THE OWL GULL: EXCLUSIVELY NOCTURNAL FORAGING BY THE SWALLOW-TAILED GULL *CREAGRUS FURCATUS* IN GALÁPAGOS

SEBASTIAN M. CRUZ[1,4]*, LUKE R. HALPIN[2], CAROLINA PROAÑO[1,4], DAVID J. ANDERSON[3], & MARTIN WIKELSKI[4,5]

*[1]Independent researcher, Galápagos Islands, Ecuador *(cruz.seb@gmail.com)*
[2]Gulbali Research Institute, Charles Sturt University, Albury, New South Wales, Australia
[3]Wake Forest University, Department of Biology, Winston Salem, USA
[4]Max Planck Institute of Animal Behavior, Am Obstberg 1, Radolfzell, Germany
[5]University of Konstanz, Department of Biology, Konstanz, Germany

Received 09 July 2024, accepted 09 September 2024

ABSTRACT

Cruz, S. M., Halpin, L. R., Proaño, C., Anderson, D. J., & Wikelski, M. (2025). The owl gull: Exclusively nocturnal foraging by the Swallow-tailed Gull *Creagrus furcatus* in Galápagos. *Marine Ornithology*, *53*(1), 63–69. http://doi.org/10.5038/2074-1235.53.1.1626

Colony-based observations indicate that Swallow-tailed Gulls *Creagrus furcatus* go to sea only at night. Here, we use GPS tracking technology to reveal the species' exclusively nocturnal foraging behavior at four colonies in the Galápagos Islands. All nocturnal trips proved to be foraging effort in pelagic waters 19–103 km from nests during breeding. While at sea, individuals spent approximately one-quarter of their time commuting, with half of the time dedicated to area-restricted search behavior. Three years of data from one colony indicate spatial fidelity to a general foraging area. Our research directly confirms that Swallow-tailed Gulls are the only obligate nocturnal foragers among Laridae and contributes to our understanding of nocturnal foraging strategies in tropical seabirds.

Key words: nocturnal foraging, GPS tracking, diel vertical migration, spatial fidelity, Galápagos Marine Reserve

INTRODUCTION

Most seabirds forage primarily during daylight hours, but some exploit nocturnal opportunities to some degree (Ballance & Pitman, 1999; Brooke & Prince, 1991). Aside from the seasonal, obligate nocturnal activity of high-latitude species (Ainley et al., 1992), a driving factor underlying nocturnal foraging in seabirds is the high nighttime availability of some prey, particularly those involved in diel vertical migration (DVM; Bandara et al., 2021; Gliwicz, 1986; Spear et al., 2007; Watanabe et al., 1999), whereby prey migrate from deeper waters to the surface at night. This abundance of prey may be important for seabirds, especially in tropical waters, which are generally less productive, less structured, and have an uneven distribution (Benoit-Bird et al., 2013; Weimerskirch et al., 2005; Weimerskirch, 2007). Although diurnally migrating prey represent a substantial food resource, nocturnal foraging is observed in only a minority of tropical seabirds. For example, it accounts for just 14% of prey captures across the entire eastern tropical Pacific avifauna, although the percentage is higher for some species (Spear et al., 2007). The failure of many tropical seabirds to exploit the nocturnal foraging niche may be rooted in day vs. night trade-offs in the visual system (Hall & Ross, 2007): acquiring effective nocturnal vision may compromise daylight vision, thereby increasing the vulnerability of night-foraging species to depredation during daylight hours, as well as decreasing their foraging effectiveness if they continue to forage during the day. Specialization to a specific light regime can be highly restrictive for a seabird visual predator without nocturnal adaptation, potentially causing unproductive time at sea in the dark, where the bird may simply drift with the wind and currents (e.g., Zavalaga et al., 2012).

Indirect evidence indicates that the Swallow-tailed Gull *Creagrus furcatus*, a near-endemic species of the Galápagos Islands, is an obligate nocturnally foraging seabird. It is absent from the colony between dusk and dawn, spending its daytime hours primarily on or near nests (Hailman, 1964; Harris 1970; Snow & Nelson, 1984). Its diet consists predominantly of DVM prey such as squid and myctophid fish (Nelson, 1968; Snow & Snow, 1968). Characteristics that facilitate nocturnal vision include larger corneas and elongated eyes compared to those of diurnal birds, which enhance visual acuity and light sensitivity (Hall & Ross, 2007; Iwaniuk et al., 2010). Without a measurable daily melatonin rhythm, Swallow-tailed Gulls exhibit a flexible sleep schedule, adjusting their activities in response to the lunar cycle and rapidly synchronizing with lunar illumination (Wikelski et al., 2006). Nocturnal absence from the breeding colony in this species tends to decrease as lunar illumination increases over the 28-d lunar cycle. This pattern suggests that Swallow-tailed Gulls forage at sea when DVM prey are most abundant (Cruz et al., 2013), providing further indirect evidence of nocturnal specialization. Galápagos Fur Seals *Arctocephalus galapagoensis* schedule their foraging in a similar manner (Horning & Trillmich, 1999).

