MOVEMENTS AND ACTIVITY CHARACTERISTICS OF THE BROWN BOOBY *SULA LEUCOGASTER* DURING THE NON-BREEDING PERIOD

HIROYOSHI KOHNO[1*], AKIRA MIZUTANI[1], KEN YODA[2] & TAKASHI YAMAMOTO[2,3]

[1]*Okinawa Regional Research Center, Tokai University, Taketomi, Okinawa 907-1541, Japan* [*]*(hiro-kohno@fan.hi-ho.ne.jp)*
[2]*Graduate School of Environmental Studies, Nagoya University, Nagoya, Aichi 464-8601, Japan*
[3]*Current Address: Research and Development Center for Data Assimilation,*
The Institute of Statistical Mathematics, Tachikawa, Tokyo 190-8562, Japan

Received 17 December 2018, accepted 01 April 2019

ABSTRACT

KOHNO, H., MIZUTANI, A., YODA, K. & YAMAMOTO, T. 2019. Movements and activity characteristics of the Brown Booby *Sula leucogaster* during the non-breeding period. *Marine Ornithology* 47: 169–174.

As the availability of individual-based tracking has increased, our understanding of seabird distributions outside the breeding season has advanced for a variety of species, but remains comparatively limited for species inhabiting the tropics. In this study, we investigated the at-sea movement and activity of eight Brown Boobies *Sula leucogaster* during the non-breeding period using light-level geolocators. Boobies spent the non-breeding season in the western Pacific across a large geographical range; however, at a regional scale, there was variation among individuals in their use of wintering habitats, with areas 6 575 km apart between their northernmost (the East China Sea/Yellow Sea) and southernmost (northern New Guinea) destinations. Overall, during the non-breeding period, boobies spent 17.6 % ± 5.0 % of their time on the water during the day and 11.1 % ± 8.2 % of their time on the water at night. This low percentage of time spent on the water at night indicates that they may have rested on land or roosted on rocks, a behavior that might be an anti-predatory strategy. Although individuals exhibited spatiotemporal variations in their movements, all tracked birds were absent in the breeding region for periods of time coinciding with seasonal pulses of unfavorable local environmental conditions. This study is the first to explore individual-based at-sea movements and activity characteristics of *Sula* species during the non-breeding period. Our results provide insight into how breeding phenology relates to seasonal movements.

Key words: activity, Brown Booby, geolocation, non-breeding period, migration

INTRODUCTION

Bird migration is a well-known phenomenon that often involves long distance horizontal movements over hundreds to thousands of kilometers. Migration presumably occurs in response to changes in food availability and prevailing local weather (Dingle & Drake 2007, Newton 2012), which have critical consequences to survival and reproduction (Newton 2008). The recent development of tracking devices to monitor the movement of individuals, specifically those that use light-based geolocation methods (Wilson *et al*. 1992), has advanced our understanding of the at-sea movements and activity patterns of seabirds outside of the breeding season (Croxall *et al*. 2005, Shaffer *et al*. 2006, Yamamoto *et al*. 2010). To date, most studies have focused on species that inhabit polar and temperate regions; these species tend to exhibit distinct, seasonal, long-distance movements (reviewed by BirdLife International 2004, Shaffer *et al*. 2006, Newton 2008). In contrast, research into the behaviour of birds during the non-breeding season—among species that breed partially or completely in the tropics—has lagged despite these species representing half the number of all seabirds (Schreiber & Burger 2002). However, the number of studies on foraging behaviour during the breeding period for this group is increasing (Lewis *et al.* 2004, Mendez *et al.* 2017). Bird migration is thought to be driven by energy efficiency—the balance between the energetic costs associated with environmental conditions and distance travelled, and the benefits associated with access to seasonally available resources that are needed to fuel metabolism (Newton 2008, 2012). In this way, migratory species can optimize energy acquisition (Somveille *et al*. 2018). Thus, elucidating the movement patterns of seabirds in the tropics, where seasonality is generally less pronounced (Longhurst & Pauly 1998), might provide insight into how migratory behaviour is shaped by environmental conditions.

