also known as Goat Island) is a small (3.1 ha), low (3 m), flat island that is included within the Hawai‘i State Seabird Sanctuary (Figure 1 and Figure 8). It is an important nesting site for Wedge-tailed Shearwaters and supported greater than 2,600 breeding pairs in 2012 (A. Marie, DLNR-DOFAW, unpublished data).

Marine Corps Base Hawai‘i, Kaneohe Bay, O‘ahu — The Marine Corps Base Hawai‘i supports approximately 800 nesting pairs of Red-footed Boobies at the Ulupa‘u Crater colony located at the northeastern tip of the Mokapu Peninsula (T. Russell, unpublished data, pers. comm. 5 January 2017; Figure 1 and Figure 9). The boobies here nest in introduced kiawe (*Prosopis pallida*) and haole koa (*Leucaena latisiliqua*) trees. A colony of approximately 700 breeding pairs of Wedge-tailed Shearwaters nest in two sub-colonies along the southeastern coastal strand of Marine Corps Base Hawai‘i (T. Russell, unpublished data, pers. comm. 5 January 2017). The vegetation is mostly native coastal strand consisting largely of Naupaka (*Scaevola taccada*), Akiaki Grass (*Sporobolus virginicus*), and Akulikuli (*Sesuvium portulacastrum*).

2.1.3 Kaua‘i and Ni‘ihau

Kaua‘i and Ni‘ihau are the oldest and north-westernmost islands in the MHI. Important seabird colonies include KPNWR and two small exposed, crater-rim islands off Ni‘ihau: Lehua and Ka‘ula. Kaua‘i’s north shore west of Hanalei is relatively unpopulated by humans and steep, wet, remote mountainous areas support the majority of the remaining Newell’s Shearwaters in the MHI and many of the remaining Hawaiian Petrels. Like most islands and some offshore islets in the MHI, seabird populations on Kaua‘i are threatened by introduced species, especially mammals (cats, pigs, rats, and dogs), and human disturbance (e.g., urban development and infrastructure). The offshore islets and some of the upland mountain areas are managed by the Hawai‘i State DLNR-DOFAW; KPNWR is a Federal Wildlife Refuge and remaining colony areas are occupied and used by the military (e.g., Pacific Missile Range Facility and Ka‘ula) or managed by private land owners (e.g., Waipake and Na ‘Aina Kai).

Kīlauea Point National Wildlife Refuge, Kīlauea, Kaua‘i — This refuge is located on the north coast of Kaua‘i (Figure 1 and Figure 10). Breeding seabird species tracked from this site included Red-tailed Tropicbird, Wedge-tailed Shearwater, and Red-footed Booby. Wedge-tailed Shearwaters are easily accessible at three sub-colonies (Mōli Hill, Crater Hill B, and Mōkōlea Point) and are the most abundant breeding seabird at the refuge (8,000–15,000 breeding pairs; USFWS 2016). At KPNWR, Red-tailed Tropicbirds are most-concentrated at Mōkōlea Point, where birds nest in the shade beneath larger invasive shrubs and trees (*Casuarina sp.* and *Leucaena latisiliqua*), but also in dense, native naupaka kai (*Scaevola taccada*) and on some cliff ledges. Breeding population estimates at this site range from 150–250 breeding pairs (USFWS 2016). Red-footed Boobies nest within the Crater Hill A colony, and there is a second inaccessible smaller colony located approximately midway between Crater Hill B and Mōkōlea Point; the total refuge population estimate is ~1,800 breeding pairs (USFWS 2016). Additional species found breeding at Kīlauea Point NWR include Laysan Albatross (~170 pairs), and small numbers of White-tailed Tropicbird (*Phaethon lepturus*, Koa‘e‘kea; <10 pairs) and Newell’s Shearwater (~11 pairs; USFWS 2016).

Na ‘Aina Kai, Kīlauea, Kaua‘i — Located on the northeastern shore of Kaua‘i, this privately owned botanical garden supports a small colony of ~60 breeding Laysan Albatrosses (Figure 1 and Figure 10).

The albatross here nest on the coastal bluffs exposed to wind and amidst introduced ironwood trees. Na ‘Aina Kai botanical garden staff work with local citizens in the Kaua‘i Albatross Network and the Hawai‘i DLNR-DOFAW to monitor breeding, conduct banding, and record sightings of individuals.

Waipake, Kilauea, Kaua‘i — Located on the northeastern shore of Kaua‘i, this privately-owned land supports a small colony of ~120 breeding Laysan Albatrosses (Kim Rogers, pers. comm.; Figure 1 and Figure 10). The albatross here nest in several dispersed aggregations on the coastal bluffs exposed to wind and amidst introduced ironwood trees. Waipake land managers work with the Kaua‘i Albatross Network and the Hawai‘i DLNR-DOFAW to monitor breeding and record sightings of individuals.

Queen’s Bath, Princeville, Kaua‘i— This small Wedge-tailed Shearwater colony is located along the north shore of Kaua‘i adjacent to the community of Princeville and supports approximately 55–200 breeding pairs of Wedge-tailed Shearwater (Hebshi 2008; Figure 1 and Figure 11). The small colony is well-vegetated, exposed to the tradewinds, but also is in close proximity to houses, people, dogs, and cats. The Hawai‘i State DLNR-DOFAW works with local land managers to monitor breeding numbers and maintain conservation actions here.

Lāwai Kai, Lāwai, Kaua‘i — This small colony (0.6 ha) of approximately 60 pairs of Wedge-tailed Shearwaters (K. Dickson, pers. comm., 4 January 2017) is located along the south shore of Kaua‘i on the exposed coastal bluff just east of the National Tropical Botanical Garden where the Lāwai Valley meets the ocean at Lāwai Bay (Figure 1 and Figure 12).

Lehua Islet — Lehua Islet is a large (115 ha), high (215 m) island located 1.2 km north of Ni‘ihau and 31 km west of Kaua‘i (Figure 1 and Figure 13). Managed by DLNR-DOFAW as a Hawai‘i State Wildlife Sanctuary, the island is uninhabited and closed to public access. Breeding seabird species tracked from this site included Brown Booby, Red-footed Booby, Red-tailed Tropicbird, and Wedge-tailed Shearwater. Brown Booby nests are concentrated on the summit ridge of Lehua Islet; however, nests can be found throughout the island. Nests are built on the ground on ledges or open ground. The most recent population estimate identified approximately 500 breeding pairs (VanderWerf et al. 2007). Red-footed Boobies primarily nest in shrubs and can be found wherever this vegetation type exists on Lehua Islet. Recent population estimates range from 1,200–1,800 breeding pairs (VanderWerf et al. 2007). Red-tailed Tropicbird nests are patchily distributed across the island at all elevations, particularly where small-scale topographic features create bedrock alcoves and overhanging ledges or where dense vegetation creates adequate shade. Population estimates range from 150–250 breeding pairs (Harrison 1990; VanderWerf et al. 2007). Wedge-tailed Shearwaters utilize similar, but typically smaller, alcoves and crevices, as well as burrows where vegetated soil exists at lower elevations on the island. Population estimates range from 500–23,000 breeding pairs (Harrison 1990, VanderWerf et al. 2007). Additional species found breeding at this site include Bulwer’s Petrel, Black Noddy (*Anous minutus*, Noio), Black-footed Albatross (*Phoebastria nigripes*, Ka‘upu), and Laysan Albatross.

2.2 Telemetry and Sensors

2.2.1 Global Positioning System Loggers

We deployed two types of Global Positioning System (GPS) loggers on seabirds: modified i-gotU GT-120 (Mobile Action Technologies, New Taipei City, Taiwan) and e-obs GPS tags (Bird Solar 30 g, Bird Solar 15 g, and Bird Battery 30 g; e-obs GmbH, Gruenwald, Germany). The i-gotU GT-120 GPS tags are an archival unit, requiring recapture of the tagged bird to recover the tag and download data. Because these are consumer-electronic products and not specifically designed for wildlife telemetry, we stripped GT-120 loggers from their plastic housings and sealed them within 2:1 low-shrink-temperature, polyolefin heat-shrink tubing to create a lightweight, waterproof housing (AMS-DTL-23053/ 5-310,

BuyHeatShrink.com, Deerfield Beach, Florida). With the stock 380 mAh battery, the repackaged logger weighed 17 g. The e-obs GPS tags utilized a base station to acquire and archive tracking data, thus absolving the need to recover the GPS tag to retrieve data. The e-obs Bird Solar (30 g and 15 g) tags included a solar panel to recharge the tag battery while deployed, whereas the e-obs Bird Battery 30 g tag relied on an internal battery for power supply. All e-obs GPS tags included onboard tri-axial accelerometers.

2.2.2 Temperature-Depth Recorders

We deployed miniature Temperature-Depth Recorders (TDRs; Cefas G5, 3 g, Cefas Technology Ltd., Lowestoft, UK) to measure dive depths and wet/dry condition (depending on TDR model year). TDRs have a saltwater switch that, when immersed, initiates a FastLog mode to record pressure and temperature at high resolution. The FastLog mode can be programmed to record only if the pressure is greater than a user-defined threshold (e.g., dive depth). In addition, some units have a wet/dry setting to record the start and end times of wet periods (bouts of time on the water, regardless of dive behavior). Cefas G5 TDRs are archival units and require recapture of tagged birds to recover the tag and download data.

2.2.3 Capture Methods, Tag Attachment, Tag Settings, and Ancillary Data

We captured birds at marked nests containing eggs (Brown Booby, Red-footed Booby) or chicks (all species). Nest ownership/parent identity was unambiguous for tropicbirds and boobies, but Wedge-tailed Shearwater burrow attendance was monitored to be certain that target adults were the true parents of chicks in nest burrows. Similarly, Laysan Albatrosses were only tagged if they were observed feeding a chick or were previously banded and known to be the true parent of a chick from prior monitoring. Red-tailed Tropicbirds, Laysan Albatrosses, Wedge-tailed Shearwaters, and Red-footed Boobies were captured by hand. Brown Boobies were captured using a telescoping noose pole (10 m) to prevent birds from flushing during approach.

Non-banded birds were fitted with an appropriately sized hard-metal leg-band for identification (USGS Bird Banding Lab). Morphometric measurements and blood/feather samples (for DNA-sexing and stable isotope analysis) were collected from most individuals at deployment (e-obs GPS tags) or recapture for tag recovery (i-gotU GT-120 GPS and TDR archival tags). Because tropical seabirds are relatively asynchronous in nesting phenology, we recorded chick stages (e.g., relative chick age) based on feather development and general size for boobies and tropicbirds (B. Flint, USFWS, pers. comm., 10 June 2014; Fleet 1974, Nelson 1978). Additionally, morphometric measurements were collected on Wedge-tailed Shearwater chicks. Laysan Albatross chick hatch-dates and ages were known from regular monitoring throughout the breeding season. Tagged birds were returned to their burrows within 10–20 min of initial capture. Starting 1–4 days after deployment of i-gotU GT-120 GPS and/or TDR tags, study nests were monitored approximately daily or nightly (depending on species behavior) for up to 2 weeks to recapture birds and recover tags; recovery effort varied among sites and deployment sessions.

For Red-tailed Tropicbirds (2014–2016), Wedge-tailed Shearwaters (2013–2015), Brown Boobies (2014–2015), and Red-footed Boobies (2013–2015), i-gotU GT-120s were used for all GPS tracking (Figure 14, Figure 15). For tropicbirds and boobies, tags were attached to the top (Red-tailed Tropicbirds 2016) or underside (all other deployments) of the central 2–4 retrices using tape (Tesa® 4651, Norderstedt, Germany; Figure 15). Tail-mounted tags were placed as close to the body as possible, near the insertion of tail feathers into the body, and secured so as not to interfere with access to the preening gland (Figure 15). For Wedge-tailed Shearwaters, i-gotU GPS tags were attached to several central back feathers using 4, 1-cm wide strips of Tesa Tape (Figure 15). The i-gotU GPS tags were programmed to collect location data every 2–3 min continuously for a maximum expected battery life of approximately 10–14 days.

We tracked Laysan Albatrosses (all years) and Red-footed Boobies (2016) with e-obs GPS/accelerometer tags (Figure 16). For Laysan Albatrosses in 2014, e-obs Bird Battery 30 g tags were attached to several back feathers using tape (Tesa® 4651, Norderstedt, Germany). In 2016, we taped a plastic plate to albatross back feathers to which we attached e-obs Bird Solar 30 g tags with zip ties at the tag's harness attachment points (Figure 16). For Red-footed Boobies in 2016, we used a similar plastic template and zip-tie attachment technique to attach e-obs Bird Solar 15 g GPS tags to the top of booby tail feathers (Figure 16). Tail-mounted tags were placed as close to the body as possible, near the insertion of tail feathers into the body and arranged so as not to interfere with the preening gland. E-obs GPS/accelerometer tags have four relevant settings: GPS interval, acceleration interval, acceleration frequency, and acceleration burst duration. In 2014, Laysan Albatross tags were programmed to collect locations every 15 min with a 4.8-s burst of 10.54-hz acceleration data every 2 min. The Laysan Albatross tags in 2016 were programmed with a 5-min GPS interval (15 min when battery level was low) and a 15-min acceleration interval sampling at 20 hz for 4.8 s. In 2016, Red-footed Booby tags were programmed to collect locations every 2 min (10 min when battery levels low) along with a 4.8-s burst of 20-hz acceleration every 30 s. In addition, Red-footed Booby e-obs tag programming was remotely updated 2–3 days after initial deployment to include a burst of five GPS measurements (one per second) at every 2-min sampling interval when battery level was high. These burst data are excluded from analysis here but can be used to infer near-instantaneous speed and flight direction.

TDRs were deployed on a subset of GPS-tagged birds (Red-tailed Tropicbirds, Brown Boobies, Red-footed Boobies) or on additional non-GPS-tagged birds (Wedge-tailed Shearwaters; Figure 17). Wedge-tailed Shearwater mass did not meet maximum 3% body-mass equivalent for devices recommended for procellariiform seabirds (Phillips et al. 2003) to carry both devices simultaneously. TDRs were taped to the metal leg band with the pressure transducer and saltwater switch oriented towards the bird's body to avoid potential sensor damage from the bird walking or sitting on the ground. TDRs were programmed to record depth (12-bit resolution, ± 1 m) at a background rate of 1 min, at 10 hz when wet, and, for some tags, below a pre-set threshold pressure equivalent to a depth of 1 m.

2.3 Data Analysis

2.3.1 Data Entry and Tracking Database

Raw data files from archival tags (i-gotU GT-120 GPS and Cefas G5 TDR) from successfully recovered birds were downloaded and archived. Raw data files from e-obs GPS tags were downloaded from base stations every 1–2 weeks. Deployment and recovery times, and ancillary data, were entered into a custom MS ACCESS database in a standardized format.

2.3.2 GPS Data Processing and Foraging Trip Identification

Downloaded GPS tag data were clipped to deployment and recovery times and then filtered using a speed-distance-angle filter to remove erroneous locations, which were few (Freitas et al. 2008; see Table 2 for species- and tag-specific settings). Next, individual foraging trips were defined as a sequence of consecutive locations of a tagged individual located outside a fixed radius around its nesting colony or nest, beginning with the first location after the individual left the radius and ending with the last location before the individual returned (1.0–1.5 km, Table 2). For any unique trips outside this radius, time-limit thresholds were set to determine trip start- and end-times and locations (Table 2). If the time between the last on-colony location and first at-sea location was less than Threshold A, then the first trip location/time was set to the last on-colony location (i.e., the nest). If the time difference between the last on-colony and first at-sea locations was greater than Threshold A but less than Threshold B, then the first trip location was set to the colony/nest location and trip start time was interpolated using a maximum velocity estimate (Table 2). If the time between the last on-colony and first at-sea locations was greater than Threshold B,

then the trip start time, as well as the overall trip, was marked as incomplete. The same approach was used for trip end locations/times. The threshold values used in the process were species/tag specific and are summarized in Table 2.

Individual trips were visually screened to flag trips that were potentially problematic for analyses. This included identifying trips where GPS tag functionality resulted in gaps or missing data and determining which trip parameters could be quantified. For example, if a gap in GPS coverage occurred in the middle of a trip but the start and end were well documented, then trip duration, but not total distance traveled, could be quantified for that trip. In addition, short-duration trips were flagged for removal if they were known to be caused by disturbance (e.g., flushing a bird during capture activities). Trips with durations <30 min were excluded from summary analyses. All subsequent analyses were conducted on location data from foraging trips and on-colony time was excluded from analyses.

Before summarizing trips, we rediscritized the sequence of GPS track points for each trip. Rediscrization used linear interpolation methods from the R package *adehabitatLT* (Calenge 2015). We chose the longest sampling interval per species for rediscrization: 2 min for Brown Booby and Red-footed Booby, 3 min for Red-tailed Tropicbird and Wedge-tailed Shearwater, and 15 min for Laysan Albatross. For some species, we categorized trips into different trip types (e.g., short trips and long trips) because trip duration distributions were multi-modal. In addition, we incorporated phenology (e.g., incubation, early-chick-rearing, late-chick-rearing) when appropriate. Summary statistics of foraging trip measurements (e.g., trip duration, distance traveled, and maximum range) were calculated overall, and also by trip type, island, colony, and year, depending on the species. Distance traveled and maximum range from colony were calculated for each foraging trip using the R package *geoSphere* (Hijmans et al. 2016). For each species, we also examined trip start and end times at the trip type level.

2.3.3 GPS Behavioral Classification and Flight Height

We annotated the rediscritized location points for each trip with behavioral state and day phase. We used the Residence in Space and Time (RST) algorithm to classify behavior into resting, transiting, and searching/foraging (Torres et al. 2017). This algorithm calculates a normalized residual between time- and space-intensive behaviors. Time-intensive behaviors take a long time without covering much distance (i.e., resting) and space-intensive behaviors cover a lot of space/area (not distance) in a short period of time (i.e., searching, which involves more “turning”); transiting behavior (fast, straight lines) have a residual closer to zero. Analogous to first-passage time (Fauchald and Tveraa 2003), this requires a biologically-significant radius to analyze at a given sampling interval. Torres et al. (2017) recommended a radius equal to half the product of the mean transit speed and the sampling interval. We calculated mean transit speed as the mean of all ground speeds greater than 1 m s^{-1} and having tortuosity less than the median tortuosity (where tortuosity is defined as ratio of distance traveled ± 5 locations, to net distance traveled between first and last locations of the ± 5 location window). Using Red-tailed Tropicbirds as an example, we calculated a mean transit speed of 8.6 m s^{-1} . At a sampling rate of 180 s, the resulting RST radius was 774 m. Upon initial inspection, the results of RST behavioral classification appeared to classify some birds obviously floating on the water as searching/foraging behavior; therefore, we manually set all locations with a speed value $< 1 \text{ m s}^{-1}$ to resting behavior (Figure 18, Figure 19). This speed mode ($< 1 \text{ m s}^{-1}$) was apparent in the distribution of speed values for all species, corresponded spatially to what were obvious bouts of floating on the water, and is consistent with other seabird tracking results (Shamoun-Baranes et al. 2011, Ross-Smith et al. 2016). Day phase was determined by the angle of the sun above the horizon as calculated using the R package *oce* (Kelley and Richards 2017). We used astronomical definitions of day, night, and twilight, where sun angles greater than zero degrees were day, less than -18 degrees were night, and in between were twilight. Behavioral information was summarized for each species at the trip type level by pooling all locations for all birds/trips. We calculated summary statistics for the proportion of time spent in different behavior classes during the three day phases (daytime, night, and twilight), and also examined hourly patterns in behavior across the 24-hr day.

We used GPS altitude measurements to examine species-specific flight-height and estimate the percentage of time spent flying at altitudes equivalent to an expected rotor-swept-zone (RSZ; 30–194 m) for an offshore wind turbine. Altitude values derived from GPS are thought to be of lower accuracy than the horizontal positions recorded by these units, and there is often no altitude accuracy or error estimate provided with individual measurements (dilution of precision, DOP) or for devices in general (although this is changing with newer tag development). Investigators have employed a variety of methods to account for measurement error, including the use of co-deployed GPS and altimetry (currently limited to larger bird species; Garthe et al. 2014; Cleasby et al. 2015) or development of more computationally intensive state-space models (with or without DOP; Péron et al. 2017, Ross-Smith et al. 2016) that isolate GPS altitude measurement error from actual altitudinal variance and then correct flight altitudes by that measurement error in a modeling framework. In all cases, flight altitudes are categorized using some form of behavioral classification based on GPS-derived horizontal movement information and occasionally additional activity loggers (e.g., immersion loggers, accelerometry).

We used altitude measurements from the raw GPS tracking data and made a simple behavioral classification based on speed to identify resting on the water ($<1 \text{ m s}^{-1}$) from flight behavior ($\geq 1 \text{ m s}^{-1}$; Shamoun-Baranes et al. 2011, Ross-Smith et al. 2016). We retained altitude-behavior pairings with time differences less than the nominal resolution of GPS sampling for any given tag/species combination. Only data over the ocean and beyond 500 m from land were considered, as some species fly to great heights when approaching shore to avoid klepto-parasitism by Great Frigatebirds (*Fregata minor*, Iwa) and/or to access higher elevation colonies. The WGS84 GPS altitude values were adjusted to the 2008 Earth Gravitational Model (Pavlis et al. 2012) geoid to convert them to meters above mean sea level (mamsl). We assumed that all altitude measurements in the resting behavioral state ($<1 \text{ m s}^{-1}$) represented mean sea level (0 mamsl) and that all other altitude measurements represented flight behavior. We simulated variations in the proportion of time spent flying in the RSZ while accounting for measurement (GPS altitude accuracy) and environmental (tide/wave effects on sea surface altitude) variability by randomly resampling errors from resting altitudes and subtracting from randomly resampled flight altitudes; resampling was repeated for 1,000 bootstrap iterations to calculate a mean and 95% confidence interval (CI) estimate of time spent flying in the RSZ.

2.3.4 GPS Spatial Distributions

We mapped discretized tracking data for each colony by behavioral class and trip type (when applicable) using kernel density estimates in the R package *adehabitatHR* (Calenge 2015). We combined the searching and resting behavioral types for mapping because preliminary examination showed that mapped distributions were very similar for these behaviors. In addition, we mapped distributions of tracking data within 100 km of the MHI coastline for all trip types combined. Data were projected into Hawai'i Albers Equal Area Conic projection (North American 1983 Datum) and kernel density distributions were calculated using a bandwidth (or smoothing factor, h) of 1.5% of the mean of the X and Y spatial extents of the data being mapped, which produced the best visualization at any scale. Cell size was calculated similarly as 0.4% the mean spatial extent. Bandwidth values (in km) are reported with figure captions for species-specific maps.

2.3.5 TDR Data Processing

The text file output from TDRs contained tag metadata and up to three types of additional data: background low-frequency sampling, FastLog events and wet/dry status. To systematically identify and verify dives, we used the FastLog event data and wrote a custom script that used functions in the R package *diveMove* (Luque and Fried 2011). Although TDR depth resolution (precision) was estimated by Cefas Technology, Ltd. to be better than $\pm 0.15 \text{ m}$, we determined that surface calibration was necessary because the “surface” indicated by the FastLog data could be $>1.0 \text{ m}$ different than zero. We accounted for surface discrepancies using a fixed offset equal to the minimum depth per FastLog (e.g., if the

shallowest point was recorded at -2.4 m [i.e., above the ocean's surface], we added 2.4 m to all points; see Figure 20). This correction set the dive record to a surface of 0 m. Even with high-frequency (10 Hz), post-corrected FastLog data, some apparent time-at-depth patterns could not confidently be classified as dives because pressure variability created some short, noisy patterns that may have resulted from paddling, wave-slap or other submerged movements. Therefore, we defined dives as consecutive points deeper than a minimum post-corrected surface threshold of 0.1-m depth, with a post-corrected dive threshold of 0.5 m having minimum duration of 0.5 s. We visualized our results using plots of the dive itself and the entire FastLog for context (Figure 20).

The automated dive identification script has a false-positive rate that varied by species. To ensure we only analyzed dive profiles that could reasonably be interpreted as dives, we wrote a custom QAQC tool using the R package *shiny* (Chang et al. 2016). In addition to validating dives, the QAQC tool allowed users to flag dives as questionable and record two types of errors. Split errors are caused when device noise records a point shallower than our 0.1-m threshold, splitting a dive in two. Plunge errors are caused when the sudden spike in pressure from impact is recorded as an artificially deep point, skewing the maximum depth. Dives with these errors were manually edited where possible. Three users independently verified all dive profiles, assigning a score of 2 (valid dive), 1 (questionable dive), or 0 (invalid dive). Only dives with a mean score of at least 1.5 were retained for analysis (i.e. score profiles of 2+2+2 or 2+2+1). Duration and maximum depth were calculated for valid dives, and we examined daily dive patterns for all dives pooled. For species on which GPS and TDR tags were co-deployed (Red-footed and Brown Boobies), we joined dives to the temporally nearest tracking point and evaluated the rate of diving in different behavioral states (see 2.3.2 GPS Data Processing) and per hour at sea on foraging trips. For Wedge-tailed Shearwaters (TDR only), we examined dive rates per hour of daylight for each individual deployment because this species is exclusively at sea during daylight hours (06:00–20:00 local time) while chick-rearing. We did not incorporate dives conducted at night into this calculation because, without co-deployed GPS tracking data, we could not confirm that a TDR-equipped bird did not revisit the colony on any given night between deployment and recovery.

2.4 Tables and Figures

Table 1. Summary of MHI seabird telemetry for all species, site, years, and tag types, 2013–2016. Number of birds tagged indicates all individuals with one or more sensor types attached in a single deployment. Data recovered reflects the number of individuals recovered with at least one functional sensor type.

Species	Islands (Sites, if > 1)	Years	Sensors	Birds tagged	Data recovered
Red-tailed Tropicbird	O'ahu, Kaua'i (2)	2014-2016	GPS, TDR	103	67
Laysan Albatross	O'ahu, Kaua'i (2)	2014, 2016	GPS, ACC	36	35
Wedge-tailed Shearwater	Maui (3), O'ahu (4), Kaua'i (4)	2013-2015	GPS, TDR	734	368
Brown Booby	Kaua'i	2014-2015	GPS, TDR	56	43
Red-footed Booby	O'ahu, Kaua'i (2)	2013-2016	GPS, TDR, ACC	199	172

Table 2. Speed-distance-angle filter and trip-breaker parameters used for each species and GPS tag type in MHI, 2013–2016. Red-footed Boobies (RFBO) and Laysan Albatrosses (LAAL) tagged in 2016 with e-obs tags were speed filtered, but not distance/angle filtered. “Dist Limit 1” and “Dist Limit 2” values for Laysan Albatross were used for 2014 data only.

Species	Tag Type	Max Vel (m s ⁻¹)	Angle 1 (deg)	Angle 2 (deg)	Dist Limit 1 (m)	Dist Limit 2 (m)	Colony Radius (km)	Threshold A Depart/Return (min)	Threshold B Depart (min)	Threshold B Return (min)
RTTR	i-GotU	30	15	25	250	1,000	1.5	10	30	30
LAAL	e-obs	40	15	25	2,500	5,000	1.5	10	120	360
WTSH	i-GotU	30	15	25	250	500	1.0	10	120	360
BRBO	i-GotU	30	15	25	250	1,000	1.5	10	30	30
RFBO	i-GotU	40	15	25	250	1,000	1.5	10	30	30
	e-obs	40	—	—	—	—	1.5	10	180	180

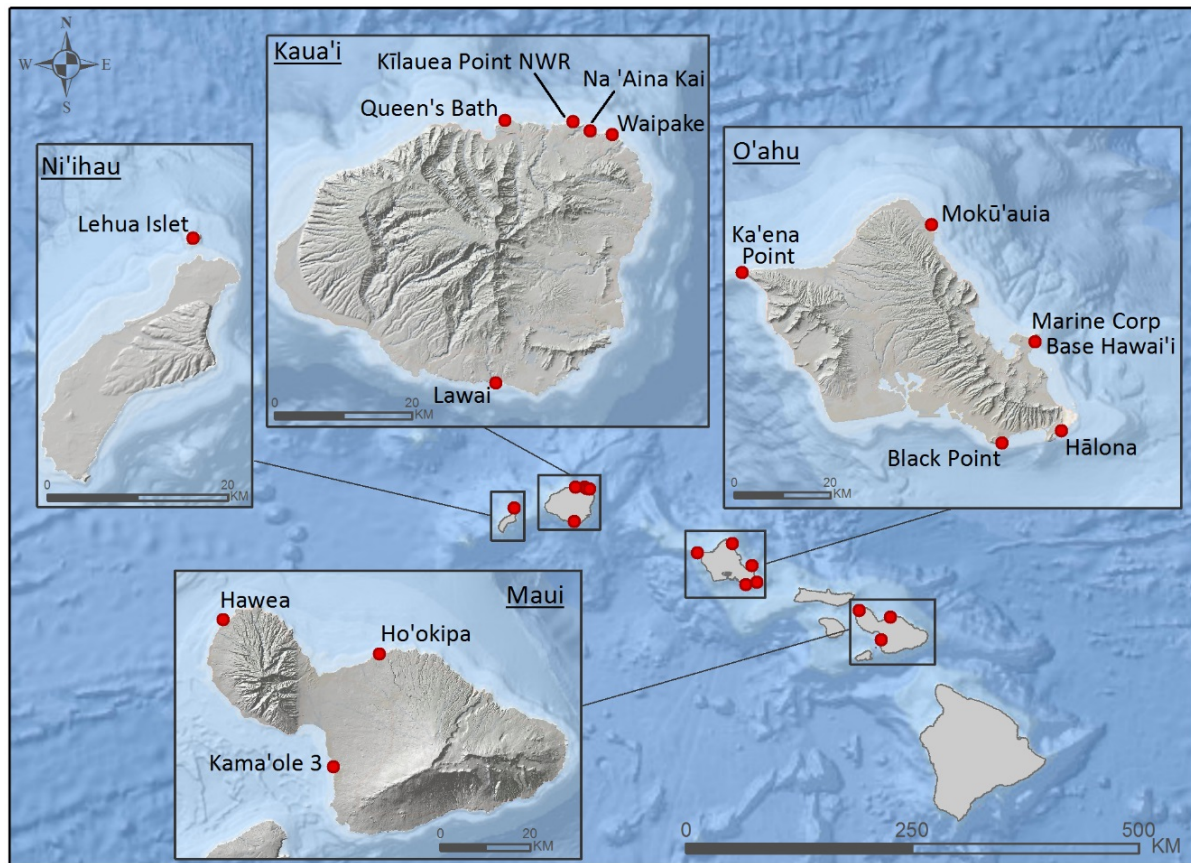


Figure 1. Study sites in the Main Hawaiian Islands where marine birds were tracked, 2013–2016.
 Study sites in the Main Hawaiian Islands where marine birds were tracked, 2013–2016.



Figure 2. Hāwea Point, Kapalua, Maui. Wedge-tailed Shearwater colony outlined in green (Google Earth™ 2017).



Figure 3. Ho'okipa, Pā'ia, Maui. Wedge-tailed Shearwater colony outlined in green (Google Earth™ 2017).



Figure 4. Kama'ole III, Kīhei, Maui. Wedge-tailed Shearwater colony outlined in green (Google Earth™ 2017).



Figure 5. Black Point, O'ahu. Wedge-tailed Shearwater colony outlined in green (Google Earth™ 2017).



Figure 6. Hālonā Point, Hawai'i Kai, O'ahu. Red-tailed Tropicbird colony outlined in green (Google Earth™ 2017).



Figure 7. Ka'ena Point Natural Area Reserve, O'ahu. Wedge-tailed Shearwater and Laysan Albatross colonies outlined in green (Google Earth™ 2017).



Figure 8. Mokū'auia Island, Lā'ie, O'ahu. Wedge-tailed Shearwater colony outlined in green (Google Earth™ 2017).



Figure 9. Marine Corps Base Hawai'i at Kaneohe Bay, O'ahu. Ulupa'u Crater Red-footed Booby (RFBO) colony located at the northeastern tip of the Mokapu Peninsula and the two Wedge-tailed Shearwater (WTSH) sub-colonies along the southeastern coastal region of Marine Corps Base Hawai'i (outlined in green; Google Earth™ 2017)



Figure 10. Kīlauea Point National Wildlife Refuge (KPNWR), Na ʻAina Kai, and Waipake, Kauaʻi. Colonies referenced in text are outlined in green (Google Earth™ 2017).



Figure 11. Queen's Bath, Princeville, Kauaʻi. This small Wedge-tailed Shearwater colony (outlined in green) is located along the northshore of Kauaʻi adjacent to the town of Princeville. Wedge-tailed Shearwater colony outlined in green (Google Earth™ 2017).



Figure 12. Lāwai Kai, Lāwai, Kaua'i. Wedge-tailed Shearwater colony outlined in green (Google Earth™ 2017).



Figure 13. Lehua Islet, located off the northern tip of Ni'ihau (Google Earth™ 2017).



Figure 14. Photographs of i-gotU GPS tags used in this study. Left: i-GotU GT-120 GPS tag removed from original packaging. This tag type was used to track Red-tailed Tropicbirds, Wedge-tailed Shearwaters, Brown Boobies, and Red-footed Boobies in MHI, 2013–2016. Upper right: Tag sealed in heat shrink with heat shrink tabs aligned with top of tag for underside tail attachments. Lower right: Tag sealed in heat shrink with heat shrink tabs aligned with bottom of tag for attachments on top of tail or back. Note that for tail attachments beginning in 2015, one heat shrink tab was folded up against the tag to allow closer placement of the tag to the bird's body.



Figure 15. Examples of i-GotU GT-120 GPS tags deployed on seabirds in MHI, 2013–2015. Upper left: Tag taped to underside of Red-tailed Tropicbird tail feathers. Upper right: Tag taped to top of Red-tailed Tropicbird tail feathers. Middle left: Tag taped to underside of Red-footed Booby tail feathers. Middle right: Red-footed Booby sitting naturally with tag taped to underside of tail feathers (only black tape is visible). Note that attachments on Brown Boobies were identical to Red-footed Boobies. Lower left: Tag being taped to back feathers on Wedge-tailed Shearwater (bird's tail is to the left, head is to the right and covered).



Figure 16. Examples of e-obs GPS solar tags attached to seabirds tagged in MHI in 2016. Top left: Attachment of plastic base plate with tape to central tail feathers of Red-footed Booby. Top right: e-obs GPS solar 15g tag zip-tied to base plate on Red-footed Booby tail feathers. Zip-ties were attached via pre-drilled holes on base plate and harness attachment points on GPS tag. Lower left and right: e-obs GPS solar 30g tag attached to Laysan Albatross back feathers using same technique described above. Note that in 2014, non-solar e-obs GPS tags were used on Laysan Albatross and were attached with tape directly to back feathers and wrapped around entire tag.



Figure 17. Example attachments of CEFAS G5 Temperature-Depth Recorders (TDRs) on seabirds in MHI, 2014–2015. TDRs were taped to the metal leg band with the pressure transducer and saltwater switch oriented towards the bird's body to avoid potential sensor damage from the bird walking on the ground. Left and top right: Brown Booby. Middle right: Red-footed Booby. Lower right: Wedge-tailed Shearwater.

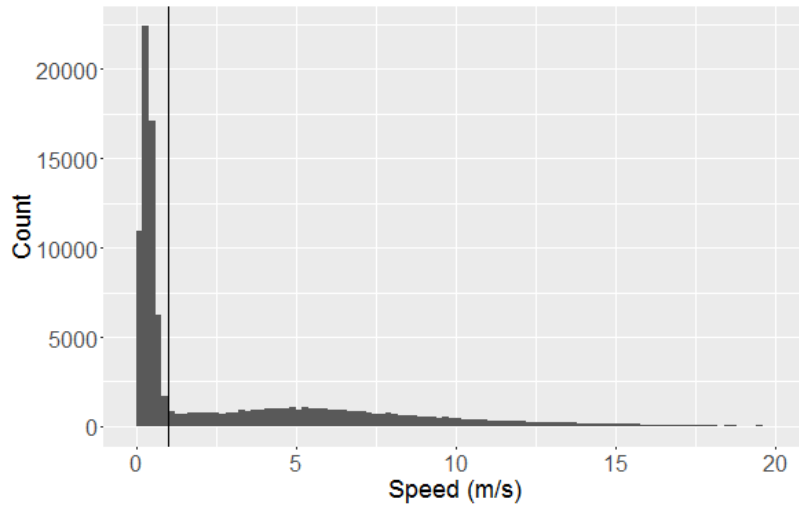


Figure 18. Example histogram of Red-tailed Tropicbird speed values from all tagged individuals, 2014–2016. Speeds were calculated as the distance moved divided by time elapsed between two locations. Sampling frequency for Red-tailed Tropicbirds was 2–3 min. Vertical black line indicates 1-m-s⁻¹ speed threshold used in behavioral classification.

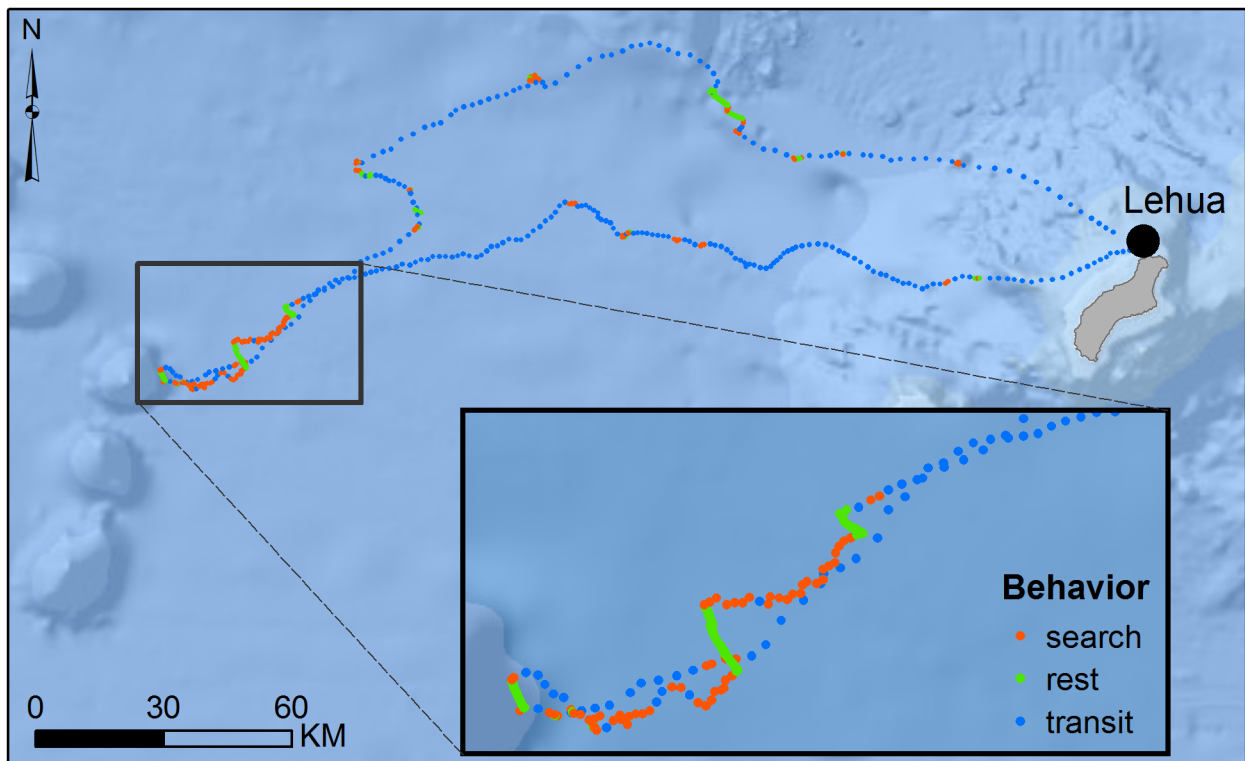


Figure 19. Example map of behaviorally-classified track of a Red-tailed Tropicbird foraging trip from Lehua Islet, 2014. Colors indicate different behavioral classifications identified by adapted Residence in Space and Time algorithm classification scheme (see text for details).