Here, we collect the first complete high-resolution records of pelagic trips of Swallow-tailed Gulls using data from Global Positioning System (GPS) loggers. Building on previous studies that relied on visual surveillance of colony absences and diet samples, our data provide a direct assessment of the strength of the association between foraging and photoperiod. Specifically, we offer an unbiased characterization of trip schedules, behavioral states at sea, and the locations of these activities. This three-year study, which involved birds from three islands and four breeding colonies, provides new insights into a seabird foraging niche that is largely unstudied in the electronic data-logging era: obligate dependence on the nocturnal diel vertical migration of prey.

METHODS

Field observations

We deployed GPS loggers on Swallow-tailed Gulls breeding in four colonies across three islands in the Galápagos Islands, spanning the Equator. The study sites included Genovesa (00.322939°N, 089.954530°W) in the north, with more than 1,000 breeding pairs; South Plazas (00.582610°S, 090.166321°W) in the center of the archipelago, with 500–1,000 breeding pairs; and two sites on Española (Punta Cevallos at 01.393228°S, 089.618577°W and Punta Suarez at 01.371901°S, 089.744395°W) in the south, where there are more than 2,000 breeding pairs (Fig. 1). Individual Swallow-tailed Gulls breed asynchronously in 9-mo cycles, leading to aseasonal breeding at the population level (Harris, 1970). This breeding pattern allowed us to deploy GPS loggers across a mix of nesting stages during short field trips between 2008 and 2010.

Birds were hand-caught at the nest, and small GPS loggers were attached to dorsal feathers between the wings using TESA® tape (model 4651; Tesa, Charlotte, North Carolina, USA; see Gillies et al., 2020). Handling time for logger attachment was ~10 min for deployment and ~5 min for logger recovery. The e-obs loggers (GmbH© Digital Telemetry, Munich, Germany) weighed 22 g (3%–4% of body mass). We deployed loggers on Genovesa Island in two sessions in 2009 only (08–16 March and 13–24 November). We also deployed loggers on South Plazas Island in 2009 only (28–31 July). At Punta Cevallos, Española Island, we deployed loggers in 2008 (02–11 August and 29 November–11 December), 2009 (14–18 April and 18–21 October), and 2010 (12–24 March). At Punta Suarez, Española Island, we deployed loggers in 2009 only (10 June).

Loggers were programmed to record GPS fixes continuously at intervals that varied among deployments (30–300 sec) and to transmit data by radio to a handheld receiver with a high-gain directional antenna when within range (~300 m). The UHF radio link attempted connection every 20 sec and transferred data at approximately 1 megabyte/min. Loggers were physically recovered within 48 h, usually after 24 h. We observed no negative effects on the logger-tagged birds (also see Geen et al., 2019; Lamb et al., 2017). All times are expressed in local time (UTC –6h00).

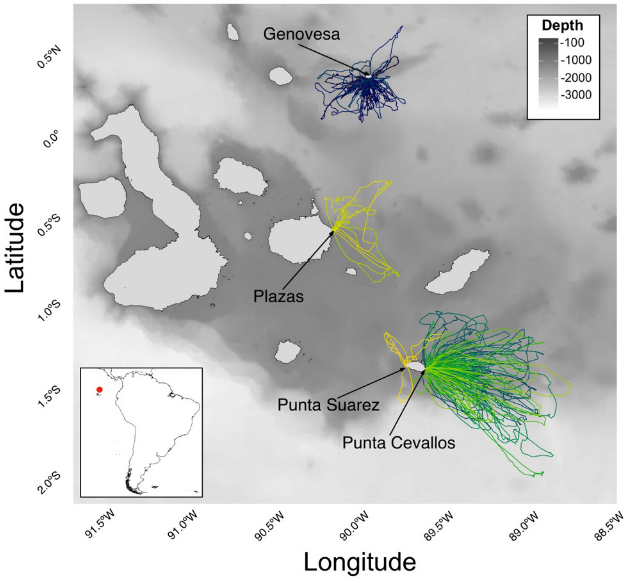

Fig. 1. Complete foraging trips recorded by GPS loggers of 114 breeding Swallow-tailed Gulls *Creagrus furcatus* (one trip per bird) at four colonies across three islands in the Galápagos Islands: one colony at Genovesa, one colony at South Plazas, and two colonies Española (Punta Cevallos and Punta Suarez). Inset: the location of the study site relative to South America is indicated by the red circle.

Data processing and analysis

Logger data were processed in R (version 4.2.3; R Core Team, 2023), using the World Geodetic System (WGS84) ellipsoid for spatial measurements. Maps were generated using R package "ggplot2" (version 3.0.2) and ArcGIS Pro (version 2.4.0; ESRI Inc., Redlands, USA). Trip characteristics were computed from complete trips only, defined as trips providing uninterrupted GPS data from the departure of the bird from the breeding colony to its return. We used the *tripSplit* function in the package "track2KBA" (version 1.0.5; Beal et al., 2021; Lascelles et al., 2016) to demarcate individual trips and separate complete trips from partial trips. For each complete foraging trip, we used the *tripSummary* function in "track2KBA" to measure the duration (in hours, from departure to return to each individual's respective colony), the maximum distance from the colony, and the cumulative distance travelled (km). GPS points within 2 km of the bird's nest were excluded from the final dataset.