The Brown Booby *Sula leucogaster* breeds in subtropical and tropical oceans between 25°S and 25°N (Nelson 1978). The breeding ecology and at-sea behaviour of this species during the breeding period have been examined at several breeding colonies (Nelson 1978, Lewis *et al*. 2005, Castillo-Guerrero *et al*. 2016), but information on their behaviour outside the breeding period remains limited. Nakanokamishima Island (southern Ryukyu Islands, Japan) is one of the study colonies for this species where many years of colony-based observations and application of animal-borne sensors have been conducted during the breeding period (Yoda & Kohno 2008, Yoda *et al.* 2011, Yamamoto *et al*. 2017, Kohno *et al*. 2018). Based on a small number of leg-ring recoveries (29 of 3 029 rings recovered outside of Japan), Brown Boobies of Nakanokamishima were found mostly around the Philippines in winter (Yamashina Institute for Ornithology 2002). However, this result may be biased to areas where there are more people available to find the rings; it is also a better reflection of where the birds died than where they lived successfully.

In this study, we used light-level geolocators to record the at-sea movements and activity of individual Brown Boobies to understand the behavioural characteristics of this tropical seabird species outside of the breeding season.

METHODS

Our study was carried out from 2009 to 2015 on Nakanokamishima Island (24°11′N, 123°34′E), a colony located close to the northern limit of the Brown Booby breeding range in the western Pacific Ocean (Nelson 1978). At night, from March to September, we captured 22 egg-incubating or chick-rearing boobies using a net, and attached geolocators (Mk-5, 3.6 g, British Antarctic Survey, UK or Mk-3006, 2.5 g, Biotrack Ltd., UK) to the tarsus of each bird using a plastic ring. The total weight of the unit was 8.5 g, which was < 1 % of the mean mass of the birds in our study (mean ± SD: 1 435 ± 201 g). After one to three years, we recovered geolocators from eight boobies. Some equipped birds were resighted, but we could not recapture them. The procedures used in this field study were approved by the Ministry of the Environment, the Agency for Cultural Affairs, and the Nature Conservation Division, Okinawa, Japan.

Geolocators measured light levels at 60-s intervals and recorded the maximum value during each 10-min period. Immersion in seawater was checked every 3 s as 0 or 1 (out of or in water, respectively); information was compiled for each 10-min period (0–200), representing the proportion of time spent wet. Water temperature was recorded every 10 min only when there was continuous immersion for at least 20 min. We analyzed light-level geolocation data within a Bayesian framework using the Solar/Satellite Geolocation for Animal Tracking (SGAT) package (Wotherspoon *et al*. 2015) for program R (version 3.3.0; R Development Core Team 2016). Sunset and sunrise times were estimated using thresholds in the light curves. Day length and night length were used to estimate latitude, whereas the relative timing of local noon and midnight were used to estimate longitude, providing two position estimates per day (Wilson