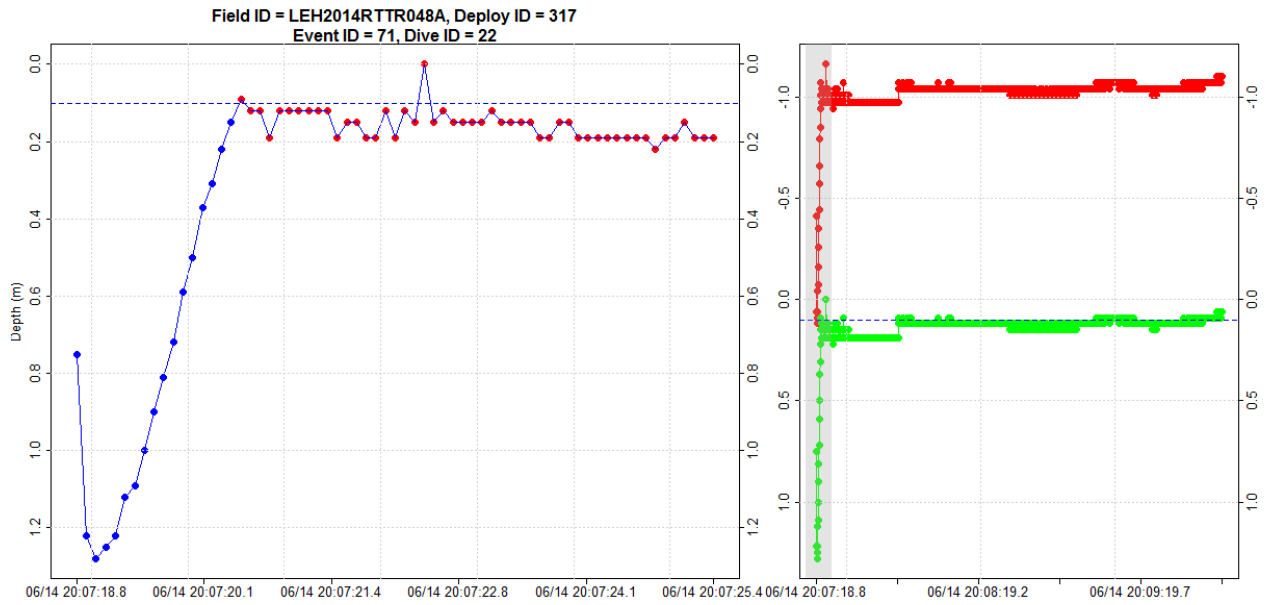


Figure 20. Sample depth profile plot from custom Temperature-Depth Recorder dive identification script. The left plot is zoomed on the dive (blue) ± 5 s before/after FastLog record (red). The right plot is the entire FastLog burst before (red) and after (green) calibration. The vertical axes of both plots represent depth, although they are not drawn at the same scale. Note the surface of the uncalibrated (blue) points in the right plot appears to be at -1.0 m, which is why we applied the fixed offset.

3 Results

3.1 Red-tailed Tropicbird (*Koa'e'ula*, *Phaethon rubricauda*)

3.1.1 Species Account

The Red-tailed Tropicbird (IUCN “Least Concern”) is one of three tropicbird species in the world and ranges across tropical and sub-tropical areas of the Pacific and Indian oceans. Of the estimated 30,000–40,000 breeding pairs worldwide (Schreiber and Schreiber 2009), approximately 9,000–12,000 pairs breed in Hawai‘i, primarily at sites throughout the northwestern Hawaiian Islands (Harrison 1990, Pyle and Pyle 2017); birds are present at nesting sites and surrounding waters predominantly during the breeding season (February–October; Harrison 1990, Laniawe 2008, Schreiber and Schreiber 2009, VanderWerf et al. 2007). An annual breeder, Red-tailed Tropicbirds lay a single egg on the ground where adequate shade exists, generally under vegetation on any slope or in natural alcoves and crevices present at steeper, rockier sites. Incubation exchanges and chick feedings occur exclusively during daylight (Harrison 1990, Tyler 1991, VanderWerf et al. 2007, Schreiber and Schreiber 2009). Nesting in MHI is restricted to steep coastal bluffs and cliffs and offshore islets where non-native predators are limited or absent (VanderWerf and Young 2014). Historically, rats (*Rattus rattus*) predating eggs and nestlings caused significant reproductive failures (up to 100%) at Kure and Midway atolls (Fleet 1972, Tyler 1991). White-tailed Tropicbirds, which can also nest farther inland in MHI and have similar behavior and flight-styles as Red-tailed Tropicbirds, have been killed in collisions with existing terrestrial wind energy infrastructure (J. Charrier, USFWS unpubl. data, pers. comm. 22 November 2016), indicating that both species are potentially at risk from offshore wind energy development.

Tropicbirds fly using flapping, directed flight, and feed mainly on surface-dwelling flying fish (Exocetidae), squid (Ommastrephidae), jacks (Scrombridae), and dolphin-fishes (Coryphoenidae), which they catch aerially or by plunge-diving from heights of up to 40 m (Le Corre 1997, Le Corre et al. 2003, Schreiber and Schreiber 2009, Spear and Ainley 2005). When observed at sea, Red-tailed Tropicbirds are typically solitary and not often found within the multi-species feeding flocks over tuna schools where many other seabirds aggregate (Spear and Ainley 2005).

Red-tailed Tropicbird foraging trip durations and ranges may vary by site and with conditions (Schreiber and Schreiber 2009). When measured by monitoring nest attendance in several studies, mean foraging trip duration during incubation ranged from 4–10 days (overall range 1–16 days; Fleet 1974, Le Corre et al. 2003, Schreiber and Schreiber 2009, Sommerfeld and Hennicke 2010, Tyler 1991). During early chick-rearing (first ~2 weeks), one adult regularly attends the chick and leaves for short, intra-day foraging trips (mean 3.0 h, range 0.8–20.4 h), typically during early morning, while the other adult conducts a longer foraging trip (mean 2.4 days, range 1–7 days; Sommerfeld and Hennicke 2010). During later chick-rearing, both adults conduct moderate-duration foraging trips (mean 34 h, range 6–78 h; Le Corre et al. 2003). Based on flight-speed estimates and foraging trip durations, Le Corre et al. (2003) calculated potential foraging ranges of 384 km during incubation and 136 km during chick-rearing. Laniawe (2008) tracked incubating Red-tailed Tropicbirds on Midway Atoll using satellite tags attached with harnesses, but all five study individuals abandoned their nests. Two studies using i-gotU 120 GPS tags taped to tail feathers have successfully tracked Red-tailed Tropicbirds breeding on Ashmore Reef (northwestern Australia; R. Mott, unpubl. data, pers. comm. April 2014) and Europa Island (Mozambique Channel; M. Le Corre and P. Pinet, unpubl. data, pers. com Sep 2016), and results are forthcoming.

Diving depths of Red-tailed Tropicbirds were measured during incubation using maximum-depth recorders (MDRs; Le Corre 1997, Sommerfeld and Hennicke 2010) and during chick-rearing using MDRs (Le Corre 1997) and TDRs (Sommerfeld and Hennicke 2010). In both studies, maximum dive depths were deeper during incubation than during chick-rearing (range of mean maximum depths

6.3–10.7 m and 0.6–2.3 m, respectively), indicating a change in behavior in response to changing prey type or availability. However, dive depths measured using MDRs may be overestimated because of condensation and/or multiple immersions on longer duration deployments (e.g., incubation foraging trips; Burger and Wilson 1998). Although Le Corre et al. (2003) found that diet varied throughout the breeding season, there was no difference in diet between tropicbirds incubating and chick-rearing concurrently.

3.1.2 Tagging Sites and Deployment Success

Red-tailed Tropicbirds were tracked from three breeding colonies in MHI: Lehua Islet (Ni‘ihau/Kaua‘i), Kīlauea Point NWR (Kaua‘i), and Hālonā Point (O‘ahu; Figure 21 and Table 3). From 2014–2016, we successfully recovered tracking data from 59 of 103 GPS deployments; TDR data was successfully recovered from 34 of 48 deployments (Table 3). Mean (\pm SD) GPS tracking duration was 5.2 ± 2.4 days and mean TDR duration was 4.6 ± 2.5 days across all sites (Table 3). Unsuccessful deployments were caused either by non-recovery of the tagged individual, tag loss, or tag technical malfunction. At Lehua Islet, we successfully recovered data from 33 of 59 GPS deployments from 2014–2015 (Table 3). Deployment sessions lasted 6–7 days and 10–12 days in 2014 and 2015, respectively, and were dictated primarily by logistical constraints; mean GPS tracking durations were longer in 2015 (6.0–6.6 days) than 2014 (2.7–3.6 days; Table 3). At Kīlauea Point NWR in 2016, we successfully recovered data from 16 of 20 GPS deployments in one 10-day session; mean tracking duration was 4.9 ± 1.8 days (Table 3). At Hālonā Point, tagging in 2014 was the first attempt to track this species during this project. GPS tags were taped to back feathers of 9 individuals; however, this method was unsuccessful, and all tags were lost while birds were at sea. In 2015, we successfully recovered data from 10 of 15 deployments in two sessions at this site; mean tracking duration ranged from 5.0–8.2 days (Table 3), although some tags experienced GPS reception issues and have less continuous tracking coverage than at other sites.

3.1.3 Foraging Trip Parameters

We identified 152 unique Red-tailed Tropicbird foraging trips made by 59 individuals across all sites; individual trip durations ranged from 38 min to 8 days (overall mean [\pm SD] 37.6 ± 52.7 h), with ~54% lasting <12 h (Figure 22, Table 4). Because previous nest attendance studies identified bimodality in foraging trip durations for early chick-rearing birds (e.g., one adult attends chick, only leaving to conduct short, intra-day trips, while the other adult conducts a multi-day foraging trip; Sommerfeld and Hennenke 2010), we examined our data in this context and found a similar pattern. Most short trips <12-h duration were conducted by tropicbirds raising chicks <2–3 weeks old ($n = 33$ of 59 birds tracked; Figure 22). For further analysis we split foraging trips into two categories: 1) “Short Trips” that occurred within the same day and 2) “Long Trips” that included at least one night spent at sea.

Mean (\pm SD) short trip duration, maximum range, and distance traveled for all site-years were 2.9 ± 1.7 h, 27.4 ± 15.9 km, and 66.5 ± 42.9 km, respectively ($n = 82$; Table 4). Mean long trip duration, maximum range, and distance traveled for all site-years were 79.9 ± 54.0 h (3.3 ± 2.25 days), 296.3 ± 206.2 km, and 888.0 ± 581.7 km, respectively ($n = 70$, Table 4). The distribution of long trip durations is right-skewed and may be bimodal (Figure 22); therefore, the mean values should be interpreted with caution. Foraging trip measurements varied across sites and years (Table 4, Figure 23), although the amount of tag recovery effort could also affect these results (e.g., Lehua 2015 deployment sessions were two times longer than in 2014, resulting in more long trips being documented). Overall, data from the Lehua 2015 and Kīlauea Point NWR 2016 deployment sessions are likely the most comprehensive because of extended recovery effort.

Red-tailed Tropicbirds exhibited different foraging trip start- and end-time patterns depending on trip type (Figure 24). Most short trips began early in the morning during twilight, with a second, smaller pulse occurring midday; end times appear to mirror that pattern 2–4 h later. In contrast, long trips almost all exclusively began and ended between 10:00 and 17:00 local time (Figure 24), perhaps indicating that

birds remain some distance away from the colony the night before they return to feed their chick and relieve their mate (early chick stages) or depart on another foraging trip (later chick stages).

3.1.4 Behavioral Classification

For RST behavioral classification of Red-tailed Tropicbird locations on foraging trips, we calculated a mean transit speed of 8.6 m s^{-1} for Red-tailed Tropicbirds. A sampling rate of 180 s (3 min) resulted in a RST radius of 774 m.

Birds on short trips spent 23.9%, 20.7%, and 55.4% of their time during the daylight hours resting, searching/foraging, and transiting, respectively; transiting was more frequent (70.1%) during twilight hours (Table 5). On long trips, tropicbirds spent 43.9%, 22.4%, and 33.6% of their time during daylight resting, searching/foraging, and transiting, respectively; resting was more prominent during twilight (56.8%) and the primary behavioral mode at night (91.4%; Table 5). An hourly behavioral breakdown further illuminates these patterns: on short trips, transit behavior peaked in early morning, midday, and late day, perhaps corresponding with peak trip start/end times (Figure 24), whereas on long trips transit and search behaviors peaked in the morning and late afternoon (Figure 25).

Tropicbird resting altitudes were normally distributed near 0 mamsl (median = 1.84 mamsl), whereas flight altitudes were bimodally distributed, with a narrow peak around 0 mamsl (likely representing time spent at or near the water's surface during searching and foraging activities) and a second, broader distribution of altitude values with a peak around 80 mamsl (overall flight median = 83.1 mamsl; Figure 26). Using our error simulation method, we estimated that Red-tailed tropicbirds spend 70.6% (95% CI 70.1–71.0%) of flight time in the RSZ. Even though there is variability in the altitude measurements, it does not induce much variation in the final proportion of time spent flying in RSZ, because underestimated and overestimated altitudes tended to cancel each other out.

3.1.5 Spatial Distribution

Red-tailed Tropicbirds utilized distinct areas at sea on foraging trips. On short trips, birds from Lehua visited waters to the west, whereas birds from Kīlauea Point NWR traveled to the east-northeast (Figure 27). Tropicbirds on long trips from Lehua Islet tended to travel either westward or northward on out-and-back or clockwise looping trajectories (Figure 27). Birds on long trips from Kīlauea Point NWR had similar trip styles, but primarily to the northeast (Figure 27). At both sites and on both trip types, we observed a shift from greater transiting behavior nearshore to greater foraging and resting behavior offshore (Figure 27). Within 100 km of the MHI, Red-tailed Tropicbirds from Lehua Islet spent some time in western nearshore waters of Kaua'i, very little time in the Kaieiewaho Channel (separating Kaua'i and O'ahu), and no time within ~100 km of O'ahu (Figure 27). Birds from Kīlauea Point NWR heavily utilized nearshore waters off northeastern Kaua'i and spent moderate time in the channel and in nearshore waters off northwestern O'ahu (Figure 27). All foraging trips from Hālonā were to the south and southeast (Figure 27).

3.1.6 Diving Behavior

We deployed 48 TDR tags on Red-tailed Tropicbirds in 2014 and 2015 (Table 3); however, TDR data were too noisy for our QAQC TDR processing scripting and we could not reliably identify dives. We suspect that the placement of the TDR on the leg band resulted in unexpected TDR sensitivity to tropicbird paddling behavior on the water. These TDR data are archived and could be reevaluated in the future.

3.1.7 Tables and Figures

Table 3. Red-tailed Tropicbird deployment and recovery success for each site and deployment session in MHI, 2014–2016. “Birds tagged” is the total number of individuals tagged with any combination of tag types. “GPS/TDR deployed” and “GPS/TDR data” indicate number of each tag type deployed and number from which data was successfully recovered, respectively. “Mean GPS/TDR duration” indicate the mean time duration (in days) between tag deployment and tag recovery.

Island	Site	Year	Deployment Session	Nest status	Birds tagged	GPS depl.	GPS data	Mean (SD)		Mean (SD) TDR duration	
								GPS duration	TDR depl. data		
Kaua'i	Kīlauea Point	2016	27-May to 4-Jun	Chick	20	20	16	4.9 ± 1.8	0	0	NA
		Lehua Islet	2014	14-May to 16-May	Chick	1	1	1	2.1	0	0
			13-Jun to 18-Jun	Chick	14	14	7	2.7 ± 1.1	13	11	2.3 ± 1.0
			14-Jul to 20-Jul	Chick	14	14	9	3.6 ± 1.5	8	6	3.3 ± 1.5
		2015	26-May to 5-Jun	Chick	16	16	10	6.6 ± 2.1	13	10	6.8 ± 2.1
			27-Jun to 5-Jul	Chick	14	14	6	6.0 ± 1.5	9	7	6.0 ± 1.4
	Kaua'i Total:					79	79	49	4.8 ± 2.1	43	34
O'ahu	Hālonā	2014	21-Apr to 26-Apr	Chick	9	9	0	NA	5	0	NA
		2015	16-Apr to 21-Apr	Chick	5	5	3	5.0 ± 0.03	0	0	NA
		6-May to 28-May	Chick	10	10	7	8.2 ± 2.9	0	0	NA	
	O'ahu Total:					24	24	10	7.3 ± 2.9	5	0
ALL SITES:					103	103	59	5.2 ± 2.4	48	34	4.6 ± 2.5

Table 4. Mean (± SD) Red-tailed Tropicbird foraging trip duration, maximum range, and distance traveled for short, long, and all trips combined in MHI, 2014–2016.

Trip Type	Site (Year)	Birds	Trips	Duration (h)	Range (km)	Dist. Traveled (km)
Short	Hālonā (2015)	8	19	2.3 ± 1.1	22.4 ± 11.0	50.2 ± 24.7
	Kīlauea Point (2016)	6	21	3.1 ± 1.7	33.6 ± 17.7	81.8 ± 48.0
	Lehua (2014)	8	19	2.7 ± 1.6	20.4 ± 12.9	51.5 ± 34.2
	Lehua (2015)	7	23	3.4 ± 2.1	31.3 ± 17.2	79.4 ± 49.7
	Short Total	29	82	2.9 ± 1.7	27.4 ± 15.9	66.5 ± 42.9
Long	Hālonā (2015)	9	13	55.4 ± 38.4	186.4 ± 176.2	460.1 ± 277.7
	Kīlauea Point (2016)	13	18	89.6 ± 55.6	387.4 ± 244.1	1,069.9 ± 642.8
	Lehua (2014)	14	18	52.4 ± 34.2	182.4 ± 135.0	534.6 ± 355.7
	Lehua (2015)	16	21	103.0 ± 59.7	352.5 ± 178.4	1,120.1 ± 555.8
	Long Total	52	70	79.9 ± 54.0	296.3 ± 206.2	888.0 ± 581.7
All	Hālonā (2015)	10	32	18.6 ± 32.2	68.3 ± 116.2	139.3 ± 210.7
	Kīlauea Point (2016)	16	39	43.0 ± 57.4	196.9 ± 242.4	537.9 ± 659.6
	Lehua (2014)	17	37	26.2 ± 34.2	99.2 ± 124.2	279.6 ± 343.9
	Lehua (2015)	16	44	54.4 ± 65.8	184.6 ± 203.2	612.4 ± 658.0
	All Trips Total	59	152	37.6 ± 52.7	146.1 ± 191.6	427.0 ± 561.7

Table 5. Percentage of time (and number of locations, N) for behavior classes during day, night, and twilight on short and long Red-tailed Tropicbird foraging trips from all MHI sites, 2014–2016.

Trip Type	Behavior	Day	Night	Twilight
Short	Rest	23.9% (970)	NA	16.2% (100)
	Search	20.7% (842)	NA	13.7% (85)
	Transit	55.4% (2,250)	NA	70.1% (434)
Long	Rest	43.9% (27,488)	91.4% (34,196)	56.8% (8,189)
	Search	22.4% (14,033)	05.3% (1,996)	18.1% (2,607)
	Transit	33.6% (21,025)	03.3% (1,239)	25.2% (3,631)

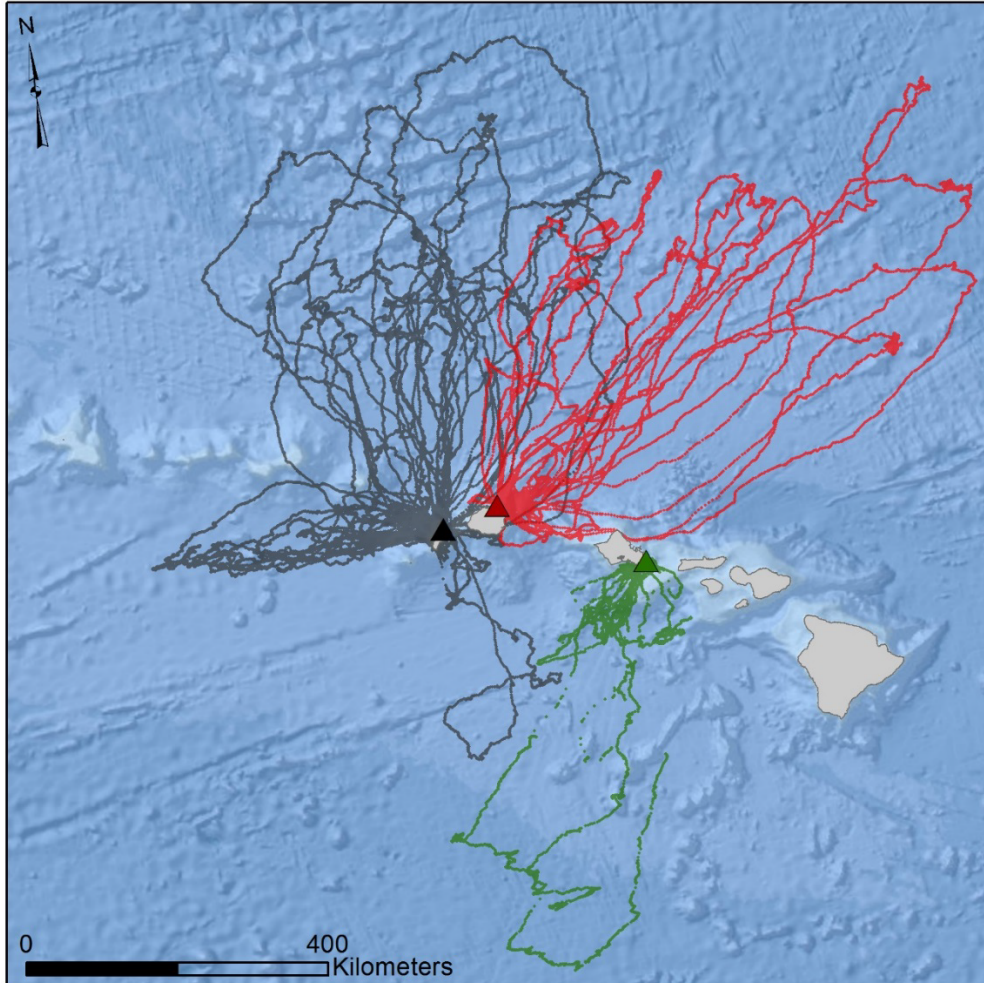


Figure 21. Raw Red-tailed Tropicbird tracking data from MHI. Birds were tracked from Lehua Islet (Ni'ihau/Kaua'i, 2014–2015, black), Kilauea Point NWR (Kaua'i, 2016, red), and Hālonā Point (O'ahu, 2015, green). Colored triangles indicate tagging sites.

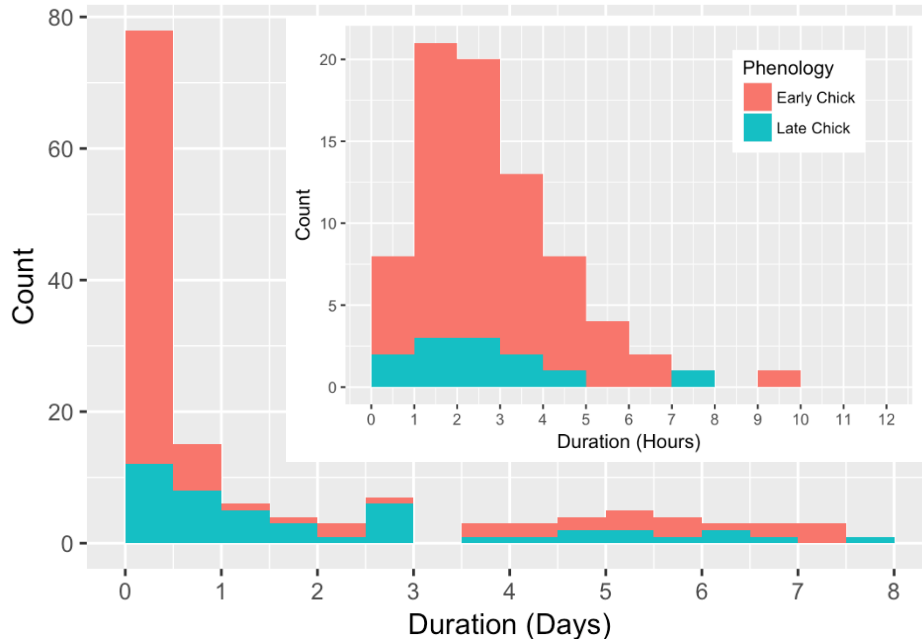


Figure 22. Stacked histogram of Red-tailed Tropicbird trip durations at all MHI sites, 2014–2016. Trips were categorized by phenology for adults rearing early- (<2–3-week-old) and late- (>2–3-week-old) stage chicks for all trips (main plot, x-axis in days) and trips <12-h duration (inset plot, x-axis in hours).

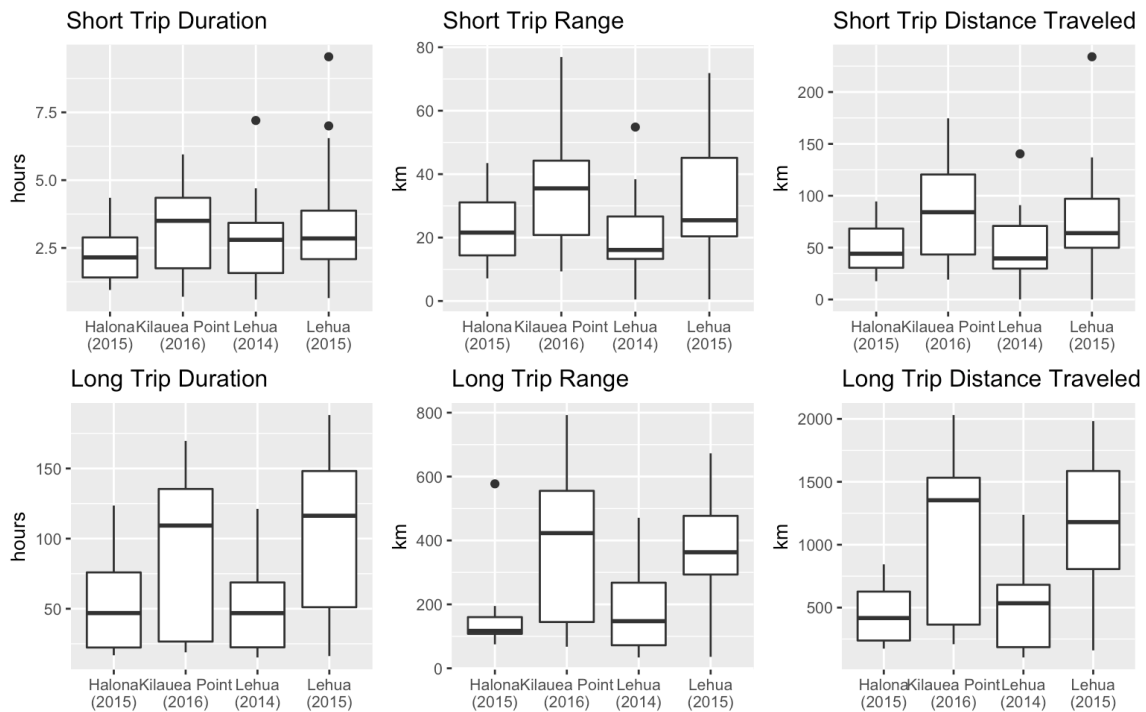


Figure 23. Box-and-whisker plots of duration, maximum range, and distance traveled on short and long Red-tailed Tropicbird foraging trips in MHI, 2014–2016. The black line in box represents the median, the box represents the inter-quartiles (25% and 75%), the whiskers extend to the furthest point within 1.5 interquartile ranges, and dots are any additional points beyond the whiskers.

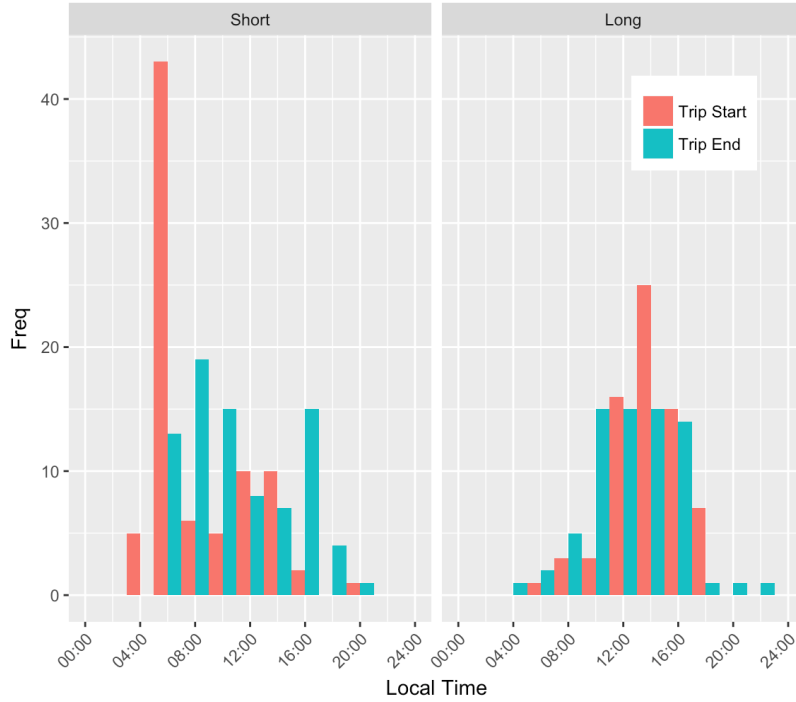


Figure 24. Histograms of trip start and end times for short (left panel) and long (right panel) Red-tailed Tropicbird foraging trips for all MHI sites, 2014–2016.

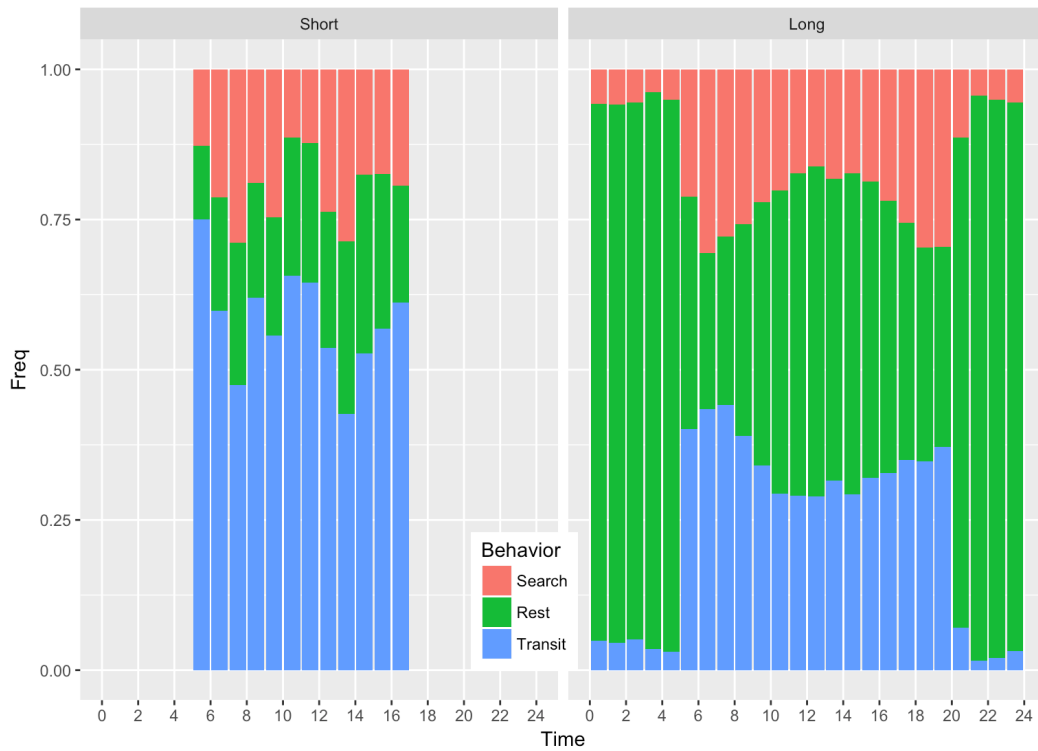


Figure 25. Daily activity patterns for all Red-tailed Tropicbirds on short (left) and long (right) foraging trips for all MHI sites, 2014–2016.

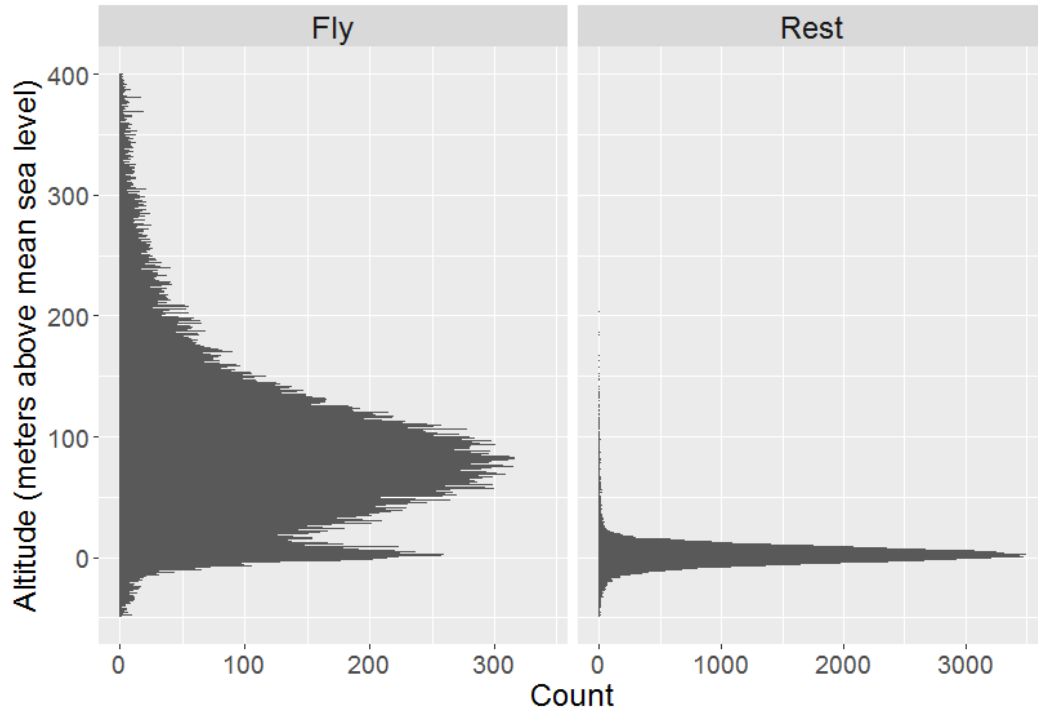


Figure 26. Histograms of Red-tailed Tropicbird altitude measurements for flying (left) and resting (right) GPS locations for all MHI sites, 2014–2016.

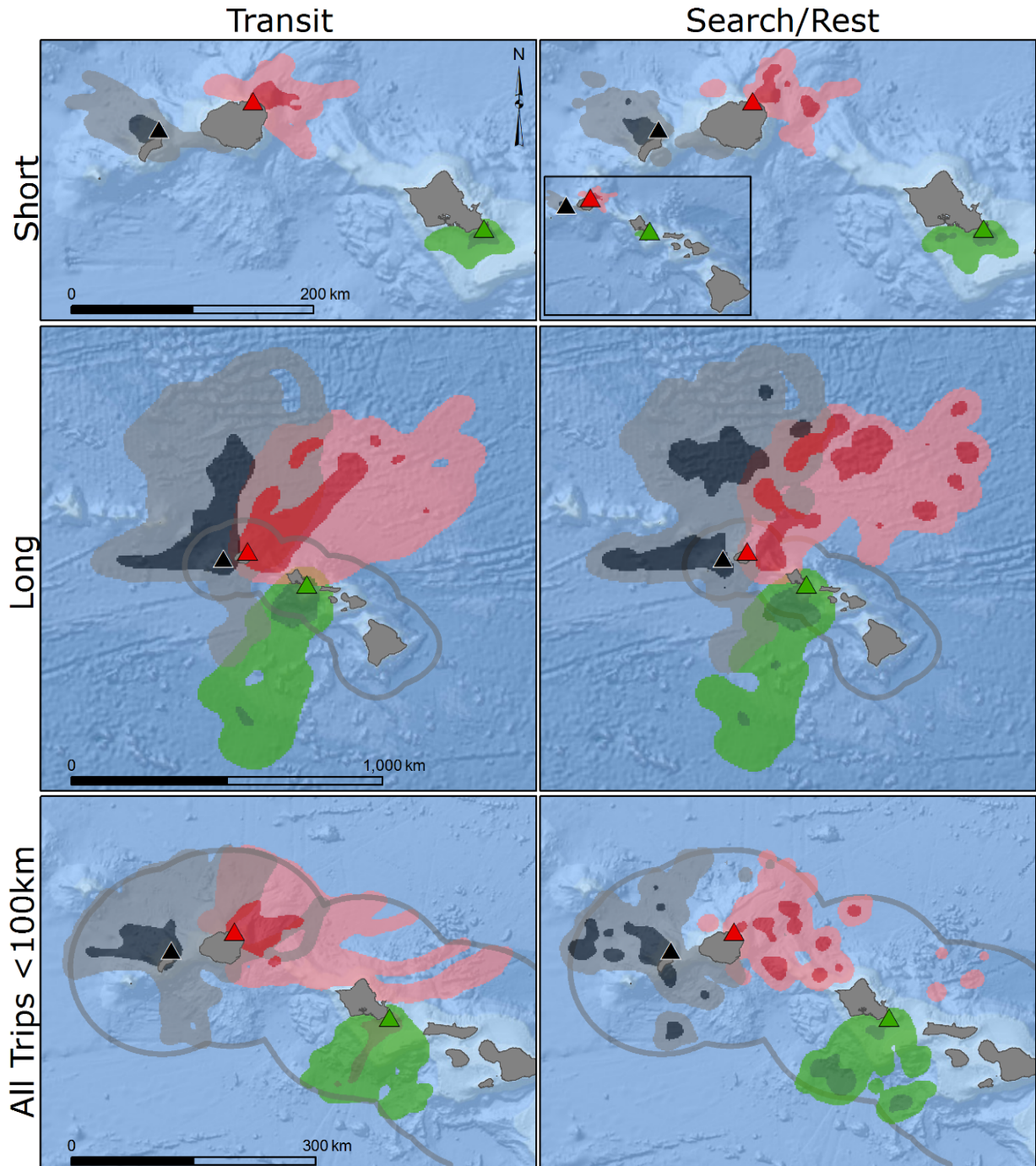


Figure 27. Kernel density distributions Red-tailed Tropicbirds tracked from MHI, 2014–2016. Distributions are mapped for short trip (intra-day; top row), long trip (multi-day; middle row), and all tracking data within 100 km of MHI (bottom row) for each behavioral state (columns) from Lehua Islet (black), Kīlauea Point NWR (red), and Hālonā (green). Colored triangles indicate site locations. Note different spatial scales of each row. Colors are shaded lighter for 99% contour and darker for 50% contour. Kernel smoothing factor set manually to 1.5% the spatial extent of the data ($h = 3.1$ km for short trips, 22.9 km for long trips, and 5.8 km for all trips <100 km).