We used the "Expectation Maximization Binary Clustering (EMbC)" package in R (version 2.0.3; Garriga et al., 2016) to estimate biologically meaningful behavioral states during time spent at sea. "EMbC", an unsupervised multivariate method, uses speed and turning angles to categorize movement sequences into distinct behavioral states: rest (low speed and low turning angle), intensive searching (low speed and high turning angle), transiting or commuting (high speed and low turning angle), and extensive searching behavior (high speed and high turning angle). We mapped the occurrences of intensive and extensive searching (which we inferred to represent area-restricted search behavior [ARS]) on a raster map in the Lambert Azimuthal Equal Area projection using a 5 × 5 km grid cell size. We used a similar raster grid cell approach to map the number of individuals foraging in each grid cell. To represent complete foraging ranges, we calculated a minimum convex hull polygon around all available tracking points for each colony.

We used the *findScale* function in "track2KBA" to estimate the spatial scale of ARS behaviour, which refers to the spatial scale at which an organism adjusts its search effort in response to encounters with prey during each complete trip. We then computed 50% utilization distributions for each individual using the R package "adehabitatHR" (Calenge, 2006), with the ARS scale from each colony's tracking data serving as the kernel smoothing parameter (h). Consistent with previous studies, we defined the 50% utilization distribution as the "core" foraging area where birds spent 50% of their time (Ford, 1979; Lascelles et al., 2016; Soanes, 2013).

We compared commuting speeds ($km \cdot h^{-1}$) between successive locations associated with commuting behaviour in the "EMbC" analysis between birds from Punta Cevallos and birds from Genovesa, estimating each bird's typical commuting speed with its median. These single speed values for each bird were then compared by colony using a Welch's t-test for unequal sample sizes.

TABLE 1
Summary statistics for complete foraging trips of breeding Swallow-tailed Gulls *Creagrus furcatus* from their respective colonies[a]

Colony	Rep.	Complete trips	Duration (h)	Foraging range (km)	Cumulative trip distance (km)
Genovesa	91%	45	3.2 (1.0–10.4)	19.4 (6.7–41.3)	46.8 (13.7–126.5)
Plazas Sur	n/a[b]	7	4.9 (1.0–11.3)	25 (6.9–47.8)	66 (13.9–143.2)
Española:					
Punta Cevallos	88%	59	7.3 (1.8–12.5)	51.2 (16.7–95.9)	118.7 (41.2–209.5)
Punta Suarez	n/a[b]	3	3.6 (2.4–5.1)	27 (24.6–31.3)	70.4 (56.2–94.1)

[a] Sample representativeness ("Rep.") is expressed as a percentage, and foraging trip characteristics for complete trips are expressed as mean (range). Additional descriptors are given in the Appendix, Table A1.

[b] Plazas Sur and Punta Suarez were omitted from the analysis because the sample size was too small ($n < 10$).

To evaluate how well our tracking datasets represented colony-level populations, we assessed the representativeness of the tracking samples from the Punta Cevallos and Genovesa colonies. The samples from Punta Suarez and Plazas Sur were omitted from this analysis because they were too small ($n < 10$) to calculate representativeness. To estimate the representativeness of the GPS datasets from each colony, we used the *repAssess* function in the "track2KBA" package. Representativeness was then estimated for each colony using the bootstrapping approach that selects track subsamples, averages them, and calculates the inclusion rate for a desired quantile (e.g., 50%). We then applied nonlinear least squares regression to model the relationship between sample size and inclusion rate, allowing us to extrapolate the data asymptotically. This approach enabled us to estimate how well the tracked sample of birds represented the space use of the broader population (Beal et al., 2021)..

RESULTS

Of 182 birds fitted with loggers across all study sites, the final dataset included only the first complete foraging trip for each bird. This resulted in 114 complete trips from 114 individual Swallow-tailed Gulls for analysis (Table 1). Of these 114 complete trips (Fig. 1), 41% occurred during the incubation stage, while 59% took place at the nestling-provisioning stage.

All 114 trips occurred within an essentially nocturnal window (Fig. 2). Departures typically occurred around dusk, although some birds departed later in the night when a returning mate relieved the tagged bird attending to an egg or young nestling. Arrivals were most common in the latter half of the night (Fig. 2), and nearly all trip time (99.5%) occurred during the night. For 113 trips, the foraging trip was completed within 11.7 h. The sole exception involved a tagged gull with a juvenile chick, which remained absent for 31.7 h, covered 100 km, departed and returned during the night, and was inactive on the ocean surface during the day (Fig. A1 in Appendix, available on the website).

Each of the 114 trips showed evidence of active foraging, characterized by either intensive or extensive searching behavior, classifying them all as "foraging trips." On average, this combination of these indicators of ARS behaviors accounted for 57.9% of the time spent at sea (standard deviation [SD] = 19.3, median = 59.9%, range 5.2–96.9%); see Table A1 in Appendix).