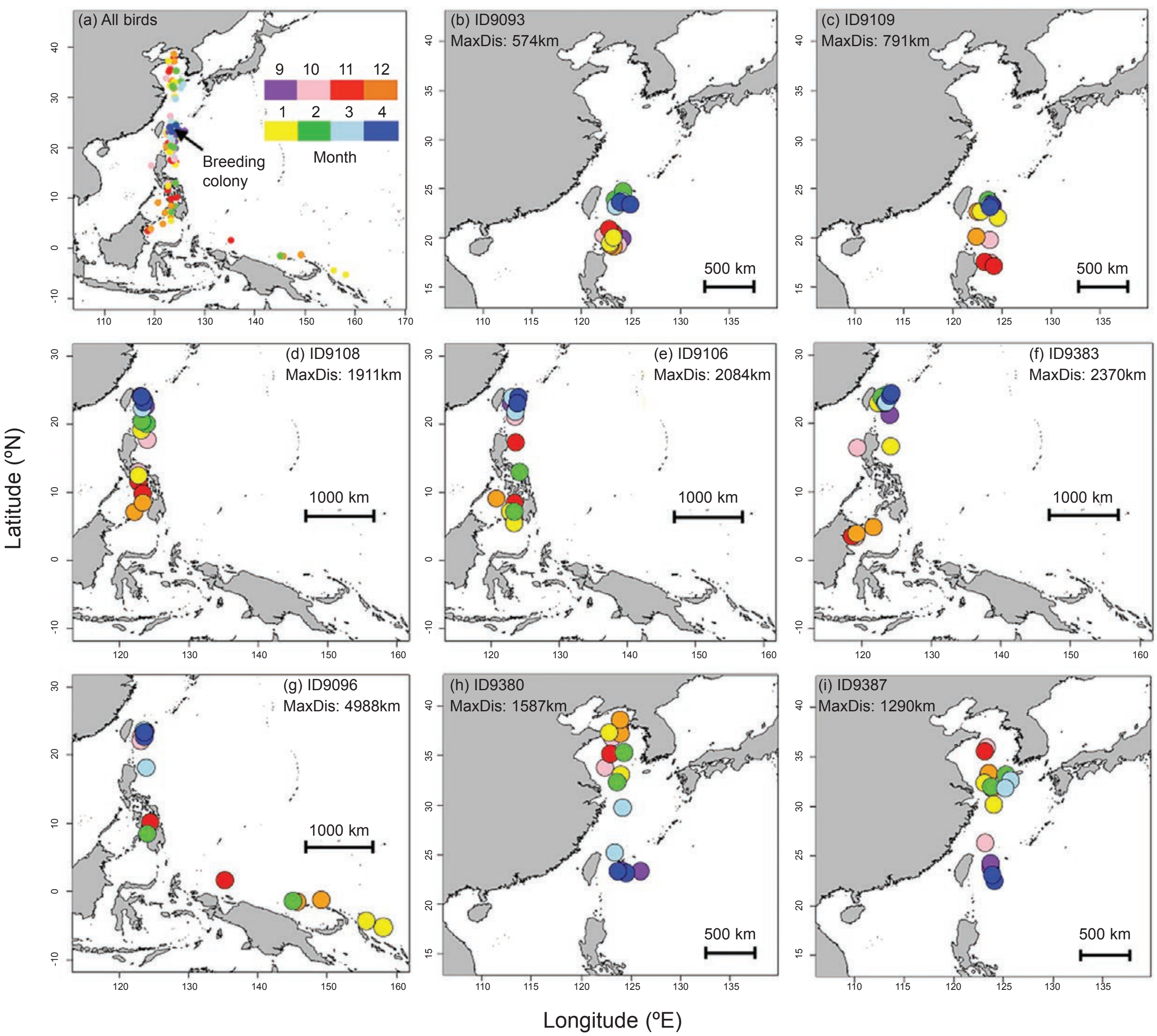

Fig. 1. At-sea movements of eight Brown Boobies breeding on Nakanokamishima Island, Japan, from September to April, including the non-breeding period. Position estimates are given for each half-month as spatial medians of daily data. Months are indicated by different colours: (a) all positions are pooled, and (b–i) different individuals are shown.

et al. 1992). SGAT uses Markov Chain Monte Carlo (MCMC) simulations to estimate locations and to quantify the error inherent in light-level geolocation based on behavioural models and spatial probability, accounting for bird flight speed, land mask (i.e., locations at sea are more likely than locations on land), and sea surface temperature mask (i.e., high probability in the range of the recorded water temperature). Despite these simulations, there was still some uncertainty in our location estimations. Therefore, we visualized overall movement patterns using half-monthly spatial medians of the latitude and longitude from September to April. This timing was chosen because fledgling independence typically occurs in early September, with egg laying occurring until mid-April (Kohno *et al*. 2018). Some boobies remained in areas around the breeding colony upon termination of breeding. Therefore, we were not able to use distance from the colony as an indicator of the beginning of the non-breeding period, despite its previous use as an indicator for other seabird species (Yamamoto *et al*. 2010).

Colony-based observations indicate that almost all boobies disappear from the colony by early November, and that peak egg-laying starts in February (Kohno *et al.* 2018). Hence, we calculated the daily proportion of time spent on the water, and the number of continuous periods of full-wet and full-dry events (i.e., periods spent on or out of the water, respectively, for 10 continuous minutes) (Yamamoto *et al.* 2010, Dias *et al*. 2012), from December to January, which represent the middle of the non-breeding period. Activities were calculated separately for light and dark periods each day; local sunset and sunrise times were assessed using light levels recorded by the geolocators.