3.2 Laysan Albatross (Mōlī, *Phoebastria immutabilis*)

3.2.1 Species Account

The Laysan Albatross (IUCN “Near Threatened”; BirdLife International 2018) is one of three northern hemisphere albatross species. Of the estimated *ca.* 800,000 breeding pairs worldwide (BirdLife International 2018), approximately 90% breed in northwestern Hawaiian Islands, primarily at Midway Atoll, Laysan Island, and French Frigate Shoals; only about 1,500 adults nest in the MHI on Kaua‘i (~1,000 birds) and O‘ahu (~555 birds in 2015; Young et al. 2009a, Young et al. 2014, Pyle and Pyle 2017). Birds are present at nesting sites and surrounding waters predominantly during the breeding season (November–July), and completely absent from near Hawaiian waters late July through mid-October (Pyle and Pyle 2017). Post-breeding dispersal among albatrosses captured at sea off Alaska indicated individuals spent most of their time in oceanic waters of the North Pacific, where they were less likely to interact with fisheries than Black-footed Albatross (Fischer et al. 2009). Breeding can be less than annually as pairs are known to skip breeding in certain years (Young et al. 2009a). Nesting in MHI is restricted to coastal bluffs and offshore islets where non-native predators are limited or absent. Laysan Albatross lay a single egg on the ground close to areas buffeted by trade-winds either in the open or where shade exists, generally near or within vegetation. Incubation exchanges and chick feedings occur mostly during daylight (Awkerman et al. 2009). Pyle and Pyle (2017) provide a comprehensive account of the history and occurrence of Laysan Albatrosses in the Hawaiian Islands.

Albatrosses fly using flapping, or dynamic soaring, and feed mainly on epi- and mesopelagic squids (Gonatidae, Ommastrephidae), mesopelagic fishes, and longline-associated bait fishes which they catch or scavenge while in direct flight or while sitting on the water (Fernandez and Anderson 2000, Conners 2015). When observed at sea, Laysan Albatross typically are solitary and not often found within multi-species feeding flocks over tuna schools (Spear and Ainley 2005). Conners et al. (2015) found that Laysan Albatrosses spent 70% of their time in flight and about 50% of their trips “actively foraging”; foraging occurred during day and night, but during the brood-guard stage (chicks 0–18 days old), individuals spent more time engaged in area-restricted search during the night.

Laysan Albatross foraging trip durations and ranges vary according to breeding period and large-scale variability in meteorology and oceanography in the north Pacific (Fernandez and Anderson 2000, Young 2009, Young et al. 2009b, Kappes et al. 2010). During the early chick-rearing brood-guard stage (chicks 0–18 days old), one adult regularly attends the chick, while the other adult conducts a foraging trip. Mean foraging trip durations during this stage were 2–3 days, with a maximum range on average of ~500 km (Fernandez et al. 2001, Conners et al. 2015); smaller (female) birds had greater maximum foraging distances than larger (male) birds (Conners et al. 2015). During the post-brooding, chick-rearing stage (chicks >18 days old), both adults conduct mostly long-distance (median max range = 2,675 km), long duration (median = 14.5 days, range: 1–29 days) foraging trips (Fernandez et al. 2001).

3.2.2 Tagging Sites and Deployment Success

Laysan Albatrosses were tracked from three breeding colonies in MHI during the mid- through the end of the chick-rearing season: Ka‘ena Point (O‘ahu; 2014), Na ‘Aina Kai (Kaua‘i; 2014) and Waipake (Kaua‘i; 2016; Figure 28 and Table 6). Chicks were 1–2 months old at the time of tagging of chick-rearing adults. During 2014 and 2016, we successfully recovered tracking data from 35 of 36 GPS-ACC deployments (Table 6). Mean GPS tracking duration was 63.4 days across all sites (Table 6). The single unsuccessful deployment was a result of tag failure. At Ka‘ena Point (2014), we successfully recovered data from 11 of 12 GPS-ACC deployments. At Na ‘Aina Kai (2014) and Waipake (2016) we successfully recovered data from all 12 GPS-ACC deployments (Table 6); however, one tag was deployed on an adult at Waipake that was incorrectly identified as a breeding bird and this deployment is not included in

further analyses. Long duration deployments were facilitated using archival transmitting tags linked to solar-powered base stations.

3.2.3 Foraging Trip Parameters

We identified 338 unique Laysan Albatross foraging trips made by 34 individuals, excluding one non-breeder, across all sites; individual trip durations lasted on average (\pm SD) 150.9 ± 183.5 h (6.3 ± 7.6 days) and were bimodally distributed. We classified 64% of trips as “short” (<6 days) and the remainder as “long” trips (Figure 29, Table 7). Mean short-trip duration, maximum range, and distance traveled for all site-years were 23.4 ± 16.7 h, 177.9 ± 239.6 km, and 418.4 ± 379.8 km, respectively ($n = 217$; Table 7). Mean long trip duration, maximum range, and distance traveled for all site-years were 379.6 ± 109.2 h (15.8 ± 4.6 days), $2,786.9 \pm 639.1$ km, and $8,727.4 \pm 2,610.3$ km, respectively ($n = 121$, Table 7). The distribution of short trips was right-skewed (Figure 29); therefore, the mean values should be interpreted with caution. The distribution of long trips was normal (Figure 29). Foraging trip parameters were consistent across sites and years (Table 7, Figure 30); however, long-trip range may be greater among albatrosses tracked from Ka‘ena in 2014 (Figure 30), because several birds from this deployment traveled to the northern Gulf of Alaska and southwestern Bering Sea (Figure 28). Although short trips outnumbered long trips, individuals spent on average $90.0 \pm 0.1\%$ of their tracking duration engaged in long trips. Laysan Albatross foraging trip start and end times were similarly distributed by trip type; peak arrivals and departures for both long and short trips were approximately bimodal with peak frequencies at 08:00 and 16:00 local time (Figure 31).

3.2.4 Behavioral Classification

For RST behavioral classification, we calculated a mean transit speed of 10.8 m s^{-1} for Laysan Albatrosses. A sampling rate of 900 s (15 min) resulted in a RST radius of 4,860 m.

Albatrosses on short trips spent 25.7%, 34.0%, and 40.3% of their time during daylight in rest, search, and transit, respectively; rest was twice as frequent during night (51.8%) than during daylight or twilight hours (Table 8). During long trips, albatrosses spent 23.9%, 19.6%, and 56.5% of their time during daylight in rest, search, and transit, respectively, with proportionately less time spent in search and more time in transit compared with short trips (Table 8). Rest was the primary behavior at night (62.1%; Table 8). On short trips, transit behavior peaked in early morning and late afternoon, corresponding with peak trip start/end times (Figure 31). On long trips, transiting behavior was slightly more frequent in the morning, and then relatively consistent throughout the rest of the day (Figure 32).

Albatross resting altitudes were normally distributed near 0 mamsl (median = -1.31 mamsl; Figure 33). Flight altitudes were also normally distributed near 0 mamsl, but slightly greater than resting altitudes (median = 0.04 mamsl). The lack of distinction in altitude values between these two behavioral states likely reflects the low flight heights of albatrosses. Using our error simulation method, we estimated that Laysan Albatrosses would spend 2.57% (95% CI 2.50–2.64%) of flight time in the RSZ. Even though there is variability in the altitude measurements, it does not induce much variation in the final proportion of time spent flying in RSZ because underestimated and overestimated altitudes tended to cancel each other out.

3.2.5 Spatial Distribution

Laysan Albatrosses tracked from Kaua‘i and O‘ahu generally utilized similar areas at sea during foraging trips (Figure 34). Short trips from Kaua‘i and O‘ahu overlapped toward the northwest. Core-use areas for transiting and search/rest during short trips extended approximately 200 km toward the northwest, with colony overlap areas at sea within 100 km northeast of Kaua‘i (Figure 34). The distribution at sea for long trips reflect the far-ranging nature of albatrosses as they seek out widely dispersed, patchy, prey resources

throughout the central north Pacific. Core-use transiting areas show overlapping distributions at sea among albatrosses tracked from both islands and the stereotypical, clockwise looping foraging trips as individuals transit around high pressure systems present north of the MHI during summer (Figure 34). Although we did not analyze spatiotemporal changes to core-use regions, core-use search/rest areas at sea for albatrosses from both islands overlapped in two distinct regions in the north Pacific: the broad region of overlap ~2,000 km north of the MHI indicated use of the North Pacific Transition Zone (NPTZ) during the earlier part of the summer, and the overlapping area ~2,500 km north of the MHI indicated use by albatrosses of the NPTZ from all colonies as this feature moves northward during the latter part of the chick-rearing period (Figure 34). Considering all trips (long and short) within 100 km of the MHI, Laysan Albatrosses from both islands maintain relatively distinct core-use areas among all behaviors; albatrosses tracked from Ka'ena Point, O'ahu occupied more area within the Ka'ie'ie Waho Channel (separating Kaua'i and O'ahu), and no time west of Kaua'i (Figure 34).

3.2.6 Tables and Figures

Table 6. Laysan Albatross deployment success for each site and deployment session in MHI, 2014–2016. “GPS deployed” and “GPS data” indicate number of tags deployed and number from which data was successfully obtained, respectively. “Mean GPS duration” indicates the mean time duration (in days) that tags transmitted data. E-obs telemetry GPS tags included accelerometry measurements on all individuals.

Island	Site	Year	Deployment Session	Nest Status	GPS deployed	GPS data	Mean (SD) GPS duration
Kaua'i	Na 'Aina Kai	2014	07-Apr–25-Jun	Chick	12	12	58.9 ± 8.9
	Waipake	2016	24-Mar–11-Jul	Chick	12	12	81.0 ± 23.2
	Kaua'i Total:				24	24	70.0 ± 20.6
O'ahu	Ka'ena Point	2014	01-Apr–29-May	Chick	12	11	49.1 ± 5.6
ALL SITES:					36	35	63.4 ± 19.8

Table 7. Mean (±SD) Laysan Albatross foraging trip duration, maximum range, and distance traveled for short, long, and all trips combined for MHI tagging sites, 2014–2016.

Trip Type	Site (Year)	Birds	Trips	Duration (h)	Range (km)	Traveled (km)
Short	Ka'ena (2014)	11	65	25.0 ± 18.7	208.6 ± 329.3	444.9 ± 426.1
	Na 'Aina Kai (2014)	12	69	23.7 ± 15.5	163.8 ± 221.4	400.9 ± 348.4
	Waipake (2016)	11	83	21.9 ± 16.0	165.6 ± 157.7	412.2 ± 369.7
	Short Total:	34	217	23.4 ± 16.7	177.9 ± 239.6	418.4 ± 379.8
Long	Ka'ena (2014)	11	31	354.5 ± 98.0	3,109.0 ± 669.6	9,118.2 ± 2,681.3
	Na 'Aina Kai (2014)	12	40	377.7 ± 116.9	2,698.1 ± 504.1	8,409.6 ± 2,575.2
	Waipake (2016)	11	50	396.7 ± 108.5	2,658.3 ± 659.2	8,739.2 ± 2,612.9
	Long Total:	34	121	379.6 ± 109.2	2,786.9 ± 639.1	8,727.4 ± 2,610.3
ALL TRIPS TOTAL:		34	338	150.9 ± 183.5	1,111.9 ± 1,323.4	3,392.9 ± 4,293.4

Table 8. Percentage of time (and number of locations, N) for behavior classes during day, night, and twilight on short and long Laysan Albatross foraging trips from all sites, 2014–2016.

Trip Type	Behavior	Day	Night	Twilight
Short	Rest	25.7% (2,493)	51.8% (3,159)	25.0% (490)
	Search	34.0% (3,295)	28.5% (1,737)	33.6% (658)
	Transit	40.3% (3,912)	19.8% (1,206)	41.4% (812)
Long	Rest	23.9% (23,722)	62.1% (29,490)	38.8% (10,628)
	Search	19.6% (19,425)	9.6% (4,549)	18.6% (5,105)
	Transit	56.5% (56,074)	28.3% (13,433)	42.5% (11,644)

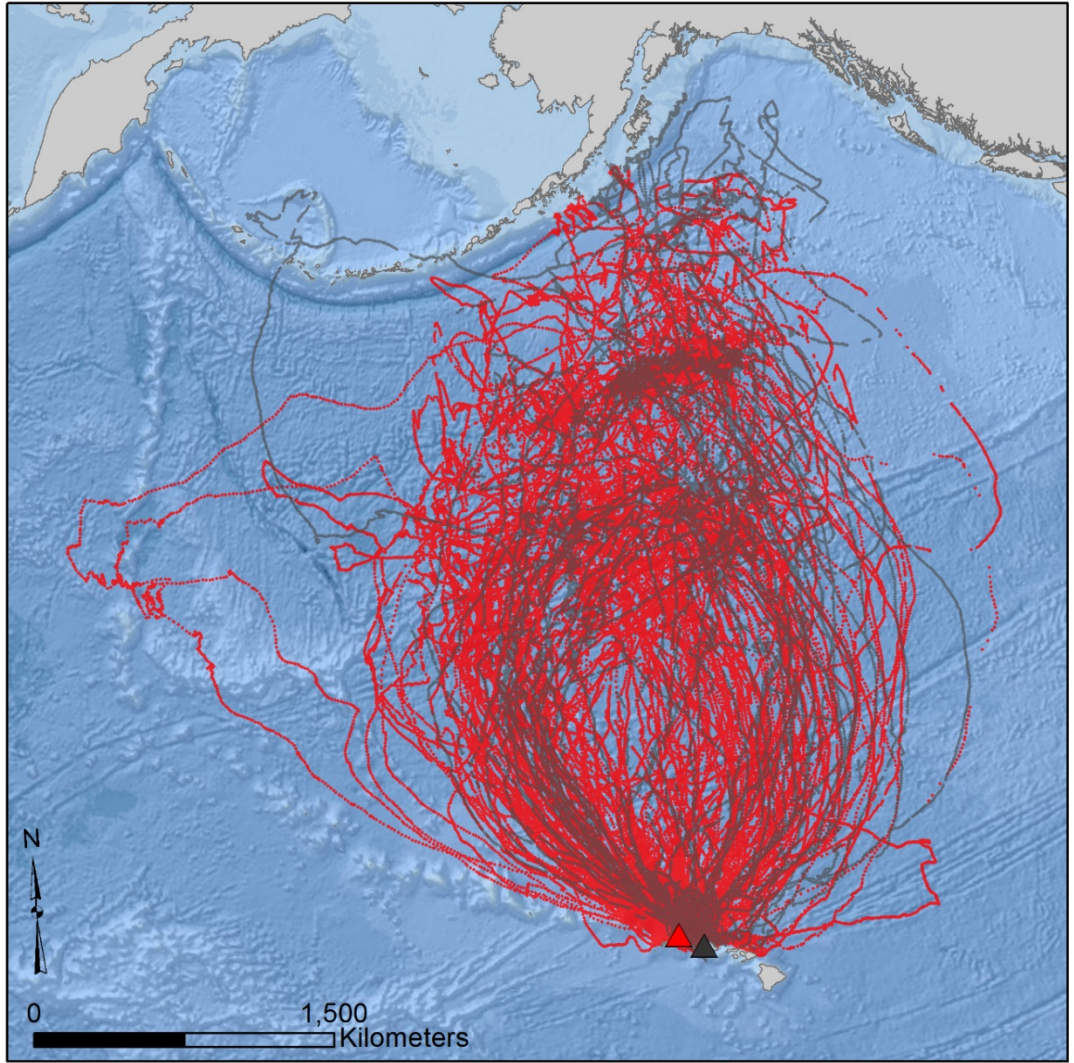


Figure 28. Raw Laysan Albatross tracking data from MHI, 2014–2016. Birds were tracked from Waipake (Kaua'i, 2016, red), Na 'Aina Kai (Kaua'i, 2014, red), and Ka'ena Point (O'ahu, 2014, dark gray). Colored triangles indicate tagging sites.

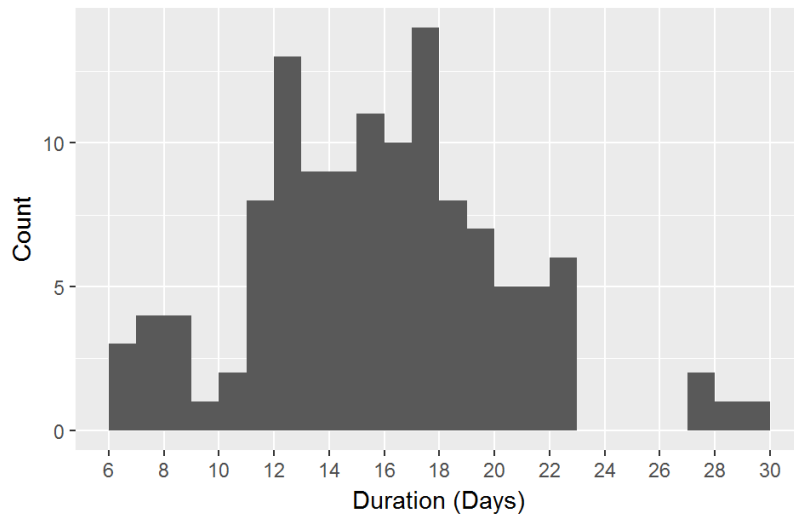
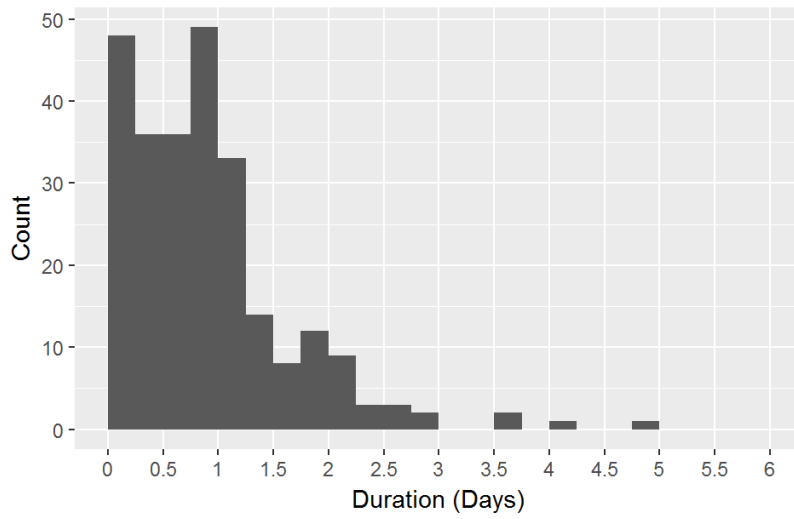
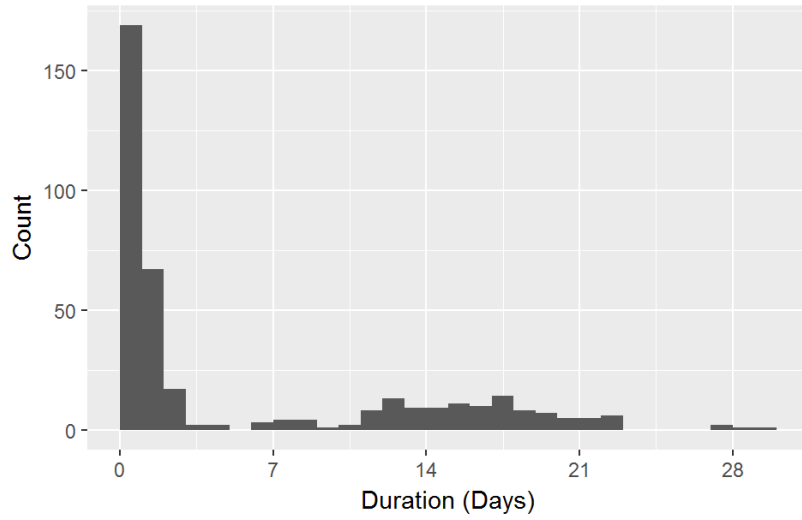


Figure 29. Histograms of Laysan Albatross foraging trip durations from all MHI sites, 2014–2016. Top: all trips. Middle: short trips (<6 days). Bottom: long trips.

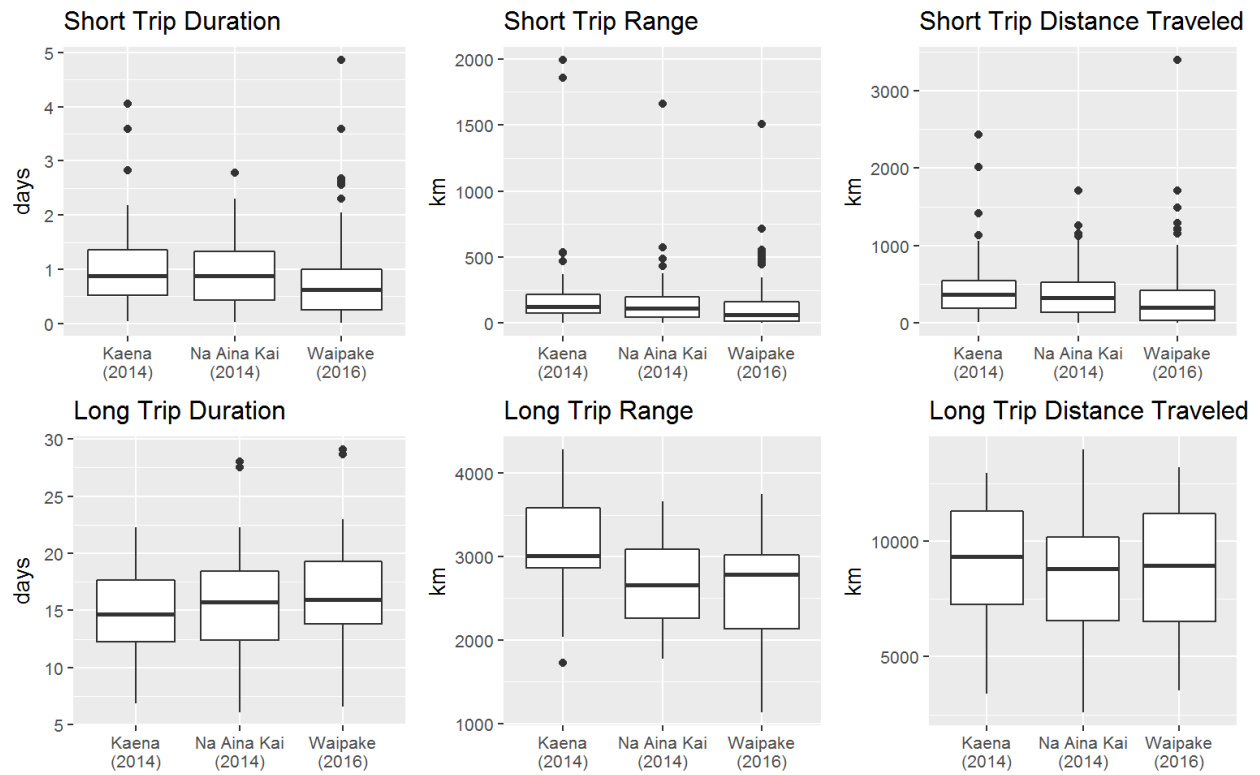


Figure 30. Box-and-whisker plots of duration (left column), range (middle column), and distance traveled (right column) for short (top row) and long (bottom row) Laysan Albatross foraging trips from all MHI sites, 2014–2016. The black line in box represents the median, the box represents the inter-quartiles (25% and 75%), the whiskers extend to the furthest point within 1.5 interquartile ranges, and dots are any additional points beyond the whiskers.

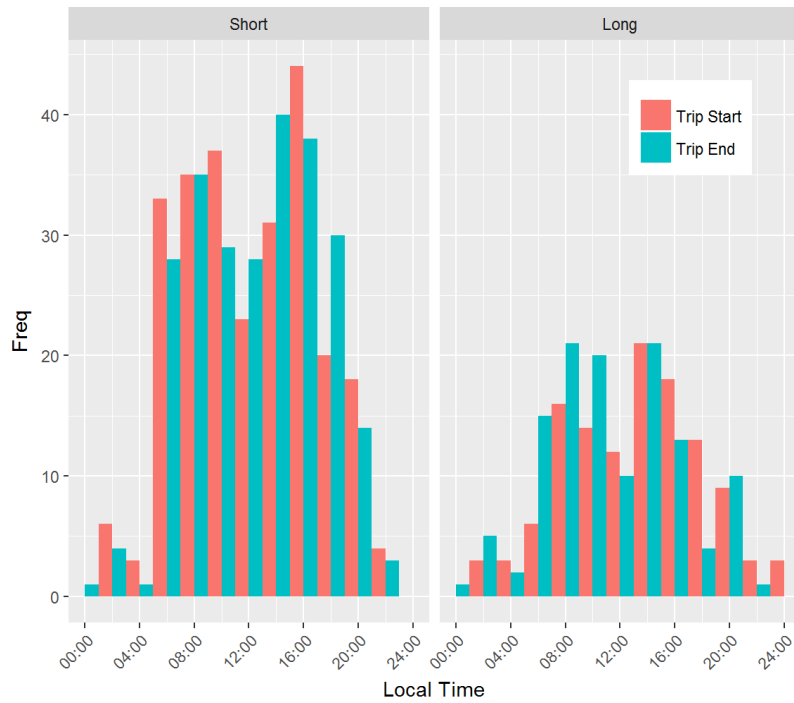


Figure 31. Histograms of trip start and end times for short and long Laysan Albatross foraging trips for all MHI sites, 2014–2016.

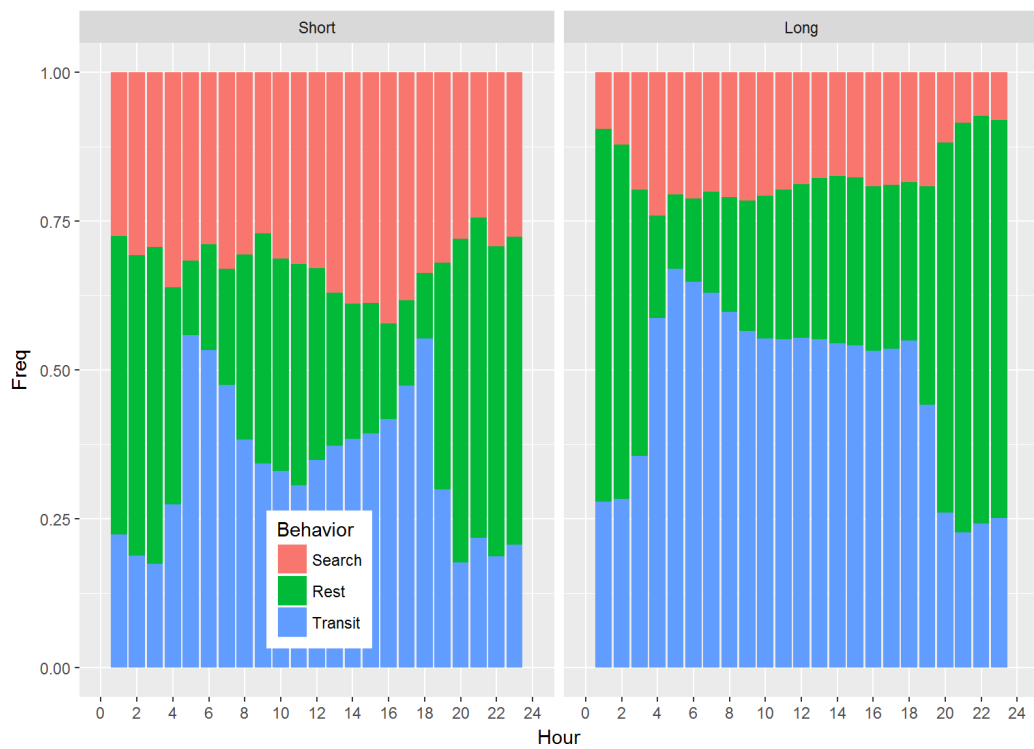


Figure 32. Daily activity patterns for all Laysan Albatrosses on short (left) and long (right) foraging trips from MHI, 2014–2016. Times are adjusted to local time at the longitude of interest (UTC time + 24 * Longitude/360).

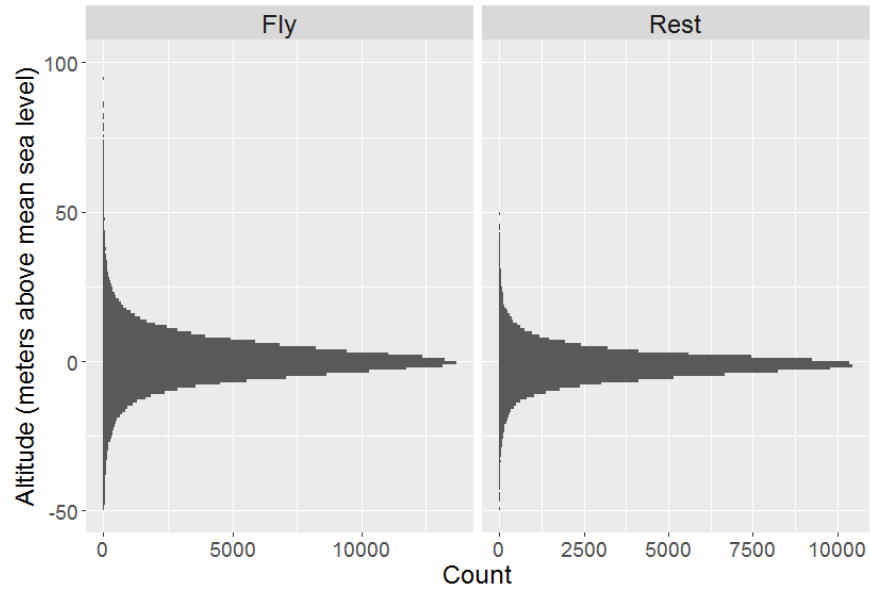


Figure 33. Histograms of Laysan Albatross altitude measurements for flying (left) and resting (right) GPS locations from all MHI sites, 2014–2016.

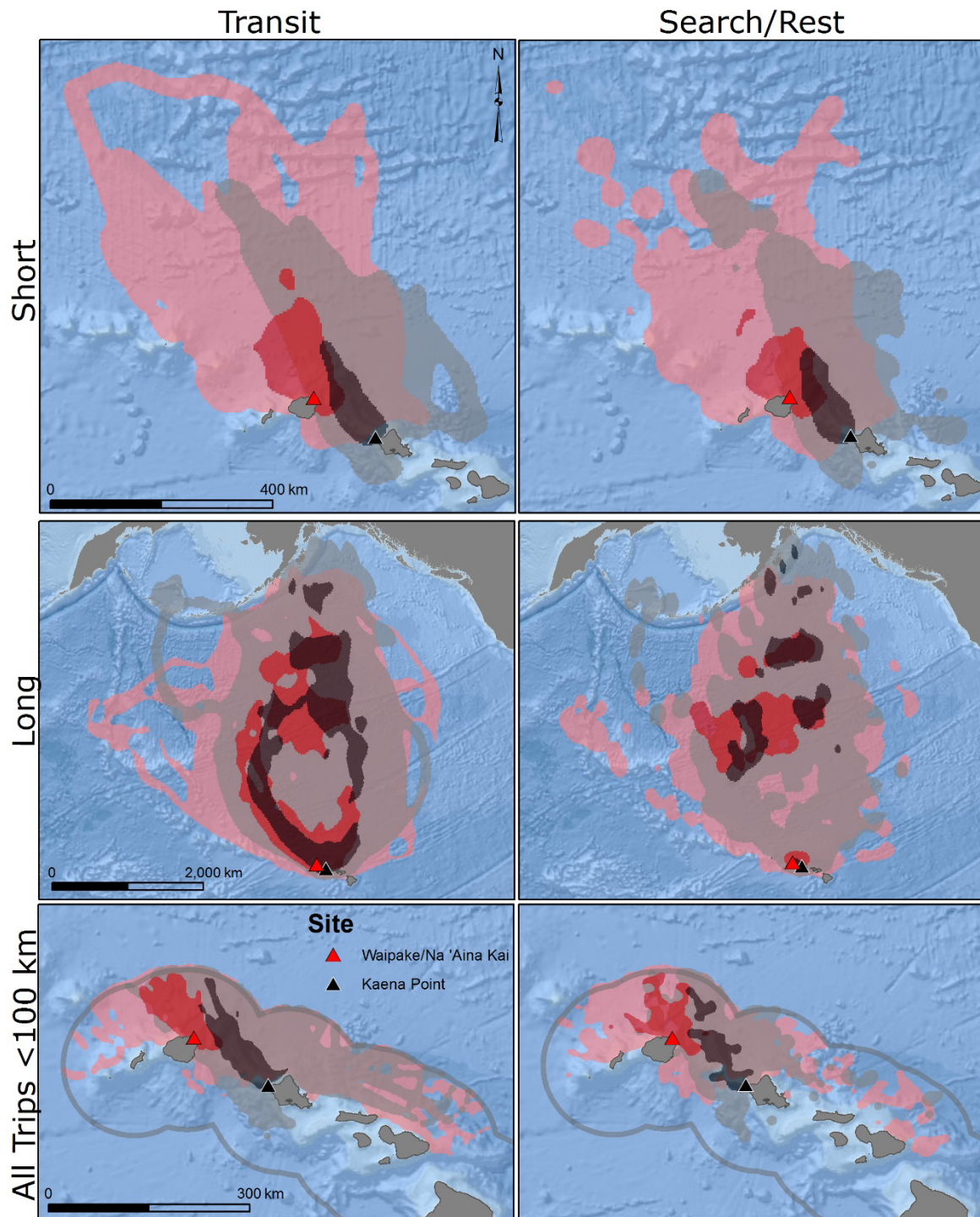


Figure 34. Kernel Density distributions for Laysan Albatrosses tracked from MHI, 2014–2016. Distributions are mapped of short trips (<6 days; top row), long trips (middle row), and all tracking data within 100 km of MHI (bottom row) for each behavioral state (columns) from Waipake/Na ‘Aina Kai (Kaua‘i; red) and Ka‘ena Point (O‘ahu; black). Colored triangles indicate site locations. Note different spatial scales of each row. Colors are shaded lighter for 99% contour and darker for 50% contour. Kernel smoothing factor set manually to 1.5% the spatial extent of the data ($h = 13.3$ km for short trips, 65.2 km for long trips, and 4.9 km for all trips <100 km).

3.3 Wedge-tailed Shearwater ('Ua'u Kani, *Ardenna pacifica*)

3.3.1 Species Account

The Wedge-tailed Shearwater (IUCN “Least Concern”) ranges across tropical and sub-tropical areas of the Pacific and Indian Oceans. Global population size is uncertain, but considered to be at least 5 million individuals, with at least one million individuals in the Hawaiian Archipelago (Whittow 1997, BirdLife International 2018). Birds are present at nesting sites and surrounding waters predominantly during the breeding season (March–November; Harrison 1990, Whittow 1997). An annual breeder, Wedge-tailed Shearwaters arrive at Hawaiian colonies early in the breeding season to bond, establish nest sites, and copulate; pre-breeding activities peak in May, after which birds go to sea for a several-week exodus before returning to lay eggs and incubate during mid-June (Whittow 1997). Incubation lasts ~50 days and young fledge in November, 3–3.5 months after hatching (Whittow 1997). Nesting usually occurs near sea level, where birds excavate burrows or occasionally nest on open ground in shaded rock alcoves or under vegetation. Travel to and from the colonies in the MHI is nocturnal (Whittow 1997). Predation by non-native predators, such as rats, cats (*Felis catus*), dogs (*Canis familiaris*), and Barn Owls (*Tyto alba*), remains a significant threat. Historically, predation by rats caused significant reproductive failures at Midway Atoll (Harrison 1990, Whittow 1997). Lighted municipalities throughout Hawaii also present significant risks for Wedge-tailed Shearwaters. Fledglings are often confused by artificial lights and become grounded before reaching the ocean (Whittow 1997).

Wedge-tailed Shearwaters fly at low altitude above the sea surface by flap-gliding or, as wind strength increases, primarily by gliding (Whittow 1997, Ainley et al. 2015). In Hawaiian waters, diet consists primarily of larval fish (goatfish [Mullidae], mackerel scad [Carangidae], and flying fish [Exocoetidae]), and, to a lesser extent, flying squid (Ommastrephidae; Harrison et al. 1983, Harrison 1990, Whittow 1997). Wedge-tailed Shearwaters are most frequently observed feeding by contact-dipping, surface-seizing, aerial pursuit, and pursuit-diving, and almost always forage in mixed-species flocks in association with subsurface predators (e.g., tunas, dolphins; Whittow 1997, Hebshi et al. 2008, Hyrenbach et al. 2014).

Wedge-tailed Shearwater foraging trip durations and ranges may vary by site and with conditions. When measured by monitoring nest attendance, mean trip durations were 1.6–1.9 days (range 1–11 days) at Tern Island (Northwestern Hawaiian Islands; Baduini 2002) and Lord Howe Island (southeastern Australia; Peck and Congdon 2006). At Heron Island in the Great Barrier Reef (east central Australia), Congdon et al. (2005) observed a distinctly bi-modal cycle in which chick-rearing adults conducted a series of short trips (mean 1.3 days, range 1–4 days) followed by a long trip (mean 8.1 days, range 6–10 days). Switching between opposite trip modes was coordinated between mates; short trips were for chick-provisioning (adults lost mass) and long trips were for self-provisioning (adults gained mass), and an equal proportion of time was spent on each trip-type during the entire chick-rearing period (Congdon et al. 2005). By tracking chick-rearing birds conducting long trips from Heron Island using platform transmitting terminal (PTT) satellite tags, McDuie et al. (2015) reported that although individuals varied their foraging destinations during self-provisioning, long trips did not represent more time foraging near the colony, but rather, long trips were conducted to access distant, and perhaps more productive, foraging sites (mean max range = 615 km from colony, well beyond the potential range of short trips). McDuie et al. (2018) found 70–85% of GPS tracks among Wedge-tailed Shearwaters from Great Barrier Reef, Australia were <24 h and within 300 km of their colony. Short-duration deployments (i.e., not long enough to capture long trips if present) of GPS tags on Wedge-tailed Shearwaters in the Seychelles recorded individually consistent short trips (mostly 1 day, maximum = 4 days) to a mean maximum range of 132 km (Cecere et al. 2013).

3.3.2 Tagging Sites and Deployment Success

Wedge-tailed Shearwaters were tracked from 11 breeding colonies in MHI, including three sites on Maui (Hāwea, Ho‘okipa, and Kama‘ole), four sites on O‘ahu (Black Point, Ka‘ena Point, Marine Corps Base Hawai‘i, and Mokū‘auia), and four sites on/near Kaua‘i (Kīlauea Point NWR, Lāwai, Lehua, and Queen’s Bath; Table 9, Figure 35). From 2013–2016, we successfully recovered tracking data from 313 of 650 GPS deployments; TDR data was successfully recovered from 55 of 84 deployments (Table 9). Unsuccessful deployments were caused either by tag loss or functionality issues, or when prolonged effort to recapture birds returning after long trips was not logistically possible. Mean GPS and TDR tracking durations were 5.1 days and 6.8 days, respectively, across all sites and years (Table 9). In 2013, tagged Wedge-tailed Shearwaters were recovered and their tags were removed any subsequent night following initial deployment, with many deployments only lasting 1–2 days. Because of concerns that this recovery scheme could cause a bias towards short foraging trips, we lagged recovery effort by 1–2 days after initial deployment in 2014–2015 to more effectively record both short and long foraging trips. As a result, tracking durations were typically less in 2013 than in subsequent years, except for at Kīlauea Point NWR (Kaua‘i) where extended recovery effort was conducted in 2013 (Table 9).