The high representativeness values for the Punta Cevallos and Genovesa colonies indicated that the foraging distributions at these sites adequately reflected those of the colony-level populations (Table 1). The results from Punta Suarez and Plazas Sur, with samples too small to estimate representativeness, were more anecdotal but useful, as they contributed information on the foraging distribution of birds in these areas.

Foraging trips typically began with rapid, directed movements away from the colony, followed by movements with more variable direction and speed once farther from land, where foraging activity commenced. Return flights to the colony followed consistent, straight trajectories, with occasional short periods of floating on the sea surface. Analysis of trips from sufficiently representative colonies revealed that the cumulative distance travelled by birds originating from Punta Cevallos exceeded the distance travelled by those from Genovesa by 44% (Mann-Whitney $U = 601.0$, $n_1 = 70$, $n_2 = 47$, $P = .04$). Notably, 46% of Genovesa birds completed two foraging trips in a single night (only the first trip was included in other analyses), while no birds from Española Island did so. Punta Cevallos birds commuted at faster speeds (mean ± SD = $27 \pm 11.9\ \text{km}\cdot\text{h}^{-1}$) than those from Genovesa ($21.1 \pm 13.4\ \text{km}\cdot\text{h}^{-1}$; Welch's *t*-test, $t(100.44) = 3.70$, $P = .0004$).

Swallow-tailed Gulls from Punta Cevallos (the east point of Española Island) foraged mostly between northeast and southeast,

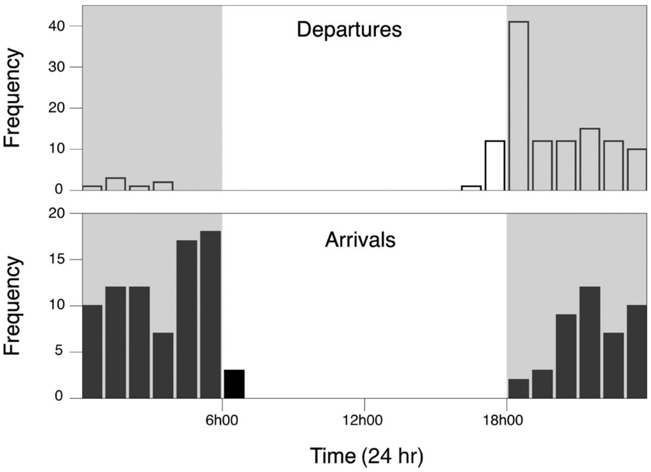

Fig. 2. Temporal distribution of departures and arrivals for complete foraging trips by 114 Swallow-tailed Gulls *Creagrus furcatus* (one trip per bird) from four colonies in the Galápagos Islands. Grey vertical shading indicates local nighttime.

usually over waters shallower than 2,000 m and mainly over the Galápagos platform and its slope (Fig. 1, Fig. A2 in Appendix). Several birds reached areas over abyssal depths southeast of Española Island. In contrast, gulls in the small sample from Punta Suarez (the west point of Española Island) did not occupy the eastern compass quadrant at all, using mostly shallower platform waters. Gulls in the small Plazas Sur sample used much of the available marine surface (i.e., areas not obstructed by the nearby Santa Cruz Island to the west) within 30 km, over waters up to 500 m deep. Most gulls from Genovesa occupied ocean within 15 km of the island, to the south of an east–west axis through the island, mainly over pelagic waters < 1,000 m deep. The large sample from Punta Cevallos (*n* = 59 trips) suggested consistency in the areas visited over the 3-y period (Fig. 3).

The behavioral state-space ("EMbC") analysis identified biologically significant behavioral states, which we evaluated for the large samples from Punta Cevallos and Genovesa. The time spent searching was similar for the two populations (Table A1 in Appendix; $t = 0.39$, $df = 124$, $P = .70$). On average, approximately half the time at sea was dedicated to searching behavior, including both intensive and extensive searching. Intensive searching accounted for 36% of the time spent at sea for birds from Genovesa and 37% for birds from Punta Cevallos, while extensive searching made up 24% and 21% of the time spent at sea for birds from these two colonies, respectively. Birds from Genovesa spent 16% of their time resting and 23% of their time commuting, compared to 13% and 25% for Punta Cevallos birds. Unclassifiable locations were infrequent for both colonies, but slightly more common for Punta Cevallos (5%) than Genovesa (1%). These findings suggest behavioral consistency in foraging strategies across colonies, with a notable proportion of time devoted to searching behavior during foraging trips.

DISCUSSION

To our knowledge, this is the first detailed GPS tracking study of the foraging activities of an exclusively nocturnal foraging seabird. Swallow-tailed Gulls meet the biological expectations for a nocturnal predator, as all foraging trips recorded in this study occurred during the night. Foraging trips at all study sites began around dusk (~18h00) and ended before dawn (~06h00), consistent with descriptions at the nest by Hailman (1964). During the day, the birds stayed at or near their nests, resting, incubating eggs, or attending chicks. Among the tracked birds, one exceptional individual, which had a fledgling at the nest, remained at sea for an extended period. This bird remained at sea for more than 12 h during the night, continued to stay at sea throughout the following day, and returned to the colony the next night, resulting in 31 h away. The tracking data from this bird supports our conclusion that foraging is strictly nocturnal: during the day, the bird floated on the water's surface, drifting with the ocean currents (Fig. A1 in Appendix).