RESULTS

The at-sea movements of Brown Boobies outside the breeding season occurred in a north-south direction (Fig. 1a). Their wintering areas were north of the Republic of the Philippines (Fig. 1b,c), in the Sulu/Celebes Sea (Fig. 1d,e,f), off northern New Guinea (Fig. 1g), and in the East China Sea/Yellow Sea (Fig. 1h,i). Most study birds stayed near the colony in September and started to move during October and the first half of November. They were most distant from the breeding site from November to January. The shortest direct maximum distance from the colony varied among individuals, ranging from 574–4 988 km. Wintering habitats were located up to 6 575 km apart between the northernmost and southernmost destinations. Boobies started to return to the breeding region in January, but the timing varied among individuals: ID9109, ID9108, and ID9383 in January; ID9093 in February; ID9106, ID9096, and ID9380 in March; and ID9387 in April (Fig. 1).

Within the non-breeding period, boobies spent 17.6 % ± 5.0 % of their time on the water during the day and 11.1 % ± 8.2 % of their time on the water at night. Overall, they spent < 10 % of their time on the water at night (Fig. 2). Boobies rarely spent long periods of time sitting on water; continuous wet periods > 30 min for each individual represented just 1.1 % ± 0.5 % (0.2 % to 2.0 %) of all events during the day and 4.4 % ± 2.8 % (0 % to 8.6 %) of all events at night. Moreover, the longest period immersed was 2.6 ± 1.4 h (1–5.7 h) during the day and 4.0 ± 2.5 h (0.5–9 h) at night. In comparison, continuous dry periods (i.e., time spend out of water) typically lasted < 60 min during the day and > 3 h at night (Fig. 3).