3.3.3 Foraging Trip Parameters

We identified 614 complete Wedge-tailed Shearwater foraging trips made by 299 individuals across all sites; individual trip durations ranged from 0.5 to 15 days, with an overall mean (\pm SD) of 45.6 ± 59.6 h, (1.9 ± 2.8 days; Table 10). We did document some trips <12-h long; because these occurred within the same night and often immediately after tag deployment or before tag recovery, we assumed they were caused by disturbance and therefore did not include these excursions in summaries or analysis. We categorized trips into three duration categories based on the distribution of trips and previous studies: 1) intraday trips (bird departs one night and returns the next night), 2) short trips (bird spends at least one entire night at sea and ≤ 4 -days long), and 3) long trips (trips > 4 days long; Figure 36).

Mean (\pm SD) intraday trip duration, maximum range, and distance traveled for all site-years were 16.5 ± 2.9 h, 68.2 ± 32.2 km, and 227.0 ± 68.2 km, respectively ($n = 404$; Table 10). Mean short trip duration, maximum range, and distance traveled for all site-years were 56.6 ± 17.7 h (2.4 ± 0.7 days), 152.1 ± 57.5 km, and 636.6 ± 195.8 km, respectively ($n = 115$; Table 10). Mean long trip duration, maximum range, and distance traveled for all site-years were 180.3 ± 62.1 h (7.5 ± 2.6 days), 341.9 ± 153.1 km, and $1,798.8 \pm 712.4$ km, respectively ($n = 95$; Table 10). Foraging trip parameters were consistent at the island level for each trip category (Table 10, Figure 37). Assessing the relative importance of longer trips, and how these vary across sites and islands, was challenging given variable recovery effort and low sample sizes documenting longer trips (Table 10). Deployments at Kīlauea Point NWR (Kaua‘i), however, provide the most comprehensive recovery effort and data.

Wedge-tailed Shearwater foraging trip start times were almost always at the end of the night between 04:00 and 06:00 local time, regardless of trip type (Figure 38). Whereas trip end times were clustered during the first few hours of night for intraday trips, birds conducting short trips returned to colonies during a more prolonged period throughout the first half of the night; long trips ended throughout the night, with no clear modality (Figure 38).

3.3.4 Behavioral Classification

For RST behavioral classification, we calculated a mean transit speed of 6.0 m s^{-1} for Wedge-tailed Shearwaters. A sampling rate of 180 s (3 min) resulted in a RST radius of 537 m.

Across all trip types, birds spent approximately equal proportions of their time during daylight in transit, search, and rest (Table 11). At night, transiting was the dominant behavior (53.4%) on intraday trips—by

definition, birds spent some portion of the night traveling to or from the colony; however, rest was the dominant behavior at night during short and long trips (73.0 and 71.6%, respectively; Table 11). During twilight, transit was the dominant behavior among intraday trips (74.8%) and occurred to a lesser extent during short trips (44.8%; Table 11). Behaviors during twilight among long trips were proportioned approximately equally (Table 11).

Hourly behavioral classifications of foraging trip locations revealed more detailed activity patterns. During intraday trips, transit was the dominant behavior and rest was almost entirely absent 1–2 h around sunset and sunrise (Figure 39), corresponding with peak trip end and start times, respectively (Figure 38). By mid-morning during intraday trips, the three behavioral states were proportioned equally, with transit and search increasing throughout the day (Figure 39). Peaks in flight behavior (transit and search) at the beginning and end of the day were also apparent during short and long trips; these behaviors were more frequent than rest, which reached a mid-morning maximum and then decreased throughout the day (Figure 39).

Wedge-tailed Shearwater resting and flight altitudes were all normally distributed around 0 mamsl (medians = 0.93 mamsl and 0.84 mamsl, respectively; Figure 40). The lack of distinction in altitude values between these two behavioral states likely reflects low flight heights of shearwaters. Using our error simulation method, we estimated that Wedge-tailed Shearwaters spend 5.20% (95% CI 5.13–5.27%) of flight time in the RSZ. Even though there was variability in the altitude measurements, it did not induce appreciable variation in the final proportion of time spent flying in RSZ, because underestimated and overestimated altitudes tended to cancel each other out.

3.3.5 Spatial Distribution

Wedge-tailed Shearwaters tracked from Kaua‘i, O‘ahu, and Maui are shown in different figures (one island per figure) for convenience and so that area-use could be better visualized according to each colony/island (Figure 41, Figure 42, Figure 43). Kernel density estimates 1) do not always represent concurrent deployments and 2) deployment effort, tag recovery success, and deployment duration were variable across sites (see Table 9); overlap depicted in these figures should be interpreted with these caveats in mind. Tracks from shearwaters tagged at the Black Point (O‘ahu) and Queen’s Bath (Kaua‘i) colonies are not included here because data were too few for calculating meaningful kernel density estimates.

On Maui, Wedge-tailed Shearwater intraday trips were primarily restricted to areas immediately offshore of colonies, with core-use focused within 100 km of shore (Figure 41). The distributions of shearwaters tracked from Ho‘okipa and Hāwea, both on the northern side of Maui, partially overlapped, whereas birds tracked from Kama‘ole 3 on the south side of Maui remained mostly isolated from the other two colonies (Figure 41). Similar patterns persisted for short trips; however, core-use areas extended up to 150 km from colonies and birds from northshore Ho‘okipa and Hāwea colonies had additional core-use areas that overlapped with Kama‘ole 3 birds along the west and north shores of the island of Hawai‘i (Figure 41). Long trip core-use extended to 350 km from colonies and, in addition to using areas similar to short trips, included more offshore waters from north of Kaua‘i to northwest of Hawai‘i (Hāwea), north of Maui and Hawai‘i (Ho‘okipa), and northwest and south of Hawai‘i (Kama‘ole 3; Figure 41). The tri-colony use of Hawai‘i extended around the entire island during long trips (Figure 41). When considering the distributions of all trips that occurred within 100 km of MHI, there was significant overlap among all three Maui colonies at the home range level, but core-use overlap predominantly occurred between the northshore colonies (Hāwea and Ho‘okipa) in waters north of Maui (Figure 41).

Core-use of Wedge-tailed Shearwaters tracked during intraday trips from O‘ahu colonies included areas adjacent to and 50–100 km offshore from colony locations; however, shearwaters from Mokū‘auia and Marine Corps Base Hawai‘i overlapped with Ka‘ena Point birds immediately offshore of Ka‘ena Point

(Figure 42). Short trip core-use extended up to 100–200 km offshore. There was significant core-use overlap among all three O‘ahu colonies in the eastern Kaua‘i Channel between Kaua‘i and O‘ahu, and to the northwest and southwest of O‘ahu (Figure 42). Shearwaters on short trips from Marine Corps Base Hawai‘i also traveled offshore toward the northeast. On long trips, shearwaters from Marine Corps Base Hawai‘i mostly utilized waters 200–500 km north of O‘ahu, although some core-use occurred south of the MHI and along the west shore of the island of Hawai‘i (Figure 42). Birds on long trips from Mokū‘auia mostly utilized waters in the channel between O‘ahu and Kaua‘i, waters around Kaua‘i, offshore waters 300–400 km north and south of the MHI, and the western shore of Hawai‘i (Figure 42). Transiting behavior core-use of shearwaters during long trips from Ka‘ena Point was focused in the channel between O‘ahu and Kaua‘i, but most searching core-use was concentrated in waters 300–500 km north and south of the MHI (Figure 42). Overlap of long trip home ranges was substantial when considering all three O‘ahu colonies, but tri-colony core-use overlap was more limited to the channel between O‘ahu and Kaua‘i, waters 200–300 km south of Kaua‘i/O‘ahu, and waters 300–500 km north of the MHI (Figure 42). Within 100 km of the MHI, core-use among all Wedge-tailed Shearwater foraging trips from O‘ahu colonies was concentrated near- and offshore of northwest, northern, and northeast O‘ahu, and we documented significant overlap among birds from all three colonies near Ka‘ena Point, O‘ahu (Figure 42).

During intraday trips from Kaua‘i (Kīlauea Point NWR, Lāwai) and Ni‘ihau (Lehua Islet), Wedge-tailed Shearwaters used waters adjacent to and within 50–100 km of colony sites, with little overlap (Figure 43). During short trips, birds from Kīlauea Point NWR ranged from north coastal waters to 150 km north of Kaua‘i, Lāwai shearwaters traveled up to 150 km south-southwest of Kaua‘i, and birds from Lehua used waters west and south of Ni‘ihau/Kaua‘i. Core-use areas among Lāwai and Lehua shearwaters partially overlapped south of Ni‘ihau/Kaua‘i (Figure 43). During long trips, core-use areas of Wedge-tailed Shearwaters from Kīlauea Point NWR extended from northern, western, and southern coastal Kaua‘i to 200 km offshore, and additional core-use areas were located 300–500 km north of and 300–400 km southwest of Kaua‘i (Figure 43). During long trips, core-use areas from Lehua were located 50–200 km southwest and northwest of Ni‘ihau, and the core-use area of shearwaters from Lāwai was located 150–450 km southeast of Kaua‘i (Figure 43). Due to limited tracking effort at Lehua and Lāwai, long trip sample sizes were low and trip durations were shorter than the range of long trips measured at other sites (Table 9, Table 10); therefore, interpretation of inter-colony spatial overlap should be done with caution. Within 100 km of the MHI, core-use areas of Wedge-tailed Shearwater transiting behavior on all trip types from Kaua‘i/Ni‘ihau colonies occurred in coastal waters adjacent to and up to 100 km from colony sites; inter-colony core-use area overlap mostly occurred associated with search/rest behavior in coastal and offshore waters south of Kaua‘i/Ni‘ihau (Figure 43).

When all Wedge-tailed Shearwater tracking data within 100 km of MHI (all trips combined) were mapped at the island-level, kernel density estimates revealed almost no inter-island overlap among core-use areas for birds from Maui, O‘ahu, and Kaua‘i sites, with the exception of shearwaters from O‘ahu and Maui that used western coastal waters off the island of Hawai‘i (Figure 44).

3.3.6 Diving Behavior

We recovered data from 55 TDR deployments on Wedge-tailed Shearwaters (Table 9); data were excessively noisy and uninterpretable for 11 deployments, limiting our sample to 44 deployments. We identified 897 valid dives made by 39 Wedge-tailed Shearwaters and 5 shearwaters performed no valid dives (Table 12). The distribution of Wedge-tailed Shearwaters dive depths was right-skewed; mean (\pm SD) depth was 1.78 ± 1.35 m (median = 1.38 m; Table 12; Figure 45). The average maximum dive depth per individual was 4.40 ± 1.17 m and the deepest dive recorded was to 10.06 m. The distribution of Wedge-tailed Shearwater dive durations was right-skewed; mean (\pm SD) duration was 3.12 ± 3.44 s (median = 1.80 s; Table 12; Figure 46). The average maximum dive duration per individual was 9.11 ± 5.24 s and the longest dive lasted 25.2 s. These distributions are likely skewed slightly toward deeper and longer dives because dives shallower than 0.5 m were excluded due to TDR limitations. Recorded dive durations

were shorter in 2015 than 2014, but this was likely due to a change in the tag programming rather than an inter-annual change in behavior (Table 12). A 1-m threshold was used for the TDRs deployed in 2015, which improved memory and battery performance, but likely truncated the shortest and shallowest dives.

Diving activity peaked during the late morning and early afternoon, and no diving occurred at night (Figure 47). The results of the behavioral classification also detected peaks in searching activity at similar times (see 3.3.4 Behavioral Classification). To analyze dive frequency for Wedge-tailed Shearwaters, we calculated the number of dives per hour during daylight (06:00–20:00 local time) per deployment. Shearwaters performed on average 0.24 ± 0.27 dives h^{-1} (median = 0.13 dives h^{-1} , range = 0.00–1.09 dives h^{-1} , $n = 44$ deployments). Note that sample size is greater than reported in the previous paragraph and in Table 12 because no valid dives were recorded for 5 shearwater TDR deployments (Figure 48). Most shearwaters (70%) dove <0.3 dives h^{-1} during daylight, but we observed sex-specific differences: all females performed <0.4 dives h^{-1} during daylight, but males dove as frequently as 1.1 dives h^{-1} of daylight (Figure 48).

3.3.7 Tables and Figures

Table 9. Wedge-tailed Shearwater deployment and recovery success for each site and deployment session in MHI, 2013–2015. “Birds tagged” is the total number of individuals tagged with any combination of tag types. “GPS/TDR deployed” and “GPS/TDR data” indicate number of each tag type deployed and number from which data was successfully recovered, respectively. “Mean GPS/TDR duration” indicate the mean time duration (in days) between tag deployment and tag recovery.

Island	Site	Year	Deployment Session	Nest Status	Birds tagged	GPS depl.	GPS data	Mean (SD) GPS duration	TDR depl.	TDR data	Mean (SD) TDR duration	
Kaua'i	Kīlauea Point	2013	12-Aug–28-Aug	Chick	20	20	19	4.3 ± 4.4	0	0	NA	
			31-Aug–10-Sep	Chick	20	20	14	4.2 ± 3.7	0	0	NA	
			20-Sep–29-Sep	Chick	20	20	3	4.0 ± 4.2	0	0	NA	
		2015	19-Aug–01-Sep	Chick	30	20	8	8.8 ± 3.2	10	10	6.6 ± 2.9	
			12-Sep–01-Oct	Chick	29	20	13	7.2 ± 5.2	9	9	4.9 ± 4.6	
	Lāwai	2014	26-Aug–05-Sep	Chick	20	20	16	5.9 ± 1.4	0	0	NA	
			01-Oct–09-Oct	Chick	15	0	0	NA	15	6	4.3 ± 1.7	
	Lehua	2014	03-Sep–13-Sep	Chick	20	20	8	7.1 ± 1.5	0	0	NA	
	Queen's Bath	2014	14-Sep–28-Sep	Chick	20	20	8	9.4 ± 2.8	0	0	NA	
	Kaua'i Total:					194	160	89	6.1 ± 3.93	34	25	5.5 ± 3.43
Maui	Hāwea	2013	20-Aug–22-Aug	Chick	20	20	11	1.2 ± 0.4	0	0	NA	
			07-Oct–09-Oct	Chick	18	18	9	1.3 ± 0.5	0	0	NA	
		2014	08-Oct–16-Oct	Chick	27	20	10	5.7 ± 0.7	7	5	6.0 ± 1.2	
			2015	18-Aug–02-Sep	Chick	25	20	10	5.7 ± 3.4	5	4	11.8 ± 5.3
				16-Sep–28-Sep	Chick	23	20	7	6.9 ± 3.5	3	3	5.6 ± 0.6
	Ho'okipa	2013	10-Sep–16-Sep	Chick	20	20	14	2.3 ± 2.0	0	0	NA	
			2014	10-Sep–23-Sep	Chick	30	20	3	12.0 ± 1.6	10	4	9.5 ± 2.8
			2015	15-Sep–25-Sep	Chick	23	20	10	6.2 ± 2.0	3	3	4.7 ± 1.2
	Kama'ole 3	2014	19-Aug–27-Aug	Chick	20	20	8	5.9 ± 1.4	0	0	NA	
			2015	17-Aug–31-Aug	Chick	25	20	11	9.4 ± 3.6	5	5	6.6 ± 0.9
Maui Total:					231	198	93	5.0 ± 3.7	33	24	7.5 ± 3.3	
O'ahu	Black Point	2013	19-Aug–22-Aug	Chick	10	10	4	2.0 ± 0.1	0	0	NA	
	Ka'ena Point	2013	15-Aug–19-Aug	Chick	20	20	8	3.2 ± 0.5	0	0	NA	
			08-Sep–11-Sep	Chick	20	20	16	1.4 ± 0.6	0	0	NA	
			29-Sep–02-Oct	Chick	20	20	12	1.7 ± 0.9	0	0	NA	
		2014	15-Aug–21-Aug	Chick	20	20	12	4.4 ± 0.7	0	0	NA	
			13-Sep–27-Sep	Chick	26	20	4	11.5 ± 5.0	6	1	13.9	
		2015	17-Aug–29-Aug	Chick	30	20	10	7.9 ± 2.6	10	4	7.0 ± 3.4	
			Marine Corps Base Hawai'i	2014	15-Aug–26-Aug	Chick	20	20	5	7.1 ± 2.2	0	0
	12-Sep–21-Sep	Chick			22	22	6	5.4 ± 2.5	0	0	NA	
	Mokū'auia	2013	12-Aug–20-Aug	Chick	20	20	11	3.1 ± 1.8	0	0	NA	
08-Sep–12-Sep			Chick	20	20	12	2.0 ± 1.3	0	0	NA		

Island	Site	Year	Deployment Session	Nest Status	Birds tagged	GPS depl.	GPS data	Mean (SD) GPS duration	TDR depl.	TDR data	Mean (SD) TDR duration
			26-Sep–01-Oct	Chick	20	20	7	1.6 ± 1.5	0	0	NA
		2014	13-Aug–23-Aug	Chick	20	20	12	5.8 ± 2.6	0	0	NA
			10-Sep–26-Sep	Chick	21	20	3	9.3 ± 3.7	1	1	15.2
O'ahu Total:					309	292	131	4.5 ± 3.7	17	6	9.5 ± 4.8
ALL SITES TOTAL:					734	650	313	5.1 ± 3.8	84	55	6.8 ± 3.7

Table 10. Mean (\pm SD) Wedge-tailed Shearwater foraging trip duration, maximum range, and distance traveled for intraday, short, long, and all trips combined for all MHI tagging sites, 2013–2015.

Trip Type	Island	Site (Year)	Birds	Trips	Duration (h)	Range (km)	Traveled (km)
Intraday	Kaua'i	Kīlauea Point (2013)	22	29	16.7 ± 2.5	74.9 ± 30.8	248.1 ± 65.7
		Kīlauea Point (2015)	14	27	16.5 ± 2.3	70.6 ± 34.5	239.0 ± 71.4
		Lāwai (2014)	11	22	16.2 ± 2.6	44.7 ± 27.2	199.5 ± 52.6
		Lehua (2014)	7	14	16.5 ± 2.2	51.0 ± 22.5	205.9 ± 56.5
		Queens Bath (2014)	4	6	17.4 ± 2.4	44.3 ± 26.1	182.5 ± 92.0
		Kaua'i Total:	58	98	16.6 ± 2.4	61.7 ± 32.1	224.6 ± 67.8
	Maui	Hāwea (2013)	16	19	18.4 ± 4.8	76.9 ± 41.8	230.7 ± 88.3
		Hāwea (2014)	4	12	19.3 ± 3.0	87.6 ± 12.6	262.8 ± 27.4
		Hāwea (2015)	15	41	16.6 ± 3.2	85.6 ± 33.2	266.8 ± 78.9
		Ho'okipa (2013)	12	15	16.0 ± 2.1	63.1 ± 20.3	190.7 ± 43.9
		Ho'okipa (2015)	6	11	17.1 ± 4.1	41.7 ± 14.0	183.5 ± 55.2
		Kama'ole 3 (2014)	7	17	17.0 ± 2.1	83.3 ± 21.1	253.9 ± 56.8
		Kama'ole 3 (2015)	11	24	16.3 ± 2.3	84.6 ± 23.3	260.1 ± 39.5
		Maui Total:	71	139	17.0 ± 3.3	78.2 ± 30.4	244.0 ± 69.3
	O'ahu	BlackPoint (2013)	3	5	16.2 ± 2.2	102.6 ± 19.1	255.2 ± 29.9
		Ka'ena (2013)	32	52	16.1 ± 3.2	56.0 ± 22.9	208.2 ± 51.3
		Ka'ena (2014)	11	32	15.6 ± 1.5	45.8 ± 20.0	177.9 ± 55.8
		Ka'ena (2015)	7	24	14.8 ± 2.1	62.3 ± 39.5	208.9 ± 73.3
		MCBH (2014)	1	2	19.6 ± 4.6	77.6 ± 14.3	318.7 ± 83.3
		MCBH (2015)	3	4	17.0 ± 4.0	92.2 ± 35.8	236.7 ± 73.2
Mokū'auia (2013)		23	32	16.7 ± 3.2	79.3 ± 34.0	240.5 ± 59.8	
Mokū'auia (2014)		9	16	15.7 ± 2.4	73.4 ± 35.1	232.4 ± 82.3	
O'ahu Total:		89	167	15.9 ± 2.7	63.6 ± 31.9	214.3 ± 64.8	
Intraday Total:			218	404	16.5 ± 2.9	68.2 ± 32.2	227.0 ± 68.2
Short	Kaua'i	Kīlauea Point (2013)	5	5	57.2 ± 12.2	179.8 ± 109.5	659.8 ± 214.9
		Kīlauea Point (2015)	8	8	40.6 ± 3.7	136.1 ± 48.6	475.4 ± 95.4
		Lāwai (2014)	6	8	59.4 ± 20.6	150.6 ± 62.1	653.7 ± 207.8
		Lehua (2014)	4	5	71.8 ± 26.9	168.5 ± 35.2	788.0 ± 209.0
		Queens Bath (2014)	2	4	61.0 ± 24.2	132.5 ± 58.7	624.0 ± 278.2
		Kaua'i Total:	25	30	56.3 ± 20.0	152.2 ± 63.1	625.6 ± 210.3
	Maui	Hāwea (2013)	2	2	41.2 ± 5.2	131.2 ± 57.7	478.1 ± 151.0
		Hāwea (2014)	3	3	45.7 ± 4.3	137.6 ± 52.2	507.3 ± 44.7
		Hāwea (2015)	9	11	55.8 ± 16.9	190.7 ± 69.0	723.8 ± 192.3
		Ho'okipa (2013)	3	3	65.7 ± 22.5	174.6 ± 26.9	682.1 ± 192.7
		Ho'okipa (2015)	6	7	70.1 ± 23.4	122.6 ± 36.4	653.8 ± 219.5
		Kama'ole 3 (2014)	6	7	57.0 ± 20.7	132.0 ± 38.6	664.5 ± 183.5

Trip Type	Island	Site (Year)	Birds	Trips	Duration (h)	Range (km)	Traveled (km)
		Kama'ole 3 (2015)	7	9	55.9 ± 15.7	180.9 ± 57.5	709.2 ± 199.2
		Maui Total:	36	42	57.4 ± 18.2	161.3 ± 57.6	669.5 ± 189.4
	O'ahu	BlackPoint (2013)	1	1	41.4	135.1	469.9
		Ka'ena (2013)	5	5	50.7 ± 12.5	106.0 ± 38.1	478.1 ± 135.8
		Ka'ena (2014)	2	2	56.4 ± 16.5	164.4 ± 63.3	744.0 ± 137.3
		Ka'ena (2015)	4	6	44.1 ± 9.4	97.5 ± 21.3	415.4 ± 116.6
		MCBH (2014)	6	7	61.0 ± 11.6	187.0 ± 80.4	748.1 ± 135.3
		MCBH (2015)	4	5	52.5 ± 21.9	175.5 ± 10.5	647.2 ± 243.2
		Mokū'auia (2013)	9	10	65.9 ± 15.3	128.3 ± 37.6	635.4 ± 149.0
		Mokū'auia (2014)	7	7	55.4 ± 17.9	159.6 ± 42.6	674.1 ± 219.9
		O'ahu Total:	38	43	56.0 ± 15.8	143.4 ± 53.0	613.6 ± 191.6
		Short Total:	99	115	56.6 ± 17.7	152.1 ± 57.5	636.6 ± 195.8
Long	Kaua'i	Kīlauea Point (2013)	11	11	210.0 ± 55.8	412.4 ± 177.6	1737.0
		Kīlauea Point (2015)	13	13	186.4 ± 59.4	397.9 ± 253.2	1,998.7 ± 908.1
		Lāwai (2014)	8	8	130.7 ± 37.6	304.1 ± 84.7	1,333.5 ± 558.8
		Lehua (2014)	4	4	155.9 ± 11.5	191.9 ± 6.0	1,453.5 ± 43.7
		Queens Bath (2014)	6	6	201.0 ± 15.5	235.7 ± 21.3	1,641.7 ± 252.5
		Kaua'i Total:	42	42	180.0 ± 57.4	352.1 ± 188.0	1,690.9 ± 742.5
	Maui	Hāwea (2014)	4	4	130.0 ± 14.6	228.7 ± 114.9	1,262.7 ± 65.3
		Hāwea (2015)	4	4	200.9 ± 61.6	364.8 ± 63.5	2,280.9 ± 691.1
		Ho'okipa (2013)	1	1	113.2	200.9	763.4
		Ho'okipa (2014)	1	1	NA	NA	NA
		Ho'okipa (2015)	3	3	169.4 ± 60.2	193.9 ± 98.3	1,442.1 ± 455.6
		Kama'ole 3 (2014)	1	1	183.1	300.3	1,808.6
		Kama'ole 3 (2015)	6	6	209.8 ± 51.5	352.6 ± 90.9	2,078.7 ± 478.2
		Maui Total:	20	20	174.5 ± 54.1	290.0 ± 107.6	1,728.7 ± 628.0
	O'ahu	Ka'ena (2014)	3	3	111.3	233.3	1,325.2
		Ka'ena (2015)	5	5	190.4 ± 53.4	407.5 ± 133.0	2,012.8 ± 630.8
		MCBH (2014)	7	7	154.6 ± 56.4	313.5 ± 80.4	1,501.2 ± 463.5
		MCBH (2015)	9	9	242.0 ± 84.1	435.2 ± 115.3	2,456.2 ± 824.3
		Mokū'auia (2013)	1	1	110.2	251.6	1,048.1
		Mokū'auia (2014)	8	8	157.1 ± 58.0	299.5 ± 111.8	1,950.5 ± 671.4
		O'ahu Total:	33	33	184.3 ± 73.6	361.8 ± 120.1	1,938.8 ± 736.9
		Long Total:	95	95	180.3 ± 62.1	341.9 ± 153.1	1,798.8 ± 712.4
		Grand Total:	299	614	45.6 ± 59.6	121.8 ± 115.5	489.3 ± 566.3

Table 11. Percentage of time (and number of locations, N) for behavior classes during day, night, and twilight on intraday, short, and long Wedge-tailed Shearwater foraging trips from all MHI sites, 2013–2015.

Trip Type	Behavior	Day	Night	Twilight
Intraday	Rest	31.4% (31,483)	38.0% (6,238)	9.4% (1,488)
	Search	31.5% (31,570)	8.6% (1,404)	15.7% (2,478)
	Transit	37.1% (37,127)	53.4% (8,753)	74.8% (11,802)
Short	Rest	26.5% (19,730)	73.0% (30,323)	27.2% (4,050)
	Search	33.1% (24,605)	10.4% (4,339)	28.1% (4,185)
	Transit	40.4% (30,050)	16.6% (6,896)	44.8% (6,670)
Long	Rest	27.1% (49,468)	71.6% (87,740)	37.2% (14,307)
	Search	36.2% (66,019)	16.0% (19,662)	30.7% (11,798)
	Transit	36.7% (66,874)	12.4% (15,172)	32.1% (12,369)

Table 12. Mean (\pm SD) dive duration and depth of Wedge-tailed Shearwaters tagged with temperature-depth recorder (TDR) tags from MHI sites, 2014–2015. Note that sample sizes may be slightly lower than reported in Table 9 because no dives were recorded or no valid dives were identified from some TDR deployments.

Year	Birds	Dives	Duration (s)	Depth (m)
2014	17	489	4.02 \pm 3.86	1.91 \pm 1.52
2015	22	408	2.04 \pm 2.45	1.63 \pm 1.09
All	39	897	3.12 \pm 3.44	1.78 \pm 1.35

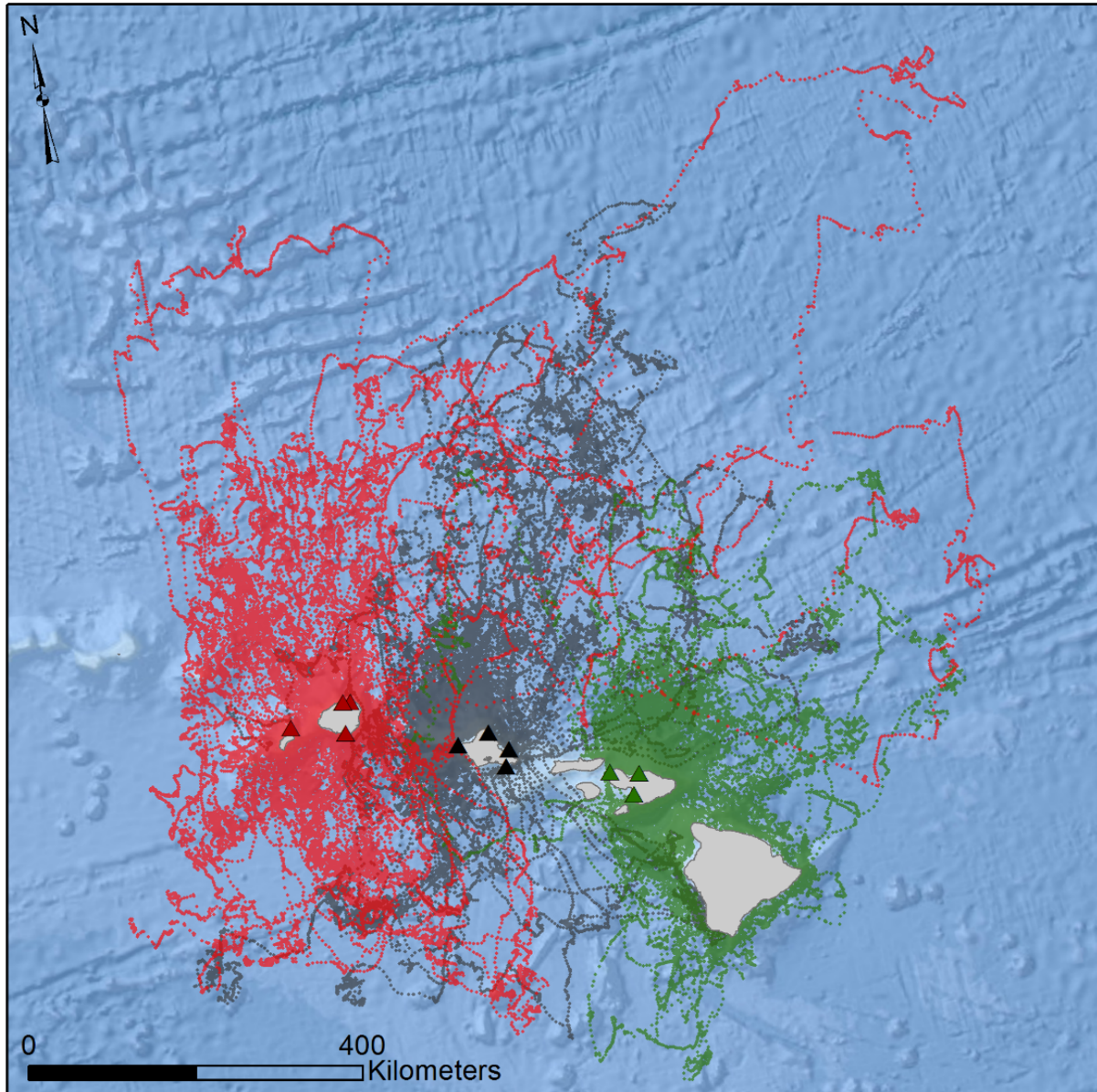


Figure 35. Raw Wedge-tailed Shearwater tracking data from MHI, 2013–2015. Birds were tracked from Kaua'i/Lehua (2013–2016, red), O'ahu (2013–2015, black), and Maui (2013–2015, green). Colored triangles indicate tagging sites.

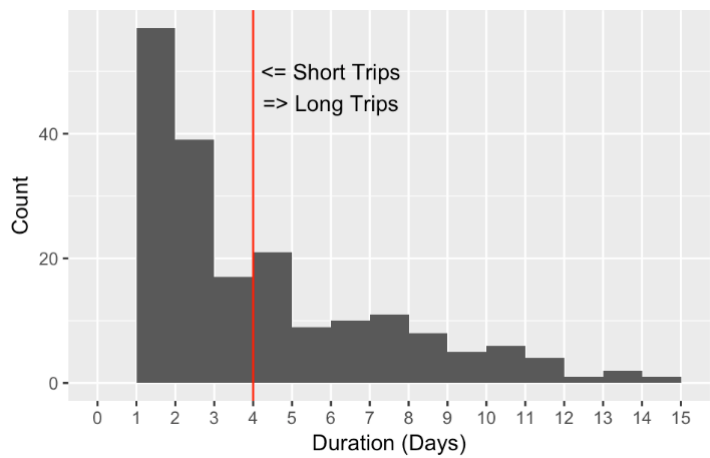
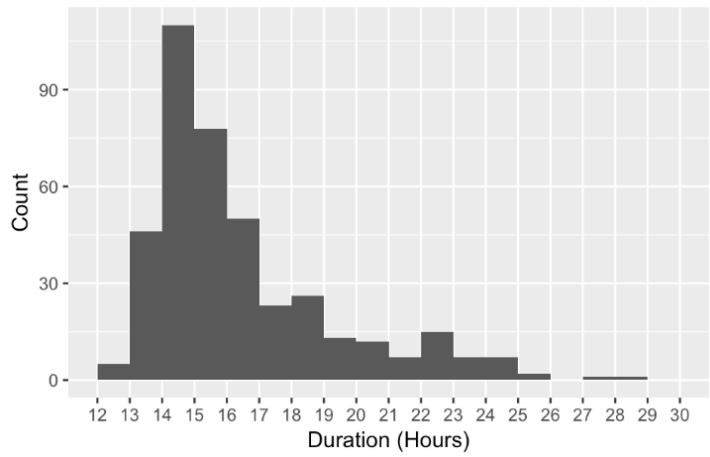
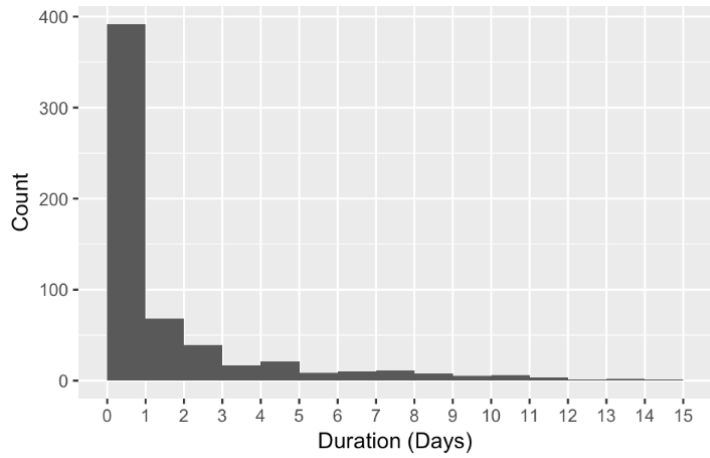


Figure 36. Histograms of Wedge-tailed Shearwater foraging trip durations from all MHI sites, 2013–2015. Top: all trips. Middle: intra-day trips, defined as a trip in which a bird left the colony one night and returned the subsequent night. Bottom: multiday trips, defined as both short trips (>1 day and ≤4 days) and long trips (>4 days).

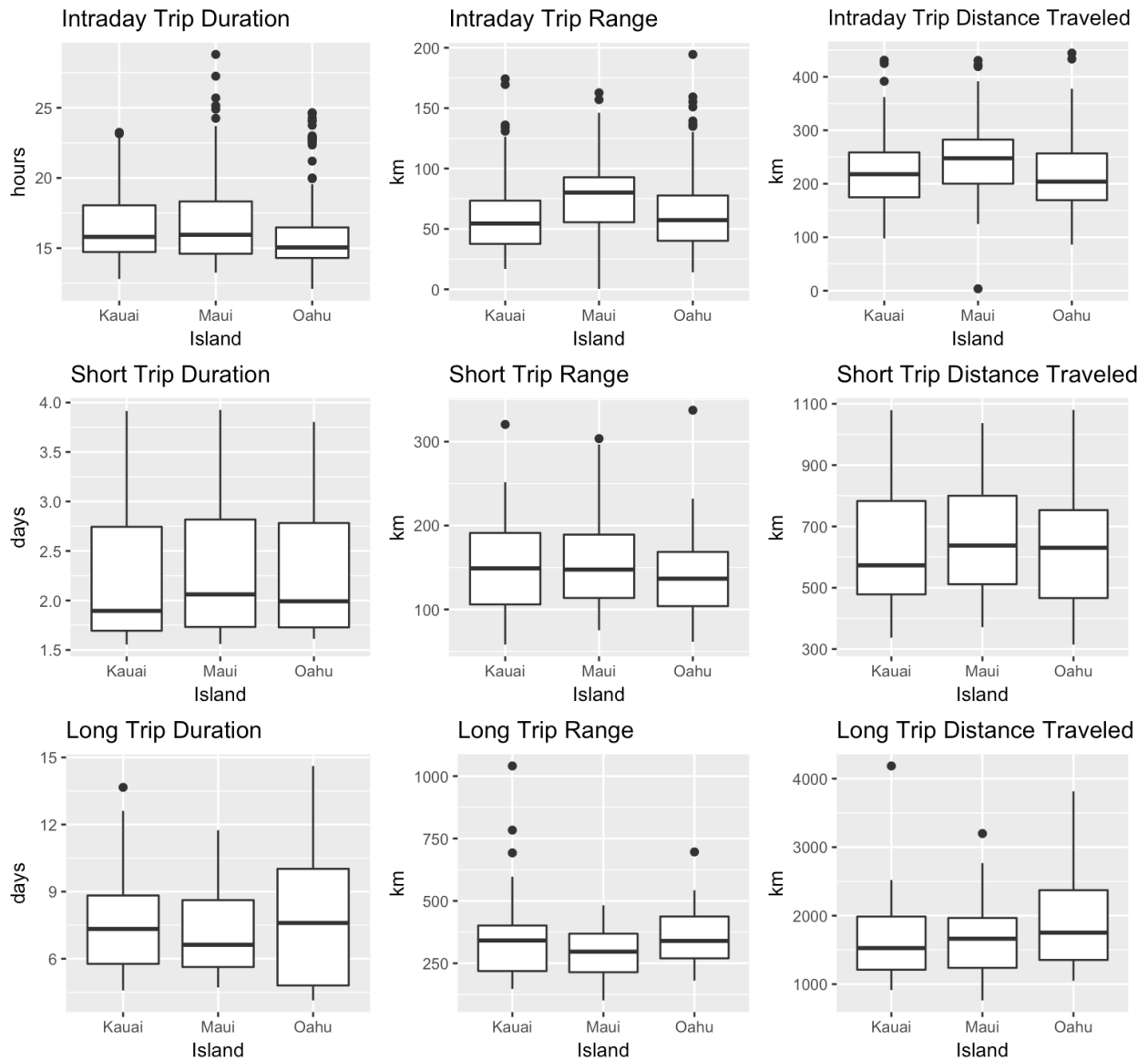


Figure 37. Box-and-whisker plots of duration (left column), range (middle column), and distance traveled (right column) for intraday (top row), short (middle row), and long (bottom row) Wedge-tailed Shearwater foraging trips from all MHI sites on Kaua'i, O'ahu, and Maui, 2013–2015. The black line in box represents the median, the box represents the inter-quartiles (25% and 75%), the whiskers extend to the furthest point within 1.5 interquartile ranges, and dots are any additional points beyond the whiskers.