Swallow-tailed Gulls from different colonies had separate foraging zones with no overlap (Fig. 1). Most foraging trips occurred over waters < 2,000 m deep, although some birds ventured into deeper waters. The slope of the Galápagos platform appears to provide an important habitat for foraging, possibly due to increased productivity at shelf edges, a pattern also observed in other pelagic seabird species (e.g., Weimerskirch, 2007). The longer trip distances and faster commuting speeds of birds from Punta Cevallos, compared to those from Genovesa, suggest that foraging conditions were more challenging for Punta Cevallos birds during the study period. Most foraging trips occurred entirely within the Galápagos Marine Reserve (GMR), emphasizing the importance of this protected area for the species during breeding. The foraging area of Punta Cevallos birds was consistent across the three years of tracking (Fig. 3), possibly indicating consistently favourable foraging opportunities at this site. Similarly, five years of tracking the foraging behavior of Nazca Boobies *Sula granti*, a diurnal predator, from the same Punta Cevallos colony revealed a consistent and nearly exclusive use of the compass quadrant east of the colony (McKee et al., 2023). This overlap in foraging zones between the two species suggests that this area within the GMR may be of significant trophic importance.

The existence of nocturnal foraging among seabirds, while limited, can be attributed to factors such as increased prey availability due to diel vertical migration of prey and avoiding competition for food with diurnal predators (Ballance & Pitman, 1999; Brooke & Prince, 1991; Hailman, 1964; Spear et al., 2007). Competition for non-planktonic animal prey (primarily fish and squid) is important in the eastern tropical Pacific, where the primary foraging mode involves aggregation of large multi-species flocks following sub-surface predators (Balance & Pitman, 1999; Spear et al., 2007). Indeed, Spear et al. (2007) found a marked sorting of prey size among species foraging in the same flocks. Peruvian Pelicans *Pelecanus thagus* also engage in nocturnal foraging, a behavior that may help them avoid competition with diurnal foragers, such as boobies and

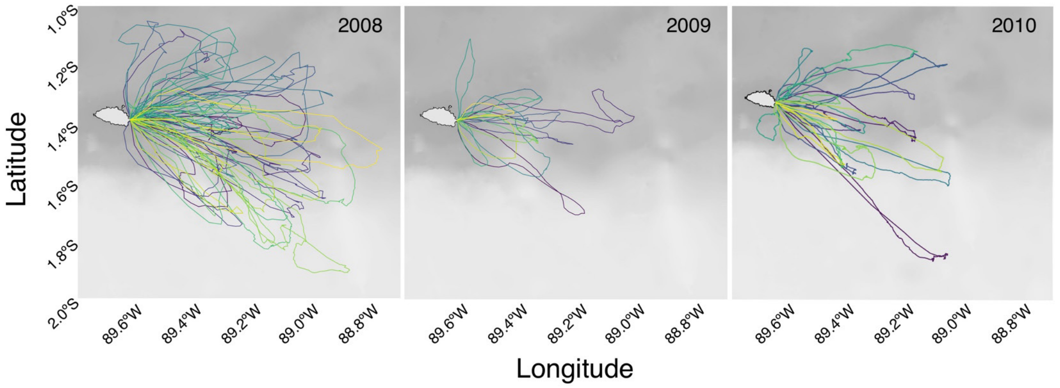

Fig. 3. GPS tracks (first trips only) of foraging Swallow-tailed Gulls *Creagrus furcatus* from the Punta Cevallos colony over three years (2008–2010).

Fig. 4. Adult Swallow-tailed Gull *Creagrus furcatus*, highlighting the distinctive eye of this species.

cormorants, which forage in large, dense flocks and are capable of diving to greater depths (Zavalaga et al., 2011).

Nonetheless, on average, nocturnal foraging is relatively rare in tropical seabirds, especially among larid, suliform, and pelecaniform species, though it is more prevalent in some petrel species (Balance & Pitman, 1999; Spear et al., 2007). The benefits of avoiding competition with the diurnal predator guild are small. Alternatively, nocturnal foraging may be a beneficial adaptation, but one that requires the evolution of sensory capabilities that are mutually exclusive to those needed for diurnal performance. This may create two distinct adaptive peaks in the evolutionary landscape (Wright, 1932), separated by a low-fitness valley. The fact that some seabirds, such as Red-legged Kittiwakes *Rissa brevirostris* (Kokobun et al., 2015), forage both day and night does not invalidate this idea. Their performance in each photoperiod would likely be greater if they were not required to forage during both periods.