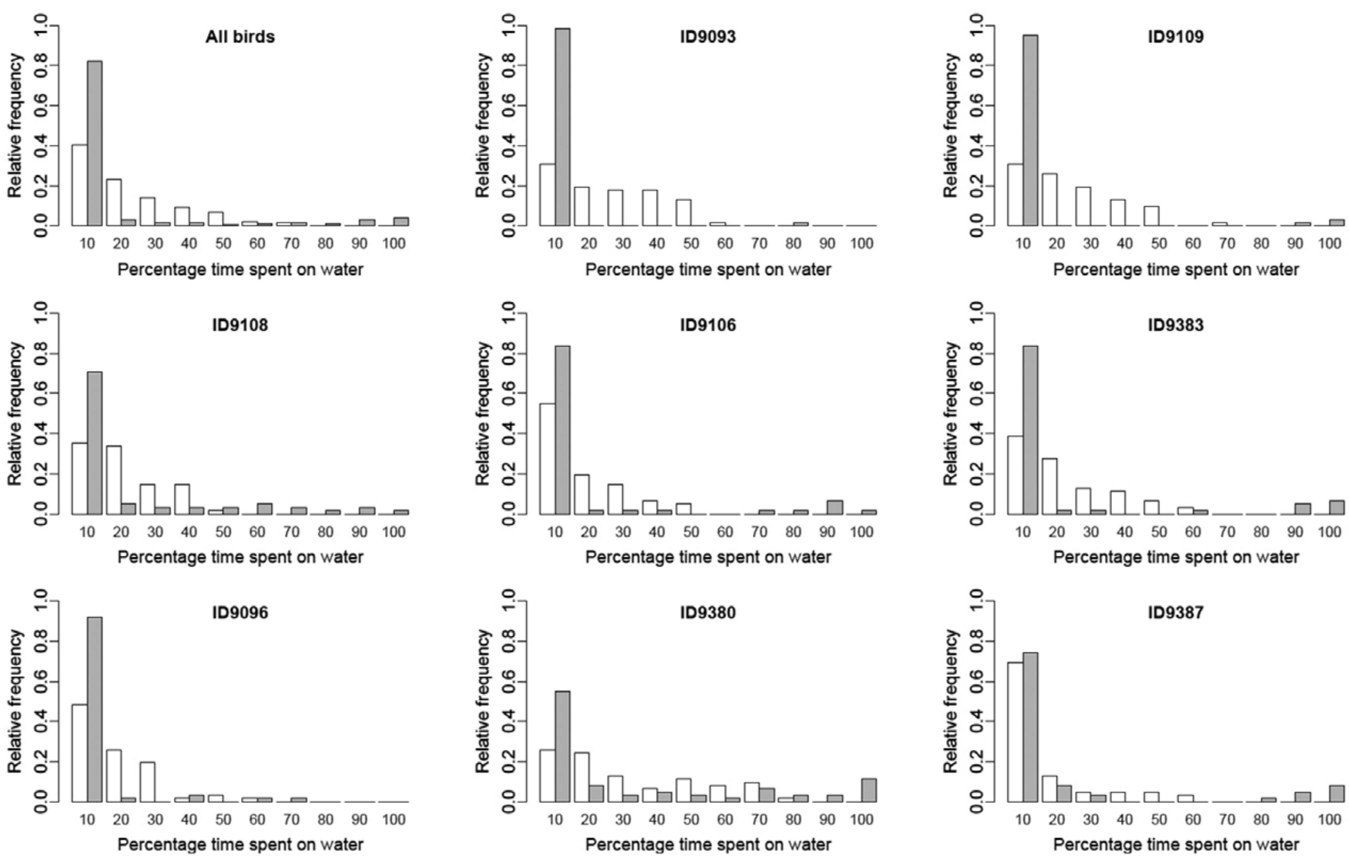

Fig. 2. Activity patterns of Brown Boobies during the wintering period from December to January. Graphs show the relative frequency of the proportion of time spent on the water during the day (white) and at night (grey), for all individuals (pooled) or each individual separately.

DISCUSSION

To our knowledge, this study is the first to explore the individual-based at-sea movements and activity characteristics of *Sula* species during the non-breeding period, although the sample size was limited to just eight birds. Brown Boobies from Nakanokamishima Island spent their non-breeding season across a large geographical range, with individuals exhibiting a large variation in wintering habitats at a regional scale. Species in temperate and polar regions primarily travel towards lower latitudes or similar latitudes in the opposite hemisphere, where the seasons are reversed (Phillips *et al*. 2005, Shaffer *et al*. 2006, Newton 2008). In contrast, a limited number of studies have shown that tropical pelagic seabirds exhibit longitudinal movements to remain in constant environmental conditions (Catry *et al*. 2009, Pinet *et al.* 2011, Ramos *et al*. 2015, Zajková *et al*. 2017). In this study, Brown Boobies, a tropical seabird, exhibited broad north-south movements. This might be related to their reliance on land throughout the non-breeding period (see discussion below), with the continental coast running north-south. This may constrain their movements to coastal waters or to areas within archipelago regions. Interestingly, some individuals even moved north. We have no information on the factors that influence the choice of wintering habitats among individual boobies, but their movement patterns do indicate multi-directional movement. Multi-directional movements are typical of tropical seabirds owing to lower seasonality in surrounding environments (Spear & Ainley 2005, Ramos *et al*. 2015). On the other hand, our observations could reflect movement patterns typical of the Sulidae family (e.g., Northern Gannets *Morus bassanus*; Kubetzki *et al*. 2009).

Brown Boobies spent 17.6 % ± 5.0 % of their time on the water during the day during the non-breeding period. Previous studies reported that Brown Boobies spent 3 % to 30 % of their time, on average, sitting on the water during a foraging trip (Lewis *et al.* 2004, Weimerskirch *et al*. 2009). The dominance of short, continuous wet and dry periods during the day indicates the frequent use of plunge dives during foraging, given that boobies conduct several dives per hour during the breeding period (Lewis *et al*. 2004, Weimerskirch *et al*. 2009). Thus, foraging activities during the non-breeding period are similar to those during the breeding period. Compared to temporal and polar seabird species, including Procellariiformes and Sulidae that generally spend > 80 % of time on water at night during the non-breeding period (Catry *et al*. 2009, Yamamoto *et al*. 2010, Garthe *et al*. 2012), the percentage of time spent on water at night was notably low in Brown Boobies, even when they were not associated with a specific island (i.e., breeding colony). Immersion records allowed us to determine if the birds were in or out of water, but they did not allow us to determine if the birds were in flight or resting on land (because both activities were recorded as dry). The Brown Booby is a diurnal feeder that usually spends the night on land during the breeding period (Lewis *et al*. 2004, Yoda & Kohno 2008, Miller *et al*. 2018). Furthermore, although some *Sula* species overnight at sea, they spend this time floating on the water surface rather than foraging and/or travelling (Mendez *et al*. 2017); this is likely because nocturnal foraging is constrained by the lack of ambient light. Thus, the increased continuous period of dry events at night recorded for Brown Boobies during the non-breeding period likely indicates that they were resting on land or roosting on rocks (Nelson 1978). In support of this hypothesis, the Brown Boobies in our study wintered in archipelago regions or close to the coast (Fig. 1). This behaviour might be related to anti-predatory behaviour (Weimerskirch *et al*. 2005, Mendez *et al*. 2017). Sharks are dominant predators in tropical oceans (Johnson *et al*. 2006, Cairns *et al*. 2008), and they attack from underwater when seabirds are sitting on the water surface (Zavalaga *et al.* 2012). In fact, at the Nakanokamishima colony, Brown Boobies with foot injuries or missing feet have been observed during the breeding period (HK unpubl. data).