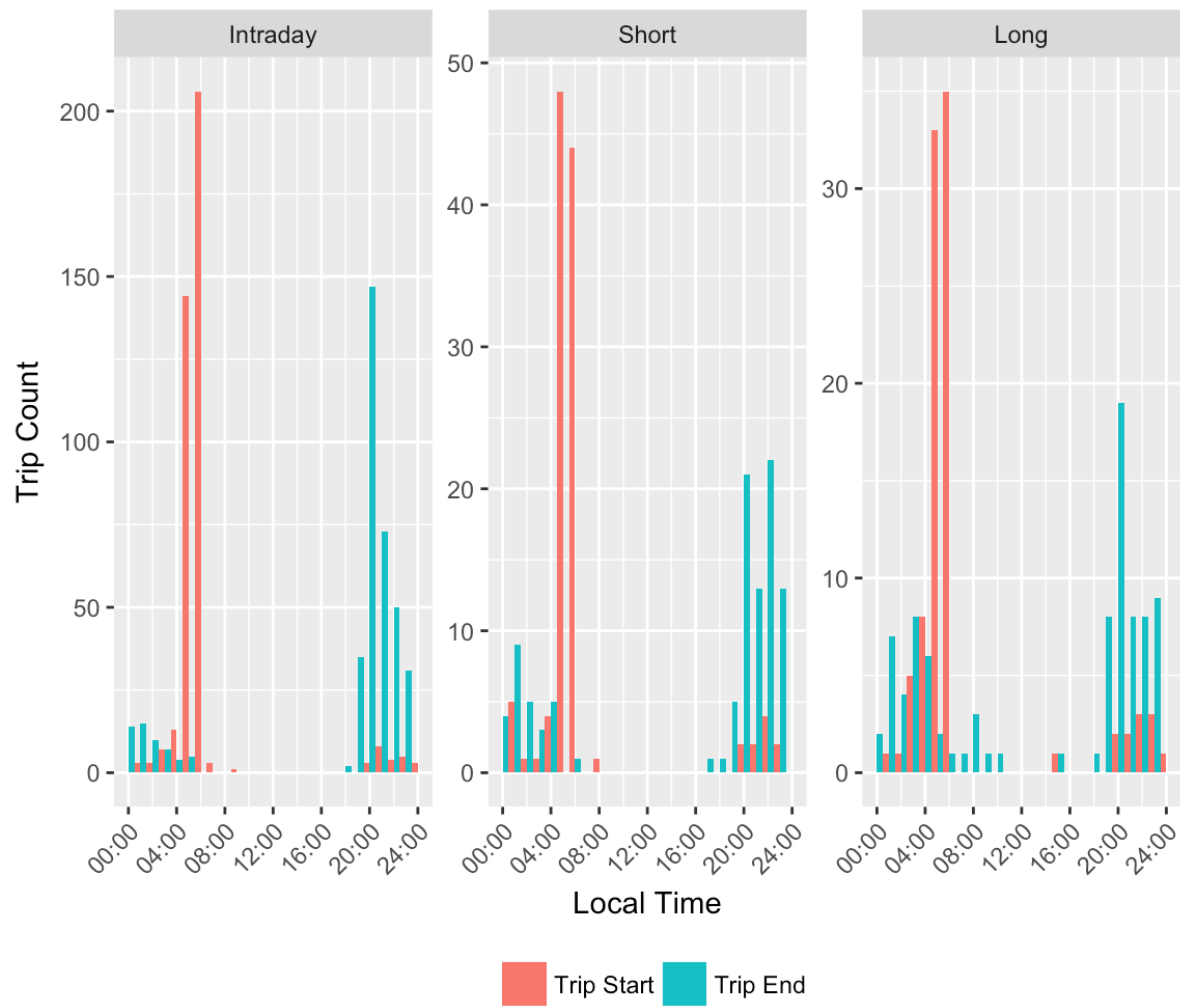


Figure 38. Histograms of trip start and end times for intraday, short, and long Wedge-tailed Shearwater foraging trips for all MHI sites, 2013–2015.

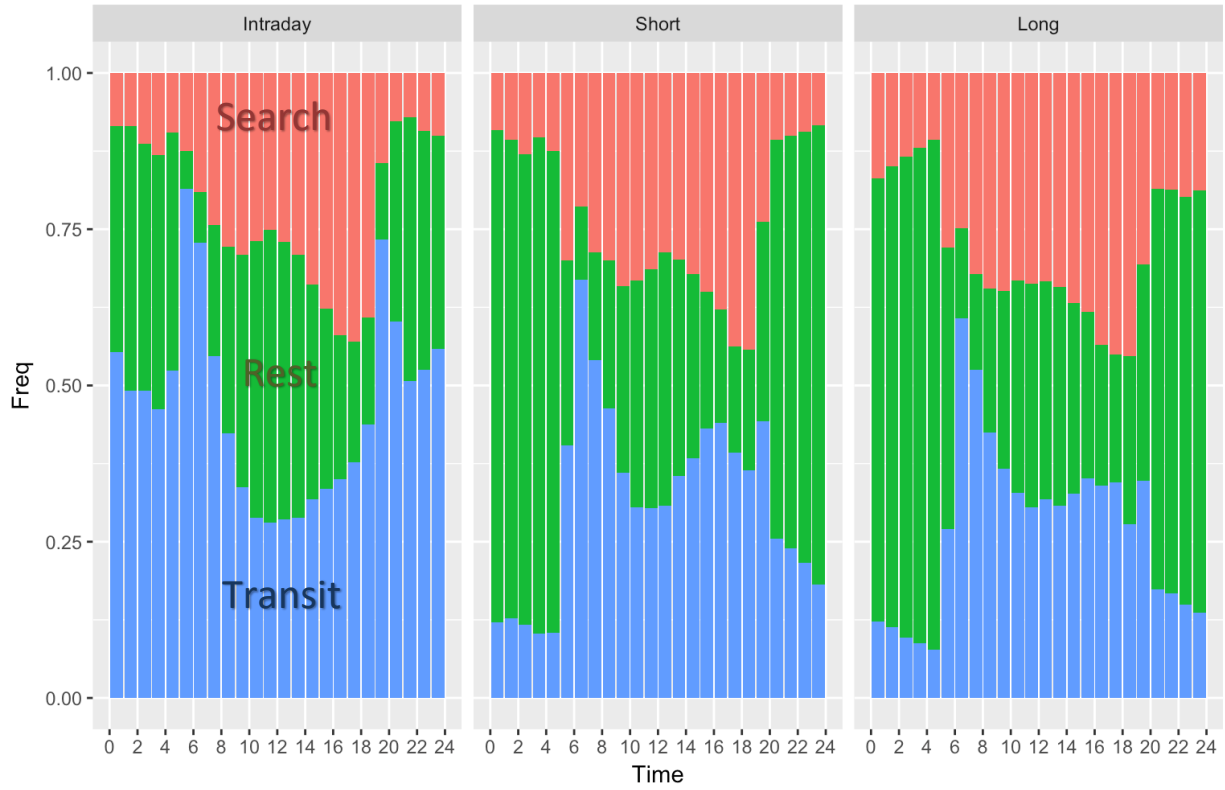


Figure 39. Daily activity patterns for all Wedge-tailed Shearwaters on intraday (left), short (middle), and long (right) foraging trips from all MHI sites, 2013–2015.

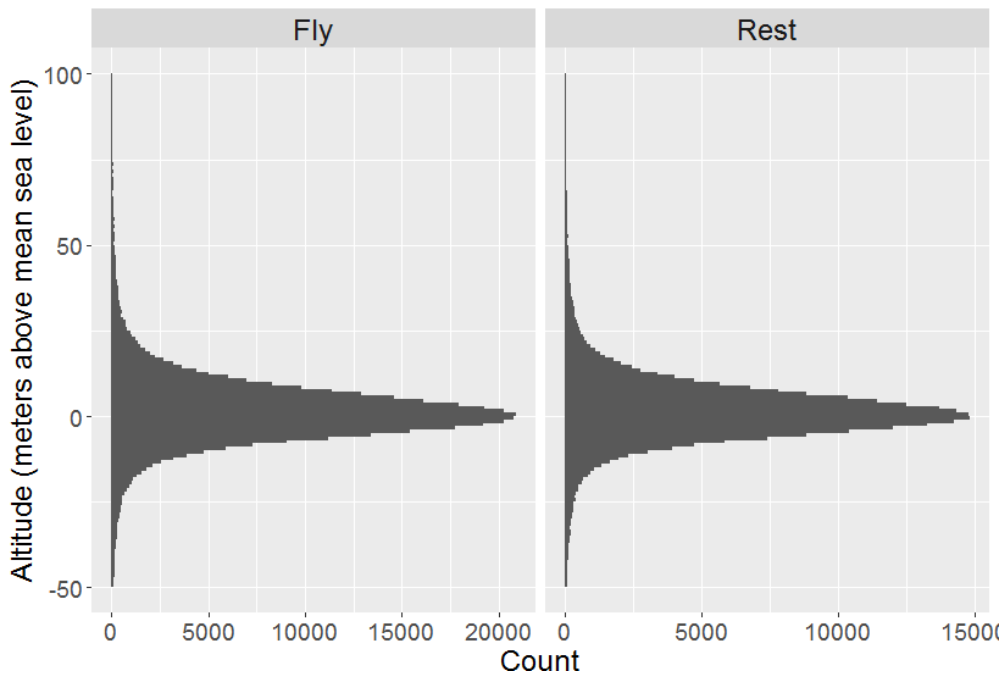


Figure 40. Distributions of Wedge-tailed Shearwater altitude measurements for flying (left) and resting (right) GPS locations for all MHI sites, 2013–2015.

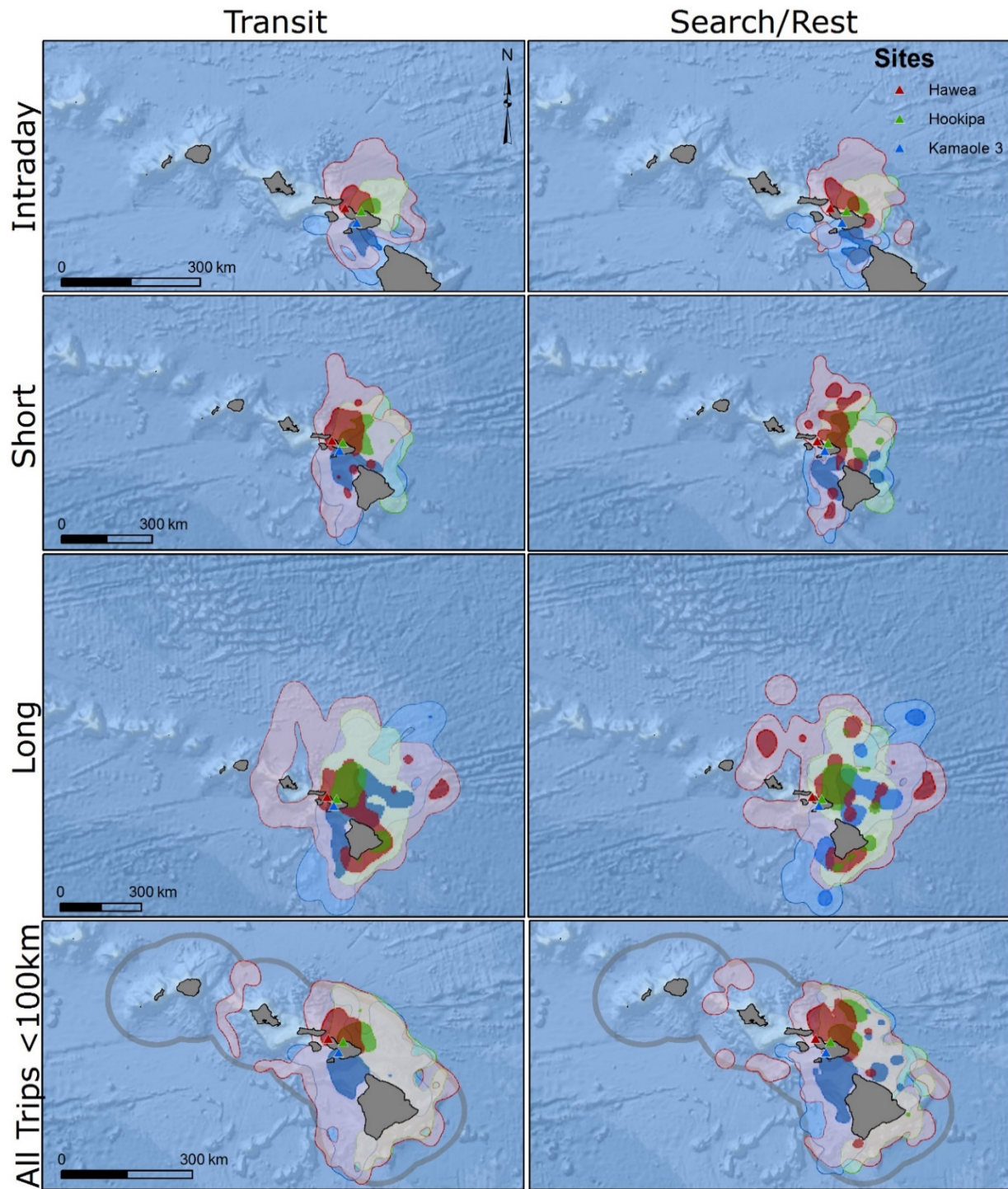


Figure 41. Kernel density distributions Wedge-tailed Shearwaters tracked from Maui, 2013–2015. Distributions are mapped of intraday trips (top row), short trips (second row), long trips (third row), and all tracking data within 100 km of MHI (bottom row) for each behavioral state (columns) from Maui colonies: Hāwea (red), Ho’okipa (green), and Kama’ole 3 (blue). Colored triangles indicate site locations. Colors are shaded lighter for 99% contour and darker for 50% contour. Kernel smoothing factor set manually to 1.5% the spatial extent of the data ($h = 8.4$ km for intraday trips, 13.8 km for short trips, 21.5 km for long trips, and 10.1 km for all trips <100 km). Note varying spatial scale of each row of maps.

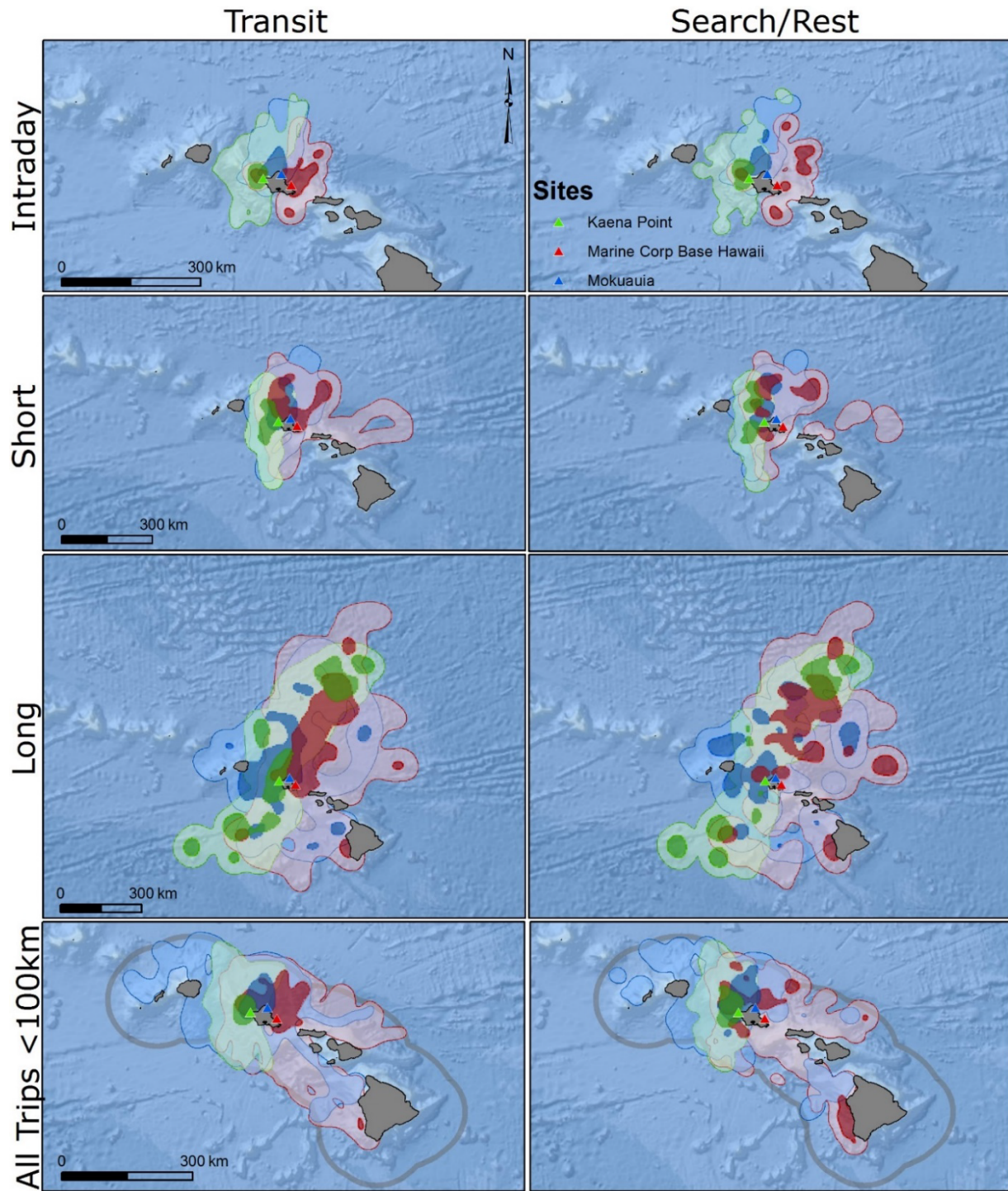


Figure 42. Kernel density distributions of Wedge-tailed Shearwaters tracked from O‘ahu, 2013–2015. Distributions are mapped of intraday trips (top row), short trips (second row), long trips (third row), and all tracking data within 100 km of MHI (bottom row) for each behavioral state (columns) from O‘ahu colonies: Marine Corps Base Hawai‘i (red), Mokū‘auia (blue), and Ka‘ena Point (green). Colored triangles indicate site locations. Colors are shaded lighter for 99% contour and darker for 50% contour. Kernel smoothing factor set manually to 1.5% the spatial extent of the data ($h = 8.4$ km for intraday trips, 13.8 km for short trips, 21.5 km for long trips, and 10.1 km for all trips <100 km). Note varying spatial scale of each row of maps.

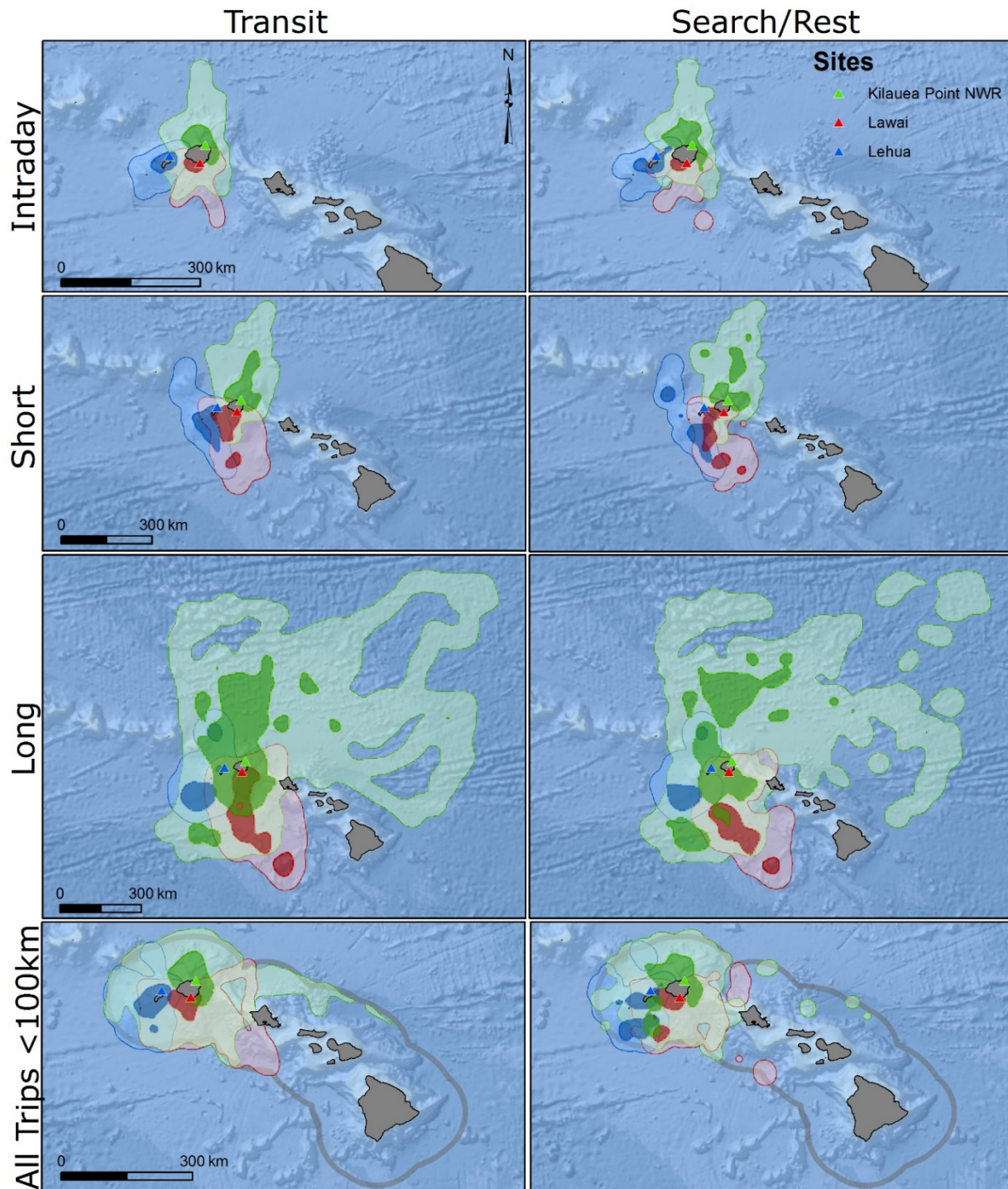


Figure 43. Kernel density distributions of Wedge-tailed Shearwaters tracked from Kaua'i, 2013–2015. Distributions are mapped of intraday trips (top row), short trips (second row), long trips (third row), and all tracking data within 100 km of MHI (bottom row) for each behavioral state (columns) from Kaua'i/Ni'ihau colonies: Lāwai (red), Kīlauea Point NWR (green), and Lehua (blue). Colored triangles indicate site locations. Colors are shaded lighter for 99% contour and darker for 50% contour. Kernel smoothing factor set manually to 1.5% the spatial extent of the data ($h = 8.4$ km for intraday trips, 13.8 km for short trips, 21.5 km for long trips, and 10.1 km for all trips <100 km). Note varying spatial scale of each row of maps.

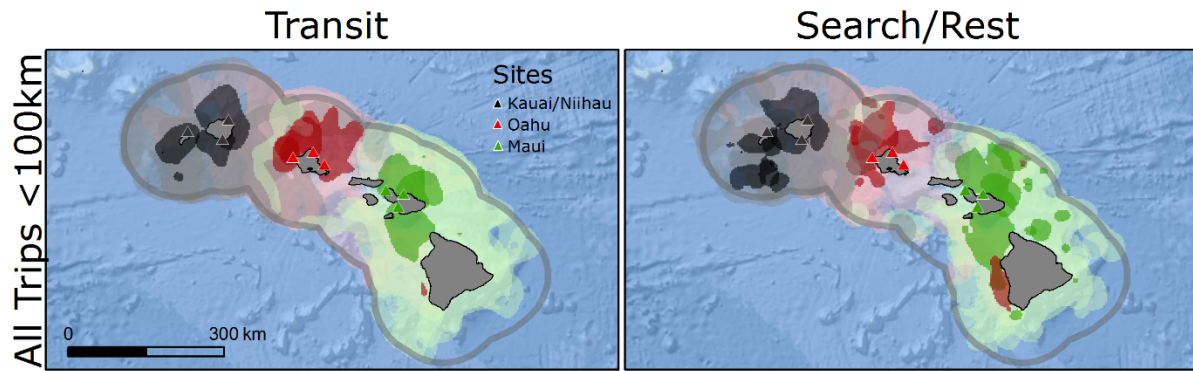


Figure 44. Kernel density distributions of all tracking data within 100 km of MHI for each behavioral state of Wedge-tailed Shearwaters tracked from sites on Maui (green), O'ahu (red), and Kaua'i (black), 2013–2015. Colored triangles indicate site locations. Colors are shaded lighter for 99% contour and darker for 50% contour. Kernel smoothing factor set manually to 1.5% the spatial extent of the data ($h = 10.1$ km for all trips <100 km).

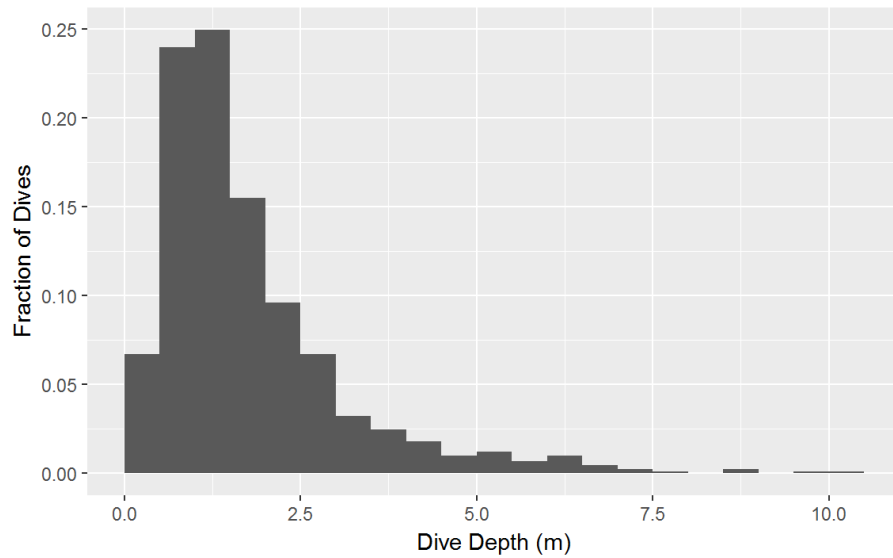


Figure 45. Distribution of Wedge-tailed Shearwater dive depths at all MHI sites, 2014–2015.

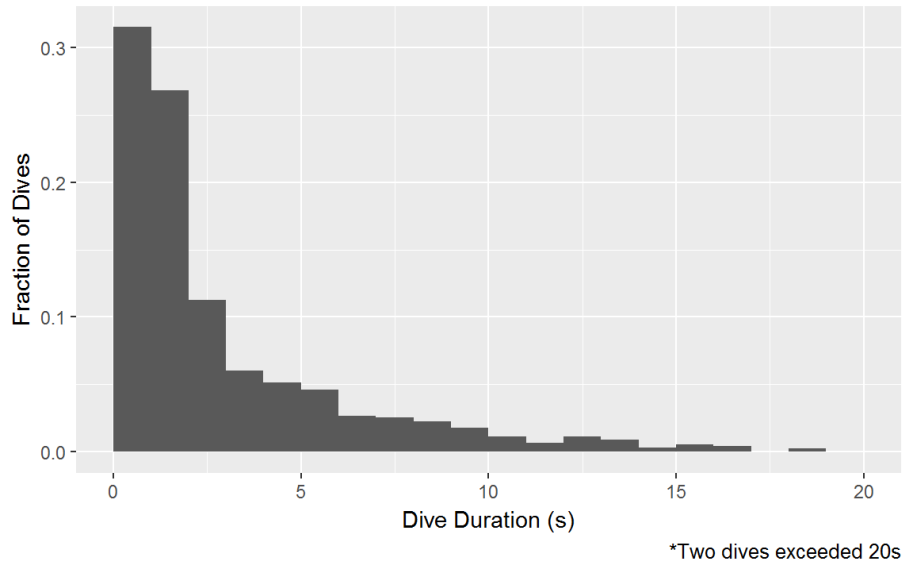


Figure 46. Distribution of Wedge-tailed Shearwater dive durations for all MHI sites, 2014–2015.

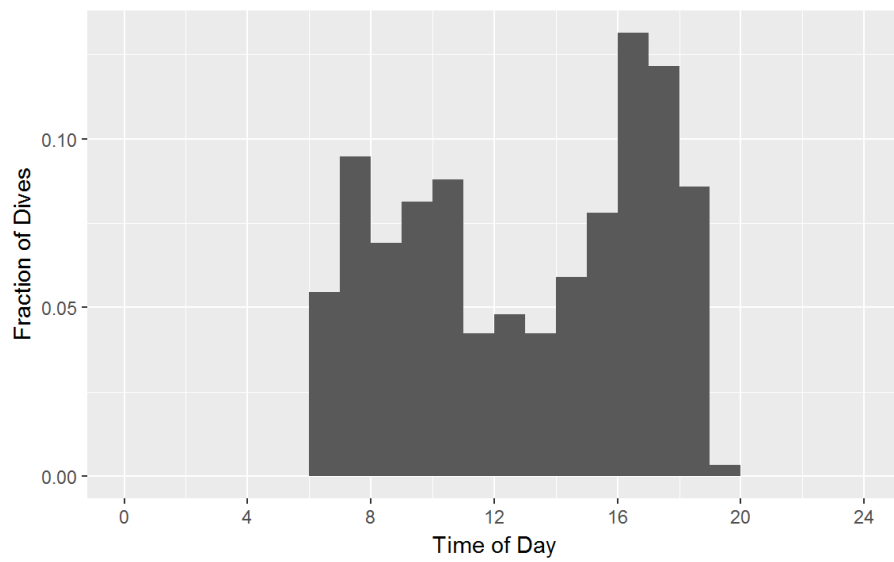


Figure 47. Distribution of Wedge-tailed Shearwater dives by hour of the day for all MHI sites, 2014–2015.

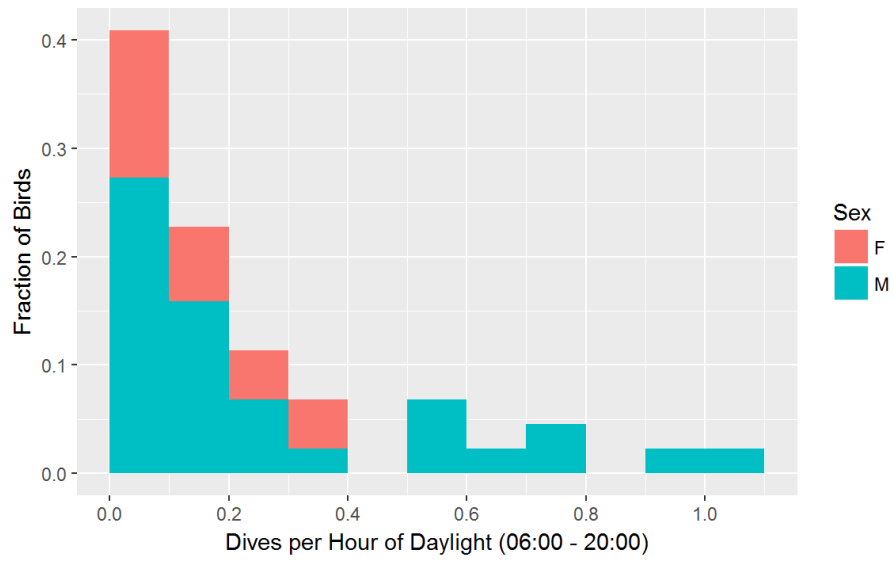


Figure 48. Stacked histogram of dives per hour (during daylight) per deployment of temperature-depth records (TDRs) on male and female Wedge-tailed Shearwaters from all MHI sites, 2014–2015.

3.4 Brown Booby ('A, *Sula leucogaster*)

3.4.1 Species account

Brown Booby (IUCN “Least Concern”) is a dark, medium-sized sulid found throughout the tropics (Nelson 1978). With a 1.5 m wing span and mass of 1260 g, they are intermediate in size between their more pelagic congeners, Red-footed and Masked Boobies (Hertel and Ballance 1999). Most individuals in the central Pacific belong to subspecies *Sula leucogaster plotus*, but a few *S. leucogaster brewsteri* from the eastern Pacific have been seen in Hawai‘i and at other central Pacific islands (VanderWerf et al. 2008).

Brown Boobies tend to breed in smaller, but more numerous, colonies than their congeners (Nelson 1978, Harrison 1990). They are the most common sulid in the Caribbean (Nelson 1978); however, in Hawai‘i there are approximately 1,500 breeding pairs (Pyle and Pyle 2017). About 500 pairs nest in the Northwestern Hawaiian Islands, mostly on Nihoa, and twice that many breed in the MHI at Lehua Islet (Ni‘ihau/Kaua‘i; ~500 breeding pairs) and on Ka‘ula Rock (Ni‘ihau/Kaua‘i; ~400 breeding pairs; VanderWerf et al. 2007, Pyle and Pyle 2017).

Though they may be found on shore year-round, Hawaiian Brown Boobies breed in the spring through early fall (Nelson 1978, VanderWerf et al. 2007). Most breeding females lay two eggs but rarely raise more than one chick (Nelson 1978). Parents incubate their eggs for approximately 6 weeks and chicks fledge after 96 days (Nelson 1978). Brown Boobies nest on the ground and build nests on terrain ranging from flat ground to steep cliffs and lava stacks (Harrison 1990).

Brown Boobies exhibit reversed sexual dimorphism; females are approximately 20–25% heavier than males (Nelson 1978, Weimerskirch et al. 2009) and up to 35% heavier than males on Johnston Atoll (Lewis et al. 2005). Males are more active foragers and appear to dive more frequently than females (Lewis et al. 2005, Weimerskirch et al. 2009). Unlike the other Hawaiian boobies, the Brown Booby’s diet reflects its coastal habitat and varies widely between locations. In Hawai‘i, Brown Boobies heavily predate jacks (Family Carangidae, mostly *Decapterus* spp. and *Seriola* spp.) but also take flyingfishes and juvenile goatfish (Harrison et al. 1983). Squid make up a much smaller percentage of Brown Booby diet than Red-footed Booby diet, but the squids taken by Brown Boobies are larger (Harrison et al. 1983). Like their diet, Brown Booby foraging behavior is dependent on location and the local environment. Brown Booby is the only booby species known to kleptoparasitize food from other seabirds (Tershy and Breese 1990). Variability in diet and intrasexual behavioral differences between regions, and evidence of kleptoparasitism, indicate Brown Boobies are flexible, opportunistic predators.

Brown Boobies forage closer to land than other boobies and tend not to form aggregations with conspecifics or other seabirds (Nelson 1978, Harrison 1990). Brown Boobies forage only 30 km from their colonies in the Gulf of California and 45–50 km in the Caribbean (Weimerskirch et al. 2009, Soanes et al. 2016). Maximum foraging range may be greater during courtship or incubation; Michael et al. (2018) found males during courtship ranged 169–315 km from their colony on Isla Larga, Parque Nacional Islas Marietas, Mexico. Differences between the sexes in trip duration and range vary by location. Studies in the eastern Pacific found females ranged farther from the colony than males (Gilardi 1992, Weimerskirch et al. 2009). But on Johnston Atoll in the central Pacific, males took longer trips than females (Lewis et al. 2005), and in the Caribbean, there was no significant difference in range or duration between sexes.

3.4.2 Tagging Sites and Deployment Success

Brown Boobies were tracked from one breeding colony in the MHI: Lehua Islet (Ni‘ihau/Kaua‘i; Figure 49 and Table 13). From 2014–2015, we successfully recovered tracking data from 42 of 56 i-gotU GPS

deployments; TDR data were recovered from 37 of 47 deployments (Table 13). Unsuccessful deployments resulted from inability to recapture the tagged individual, tag loss, or tag technical malfunction. GPS/TDR deployment sessions were longer in 2015 (8–10 days) than in 2014 (4–5 days; Table 13). Mean (\pm SD) i-gotU GPS tracking duration was 3.8 ± 1.8 days and mean TDR duration was 3.8 ± 2.0 days across all sites/years, with shorter mean deployment durations in 2014 (2.1–2.3 days) than in 2015 (5.1–5.8 days; Table 13). Tags were deployed primarily on chick-rearing adults at all sites, although some incubating birds were also tagged during the first deployment session in 2015 at Lehua Islet (Table 13).

3.4.3 Foraging Trip Parameters

We identified 189 unique foraging trips made by 42 individual Brown Boobies tracked from Lehua Islet: 21 birds (61 trips) in 2014 and 21 birds (123 trips) in 2015 (Table 14). Foraging trips lasted on average (\pm SD) 4.9 ± 3.7 h and birds ranged 35.7 ± 19.6 km from the colony (Table 14). Almost all foraging trips (97%) were conducted during a single day and we did not detect any bimodality in the distribution of single day trips; therefore, we classified single day trips as “short” and multiday trips ($n = 5$, 2015 only) as “long” (Table 14; Figure 50). Long (multiday) trips conducted during 2015 all involved birds spending one or multiple nights roosting along coastal Kaua‘i or Ni‘ihau (Table 14, Figure 49).

We classified phenology into three categories: incubation, early chick ($<$ half adult body size), and late chick (\geq half adult body size). Distributions of trip durations for the two chick-rearing stages were similar, except for a few longer single-day trips for late-chick-rearing birds (Figure 50). The sample size of incubating birds was small, but most trip duration values fell within the range of chick-rearing birds (Figure 50). Mean (\pm SD) short trip duration and range were greater in 2015 than 2014 (5.6 ± 4.1 h and 3.3 ± 1.9 h, respectively; Table 14; Figure 51). Year may have been a more important factor affecting foraging trip parameters because we tagged early- and late-chick-rearing birds in similar proportions in both years (50% early chick-rearing in 2014, 60% early chick-rearing in 2015).

Most Brown Booby foraging trips started early in the morning, but departures continued throughout the day (Figure 52). Foraging trip end times peaked during mid-morning and at the end of the day, but arrivals occurred during all times of day (Figure 52).

3.4.4 Behavioral Classification

Brown Boobies flew at an average ground speed of 8.75 m s^{-1} during transit. We sampled locations every 120 s (2 min), resulting in a RST radius of 525 m. We restricted behavioral summaries to only include single day (“short”) trips because multiday (“long”) trips were rare.

While on foraging trips, Brown Boobies spent 32.4% of daylight hours resting, 28.5% of their time searching, and the remaining 39.1% transiting (Table 15). Peak searching took place in the late morning and afternoon, with more resting around noon. Brown Boobies transited more during dawn and dusk (05:00–07:00 and 19:00–20:00 local time) than during any other time of day (Figure 53). Transiting corresponded with peak trip start and end times (Figure 52).

Brown Booby resting and flight altitudes were all normally distributed near 0 mamsl (medians = -2.16 mamsl and -1.03 mamsl, respectively; Figure 54). The lack of distinction in altitude values between these two behavioral states likely reflects low flight heights at sea. Using our error simulation method, we estimated that Brown Boobies spend 3.41% (95% CI 3.16–3.67%) of flight time in the RSZ. Even though there is variability in the altitude measurements, it does not affect our estimate of proportion of time spent flying in RSZ because underestimated and overestimated altitudes tended to cancel each other out.

3.4.5 Spatial Distribution

Brown Boobies tracked from Lehua Islet transited in all directions from the island, but primarily to the west and east-southeast (Figure 55). Core-use search/rest areas included along and offshore of the northwest coast Ni‘ihau, northeast coastal Ni‘ihau, throughout the channel between Ni‘ihau and Kaua‘i, and along the west coast of Kaua‘i (Figure 55).