Each of these ideas is broadly consistent with the biology of Swallow-tailed Gulls. In gulls (family Laridae), the ancestral foraging window was likely diurnal, and Swallow-tailed Gulls are the only species in the group that fully transitioned to nocturnal foraging. Swallow-tailed Gulls are distinctive in the Laridae in ways that suggest food limitation: one-egg clutch, delayed sexual maturity, and relatively pelagic foraging (Snow & Snow, 1984). These characteristics resemble those of the Procellariidae (petrels and shearwaters) and are consistent with the possibility of disadvantages to a gull in the diurnal foraging space in waters around the Galápagos (Snow & Nelson, 1984). These include scarce inshore resources for an opportunistic scavenger, ubiquitous daytime attacks by kleptoparasitic Magnificent Frigatebirds *Fregata magnificens* (Gibbs & Gibbs, 1987; Grant et al., 2014), and many potential competitors for food (Hailman, 1964; Harris, 1970). Similar to owls (Order Strigiformes; Martin, 1990), Swallow-tailed Gulls may have evolved nocturnal foraging as a strategy to avoid hazards and reduce competition, making them the only gull species to do so.

CONCLUSION

This is the first study to track the foraging trips of Swallow-tailed Gulls using GPS loggers. Their nocturnal foraging strategy differs from most other seabirds, particularly in tropical waters, where daytime foraging of sub-surface prey predominates. These results highlight the importance of diel patterns in prey availability for avian marine predators. Furthermore, the observed differences in foraging zones and trip lengths among different colonies underscore the need for continued monitoring and research to understand the factors driving these patterns. These findings enhance our understanding of the ecological dynamics in the Galápagos and the unique foraging strategies of its avian predators. The study provides valuable insights into the foraging behaviour of Swallow-tailed Gulls, including their nocturnal activity, specific foraging zones, and the variations in behavior across different colonies. It also highlights several distinct nocturnal traits of Swallow-tailed Gulls, such as their elongated eyes with larger corneas and their propensity for foraging at sea during new moons. These specialized behavioral, morphological, and physiological adaptations appear to limit them to nocturnal foraging, distinguishing them from other tropical seabirds and offering a unique example of nocturnal foraging behavior in tropical marine ecosystems.

ACKNOWLEDGEMENTS

This study was approved by the Galápagos National Park Service, with research conducted under permit number PC-08-10. We thank the Galápagos National Park Service for permission to work in the park, and The Beagle Cruises for logistical support. We are grateful to Kate Huyvaert for her comments on earlier versions of the manuscript. Our gratitude extends to the Max Planck Society and the International Max Planck Research School for Organismal Biology. This research was partially funded by the National Science Foundation under grant DEB 0842199 to DJA. This publication is contribution 2675 of the Charles Darwin Foundation for the Galapagos Islands. The insightful comments from reviewers were invaluable in improving the manuscript.

AUTHOR CONTRIBUTIONS

Sebastian Cruz: Conceptualization, Methodology, Investigation, Writing-Original draft preparation, Formal analysis, Data curation. Luke Halpin: Formal Analysis, Writing, Visualization. Carolina Proaño: Investigation. David Anderson: Conceptualization, Writing, Reviewing, Editing, Investigation. Martin Wikelski: Conceptualization, Funding acquisition.

AVAILABILITY OF SUPPORTING DATA

The dataset supporting the results of this study is available in the Movebank Data Repository, https://doi.org/10.5441/001/1.605

REFERENCES

Ainley, D. G., Ribic, C. A., & Fraser, W. R. (1992). Does prey preference affect habitat choice in Antarctic seabirds? *Marine Ecology Progress Series*, *90*(3), 207–221.

Ballance, L. T., & Pitman, R. L. (1999). Foraging ecology of tropical seabirds. In N. J. Adams & R. H. Slotow (Eds.), *Proceedings of the 22nd International Ornithology Congress* (pp. 2057–2071). BirdLife South Africa.

Bandara, K., Varpe, Ø., Wijewardene, L., Tverberg, V., & Eiane, K. (2021). Two hundred years of zooplankton vertical migration research. *Biological Reviews*, *96*(4), 1547–1589. https://doi.org/10.1111/brv.12715

Beal, M., Oppel, S., Handley, J., Pearmain, E. J., Morera-Pujol, V., & Carneiro, A. P. B. (2021). Track2kba: An R package for identifying important sites for biodiversity from tracking data. *Methods in Ecology and Evolution*, *12*(12), 2372–2378. https://doi.org/10.1111/2041-210X.13713

Benoit-Bird, K. J., Battaile, B. C., Heppell, S. A., Hoover, B., Irons, D., Jones, N., Kuletz, K., J., Nordstrom, C. A., Paredes, R., Suryan, R. M., Waluk, C. M., & Trites, A. W. (2013). Prey patch patterns predict habitat use by top marine predators with diverse foraging strategies. *PLOS One*, *8*(1), e53348. https://doi.org/10.1371/journal.pone.0053348

Brooke, M. D. L., & Prince, P. A. (1991). Nocturnality in seabirds. *Proceedings of the International Ornithological Congress*, *20*, 1113–1121.