Colony-based observations have reported large variations in the breeding phenology of tropical sulids, as some populations breed annually while others breed irregularly or in all months (Nelson 1987, Schreiber & Norton 2002). In our study colony, the breeding period occurs broadly from February to November (Kohno *et al*. 2018). Although one bird used areas just 574 km from the breeding colony during the non-breeding period, this distance exceeded that of typical foraging excursions during the breeding period, which were a mean distance of 40 km from the colony and always within 100 km of the colony (HK unpubl. data; consistent with findings from other populations, in which distances from the colony were < 80 km: Weimerskirch *et al*. 2009, Miller *et al.* 2018). In the southern Ryukyu Islands, where Nakanokamishima is located, stormy seas prevail during November to February due to the East Asian Monsoon (Zhang *et al*. 1997, Kohno 2000, Ikema *et al*. 2013). These seasonal local environmental conditions, which may reduce prey detectability (Finney *et al*. 1999, Baptist & Leopold 2010, Dehnhard *et al*. 2013) and flight performance due to strong winds (Hertel & Ballance 1999, Zavalaga *et al*. 2012, Yamamoto *et al*. 2017), might force boobies to leave the breeding region. Therefore, the seasonal movements in this study might indicate, in part, that breeding phenology is shaped by changes in the local environment of the breeding region. Nonetheless, the timing of return to the breeding colony appeared to vary among individuals, which coincides with the observed variation in the breeding phenology of this population (e.g., among individuals, egg laying takes place over a two-month range; Kohno *et al*. 2018). The consequences of individual differences in wintering habitat may vary with differing energy or time costs, the time available for feeding, and the timing of the return to the colony (Phillips *et al*. 2017). Further investigations are needed to elucidate the advantages and disadvantages to survival or reproduction of each migratory characteristic, and to predict the effect of these differences on population dynamics.

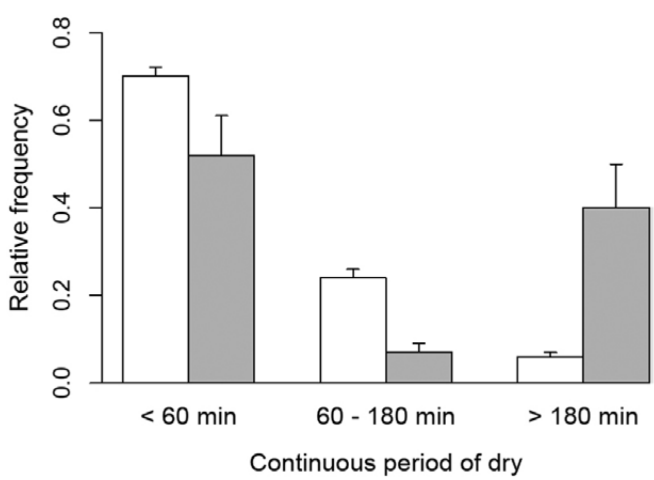

Fig. 3. Activity patterns of Brown Boobies during the wintering period from December to January. The graph shows the relative frequency of the proportion of the continuous period (mean ± standard deviation) of dry during day (white) and night (grey). Data from all individuals are pooled.

ACKNOWLEDGEMENTS

We would like to thank Ken Sakihara, the staff of the Okinawa Regional Research Centre (ORRC) at Tokai University, and Yonezo Ikeda for providing logistical support in the field. We are also grateful for the assistance of students who undertook research for their dissertations as part of this study. An anonymous reviewer provided edits that improved our paper. This work was financially supported by grants from ORRC and JSPS KAKENHI (Grant Numbers 23657023, 25281056, and 15J07507).

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