3.4.6 Diving Behavior

We identified 1,618 valid dives made by 35 Brown Boobies (Table 16). The distribution of Brown Booby dive depths was right-skewed. Brown Boobies dove to a mean (\pm SD) depth of 1.42 ± 0.75 m (median = 1.25 m; Table 16; Figure 56). The average maximum dive depth per individual was 3.32 ± 1.21 m and the deepest dive recorded was to 8.19 m. The distribution of dive durations also was right-skewed. Mean dive duration for Brown Boobies was 1.87 ± 1.69 s (median = 1.50 s; Table 16; Figure 57). The average maximum dive duration across individuals was 7.35 ± 6.40 s and the longest dive lasted 35.0 s. These distributions are likely biased deeper and longer because dives shallower than 0.5 m were excluded due to TDR device limitations. Recorded dive durations were shorter in 2015 than in 2014, but this was likely due to a change in the tag programming rather than an inter-annual change in behavior (Table 16). A 1-m threshold was used for the TDRs deployed in 2015, which improved memory and battery performance but likely truncated the shortest and shallowest dives.

All Brown Booby dives took place during daylight (06:00–20:00 local time) with peak activity during the late morning (~08:00 local time) and early evening (~16:00 local time; Figure 58). When combined with behavioral classifications, we found that more than half of the dives took place while birds were engaged in searching behavior (Figure 59; see 3.4.4 Behavioral Classification). Another 30% occurred during rest and less than 10% during transit (Figure 59). The distribution of dive rates was right-skewed (Figure 60); on a per trip basis, birds performed 2.1 ± 3.3 dives h^{-1} (median = 1.0 dives h^{-1} , range = 0–26.9 dives h^{-1} , $n = 157$ trips). Excluding trips where no dives were measured, the dive rate was 2.8 ± 3.5 dives h^{-1} (median = 1.6 dives h^{-1} , $n = 120$ trips).

3.4.7 Tables and Figures

Table 13. Brown Booby deployment and recovery success for each site and deployment session in MHI, 2014–2015. “Birds tagged” is the total number of individuals tagged with any combination of tag types. “GPS/TDR deployed” and “GPS/TDR data” indicate number of each tag type deployed and number from which data was successfully recovered, respectively. “Mean GPS/TDR duration” indicate the mean time duration (in days) between tag deployment and tag recovery.

Island	Site	Year	Deployment Session	Nest Status	Birds tagged	GPS depl.	GPS data	Mean (SD) GPS duration	TDR depl.	TDR data	Mean (SD) TDR duration
Kaua'i	Lehua	2014	15-May–18-May	C	7	7	6	2.2 ± 0.8	7	6	2.2 ± 0.17
			14-Jun–18-Jun	C	10	10	7	2.3 ± 0.6	10	7	2.3 ± 0.6
			15-Jul–18-Jul	C	9	9	8	2.1 ± 0.4	8	7	2.1 ± 0.4
	2015	26-May–04-Jun	I, C	15	15	11	5.8 ± 1.0	12	10	6.1 ± 1.2	
		27-Jun–04-Jul	C	15	15	10	5.1 ± 0.9	10	7	5.2 ± 0.9	
ALL:					56	56	42	3.8 ± 1.8	47	37	3.8 ± 2.0

Table 14. Mean (± SD) Brown Booby foraging trip duration, maximum range, and distance traveled for short, long, multiday, and all trips combined from MHI sites, 2014–2016.

Trip Type	Site (Year)	Birds	Trips	Duration (h)	Range (km)	Traveled (km)
Short	Lehua (2014)	21	61	3.3 ± 1.9	28.5 ± 13.2	76.0 ± 40.2
	Lehua (2015)	21	123	5.6 ± 4.1	39.2 ± 21.2	105.9 ± 58.7
	Short Total:	42	184	4.9 ± 3.7	35.7 ± 19.6	96.1 ± 55.0
Long	Lehua (2015)	5	5	50.3 ± 34.3	91.7 ± 17.3	445.3 ± 129.2
ALL TRIPS TOTAL:		42	189	6.1 ± 9.7	37.2 ± 21.5	105.5 ± 80.8

Table 15. Percentage of time (and number of locations, N) for behavior classes during day, night, and twilight on short, long, and multiday Brown Booby foraging trips from Lehua Islet, 2014–2015. Sample sizes are indicated in parentheses.

Behavior	Day	Night	Twilight
Rest	32.4% (9,156)	99.3% (1,244)	43.1% (581)
Search	28.5% (8,048)	0.6% (7)	4.5% (60)
Transit	39.1% (11,028)	0.2% (2)	52.4% (706)

Table 16. Mean (± SD) dive duration and depth of Brown Boobies tagged with temperature-depth recorder (TDR) tags from MHI sites, 2014–2015. Note that sample sizes may be lower than reported in Table 13 because no dives were recorded or no valid dives were identified from some TDR deployments.

Year	Birds	Dives	Duration (s)	Depth (m)
2014	18	656	2.04 ± 2.07	1.26 ± 0.79
2015	17	962	1.75 ± 1.37	1.54 ± 0.69
All	35	1,618	1.87 ± 1.69	1.42 ± 0.75

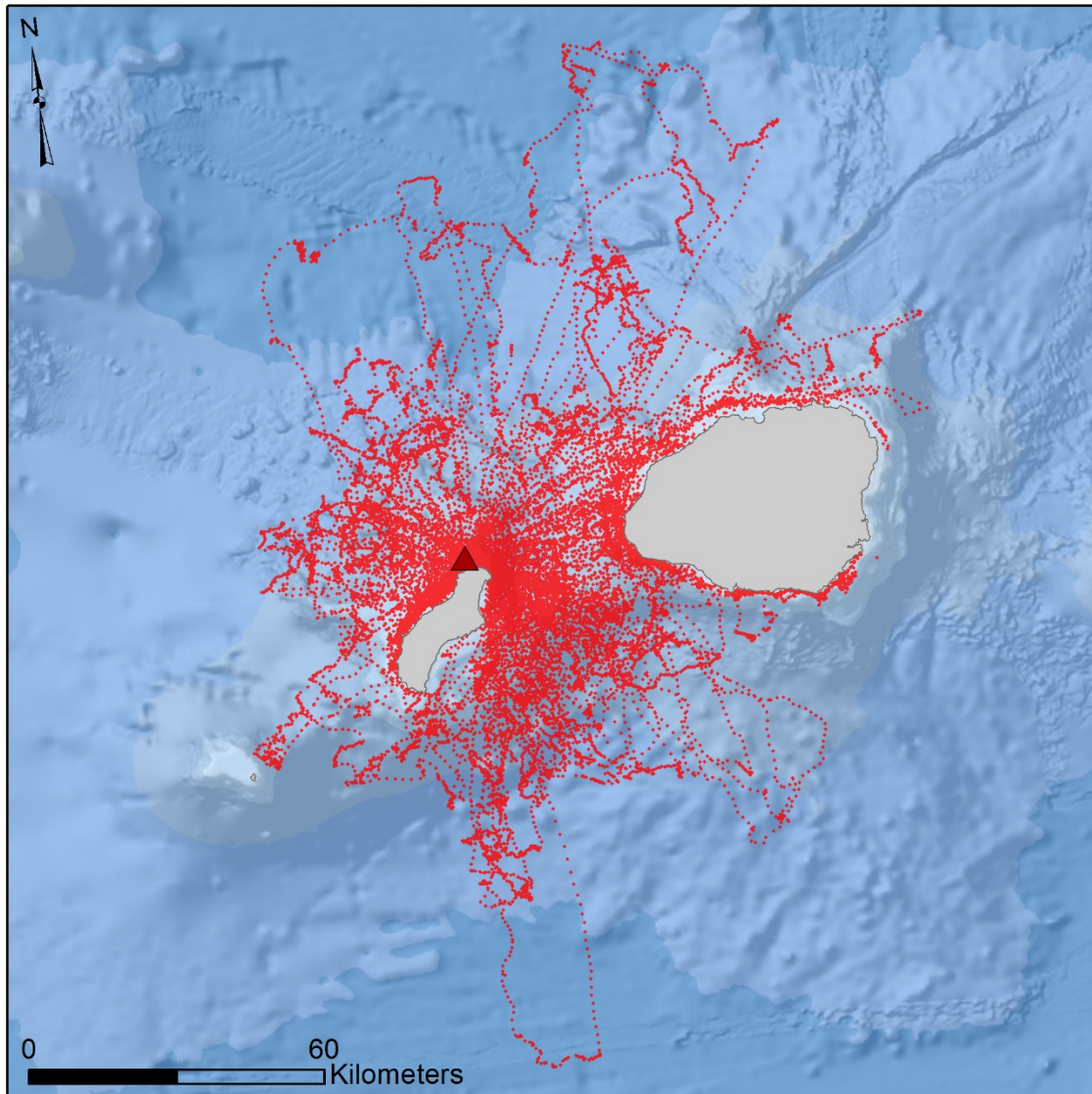


Figure 49. Raw GPS locations for Brown Boobies tracked from Lehua Islet off Ni'ihau/Kaua'i (red triangle), 2014–2015.

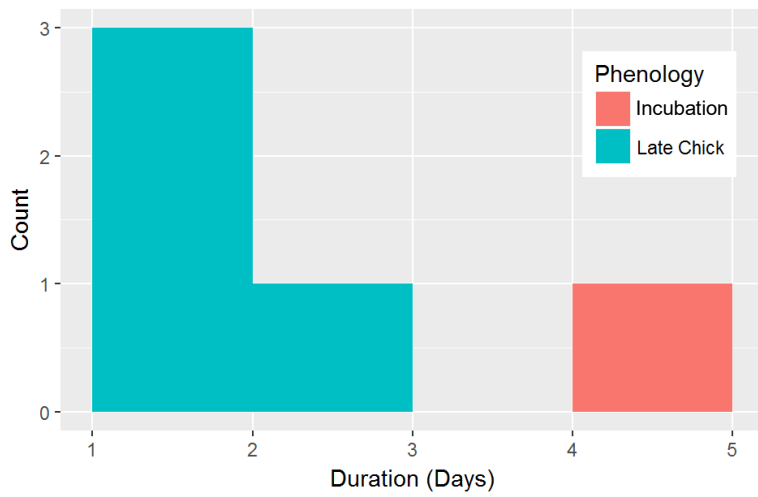
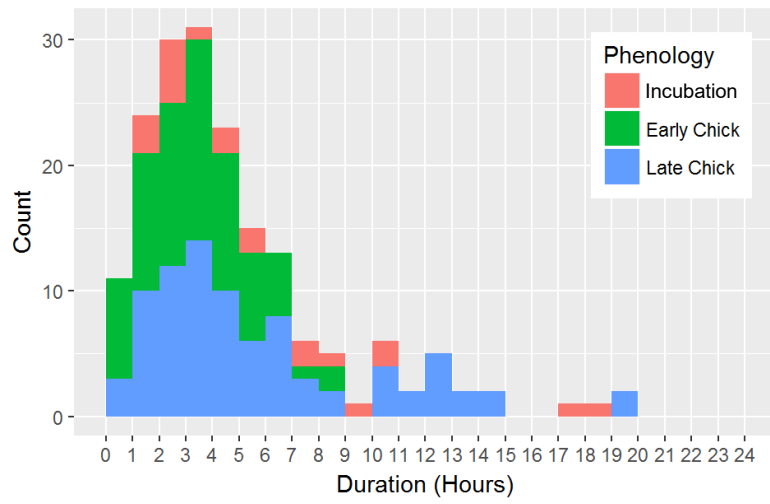


Figure 50. Distributions of trip durations for single day (top) and multiday (bottom) Brown Booby foraging trips from Lehua Islet, 2014–2015. Colors indicate phenology categories.

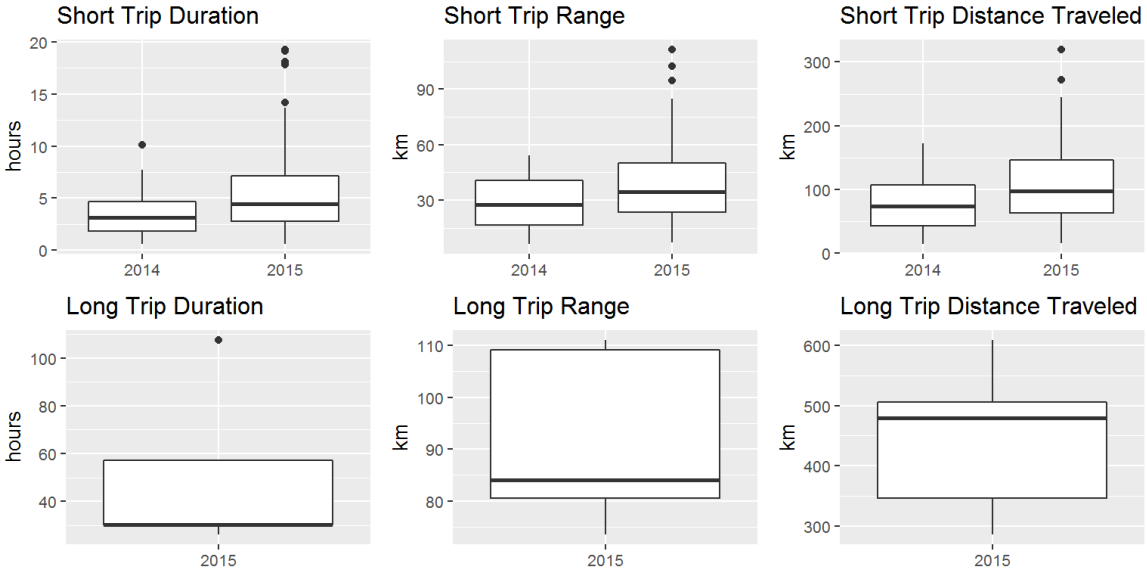


Figure 51. Box-and-whisker plots of duration, range, and distance traveled for short, long, and multiday Brown Booby foraging trips by year from Lehua Islet, 2014–2015. Sample size for long trips (multiday, $n = 5$) is small and results should be interpreted with caution. The black line in box represents the median, the box represents the inter-quartiles (25% and 75%), the whiskers extend to the furthest point within 1.5 interquartile ranges, and dots are any additional points beyond the whiskers.

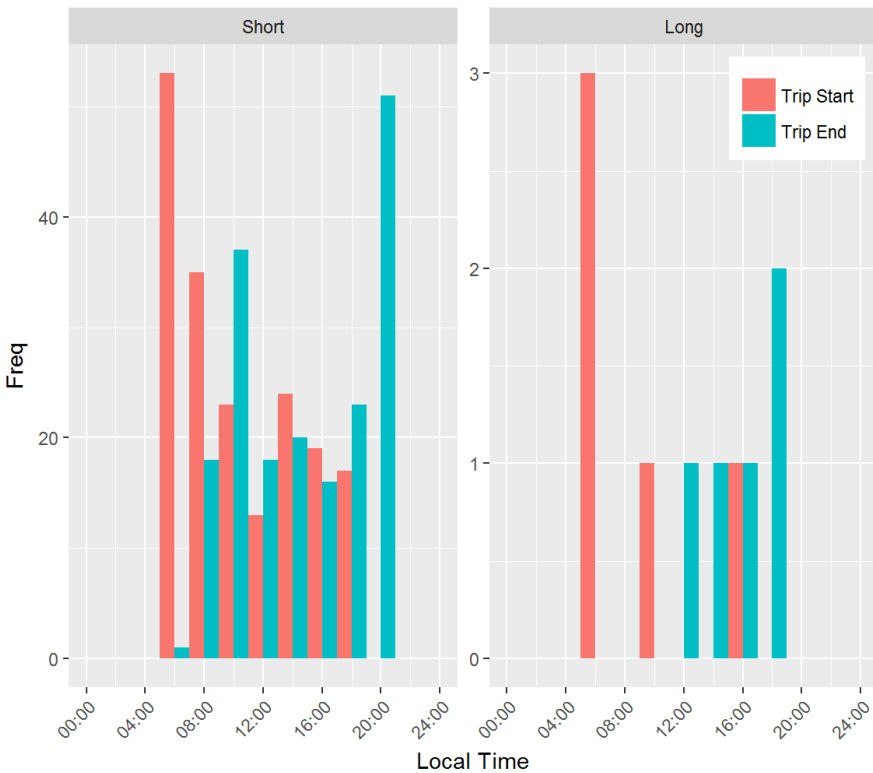


Figure 52. Histograms of trip start and end times for short (single day) and long (multiday) Brown Booby foraging trips from Lehua Islet, 2014–2015.

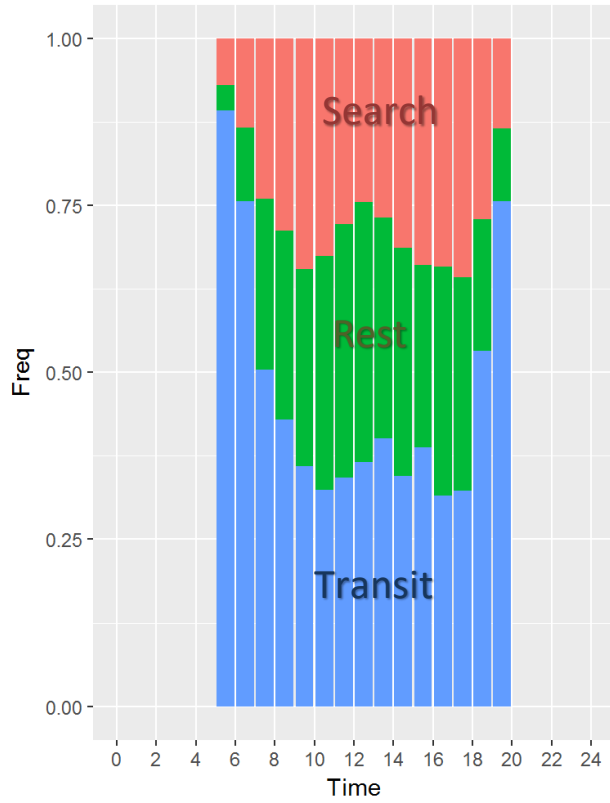


Figure 53. Daily activity patterns for all Brown Boobies on single day foraging trips from Lehua Islet, 2014–2015.

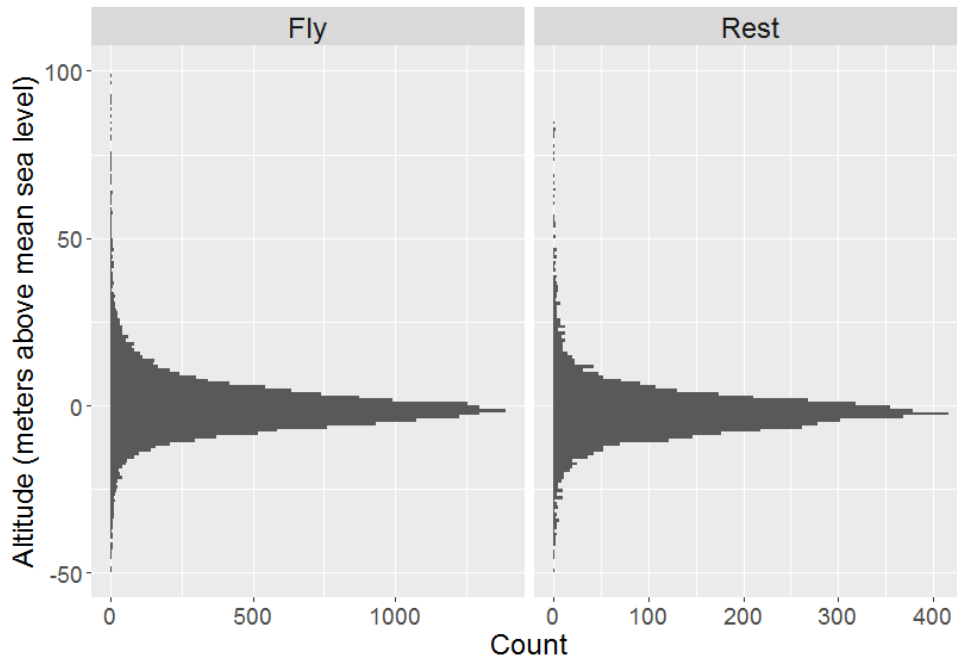


Figure 54. Distributions of Brown Booby altitude measurements for flying (left) and resting (right) GPS locations of birds tracked from Lehua Islet, 2014–2015.

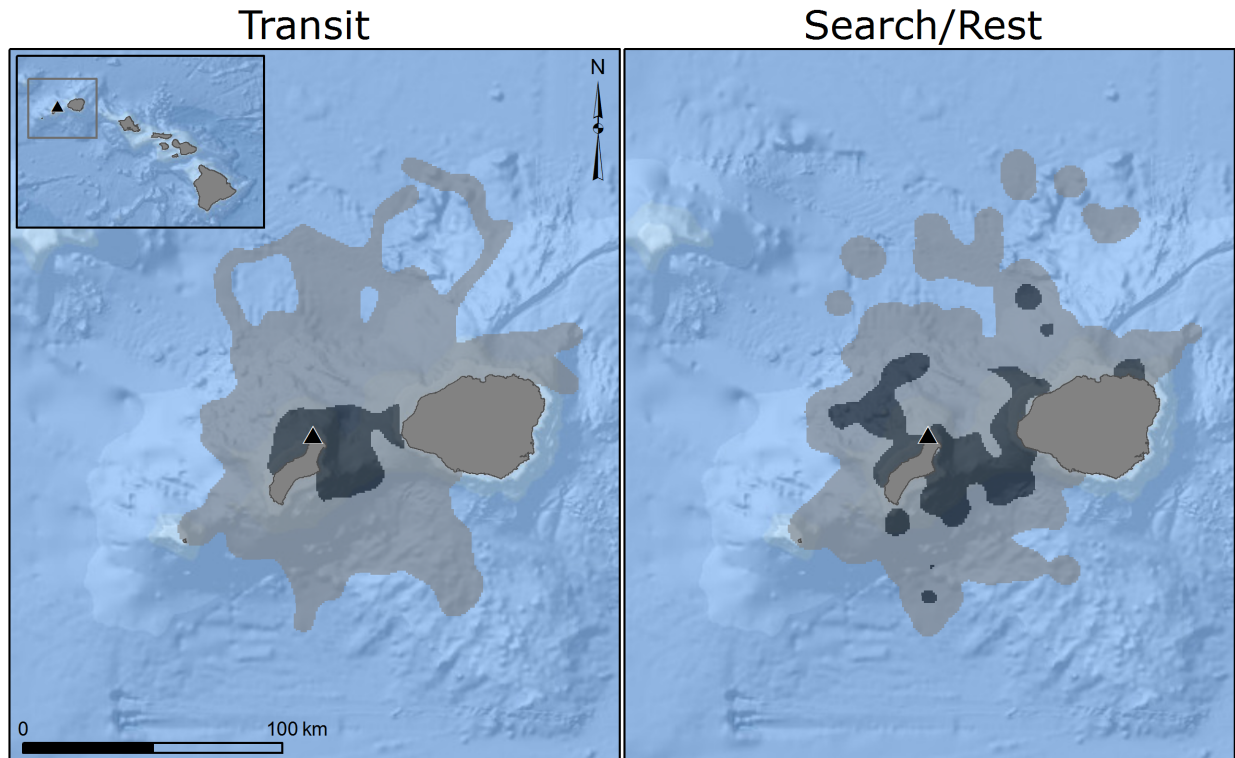


Figure 55. Kernel Density distributions of all single-day trips for each behavioral state (columns) of Brown Boobies tracked from Lehua Islet, 2014–2015. Colored triangle indicates site location. Five multi-day trips (2.6% of all trips) were excluded from analysis. Colors are shaded lighter for 99% contour and darker for 50% contour. Kernel smoothing factor set manually to 1.5% the spatial extent of the data ($h = 3.2$ km).

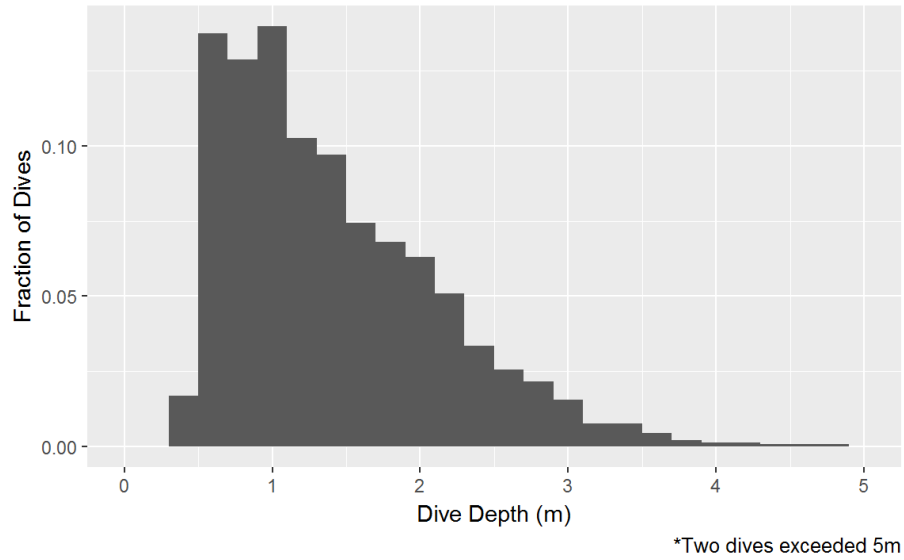


Figure 56. Distribution of Brown Booby dive depths at all MHI sites, 2014–2015.

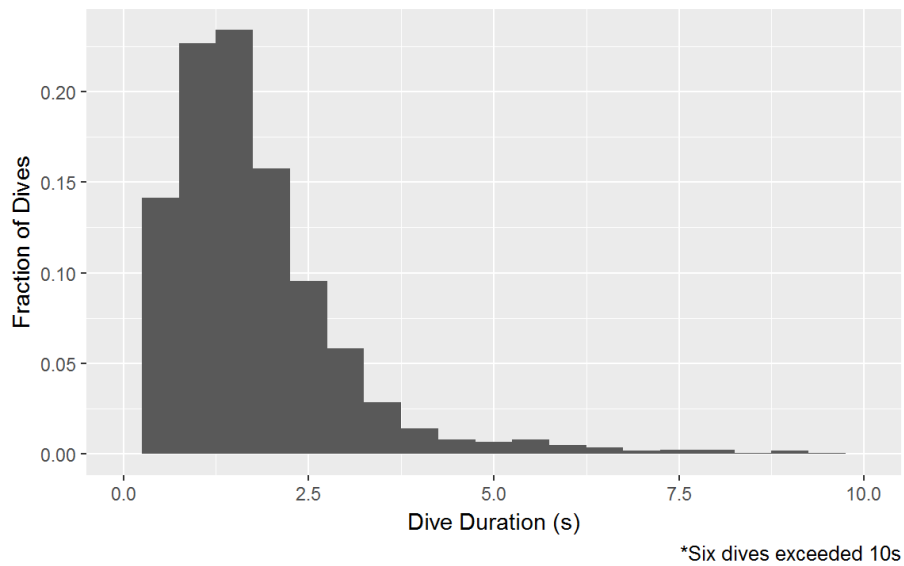


Figure 57. Distribution of Brown Booby dive durations for all MHI sites, 2014–2015.

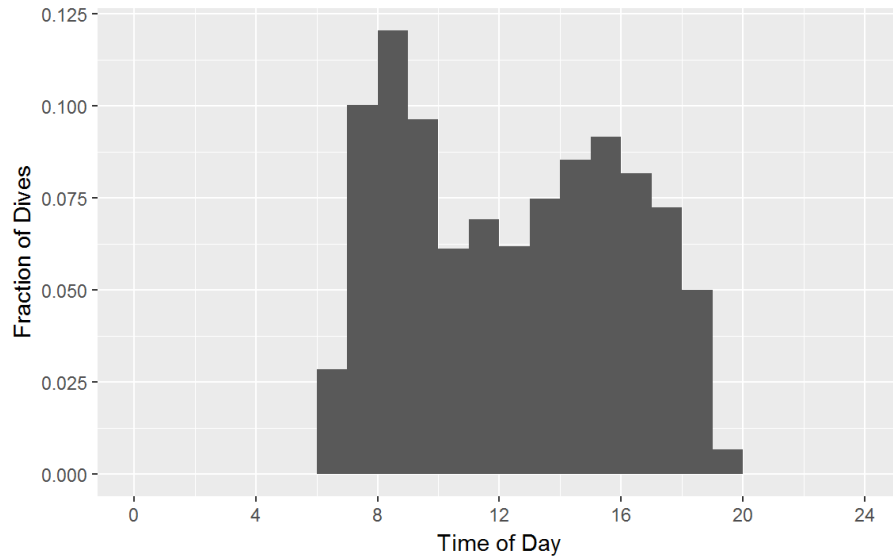


Figure 58. Distribution of Brown Booby dives by hour of the day for all MHI sites, 2014–2015.

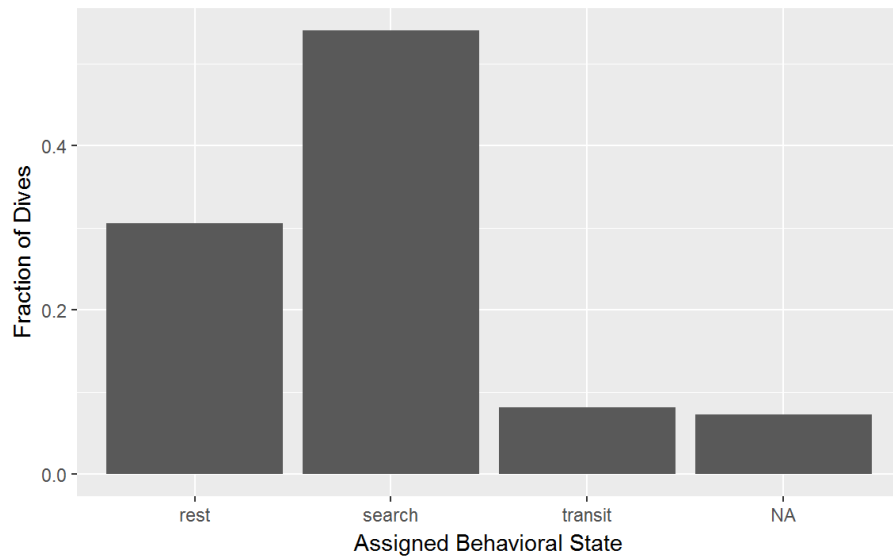


Figure 59. Distribution of Brown Booby dives in each behavioral state for all MHI sites, 2014–2015. NA records are for dives that occurred at a GPS location where behavior could not be assigned (e.g. first and last locations of a trip).

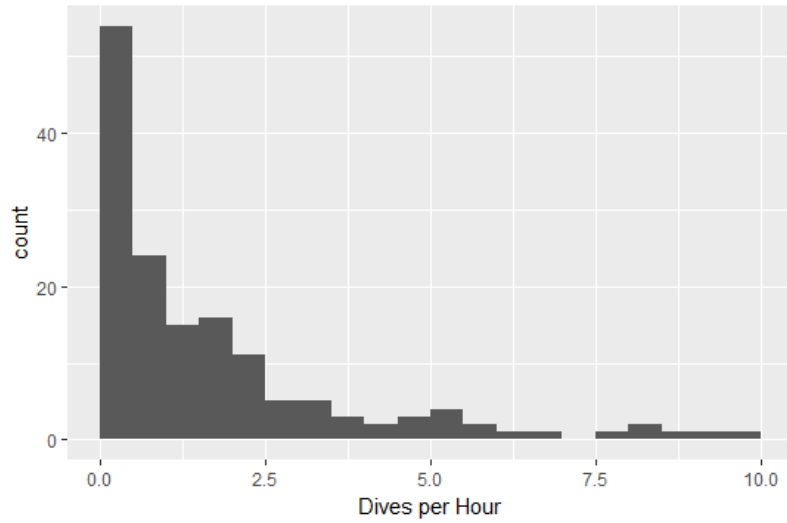


Figure 60. Distribution of dives per hour per trip for Brown Boobies from all MHI sites, 2014–2015. This metric was only calculated for deployments where both GPS and TDR data were collected, allowing for the assignment of dives to specific foraging trips. Note that five dive rate values were measured beyond x axis limit (10.3, 11.5, 11.9, 13.1, and 26.9 dives h⁻¹).

3.5 Red-footed Booby ('A, *Sula sula rubripes*)

3.5.1 Species Account

Red-footed Boobies (IUCN “Least Concern”) are the smallest and most pelagic of the six booby species (Nelson 1978). At 850–1,100 g, they are less than half the mass of Masked Boobies (*S. dactryla*; Schreiber et al. 1996). Worldwide, there are three Red-footed Booby color morphs and the number of subspecies is debated. Color morphs are not related to particular subspecies, but most of the birds in Hawai‘i (*S. sula rubripes*) are the white morph.

An estimated 300,000 breeding pairs of Red-footed Boobies are distributed across the world’s tropical oceans (Schreiber et al. 1996). Hawai‘i is home to approximately 23,000 individuals (breeders and non-breeders combined), with the largest colonies located on Nihoa and French Frigate Shoals in the Northwestern Hawaiian Islands (Seki and Harrison 1989, Harrison 1990, Pyle and Pyle 2017). In the MHI, Red-footed Boobies breed on Lehua, Kaua‘i, and O‘ahu. VanderWerf et al. (2007) reported 4,288 individuals in 2002, compared with a previous count of 3,000 in 1947 (Fisher 1951). Colonies on Kaua‘i and O‘ahu were established in the mid-1900s. Recent surveys from 2004 to 2008 found an average of 1,882 breeding pairs at Kīlauea Point NWR, Kaua‘i (USFWS 2016). On O‘ahu, Red-footed Boobies breed at Marine Corps Base Hawai‘i (1,473 individuals in 2014) and offshore on Moku Manu (200 nests in 2016; Pyle and Pyle 2017).

With a foraging range of approximately 150 km, Red-footed Boobies may be found farther to sea than most of their congeners (Nelson 1978, Young et al. 2010). Previous tracking efforts found trips typically last 7–9 hours, though range and duration vary with location and breeding stage (Weimerskirch et al. 2005, Young et al. 2010). At one end of the spectrum, Red-footed Boobies breeding on Europa (40.3°E, 22.3°S) returned to the colony each day, but individuals breeding on Christmas Island (105.6°E, 10.5°S) regularly undertook trips of two or more days (Mendez et al. 2016). Red-footed Boobies feed primarily on flying fish (Exocetidae) and squid (Ommastrephidae) by plunge diving to 2.4 m depth or by catching prey in the air (Nelson 1978, Seki and Harrison 1989, Weimerskirch et al. 2005). Like many other tropical seabirds, Red-footed Boobies often feed in association with subsurface predators that push prey to the surface. This facilitated foraging is well documented in the eastern Tropical Pacific, though it appears to be less important for boobies foraging in the central Pacific (Ballance et al. 1997, Maxwell and Morgan 2013). In Hawaiian waters, seabirds most frequently associate with skipjack tuna (*Katsuwonus pelamis*), but Red-footed Boobies may also be found with schools of mahimahi (*Coryphaena hippurus*) and spotted dolphins (*Stenella attenuate*) (Hebshi et al. 2008).

Other than Abbott’s Booby (*Sula abbotti*), Red-footed Booby is the only sulid to nest in trees and shrubs (Nelson 1978). Commonly used vegetation includes ironwood (*Casuarina equisetifolia*), aweoweo (*Chenopodium O‘ahuense*), and beach heliotrope (*Tournefortia argentea*) (Starr and Starr 2006). Though present in MHI year-round, breeding predominantly takes place between February and October (VanderWerf et al. 2007, USFWS 2016). Similar to Abbott’s Boobies, Red-footed Boobies almost exclusively lay single-egg clutches (Nelson 1978). As may be expected of a tropical seabird, chick growth is long and slow, requiring 70 days to reach 1,000 g (Schreiber et al. 1996). Depending on the location of the colony—and available quantity of prey—fledging may take place between 90 and 135 days (Nelson 1978).

3.5.2 Tagging Sites and Deployment Success

Red-footed Boobies were tracked from three breeding colonies in the MHI: Lehua Islet (Ni‘ihau/Kaua‘i), Kīlauea Point NWR (Kaua‘i), and Marine Corps Base Hawai‘i (O‘ahu; Figure 61 and Table 17). In 2014–2015 we successfully recovered tracking data from 149 of 184 i-gotU GPS deployments; TDR data were recovered from 118 of 133 deployments (Table 17). Unsuccessful deployments were caused either by an

inability to recapture the tagged individual, tag loss, or tag technical malfunction. GPS/TDR deployment sessions were longer in 2015 (8–11 days) than 2014 (5–7 days; Table 17). Mean i-gotU GPS tracking duration was 4.6 days and mean TDR duration was 4.3 days across all sites, with shorter mean deployment durations in 2014 (3.0–3.8 days) than in 2015 (5.6–7.6 days; Table 17). Tags were deployed primarily on chick-rearing adults at all sites; however, some incubating birds were also tagged during the first deployment session of each year at Lehua Islet (Table 17). We deployed 15 e-obs 15 g Bird Solar GPS tags on chick-rearing Red-footed Boobies at Kīlauea Point NWR in late May 2016 (Table 17). These tags, which wirelessly transfer data to a base station at the colony, did not require recapture and recovery and therefore were left on birds until they fell off. The mean GPS tracking duration for this deployment was 61.6 days, and we assume tags either fell off and/or birds left the area after completing the breeding season (Table 17).

3.5.3 Foraging Trip Parameters—i-gotU GPS Tags

Data from i-gotU (archival GPS tags, shorter deployments) and e-obs (remote download GPS tags, longer deployments) units were qualitatively different, so we present our findings for these two datasets separately. The following summarizes the i-gotU results.

We identified 512 unique Red-footed Booby foraging trips made by 144 individuals across all sites; individual trip durations ranged from 30 min to 5 days, with an overall mean (\pm SD) of 13.6 ± 13.4 h (Figure 62, Table 18). Trips were categorized as short (≤ 12 h), long (12 h $<$ duration < 24 h), or multiday (> 24 h) for analysis; the decision to split short and long trips at 12 h was based on an observed bimodality in the trip duration histogram (Figure 62). Short trips lasted 6.7 ± 2.9 h and boobies ranged 51.5 ± 24.8 km from the colony. Long trips lasted 14.3 ± 1.2 h and boobies ranged 101.7 ± 29.7 km (Table 18). Foraging trip duration, range, and distance traveled appeared consistent across sites and years for both short and long trips (Figure 63). The distribution of multiday trip durations was right-skewed, with the majority of trips lasting for 2 days (one night away) with a maximum duration of 4.5 days (Figure 62). Most multiday trips occurred in 2015, particularly at Lehua (Table 18), and involved birds spending the night at sea. All multiday trips in 2014 and some in 2015 were from boobies roosting offsite at other islands (primarily Ka‘ula, and in one case, Nihoa).

Trip length varied with three phenology categories: incubation, early chick ($<$ half adult body size), and late chick (\geq half adult body size). Proportions of long and multiday trips were greatest for incubating parents and least for parents with early chicks; behavior of parents of late chicks was intermediate (Figure 64). Deployment session-specific environmental conditions may also affect foraging trip parameters, but these were not considered herein.

Trip start times varied by trip duration, but colony returns were tightly distributed around twilight ($\sim 20:00$ local time; Figure 65). Birds foraging on short trips displayed the greatest variability in start and end times, whereas long and multiday trips most frequently began close to dawn (Figure 65).

3.5.4 Foraging Trip Parameters—e-obs GPS tags

GPS data for Red-footed Boobies outfitted with e-obs solar GPS tags were occasionally interrupted by insufficient battery power or GPS reception problems; therefore, we limited our analysis of foraging trip parameters to trips with $\geq 75\%$ coverage and ≤ 10 min sampling intervals. In addition, because nest status was not monitored post-deployment, we limited analysis to trips starting on or before 11 July 2016. After this date, sample size dropped to less than 10 tagged birds, chicks started fledging the colony (Kim Rogers, pers comm), and this time period was most comparable with timing of data collected during i-gotU deployments at other sites.