Calenge, C. (2006). The Package "Adehabitat" for the R Software: A tool for the analysis of space and habitat use by animals. *Ecological Modelling*, *197*(3–4), 516–519. https://doi.org/10.1016/J.ECOLMODEL.2006.03.017

Cambra, M., Lara-Lizardi, F., Peñaherrera-Palma, C., Hearn, A., Ketchum, J. T., Zarate, P., Chacón, C., Suárez-Moncada, J., Herrera, E., & Espinoza, M. (2021). A first assessment of the distribution and abundance of large pelagic species at Cocos Ridge seamounts (Eastern Tropical Pacific) using drifting pelagic baited remote cameras. *PLOS One*, *16*(11), e0244343. https://doi.org/10.1371/journal.pone.0244343

Cruz, S. M., Hooten, M., Huyvaert, K. P., Proaño, C. B., Anderson, D. J., & Wikelski, M. (2013). At–sea behavior varies with lunar phase in a nocturnal pelagic seabird, the Swallow-Tailed Gull. *PLOS One*, *8*(2), e56889. https://doi.org/10.1371/journal.pone.0056889

Ford, R. G., & Krumme, D. W. (1979). The analysis of space use patterns. *Journal Theoretical Biology, 76*(2), 125–155. https://doi.org/10.1016/0022-5193(79)90366-7

Garriga, J., Palmer, J. R. B., Oltra, A., Bartumeus, F. (2016). Expectation-maximization binary clustering for behavioural annotation. *PLOS One*, *11*(3), 1–26. https://doi.org/10.1371/journal.pone.0151984

Geen, G. R., Robinson, R. A., & Baillie, S. R. (2019). Effects of tracking devices on individual birds, a review of the evidence. *Journal of Avian Biology*, *50*(2), e01823. http://doi.org/10.1111/jav.01823

Gibbs, L. H., & Gibbs, J. P. (1987). Prey robbery by nonbreeding Magnificent Frigatebirds (*Fregata magnificens*). *The Wilson Bulletin*, *99*(1), 101–104.

Gillies, N., Fayet, A. L., Padget, O., Syposz, M., Wynn, J., Bond, S., Evry, J., Kirk, H., Shoji, A., Dean, B., Freeman, R., & Guilford, T. (2020). Short-term behavioural impact contrasts with long-term fitness consequences of biologging in a long-lived seabird. *Scientific Reports*, *10*, 15056. https://doi.org/10.1038/s41598-020-72199-w

Gliwicz, Z. M. (1986). A lunar cycle in zooplankton. *Ecology*, *67*(4), 883–897. https://doi.org/10.2307/1939811

Grant, T., Estes, O., & Estes, G. (2014). Observations on the breeding and distribution of Lava Gull (*Leucophaeus fuliginosus*). *Cotinga*, *37*, 1–16.

Hailmain, J. (1964). The Galapagos swallow-tailed gull is nocturnal. *The Wilson Bulletin*, *76*(4), 347–354. https://www.jstor.org/stable/4159327

Hall, M. I., & Ross, C. F. (2007). Eye shape and activity pattern in birds. *Journal of Zoology*, *271*(4), 437–444. https://doi.org/10.1111/j.1469-7998.2006.00227.x

Harpp, K. S., Fornari, D. J., Geist, D. J., & Kurz, M. D. (2003). Genovesa Submarine Ridge: A manifestation of plume-ridge interaction in the northern Galápagos Islands. *Geochemistry, Geophysics, Geosystems*, *4*(8511), 9. http://doi.org/10.1029/2003GC000531

Harris, M. (1970). Breeding ecology of the Swallow-tailed Gull, *Creagrus furcatus*. *The Auk*, *87*(2), 215–243. https://doi.org/10.2307/4083917

Harris, M. (1977). Comparative ecology of seabirds in the Galapagos Archipelago. In B. Stonehouse & C. Perrins (Eds.), *Evolutionary Ecology* (pp. 65–76). Methuen. https://doi.org/10.1007/978-1-349-05226-4_7

Horning, M., & Trillmich, F. (1999). Lunar cycles in diel prey migrations exert a stronger effect on the diving of juveniles than adult Galápagos fur seals. *Proceedings of the Royal Society B*, *266*(1424), 1127–1132. http://doi.org/10.1098/rspb.1999.0753

Howard, J. L., Tompkins, E. M., & Anderson, D. J. (2021). Effects of age, sex, and ENSO phase on foraging and flight performance in Nazca boobies. *Ecology & Evolution*, *11*(9), 4084–4100. http://doi.org/10.1002/ece3.7308

Iwaniuk, A. N., Heesy, C. P., & Hall, M. I. (2010). Morphometrics of the eyes and orbits of the nocturnal Swallow-tailed Gull (*Creagrus furcatus*). *Canadian Journal of Zoology*, *88*(9), 855–865. https://doi.org/10.1139/Z10-051

Jackson, M. H. (1993). *Galapagos: A natural history*. University of Calgary Press.