We documented 510 unique foraging trips made by 15 birds from Kīlauea Point NWR in 2016 (Table 19). Trips were categorized as short (≤ 12 h), long ($12 \text{ h} < \text{duration} \leq 24 \text{ h}$), or multiday ($>24 \text{ h}$) for analysis; the decision to split short and long trips at 12 h was based on an observed bimodality in the trip duration histogram (Figure 66). Short trips lasted on average (\pm SD) 7.3 ± 2.8 h and ranged 60.5 ± 32.4 km from the colony (Table 19). Long trips lasted 14.7 ± 1.6 h and ranged 139.7 ± 42.2 km (Table 19). Multiday trips lasted 39.2 ± 8.7 h and boobies ranged 226.8 ± 58.8 km (Table 19); almost all multiday trips involved just one night away from the colony spent at sea or at an offsite roost.

3.5.5 Behavioral Classification—i-gotU GPS Tags

For i-gotU GPS tags, we calculated a mean transit speed of 9.15 m s^{-1} for Red-footed Boobies. A 120 s (2 min) sampling interval yielded an RST radius of 549 m.

Activity budgets for short and long trips were similar. During daytime hours boobies allocated approximately equal time for rest, search, and transit with slightly more searching than resting (Table 20). During twilight and night, birds spent most of their time transiting to and from the colony (Table 20). Individuals were most active during the late morning and early afternoon (Figure 67). Transiting was most frequent at dusk and dawn and peak hours for foraging occurred around 09:00 and 17:00; proportion of time resting reached a maximum during midday (Figure 67). During daytime, individuals on multiday trips spent 42.0% of their time searching, compared with 37.8% and 37.6% of time searching during short and long trips, respectively (Table 20). Furthermore, birds on multiday trips engaged in searching behavior almost three times more (9.2%) during twilight hours compared with birds on single day trips (3.5%) and spent one third as much time transiting (31.4%) during multiday trips compared with single day trips (93.2% and 93.6% for short and long trips, respectively; Table 20).

Red-footed Booby resting and flight altitudes were all normally distributed near 0 mamsl (medians = -2.40 mamsl and -0.81 mamsl, respectively; Figure 68), and flight altitudes were slightly greater. The lack of distinction in altitude values between these two behavioral states likely reflects mostly low flight heights detected for Red-footed Boobies. Using our error simulation method, we estimated that Red-footed Boobies spent 2.74% (95% CI 2.63–2.84%) of their flight time in the RSZ. Even though there was variability in the altitude measurements, this did not affect the estimated proportion of time spent flying in RSZ, because underestimated and overestimated altitudes canceled each other.

3.5.6 Behavioral classification—e-obs GPS tags

We did not conduct behavioral classification of Red-footed Booby e-obs GPS tag data. These tags functioned at variable sampling intervals, both 1) as programmed due to battery charge and solar power, and 2) due to occasional GPS reception issues. These data were less continuous than i-gotU GPS data and along-track behavioral classification would have been more complicated given our approach for the i-gotU data.

3.5.7 Spatial Distribution—i-gotU and e-obs Tags

Red-footed Boobies from the three major MHI colonies showed little spatial overlap at sea, regardless of trip type (Figure 69). On short trips, birds from all colonies mostly spent time 25–75 km from shore; Lehua birds traveled northwest and south to forage, the Kīlauea Point NWR core-use area was to the north-northeast of Kaua‘i, and Marine Corps Base Hawai‘i birds traveled north, east, and to a lesser extent toward the south (Figure 69). The same spatial patterns persisted for long trips; however, core-use areas extended farther offshore, to ~ 150 km for Lehua and Marine Corps Base Hawai‘i, and ~ 200 km for Kīlauea Point NWR (Figure 69). Whereas multiday trips from Lehua were mostly to the southwest and south, at the other sites, patterns were similar to long trips (Figure 69).

We mapped the spatial distribution of Red-footed Boobies tracked with i-gotU (Lehua, Marine Corps Base Hawai‘i) and e-obs (Kīlauea Point NWR) GPS tags together; however, it is important to consider that kernel density estimates for Kīlauea Point NWR integrated up to 45 days of tracking data in a single year for a small sample of individuals ($N = 15$) whereas Lehua and Marine Corps Base Hawai‘i integrated shorter deployments (mean = 3–8 days) across multiple years for a much larger sample of individuals ($N = 82$ for Lehua and $N = 66$ for Marine Corps Base Hawai‘i; Table 17). We also restricted kernel density estimates for e-obs (Kīlauea Point NWR) GPS tags to trips beginning on or before 11 July 2016 (see section 3.5.4 Foraging Trip Parameters–e-obs GPS tags).

3.5.8 Diving Behavior

We identified 6,330 valid dives made by 107 Red-footed Boobies (Table 21). The distribution of Red-footed Booby dive depths was right-skewed; boobies dove to a mean depth of 1.12 ± 0.53 m (median = 1.00 m; Table 21; Figure 70). The average maximum dive depth per individual was 2.62 ± 0.96 m and the deepest dive recorded was to 7.57 m. The distribution of Red-footed Booby dive durations was right-skewed; mean dive duration was 1.50 ± 1.10 s (median = 1.30 s; Table 21; Figure 71). The average maximum dive duration across individuals was 4.14 ± 3.91 s and the longest dive lasted 36.7 s. These distributions are slightly biased deeper and longer because dives shallower than 0.5 m were excluded due to TDR device limitations. Recorded dive durations were shorter in 2015 than 2014, but this was likely due to the change in the tag programming rather than an inter-annual change in behavior (Table 21). A 1-m threshold was used for the TDRs deployed in 2015, which improved memory and battery performance, but likely truncated the shortest and shallowest dives.

Nearly all Red-footed Booby dives took place during daylight (06:00–20:00 local time) with a major peak in activity during the late evening (~16:00 local time) and a minor peak during the morning (09:00 local time; Figure 72). A small number of dives took place between 20:00 and midnight (Figure 72). When combined with behavioral classifications, we found that almost 80% of dives occurred during searching behavior, 15% occurred during resting behavior, and 5% occurred during behaviors classified as transiting (Figure 73). The distribution of dive rates was right-skewed (Figure 74); on a per trip basis, birds performed 1.5 ± 3.0 dives h^{-1} (median = 0.8 dives h^{-1} , range = 0–36.6 dives h^{-1} , $n = 316$ trips). Excluding trips where no dives were measured, the dive rate was 1.9 ± 3.2 dives h^{-1} (median = 1.2 dives h^{-1} , $n = 260$ trips).

3.5.9 Tables and Figures

Table 17. Red-footed Booby deployment and recovery success for each site and deployment session in MHI, 2014–2016. Nest status “I” = incubation and “C” = chick-rearing. “Birds tagged” is the total number of individuals tagged with any combination of tag types. “GPS/TDR deployed” and “GPS/TDR data” indicate number of each tag type deployed and number from which data was successfully recovered, respectively. “Mean GPS/TDR duration” indicate the mean time duration (in days) between tag deployment and tag recovery.

Island	Site	Year	Deployment Session	Nest Status	Birds tagged	GPS depl.	GPS data	Mean (SD)			
								GPS duration	TDR depl.	TDR data	Mean (SD) TDR duration
Kaua'i	Kīlauea Point	2016	27-May–17-Sep	C	15	15	15	61.6 ± 30.8*	0	0	NA
		Lehua	2014	13-May–18-May	I	10	10	10	3.2 ± 0.8	10	10
			13-Jun–18-Jun	C	20	20	18	3.0 ± 0.5	20	19	3.0 ± 0.5
			14-Jul–20-Jul	C	20	20	19	3.8 ± 0.7	20	19	3.8 ± 0.7
		2015	26-May–04-Jun	I, C	25	25	22	5.6 ± 1.1	24	20	5.6 ± 0.9
			27-Jun–06-Jul	C	25	25	13	6.1 ± 1.0	10	8	7.2 ± 1.2
	Kaua'i Total:					120	120	97	4.4 ± 1.5*	84	76
O'ahu	Marine Corps Base	2014	01-Jun–07-Jun	C	39	39	31	3.3 ± 1.0	30	25	3.0 ± 0.9
		2015	17-Jun–24-Jun	C	20	20	19	5.3 ± 0.5	10	9	5.3 ± 0.5
	Hawai'i		29-Jun–08-Jul	C	20	20	16	7.6 ± 0.7	9	8	7.3 ± 0.5
		O'ahu Total:					79	79	66	4.9 ± 1.9	49
ALL SITES TOTAL:					199	199	164	4.6 ± 1.7*	133	118	4.3 ± 1.7

*Red-footed Boobies tagged at Kīlauea Point in 2016 were outfitted with e-obs telemetry tags, resulting in much greater tracking durations than at all other sites. Tracking durations for these individuals are not included in calculation of mean days tracked for Kaua'i Total or All Islands Total. In addition, accelerometry data was collected for these e-obs-tagged birds.

Table 18. Mean (\pm SD) Red-footed Booby foraging trip duration, maximum range, and distance traveled for short, long, multiday, and all trips for birds tagged with i-gotU GPS tags at MHI sites, 2014-2015.

Trip Type	Site (Year)	Birds	Trips	Duration (h)	Range (km)	Traveled (km)
Short	Lehua (2014)	32	63	5.4 \pm 3.0	39.0 \pm 22.6	104.5 \pm 58.4
	Lehua (2015)	21	30	7.5 \pm 3.0	49.1 \pm 24.6	134.6 \pm 59.1
	MCBH (2014)	25	54	6.6 \pm 2.7	60.3 \pm 26.5	146.9 \pm 62.3
	MCBH (2015)	32	123	7.1 \pm 2.7	54.3 \pm 22.8	138.4 \pm 57.2
	Short Total:	110	269	6.7 \pm 2.9	51.5 \pm 24.8	132.1 \pm 60.4
Long	Lehua (2014)	24	39	14.2 \pm 1.2	104.6 \pm 31.5	281.3 \pm 61.2
	Lehua (2015)	23	42	14.6 \pm 1.2	112.8 \pm 32.1	292.5 \pm 61.2
	MCBH (2014)	23	32	14.1 \pm 0.9	110.9 \pm 29.7	302.4 \pm 61.9
	MCBH (2015)	31	80	14.3 \pm 1.1	90.9 \pm 23.8	255.1 \pm 48.2
	Long Total:	101	193	14.3 \pm 1.2	101.7 \pm 29.7	276.4 \pm 59.0
Multiday	Lehua (2014)	9	9	44.4 \pm 17.8	149.5 \pm 53.0	570.5 \pm 169.4
	Lehua (2015)	24	35	49.3 \pm 18.0	190.5 \pm 64.9	626.4 \pm 171.5
	MCBH (2015)	6	6	49.0 \pm 21.2	201.6 \pm 87.1	646.1 \pm 245.3
	Multiday Total:	39	50	48.3 \pm 18.1	184.4 \pm 66.6	618.6 \pm 178.4
ALL TRIPS TOTAL:		144	512	13.6 \pm 13.4	83.6 \pm 52.4	233.9 \pm 163.4

Table 19. Mean (\pm SD) Red-footed Booby foraging trip duration, maximum range, and distance traveled for short, long, multiday, and all trips combined for birds tagged with e-obs GPS tags at Kīlauea Point NWR, Kaua'i, 2016.

Trip Type	Site (Year)	Birds	Trips	Duration (h)	Range (km)	Traveled (km)
Short	Kīlauea Point (2016)	15	180	7.3 \pm 2.8	60.5 \pm 32.4	158.2 \pm 71.5
Long	Kīlauea Point (2016)	15	265	14.7 \pm 1.6	139.7 \pm 42.2	339.7 \pm 77.4
Multiday	Kīlauea Point (2016)	14	65	39.2 \pm 8.7	226.8 \pm 58.8	633.2 \pm 137.2
Grand Total:		15	510	15.2 \pm 10.4	122.8 \pm 68.1	313.1 \pm 170.9

Table 20. Percentage of time (and number of locations, N) for behavior classes during day, night, and twilight on short, long, and multiday Red-footed Booby foraging trips for all MHI sites, 2014–2015 (i-gotU tags only). Sample sizes are indicated in parentheses.

Trip Type	Behavior	Day	Night	Twilight
Short	Rest	27.3% (13,538)	27.2% (141)	3.2% (107)
	Search	37.8% (18,764)	27.9% (145)	3.6% (121)
	Transit	34.9% (17,310)	44.9% (233)	93.2% (3,139)
Long	Rest	29.8% (22,162)	14.5% (133)	2.9% (191)
	Search	37.6% (27,910)	0.7% (6)	3.5% (228)
	Transit	32.6% (24,229)	84.9% (780)	93.6% (6,174)
Multiday	Rest	28.4% (13,033)	87.8% (17,127)	59.4% (5,100)
	Search	42.0% (19,267)	5.7% (1,112)	9.2% (789)
	Transit	29.6% (13,609)	6.5% (1,270)	31.4% (2,691)

Table 21. Mean (\pm SD) dive duration and depth of Red-footed Boobies tagged with temperature-depth recorder (TDR) tags from MHI sites, 2014–2015. Note that sample sizes may be slightly lower than reported in Table 17 because no dives were recorded or no valid dives were identified from some TDR deployments.

Year	Birds	Dives	Duration (s)	Depth (m)
2014	64	3,854	1.57 \pm 1.31	1.02 \pm 0.49
2015	43	2,476	1.37 \pm 0.65	1.28 \pm 0.55
All	107	6,330	1.50 \pm 1.10	1.12 \pm 0.53

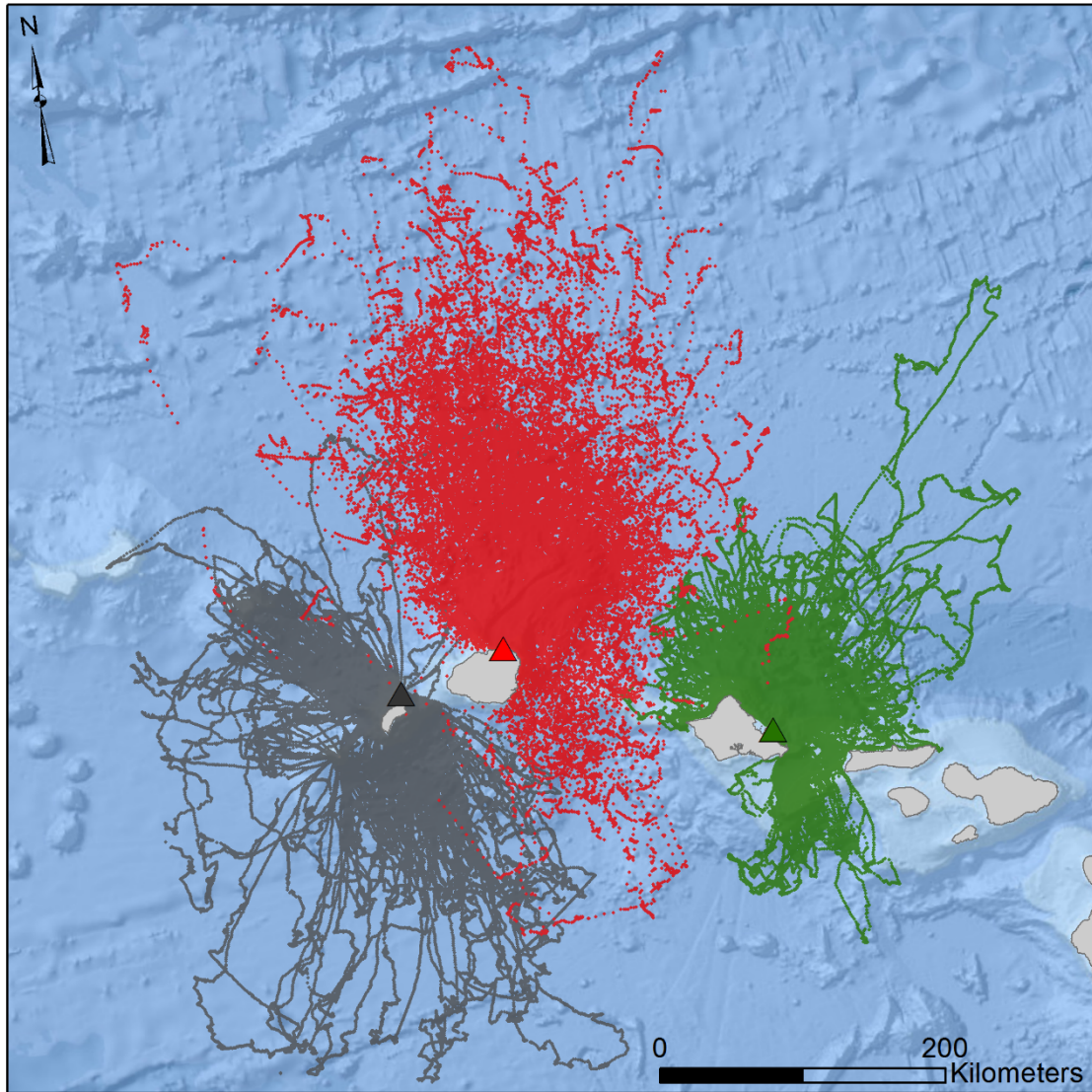


Figure 61. Raw Red-footed Booby tracking data from Lehua Islet (2014–2015, black), Kīlauea Point NWR (Kauaʻi, 2016, red), and Marine Corps Base Hawaiʻi (Oʻahu, 2014–2015, green). Colored triangles indicate tagging sites.

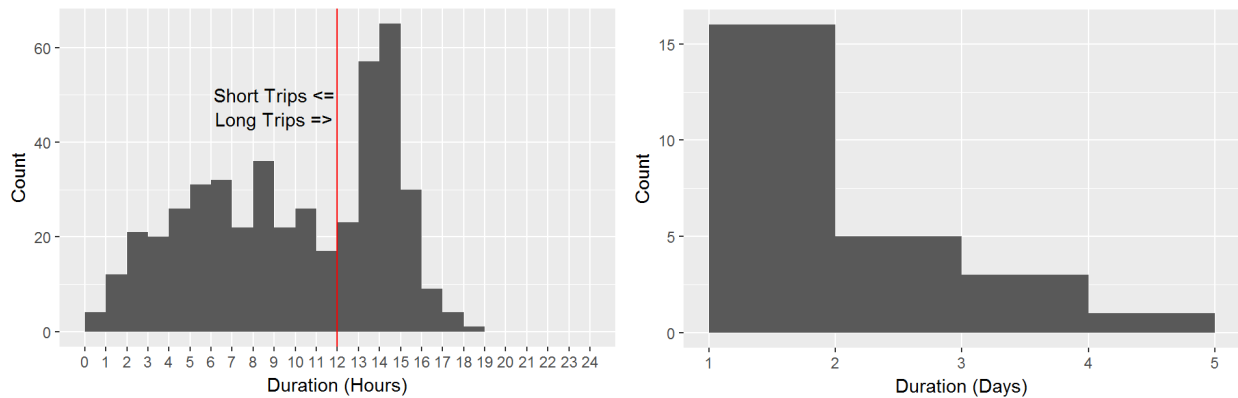


Figure 62. Distributions of trip durations for single day (left) and multiday (right) foraging trips of Red-footed Boobies tagged with iGot-U GPS tags from all MHI sites, 2014–2015. Single day trips were further categorized as short (≤ 12 h) or long (> 12 h) based on obvious bimodality in distribution.

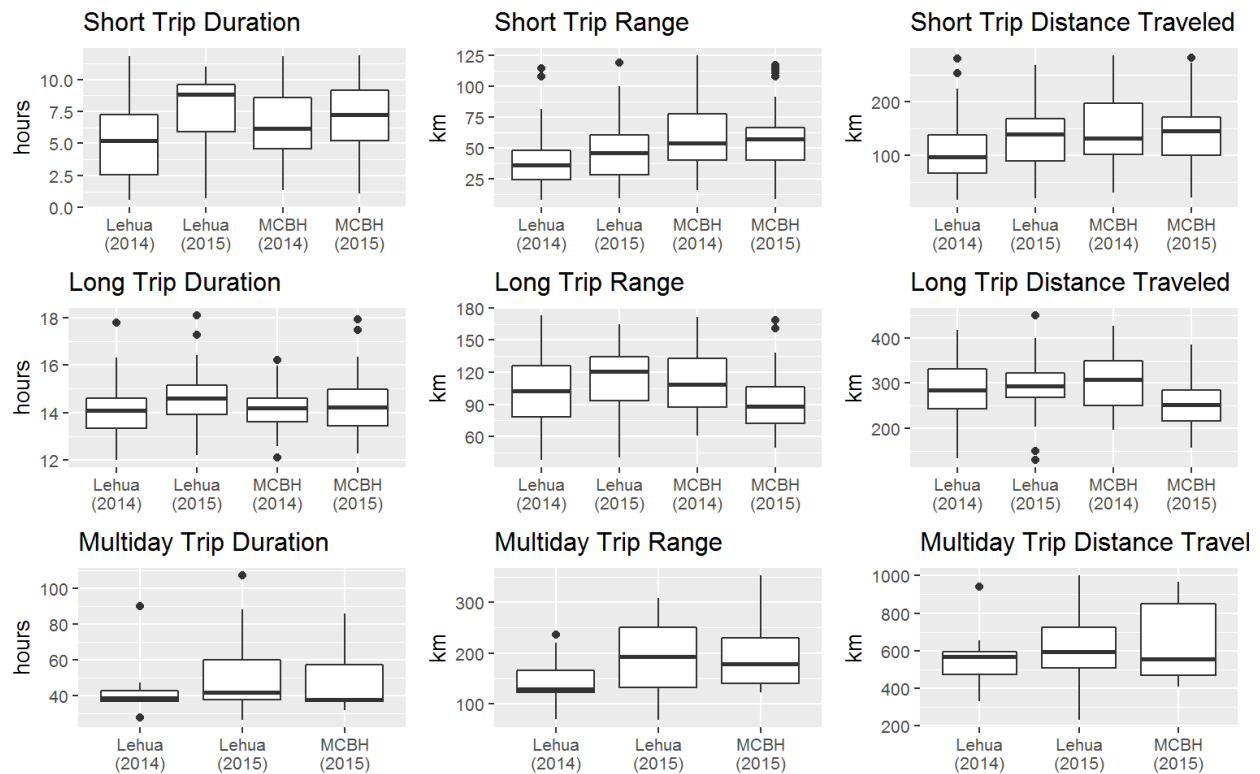


Figure 63. Box-and-whisker plots of duration, range, and distance traveled for short, long, and multiday Red-footed Booby foraging trips by year and location from MHI sites, 2014–2015 (i-gotU tags only). The black line in box represents the median, the box represents the inter-quartiles (25% and 75%), the whiskers extend to the furthest point within 1.5 interquartile ranges, and dots are any additional points beyond the whiskers.

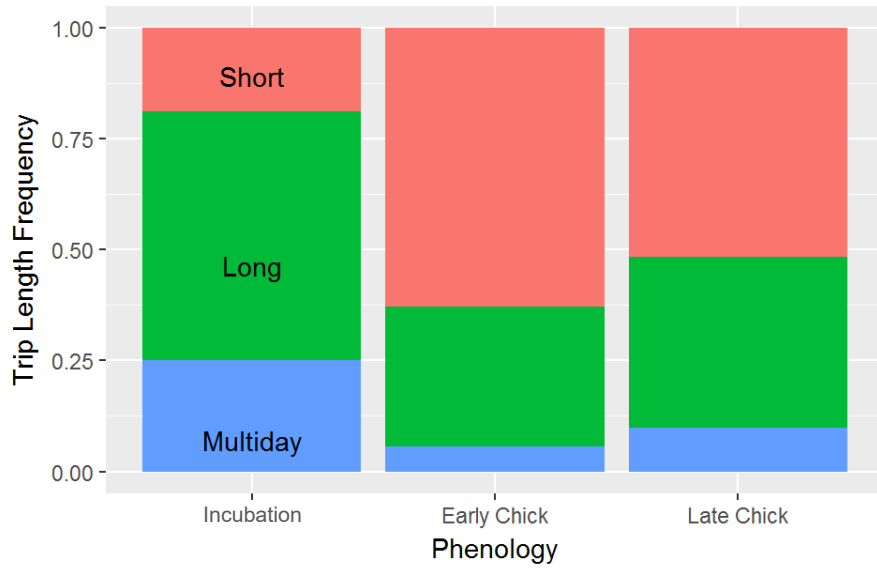


Figure 64. Proportion of Red-footed Booby foraging trip length categories by phenology for all MHI sites, 2014–2015 (i-gotU tags only).

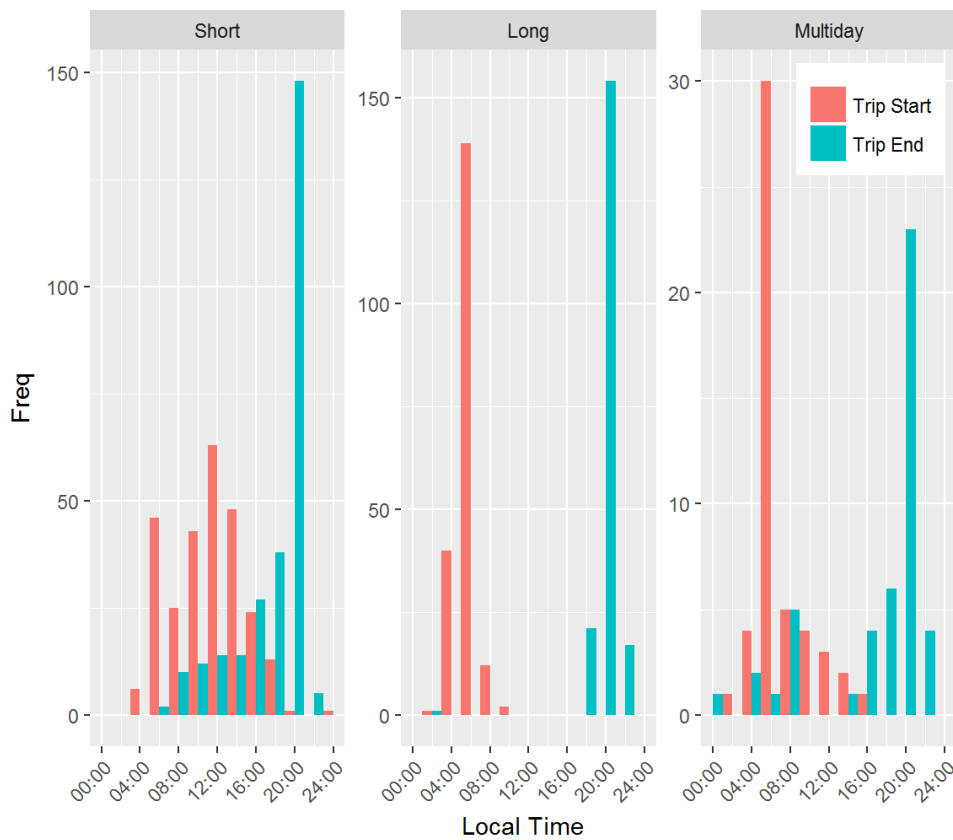


Figure 65. Histograms of trip start and end times for short, long, and multiday Red-footed Booby foraging trips for all MHI trips, 2014–2015 (i-gotU tags only).

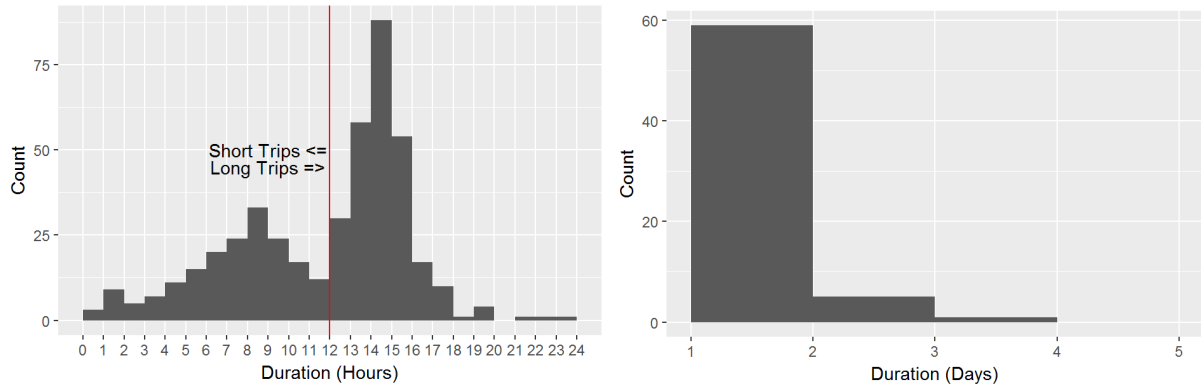


Figure 66. Distributions of trip durations for single day (left) and multiday (right) Red-footed Booby tracked with e-obs GPS tags from Kīlauea Point NWR, Kaua‘i, 2016. Single day trips were further categorized as short (≤ 12 h) or long (> 12 h) based on obvious bimodality in distribution.

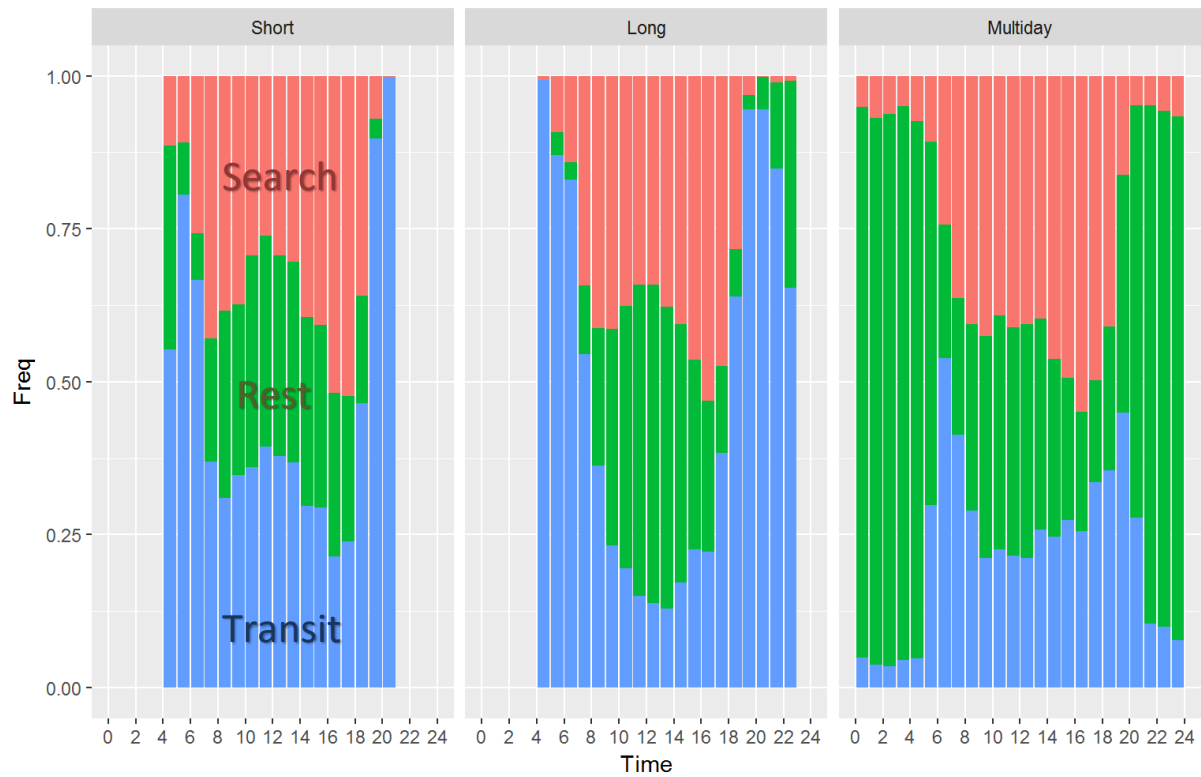


Figure 67. Daily activity patterns for all Red-footed Boobies on short (left), long (middle), and multiday (right) foraging trips from all MHI sites, 2014–2015 (i-gotU tags only).

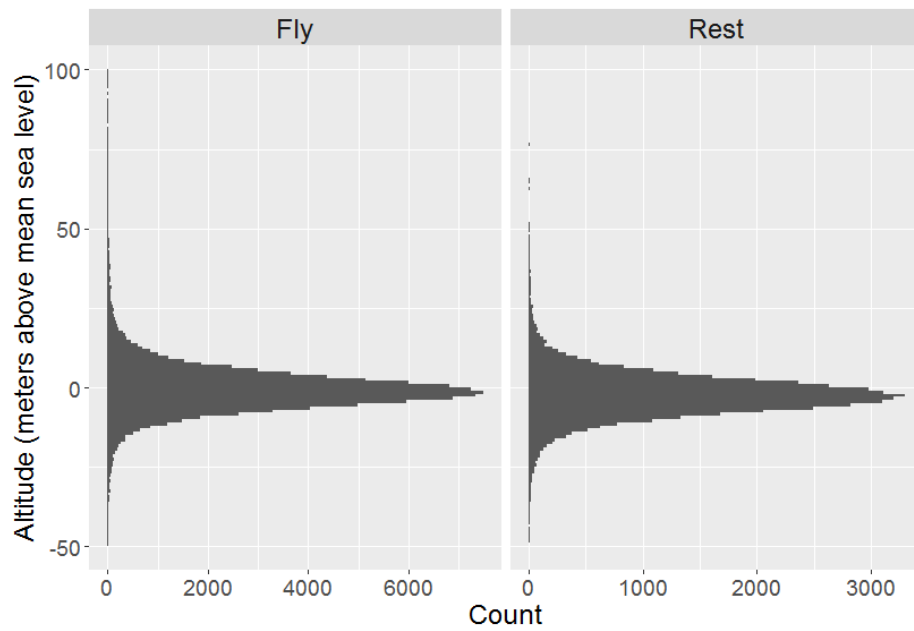


Figure 68. Distributions of Red-footed Booby altitude measurements for flying (left) and resting (right) GPS locations of birds tracked from all MHI sites, 2014–2015 (i-gotU tags only).

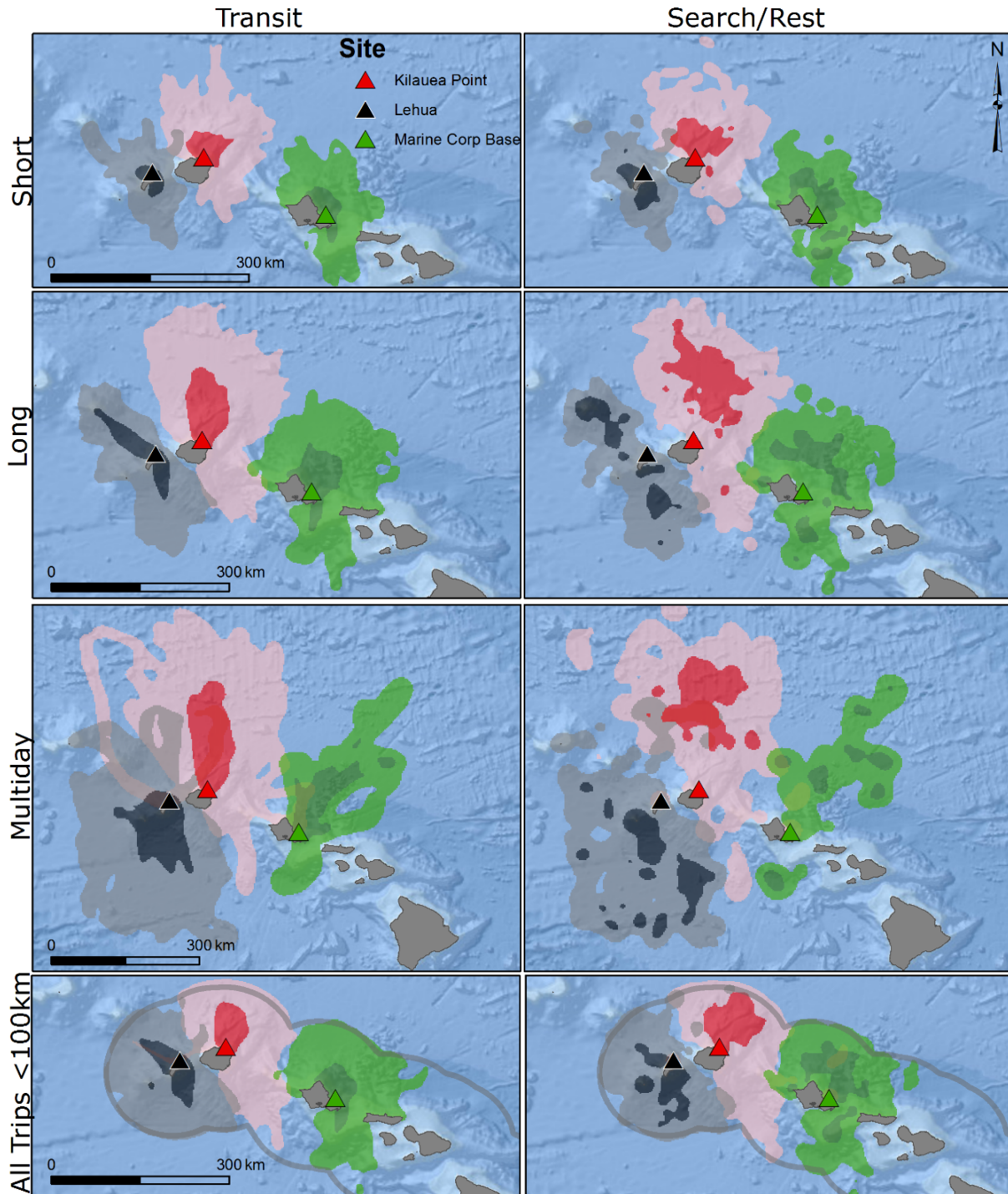


Figure 69. Kernel density distributions Red-footed Boobies tracked from MHI, 2014–2016. Distributions are mapped of short trips (top row), long trips (second row), multiday trips (third row), and all tracking data within 100 km of MHI (bottom row) for each behavioral state (columns) from Lehua Islet (2014–2015; black), Kilauea Point NWR (2016; red), and Marine Corps Base Hawai'i (2014–2015; green). Colored triangles indicate tagging sites. Colors are shaded lighter for 99% contour and darker for 50% contour. Kernel smoothing factor set manually to 1.5% the spatial extent of the data ($h = 4.6$ km for short trips, 6.3 km for long trips, 9.4 km for multiday trips, and 6.3 km for all trips <100 km). Note varying spatial scale of each row of maps.

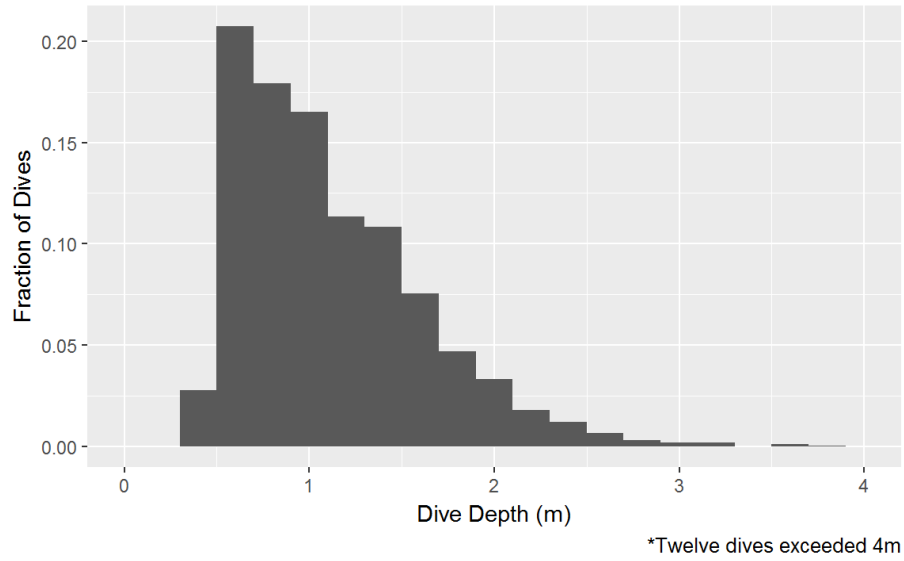


Figure 70. Distribution of Red-footed Booby dive depths at all MHI sites, 2014–2015.