Kokubun, N., Yamamoto, T., Kikuchi, D. M., Kitaysky, A., & Takahashi, A. (2015). Nocturnal foraging by red-legged kittiwakes, a surface feeding seabird that relies on deep water prey during reproduction. *PLOS One*, *10*(10), e0138850. https://doi.org/10.1371/journal.pone.0138850

Lamb, J. S., Satgé, Y. S., Fiorello, C., & Jodice, P. (2017). Behavioral and reproductive effects of bird-borne data logger attachment on Brown Pelicans (*Pelecanus occidentalis*) on three temporal scales. *Journal of Ornithology*, *158*, 617–627. https://doi.org/10.1007/s10336-016-1418-3

Lascelles B. G., Taylor, P. R., Miller, M. G. R., Dias, M. P., Oppel, S., Torres, L., Hedd, A., le Corre, M., Phillips, R. A., Shaffer, S. A., Weimerskirch, H., & Smakk, C. (2016). Applying global criteria to tracking data to define important areas for marine conservation. *Diversity and Distributions*, *22*(4), 422–431. https://doi.org/10.1111/ddi.12411

Martin, G. (1990). *Birds by night*. T. & A. D. Poyser.

McKee, J. L., Tompkins, E. M., Estela, F. A., & Anderson, D. J. (2023). Age effects on Nazca booby foraging performance are largely constant across variation in the marine environment: Results from a 5-year study in Galápagos. *Ecology and Evolution*, *13*(6), e10138. https://doi.org/10.1002/ece3.10138

Mendez, L., Borsa, P., Cruz, S., de Grissac, S., Hennicke, J., Lallemand, J., Prudor, A., & Weimerskirch. (2017). Geographical variation in the foraging behaviour of the pantropical red-footed booby. *Marine Ecology Progress Series*, *568*, 217– 230. https://doi.org/10.3354/meps12052

Nelson, J. B. (1968). Breeding behaviour of the Swallow-Tailed Gull in the Galapagos. *Behaviour*, *30*(2/3), 146–174. https://www.jstor.org/stable/4533209

R Core Team. (2023). *R* (version 4.3.1) [Computer software]. The R Foundation for Statistical Computing. https://www.r-project.org/

Snow, B., & Snow, D. (1968). Behaviour of the Swallow-tailed Gull of the Galapagos. *The Condor*, *70*(3), 252–264.

Snow, D. W., & Nelson, J. B. (1984). Evolution and adaptations of Galapagos seabirds. *Biological Journal of the Linnean Society*, *21*(1–2), 137–155. https://doi.org/10.1111/j.1095-8312.1984.tb02057.x

Soanes, L. M., Arnould, J. P. Y., Dodd, S. G., Sumner, M. D., & Green, J. A. (2013). How many seabirds do we need to track to define home-range area? *Journal of Applied Ecology*, *50*(3), 671–679. https://doi.org/10.1111/1365-2664.12069

Spear, L. B., Ainley, D. G., & Walker, W. A. (2007). Foraging dynamics of seabirds in the eastern tropical Pacific Ocean. *Studies in Avian Biology*, *35*, 1–99.

Watanabe, H., Moku, M., Kawaguchi, K., Ishimaru, K. L., & Ohno, A. (1999). Diel vertical migration of myctophid fishes (family Myctophidae) in the transitional waters of the western North Pacific. *Fisheries Oceanography*, *8*(2), 115–127. https://doi.org/10.1046/j.1365-2419.1999.00103.x

Weimerskirch, H. (2007). Are seabirds foraging for unpredictable resources? *Deep-Sea Research Part II*, *54*(3-4), 211–223. https://doi.org/10.1016/j.dsr2.2006.11.013

Wikelski, M., Tarlow, E., Eising, C., Groothuis, T., & Gwinner, E. (2006). Do night-active birds lack daily melatonin rhythms? A case study comparing a diurnal and a nocturnal-foraging gull species. *Journal of Ornithology*, *147*(1), 107–111. http://doi.org/10.1007/s10336-005-0018-4

Wilkinson, B. P., Satgé, Y. G., Lamb, J. S., & Jodice, P. (2019). Tropical cyclones alter short-term activity patterns of a coastal seabird. *Movement Ecology*, *7*, 30. https://doi.org/10.1186/s40462-019-0178-0

Wright, S. (1932). The roles of mutation, inbreeding, crossbreeding and selection in evolution. In D. F. Jones (Ed.), *Proceedings of the Sixth International Congress of Genetics. Vol. 1, Transactions and General Addresses* (pp. 356–366). Genetics Society of America.

Zavalaga, C. B., Dell'Omo, G., Becciu, P., & Yoda, K. (2011). Patterns of GPS tracks suggest nocturnal foraging by incubating Peruvian pelicans (*Pelecanus thagus*). *PLOS One*, *6*(5), e19966. https://doi.org/10.1371/journal.pone.0019966

Zavalaga, C. B., Emslie, S. D., Estela, F., Muller, M., Dell'Omo, G., & Anderson, D. J. (2012). Overnight foraging trips by chick-rearing Nazca Boobies (*Sula granti*) and the risk of attack by predatory fish. *Ibis*, *154*(1), 61–73. http://doi.org/10.1111/j.1474-919X.2011.01198.x