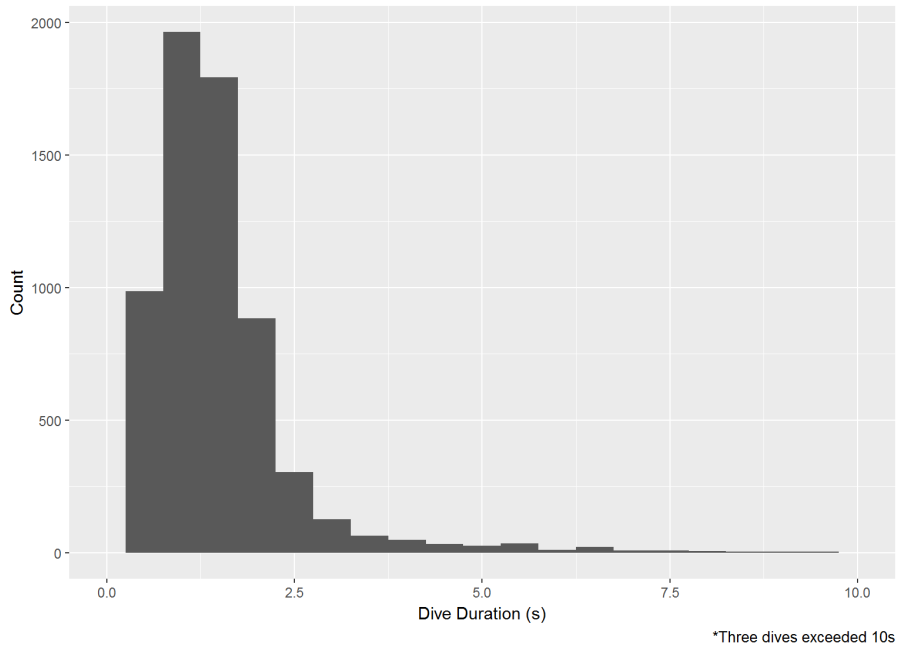


Figure 71. Distribution of Red-footed Booby dive durations for all MHI sites, 2014–2015.

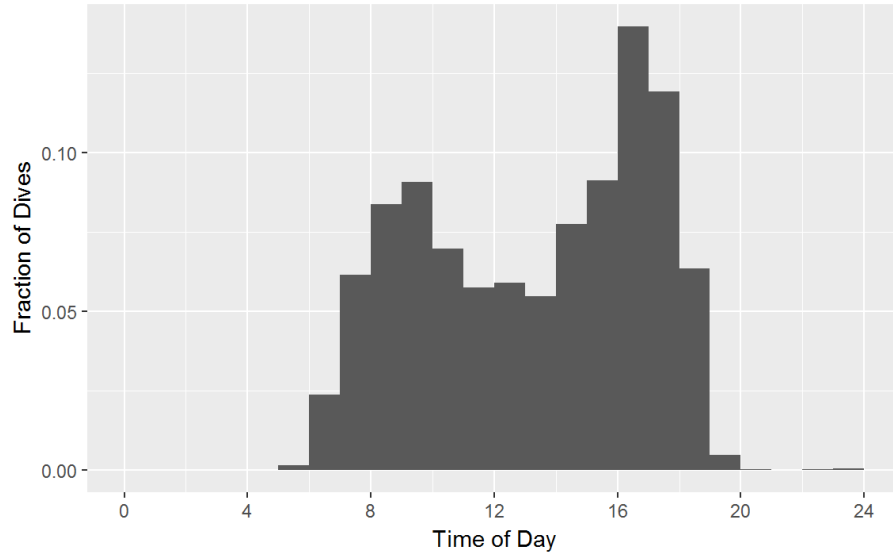


Figure 72. Distribution of Red-footed Booby dives by hour of the day for all MHI sites, 2014–2015.

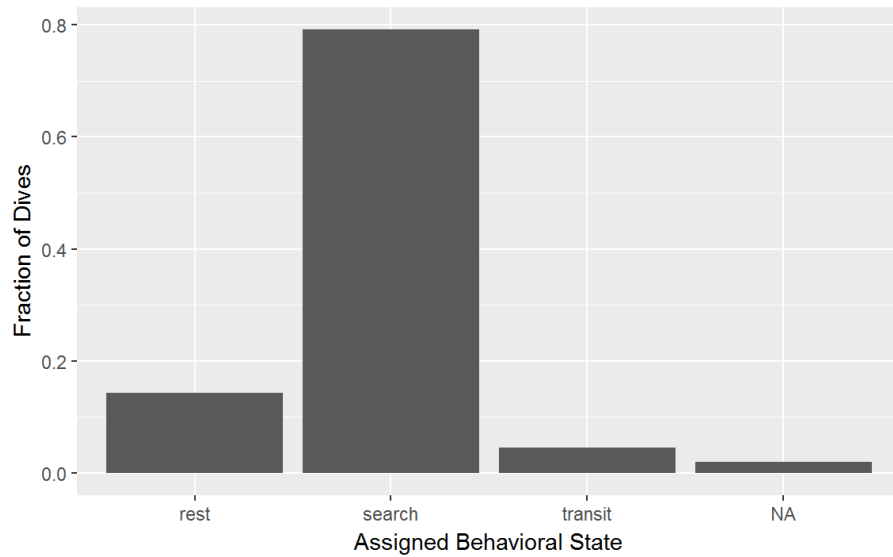


Figure 73. Distribution of Red-footed Booby dives in each behavioral state for all MHI sites, 2014–2015. NA records are for dives that occurred at a GPS location where behavior could not be assigned (e.g. first and last locations of a trip).

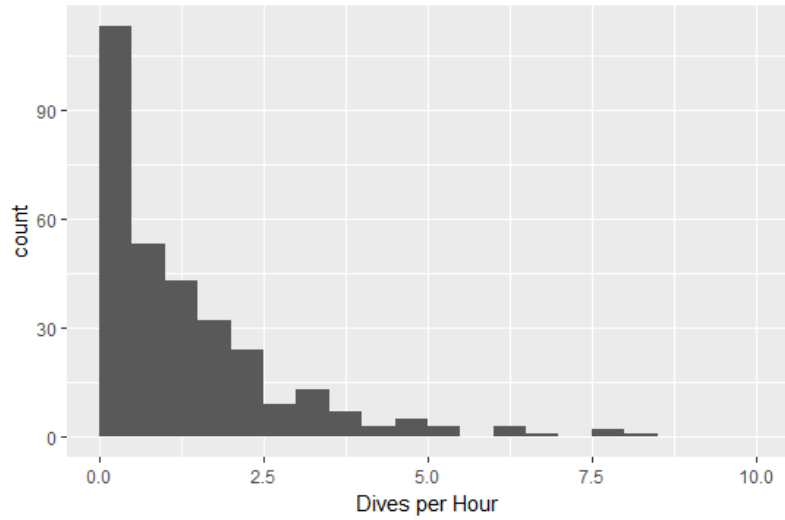


Figure 74. Distribution of dives per hour per trip for Red-footed Boobies from all MHI sites, 2014–2015. This metric was only calculated for deployments where both GPS and TDR data were collected, allowing for the assignment of dives to specific foraging trips. Note that three dive rate values were measured beyond x axis limit (13.5, 27.6, and 36.6 dives h⁻¹).

4 Discussion

This collaborative telemetry project contributed new information about the distribution at sea and ranging behaviors among five abundant, breeding seabird species throughout the MHI. A more comprehensive understanding of the movement ecology of Hawaiian seabirds from their colonies and nest sites will benefit efforts seeking to understand and minimize potential impacts of planned offshore energy infrastructure. Understanding breeding-season movements is particularly important because adult seabirds are constrained to nest on land and raise their young by making repeat forays to sea to find food. Adult survival among long-lived seabirds also is important for sustaining population growth and recovery; impacts that negatively affect adult breeding birds have a disproportionate effect on population growth rates. Species-specific foraging ranges and provisioning requirements create interspecies differences in how much time individuals spend over waters of varying distance from their nest sites. In some species, nearshore areas (i.e., <100 km from nest sites) may be important for resting, socializing, or foraging. Other more far-ranging species (e.g., petrels and albatrosses) may spend little time foraging in nearshore areas, but they likely commute to and from distant foraging areas by using relatively predictable transit corridors at sea.

4.1 Red-tailed Tropicbird

Our results are among the first to describe the ranging behaviors at sea for individual breeding Red-tailed Tropicbirds. We tracked birds using GPS from three sites on O‘ahu, Kaua‘i, and Lehua (Ni‘ihau). The species proved reasonably easy to track using tail-mounted GPS units; however, tag and tail feather loss occasionally occurred, and we recommend caution if this attachment is to be used in the future. Taping units directly to the back feathers—a relatively common approach for other seabirds—did not work well with tropicbirds because they have relatively weak and small body contour feathers. Tag attachment durations and logistic constraints that imposed limited deployment windows on remote Lehua prevented us from fully characterizing the long-trip aspects of the species’ bimodal foraging strategy, especially in 2014. Furthermore, tracking data from Hālonā (O‘ahu) was minimal compared with the Kaua‘i and Lehua sites. Since the conclusion of this study, there was additional Red-tailed Tropicbird tracking at Hālonā in 2017 that could provide more insight to ranging patterns at sea and help to resolve the bi-modality in breeding season foraging trip duration to foraging areas south and southeast of O‘ahu (O. Townsend, unpublished data). In general, longer-duration tracking (i.e., with solar-powered tags and/or better attachment techniques) and incorporation of extended nest monitoring to quantify foraging trip durations, could provide more insight into the relative importance in overall breeding season time budgets between short vs. long trip types for this species (e.g., Congdon et al. 2005).

Based on RST behavioral classification results, Red-tailed Tropicbirds spent considerable time during the daytime transiting and engaging in search/foraging modes (both behavioral modes combined: >75% and >55% of their time during short and long trips, respectively) and almost exclusively rested on the water at night. Unique among the seabirds we tracked in this study, Red-tailed Tropicbirds spent considerable time (70.6% [95% CI 70.1–71.0%] of flight time) flying at an altitude range equivalent to an expected RSZ for an offshore wind turbine. Although we do not know this species’ capacity for avoiding collision with wind turbines at sea, carcasses of White-tailed Tropicbirds, which have a similar flight style as Red-tailed Tropicbirds but nest much farther inland, have been collected and recorded in association with land-based wind energy infrastructure in Hawai‘i (J. Charrier, USFWS, unpublished data).

This study marked the first attempt to measure diving behavior among individual Red-tailed Tropicbirds nesting in Hawai‘i. Although we recovered 34 of 43 TDRs deployed on tropicbirds, data were too noisy for our QAQC TDR processing scripting and we could not reliably identify dives. During chick-rearing, breeding individuals on Europa Island (Indian Ocean) were recorded performing shallow dives to 2.3 ± 1.0 SD m indicating this species uses passive plunging to catch prey at or very close to the surface

(Le Corre 1997). Sommerfeld and Hennicke (2010) recorded similar diving capacity among incubating and chick-rearing Red-tailed Tropicbirds tagged on Christmas Island (Indian Ocean). Neither study commented on the propensity for this species to engage in aerial pursuit of prey (especially flying fishes and squids), but this behavior may be rare (Schreiber and Schreiber 2009). Further study is needed using TDRs (ideally coupled with accelerometry) on both short- and long-duration foraging trips to determine if Red-tailed Tropicbirds, when not feeding aerially, plunge-dive (limiting depth to upper few meters) or also actively pursuit-dive to greater depths.

4.2 Laysan Albatross

Although relatively small numbers of Laysan Albatross nest in the MHI compared with the northwestern Hawaiian Islands, small breeding colonies on Kaua‘i and O‘ahu are considered important to land-owners and resource managers, and they receive special conservation attention and relatively detailed monitoring (e.g., Kaua‘i Albatross Network, Hawai‘i DLNR-DOFAW, US Navy, US Fish and Wildlife Service). We tracked Laysan Albatrosses from three breeding colonies in the MHI: Ka‘ena Point (O‘ahu; 2014), Na‘Aina Kai (Kaua‘i; 2014) and Waipake (Kaua‘i; 2014). Back-mounted GPS tags taped to contour feathers worked well for this species.

Our Laysan Albatross results are focused on the mid- to late-chick-rearing period when provisioning adults typically range far from the colony in search of food (Young et al. 2009, Connors et al. 2015). During this time, most of the relatively nearshore (<100 km from nest site) ranging is associated with transit flights of birds departing on or returning from long, distant trips to provision their young. In this study, we documented more short trips than long trips; however, the majority of individual tracking duration was occupied by long, distant trips. All three North Pacific albatross species are known to associate with vessels at sea (e.g., Wahl and Heinemann 1979, Hyrenbach 2001, Deitrich and Melvin 2007, Gilman et al. 2008) in areas where fisheries overlap with albatrosses. The degree to which certain fishing activities (e.g., Hawaiian longline tuna fisheries) modify albatross distribution at sea is unknown. However, recent work has demonstrated that Black-footed Albatross (*P. nigripes*; not tracked in our study) were most likely of the three species to approach vessels, and Laysan Albatross (including those tracked in this study) were more likely to approach vessels during the return portion of their long, looping trips throughout the northeastern Pacific (Orben et al. unpublished data). Additional tracking information on short, guard-stage foraging trips, and the addition of tracking albatrosses breeding on Lehua (Ni‘ihau) could be more relevant to OWEI development around MHI (i.e., birds from Lehua might access the north Pacific by transiting through the Ka‘ie‘ie Waho Channel separating Kaua‘i and O‘ahu). Tracking data for guard-stage Laysan Albatross from Ka‘ena Point were collected by Nishizawa et al. (2018) and their data may be useful for future marine spatial planning.

Considering both long and short trips together, Laysan Albatrosses spent >70% of their time in transit or engaged in search/foraging behavior and more time resting during night than during twilight and day-time. These results are consistent with those of Connors et al. (2015) who reported that Laysan Albatrosses spent 70% of their time in flight. Whereas albatrosses can achieve impressive heights in high-wind conditions during the apex (i.e., “pullup”; Pennyquick 2002) of their characteristic sinusoidal flight path while transiting (Sachs et al. 2013), time-at-altitude is brief. Our GPS-derived altitude results revealed that for the most part, individuals occupied airspace close to the ocean’s surface (0–5 masl), and in contrast to results from GPSs deployed on Red-tailed Tropicbirds, albatrosses rarely achieved an altitude that would overlap with the expected RSZ of an offshore wind turbine. Although not considered here, the e-obs GPS tags deployed on albatrosses also collected accelerometry data that might be useful in future analyses designed to measure more detailed behavior or estimated energy expenditure at sea (see Connors et al. 2015, Czupanski et al. 2018a).

4.3 Wedge-tailed Shearwater

Wedge-tailed Shearwaters are among the most abundant and wide-spread breeding seabirds within the MHI; this numerical dominance, combined with their close associations with sub-surface predators (e.g., skipjack and big eye tuna (*Thunnus obesus*), and cetaceans) and multispecies seabird foraging aggregations (Hebshi et al. 2008), make Wedge-tailed Shearwaters good indicators within sub-tropical marine ecosystems of areas with enhanced productivity, species diversity, and nutrient transfer. We tracked Wedge-tailed Shearwaters from 11 colonies throughout Kaua‘i, O‘ahu, and Maui. Taping units directly to the back feathers—a relatively common approach for some seabirds—was moderately successful for Wedge-tailed Shearwaters, but tag loss was not insignificant, especially during longer-duration trips (see also Calabrese 2015). Attaching i-gotU-style GPS tags with tape to tail feathers minimized tag loss in other studies of this species (e.g., McDuie et al. 2018) and should be considered as an alternative approach. Tag attachment durations and logistic constraints also imposed limited deployment windows at some sites, thereby preventing full characterization of the long-trip aspects characteristic of the species’ multi-modal foraging strategy. In general, longer-duration tracking (e.g., with solar-powered tags and/or better attachment techniques), together with extended nest monitoring to quantify foraging trip durations, could provide more insight into the relative importance of tracking data from different trip types in overall breeding season time budgets for this species (e.g., Baduini 2002, Congdon et al. 2005).

Wedge-tailed Shearwaters departed from and returned to their colonies during the dark hours of night and pre-dawn and displayed three modes in trip duration. During trips lasting >12 h and <24 h (intraday trips), individuals spent considerably more time (>53%) flying in transit during the night compared with the other species tracked during this study. During multiday trips to sea, Wedge-tailed Shearwaters were consistent with other species and spent most of their time at night (>71%) resting on the surface. If vulnerability to collision with offshore wind turbines is greater for seabirds during darkness (Marques et al. 2014, Hüppop et al. 2016), then Wedge-tailed Shearwaters would be most vulnerable during colony arrival and departure for all trip modes, but perhaps more so during the relatively frequent intraday trips when they are mostly in transit during the night (assuming they are not displaced from OWEI, thus reducing collision risk; Kelsey et al. 2018). Although present to some degree, the increased hypothetical collision vulnerability associated with increased nocturnal flight and relatively nearshore (<300 km) foraging range during short trips could be ameliorated by our observations of low flight altitudes among shearwaters. For example, we estimate that Wedge-tailed Shearwaters remain close to the ocean’s surface and only spend 5.20% (95% CI 5.13–5.27%) of their total flight time within the potential RSZ of an offshore turbine. Over land however, where we lack movement behavior data, Wedge-tailed Shearwaters are among the more-frequently observed seabird carcasses associated with land-based wind-turbine sites in Hawai‘i (J. Charrier, USFWS unpublished data).

Although the maximum range of frequent intraday trips (227 km) would be most likely to overlap with potential offshore energy infrastructure located relatively close to the islands, Wedge-tailed Shearwaters on longer-duration foraging trips also spent time (e.g., core-use areas) searching and foraging <100 km from shore. Interestingly, we did observe birds from colonies located on Maui (Hāwea, Ho‘okipa, and Kama‘ole 3, and birds from eastern O‘ahu (Marine Corps Base Hawai‘i), utilizing core areas located off the island of Hawai‘i during short and long trips. Although the reasons for foraging trip destinations among individuals from these Maui and O‘ahu colonies remain undetermined, it may relate to potential interference competition associated with greater numbers of Wedge-tailed Shearwaters surrounding O‘ahu, and the lack thereof off Hawai‘i where there are very few known nesting sites. Alternatively, environmental conditions or distribution of sub-surface predators such as tunas could create advantageous foraging conditions for shearwaters off Hawai‘i.

This study contributed significantly more information (897 valid dives made by 39 individuals) related to diving behavior among individual Wedge-tailed Shearwaters provisioning chicks in Hawai‘i. Relatively shallow diving observed in this study is consistent with their observed foraging modes at sea (contact-dipping, surface-seizing, aerial pursuit, and pursuit-diving) where they almost always forage in mixed-species flocks in association with subsurface predators (e.g., tunas, dolphins; Whittow 1997, Hebshi et al. 2008, Hyrenbach et al. 2014). Our results (mean maximum depth per individual = 4.40 ± 1.17 m and the deepest dive recorded = 10.06 m, mean dive duration = 3.12 ± 3.44 s) are similar to Peck and Congdon (2006) who measured Wedge-tailed Shearwater diving behavior using Maximum-Depth Gauges deployed on chick-rearing adults conducting short (≤ 3 days) trips (mean maximum dive depth across all trips = 5 m [range: 2.0–11.7 m]). Using similar Temperature-Depth Recorders, Hyrenbach et al. (2014) documented deeper and longer dives from four individuals conducting short trips (≤ 2 days) from their colony at Lehua Islet (mean individual maximum depth = 9.7 m, range: 1.5–21.8 m; single dive mean duration = 16 s, bout dive mean duration = 48 s). However, these TDRs were programmed with a deeper threshold (depth > 1.5 m) than in our study, likely contributing to the discrepancy between results. Although it was unfortunate that we could not combine TDRs with GPSs deployed on Wedge-tailed Shearwaters, future analyses could benefit by mapping and highlighting the locations at sea during the time of day when shearwaters were recorded diving (late morning and early afternoon, no diving at night), thus providing an approximate spatial context for where most diving associated with foraging would be expected to occur.

4.4 Brown Booby

Brown Booby breeding colonies west of Kaua‘i (Lehua Islet and, to a lesser extent, Ka‘ula Rock) represent the majority of a relatively small overall Hawaiian breeding population. Although Brown Boobies were more difficult to capture for tag deployment and recovery compared with Red-footed Boobies, we were able to track 42 individuals successfully from Lehua Islet (Ni‘ihau/Kaua‘i) using a combination of GPS tags and TDRs for an average of 4–6 days. GPS tag tail attachments worked well for this species.

Consistent with previous observations that showed Brown Boobies foraging ~30 km from their colonies in the Gulf of California (Weimerskirch et al. 2009,) and 45–50 km from colonies in the Caribbean (Soanes et al. 2016), we found that Brown Boobies on Lehua made relatively short duration (< 5 h on average) nearshore (~35 km) foraging trips and observed very few birds engaging in multi-day trips involving off-colony roost sites (e.g., Kaua‘i and Ni‘ihau). Brown Boobies divided their time at sea fairly equivalently according to the three behavioral classifications, with slightly more time proportionately spent in transit (~39%). Brown Boobies appeared to spend most of their time at sea flying close to the ocean surface; we estimated that this species spent 3.41% (95% CI 3.16–3.67%) of its flight time at the altitude of the RSZ of an offshore wind turbine. The species’ propensity for roosting at sea (Pitman 1993) indicates that individuals might associate with artificial roosting habitat provided by potential offshore wind energy infrastructure if this were to be located within their foraging range from nesting colonies.

This is the first study to examine diving behavior among Brown Boobies provisioning chicks in Hawai‘i, and we contributed significantly more new data about diving behavior (1,618 valid dives from 35 individuals). Brown Boobies exhibit reversed sexual dimorphism; females are approximately 20–25% heavier than males (Nelson 1978, Weimerskirch et al. 2009) and up to 35% heavier than males on Johnston Atoll (Lewis et al. 2005). Males are more active foragers and appear to dive more frequently than females (Lewis et al. 2005, Weimerskirch et al. 2009). Despite the sexual dimorphism recorded by Lewis et al. (2005), they found no significant difference in dive depth between sexes (~0.85 m). Although we have yet to analyze sex differences in diving behavior, Brown Boobies in our study dove deeper on average (1.42 ± 0.75 m [median = 1.25 m]) than the boobies tracked by Lewis et al. (2005) from Johnston Atoll (Pacific Ocean). Excluding trips where no dives were measured, our measured dive rate (2.8 ± 3.5 dives h^{-1}) was similar to the rate measured among females from Johnston Atoll, but half as frequent as the

dive rate measured for males there (Lewis et al. 2005). Yoda et al. (2007) found that hand-raised juvenile Brown Boobies did not dive as deep as wild adults, possibly because they are not as well practiced or have not developed sufficient ability to dive as efficiently as adults.

4.5 Red-footed Booby

Red-footed Boobies are relatively common in the MHI with breeding populations on O‘ahu and Kaua‘i/Ni‘ihau. Similar to Wedge-tailed Shearwaters, Red-footed Boobies are also important ecosystem indicator species that associate with sub-surface predators (Ballance et al. 1997, Maxwell and Morgan 2013). We tracked Red-footed Boobies using a combination of tag types, including relatively short-duration (4–8 d on average) deployments of GPS loggers with and without TDRs (Marine Corps Base Hawai‘i, O‘ahu and Lehua, Kaua‘i/Ni‘ihau) and longer-duration (>60 d on average) deployments with solar GPSs outfitted with accelerometers (Kīlauea Point NWR, Kaua‘i). Tail-attachments worked well, although folded wings may have reduced e-obs GPS tag solar capacity and battery recharge while birds perched at nests and/or rested on the water surface. In addition, e-obs 15 g solar tags experienced GPS timeout and reception problems at sea that were unrelated to battery power, causing gaps in some tracks.

Red-footed Boobies displayed variability in foraging trips with a multimodal distribution of durations that included short (~50 km from colony), long (~100 km), and relatively rare, multi-day trips that were mostly associated with the individuals engaged in incubation during 2015. Their relatively nearshore (<100 km) ranging capacity generated core-use areas that could overlap with potential offshore energy infrastructure. Individuals were primarily diel foragers and activity at sea during night was rare. Individuals engaged in approximately equal proportions of time spent in each of the 3 behavioral classifications (rest, search, and transit). Our GPS-derived measurements of flight height indicated that unlike Red-tailed Tropicbirds, but similar to the other seabirds tracked, Red-footed Boobies spent their flight time near the ocean’s surface; possible rare excursions to greater heights while searching or transiting expose them to an altitude range equivalent to the estimated RSZ 2.74% (95% CI 2.63–2.84%) of the time.

On occasion we observed Red-footed Boobies engaged in “stepping stone” foraging where individuals nesting on Lehua roosted for a period during a foraging trip on Ka‘ula off Ni‘ihau. One track also indicated that an individual roosted for a period onboard an ocean-going vessel. This behavior indicates the potential for Red-footed Boobies to be attracted to offshore energy infrastructure as an artificial roost site or jump-off point during foraging, thereby increasing the species’ estimated vulnerability to OWEI (see Kelsey et al. 2018). Although not considered here, the solar e-obs GPS tags deployed on Red-footed Boobies at Kīlauea Point NWR also collected accelerometry data that might be useful in future analyses designed to measure more detailed behavior or estimated energy expenditure at sea. For example, these accelerometry data were recently used to evaluate “energy landscapes” and estimate energetic expenditure among individuals transiting through variable wind-scapes at the three colonies where we worked (Czapanskiy et al. 2018b). In addition, Donahough (2018) used diet data collected from Red-footed Boobies studied in this project in conjunction with GPS tracking data to assess the relationships between diet and ranging behavior at Marine Corps Base Hawai‘i, O‘ahu.

This is the first study to examine the diving behavior of Red-footed Boobies provisioning chicks in Hawai‘i (6,330 dives by 107 individuals). Although we measured a similar mean dive depth (1.12 ± 0.53 m) as Weimerskirch et al. (2005) among boobies tagged at Europa Island (Indian Ocean; 0.98 ± 0.47 m), we recorded a comparatively lower dive rate (1.9 ± 3.2 dives h^{-1} vs. 4.4 ± 3.7 dives h^{-1}), perhaps due to device differences in the two studies. Weimerskirch et al. (2005) estimated that during searching, Red-footed Boobies were able to climb regularly to altitudes of 20–50 m, and that dives to about 1 m were attained by plunging from an altitude of 9.2 ± 7.4 m (range 2–32 m).

4.6. Species not included in this study

For a variety of reasons, we were not able to track all species of seabirds breeding within the MHI. Additional seabird species that have relatively abundant or locally important breeding populations in MHI, but were not tracked during this study, include White-tailed Tropicbird, Black Noddy, Brown Noddy, Sooty Tern, Bulwer's Petrel, and Black-footed Albatross. In addition, there are three state- and federally-listed species that also occur in the MHI: Band-rumped Storm-Petrel (*Oceanodroma castro*, 'Ake'ake; U.S. Endangered Species Act [ESA] and Hawai'i Endangered), Hawaiian Petrel (ESA and Hawai'i Endangered), and Newell's Shearwater (ESA and Hawai'i Threatened; Hawai'i DOFAW 2019, USFWS 2019). We present relevant background information in the Appendix) for consideration and to help with planning related to understanding potential effects of OWEI off the MHI.

4.7 Summary

Our results were specific to the oceanographic conditions that affected breeding seabirds during specific deployment sessions in 2013–2016. Oceanic variability can affect trophic conditions, breeding propensity, reproductive success, and ranging behaviors at sea. More studies would be required to fully evaluate variability in the at-sea behaviors among MHI seabirds associated with interannual environmental variability. From a phenological perspective (timing of events during the breeding season), our studies focused for the most part on breeding adults that were engaged in provisioning their chicks. Additional studies that included early-breeding-season movements would be useful for evaluating seabird vulnerability to OWEI off Hawai'i. If possible, and provided researchers could minimize disturbance, tracking during incubation (all species) and guard stage (specifically, albatross) would allow for a more comprehensive assessment of species' ranging behaviors at sea. With appropriately designed studies, managers could gain insight across the entire breeding period and better understand overall use/time budgets, especially within near-MHI waters. Additionally, future tracking results would benefit by attempting to accommodate tracking durations that encapsulate multiple cycles of long trips for species like Wedge-tailed Shearwater and Red-tailed Tropicbird, to better evaluate overall time budgets and increase our understanding of seabird vulnerability to ocean energy development in near-MHI waters. Whereas, we were able to achieve long-duration tracking data among Laysan Albatross and Red-footed Booby, it is now possible to use similar tags that might also work for Wedge-tailed Shearwater and Red-tailed Tropicbird. Better resolution regarding multi-modal trip durations could be achieved also by employing extended nest monitoring (e.g., human- or camera-facilitated observation). Although tracking seabirds in challenging environments can be difficult, future studies should strive to ensure sufficient logistical capacity to recover data from a maximum number of tags, perhaps by using remote download capabilities similar to the e-obs GPS tags used on Laysan Albatross and Red-footed Booby. Lastly, as technology improves, we encourage tracking more species in order to gain a more comprehensive picture of the full MHI seabird community's behavior at sea during the breeding season (see Appendix). Alternative, lower-resolution tagging options (e.g., GLS tags) also are available to describe seasonal-use of Hawaiian waters and dispersal to other portions of the Pacific during the non-breeding season.

Lastly, the tracking data associated with the results presented in this report can be rendered using a variety of techniques available to GIS practitioners. Many techniques are available for depicting area-use at sea, point and line densities, and quantitative raster layers. These and additional telemetry data are unique and useful for future marine spatial planning; telemetry data provide for a more comprehensive assessment of the vulnerability at-sea of Hawaiian seabirds to potential OWEI. Users should be aware of the biases and limitations associated with these data and take an informed, precautionary approach when conducting analyses and drawing conclusions. Integrating telemetry data with revised population counts and MHI colony distributions will be particularly important for estimating potential colony-specific foraging areas (see Grecian et al. 2012, Baylis et al. 2019) that may overlap with planned infrastructure at sea. Ultimately, species- and colony-specific data for MHI seabirds will support better evaluations of risk and

options for mitigation strategies that allow diverse populations that characterize the Hawaiian seabird avifauna to co-exist with a changing ocean environment.

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Appendix

We were not able to track all species of seabirds breeding within the main Hawaiian Islands (MHI). Additional seabird species with relatively-abundant or locally-important breeding populations in the MHI not tracked during this study, include White-tailed Tropicbird, Black Noddy, Brown Noddy, Sooty Tern, White Tern (*Gygis alba candida*; Manu-o-ku), Bulwer's Petrel, and Black-footed Albatross. In addition, there are three state- and federally-listed species that also occur in the MHI: Band-rumped Storm-Petrel (U.S. Endangered Species Act [ESA] and Hawai'i Endangered), Hawaiian Petrel (ESA and Hawai'i Endangered), and Newell's Shearwater (ESA and Hawai'i Threatened; Hawai'i DOFAW 2019, USFWS 2019). In this appendix, we present relevant background information for consideration and to help with planning related to understanding potential effects to these taxa of offshore wind energy infrastructure (OWEI) off the MHI.

White-tailed Tropicbirds are commonly seen on all the MHI, but their nest sites tend to be more dispersed, farther inland, and much less accessible than those of Red-tailed Tropicbirds. Campos et al. (2018) tracked 11 White-tailed Tropicbirds and used nest observations to record birds using a dual long- / short-trip foraging strategy. In their study, short trips lasted ~4 h and ranged 8-70 km from their nest site. During long trips White-tailed Tropicbirds foraged at sea for ~6 days and ranged at least 157 km, but the study had limited capacity to track long-trips effectively (Campos et al. 2018). Based on morphology and flight-style, we suspect that White-tailed Tropicbird behavior at sea would be similar to the Red-tailed Tropicbird. Although we do not know this species' capacity for avoiding collision OWEI, carcasses of White-tailed Tropicbirds have been collected and recorded associated with land-based wind energy infrastructure in Hawai'i (J. Charrier, USFWS, unpublished data). Together with their congener, we suspect White-tailed Tropicbird would be among the most-vulnerable species of breeding Hawaiian seabirds when considering offshore wind energy development.

The Black Noddy population in the MHI comprises two unique subspecies (*A. m. marcusii* and *A. m. melanogenys*). Although both occur in the MHI, *A. m. melanogenys* is only found here and in greater relative numbers (Pyle and Pyle 2017). In the MHI, approximately 2,000 pairs nest in low numbers in caves and along rugged, rocky coastlines mostly at Ka'ula, Lehua, Molokai, and fewer at several other sites (Pyle and Pyle 2017). Congener Lesser Noddy (*A. tenuirostris melanops*) was tracked using GPS from Pelsaert Island, western Australia where they were recorded 4.8 to 112 km for an average trip duration of 5.7 hrs during the day (Surman et al. 2017). Black Noddies are similarly small and have yet to be tracked at sea. Their foraging distribution is thought to be relatively nearshore, probably <100 km (King 1970).

Brown Noddy breeding populations in the MHI are concentrated at Manana Island off Oahu (~20,000 pairs) and Ka'ula Island off Ni'ihau (~4,000 pairs) (Pyle and Pyle 2017). Foraging Brown Noddies are tightly-affiliated with foraging tunas (especially skipjack tuna) off O'ahu (Hebshi et al. 2008). In the Florida Keys, Brown Noddies tracked with small GPSs traveled at sea mainly between early morning and early evening and trips lasted approximately 4 to 12 hours when they ranged on average 51 km, but up to 130 km, from their colony (Maxwell et al. 2016).

Sooty Terns are relatively abundant in the MHI (~150,000 pairs) and nest primarily on 3 islands: Ka'ula off Ni'ihau, and Manana and Mokumanu islets off O'ahu (Pyle and Pyle 2017). Minimal GPS tracking data from eight Sooty Terns breeding in the Lesser Antilles revealed that individuals that retained tags, foraged a mean maximum distance of 94 km from their colony (Soanes et al. 2015); other sources indicate maximum a foraging range from colonies of ~200 km (Schreiber et al. 2002). There is little information about their ranging behaviors at sea, but birds remain largely in flight at all times of day and night when not roosting on land or floating objects (Schreiber et al. 2002).

The White Tern has a Hawaiian population that is distributed primarily throughout the northwestern Hawaiian Islands (~25,000 pairs; Pyle and Pyle 2017). White Terns are not abundant in the MHI, but there are small local breeding populations documented on Ka‘ula (~10 pairs). Since the early 1960s, White Terns have increased in abundance on southeast O‘ahu and near Honolulu. Eric VanderWerf (pers. comm. in Pyle and Pyle [2017]) estimated a population of 2,000 birds including 600 breeding pairs. Very little is known about foraging behavior in this small tern species. Parents likely forage relatively nearshore and they deliver whole fishes carried in their bills to their chicks. They are known to forage in close association with tunas and dolphins and they appear well adapted to forage in low light conditions (Niethammer and Patrick 1998).

The breeding population of Bulwer’s Petrel inhabiting the MHI is not well documented because the species’ nesting habitat is cryptic and activity at their colonies is nocturnal. Pyle and Pyle (2017) tabulate a rough estimate of 1,100 pairs throughout the MHI. Largely the result of black rat (*Rattus rattus*) predation, remaining habitat throughout the MHI is restricted to inaccessible sites that also are remote or located on offshore islets. Satellite tracking data from only 3 foraging trips lasting on average ~6 days in the Canary Islands indicated that this species ranges ~350 km from its colony (Rodríguez et al. 2013). Typical of other small petrels and large storm-petrels with similar flight styles, Bulwer’s Petrel rarely achieves flight heights greater than 2–3 m above the ocean surface (Megysi and O’Daniel 1997) and based on expected time spent flying at the RSZ, it would not be expected to be particularly vulnerable to collision with offshore wind-turbine infrastructure.

Small numbers (<100 estimated pairs) of Black-footed Albatrosses nest in the MHI only on Lehua Islet and Ka‘ula islands off Ni‘ihau (VanderWerf et al. 2007). At-sea flight style and behavior are similar to those of the Laysan Albatross. Comparative telemetry studies of both species nesting on Tern Island, French Frigate Shoals in the northwestern Hawaiian Islands (Conners et al. 2015) revealed that both species forage throughout day and night, but Black-footed Albatross are less-active than Laysan Albatross while engaged in nocturnal sit-and-wait/drift-foraging at the ocean’s surface. Laysan Albatross females tended to engage in more flight foraging than drift foraging compared with males; there were no differences between sexes of Black-footed Albatross. Given similarities in morphology, flight styles, and foraging behaviors, Black-footed Albatrosses probably share minimized risks (i.e., compared with tropicbirds) associated with flight at heights equivalent to the RSZ for offshore turbines.

Among the 3 state- and federally-listed seabird species (Band-rumped Storm-Petrel, Newell’s Shearwater, and Hawaiian Petrel) only the Newell’s Shearwater and Hawaiian Petrel have been tracked at sea. Studies on post-rehabilitated and non-rehabilitated fledgling Newell’s Shearwaters indicate that upon release at sea and departure from montane nest sites on Kaua‘i, individuals rapidly move away from Kaua‘i toward the southwest (A. Raine et al., unpublished data). Very few adult Newell’s Shearwaters have been tracked during the chick rearing season, and preliminary observations indicate individuals range within ~300 km of Kaua‘i toward feeding areas north of the island (A. Raine et al., unpublished data). Given a similar flight style as the slightly larger Wedge-tailed Shearwater, Newell’s Shearwaters also are likely to be closely affiliated with the ocean surface while at sea and only achieve flight-heights equivalent to the estimated RSZ within ~10 km of Kaua‘i during late night and early morning nocturnal departures from upper-elevation nesting areas when they descend over distance to the ocean’s surface to forage (A. Raine et al., unpublished data).

Small numbers of adult breeding Hawaiian Petrels (N=30 total) have been tracked using satellite transmitters from colonies on Hawai‘i, Maui, Lanai, and Kaua‘i. Although complete results describing foraging movements at sea are forthcoming, individuals from all islands share a dual, alternating short-long foraging trip strategy (J. Adams et al., unpublished data). Short trips (~2–3 days) generally are within about 300 km of their colony locations and long trips completed by provisioning adults constitute stereotypical clockwise loops throughout the greater northeastern Pacific—a path that hypothetically allows them to forage for an extended period throughout the north Pacific Transition Zone, characterized

by strong gradients in sea surface temperature, elevated chlorophyll concentrations, and greater relative productivity (J. Adams et al., unpublished data). Although the flight style of petrels is slightly different than shearwaters and albatross, their sail-soaring trajectories can occasionally allow them to reach heights potentially in the range of the RSZ of an offshore turbine, but more refined tracking using GPS would be required to be able to apply our altitudinal estimation technique. This species is currently being studied using high-resolution GPS tags from Lanai and these data could prove useful to further evaluate this species' ranging behavior and flight height at sea (A. Raine, unpublished data).



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