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Distribution and at-sea behavior of Bermudan White-tailed Tropicbirds (*Phaethon lepturus catesbyi*) during the non-breeding season

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ABSTRACT. The movements and behavior of many taxa of seabirds during the non-breeding season remain poorly known. For example, although studies conducted in the Pacific and Indian oceans suggest that White-tailed Tropicbirds (*Phaethon lepturus*) seldom fly more than a few thousand kilometers from nest colonies after breeding, little is known about the post-breeding movements and behavior of a subspecies of White-tailed Tropicbirds (*P. l. catesbyi*) that breeds on islands in the North Atlantic Ocean. Our objective, therefore, was to use light-based geolocators to identify the ranges and pelagic activities of White-tailed Tropicbirds from Bermuda during the non-breeding periods in 2014–2015 ($N = 25$) and 2015–2016 ($N = 16$). Locations were estimated based on changes in light intensity across time, and pelagic activities were determined based on whether geolocators attached to leg bands were wet (i.e., birds resting on the water's surface) or dry (i.e., birds in flight). In 2014, birds spent late summer (July–September) near Bermuda and the British Virgin Islands; by mid-September, most ($N = 17$; 68%) birds took a direct easterly route to the Sargasso Sea. In 2015, most post-breeders ($N = 15$; 94%) flew east from Bermuda and to the Sargasso before the end of late summer. For both years combined, fall and winter (October–February) ranges extended as far west as North Carolina and as far east as the mid-Atlantic Ridge. In both years, all birds were located between Bermuda and the British Virgin Islands during the spring (April–May). All birds then flew north to Bermuda in both years, with variations in timing, during April and May. We also found extensive overlap in the ranges of males and females during the non-breeding season in both years. During the non-breeding season, White-tailed Tropicbirds spent 5% of night periods and 41% of day periods in flight in 2014; in 2015, birds spent 8% and 42% of night and day periods, respectively, in flight. Tropicbirds spent more time flying during the day because they hunt by day, detecting prey on the wing by sight. Overall, our results suggest that White-tailed Tropicbirds that breed in Bermuda are diurnal, nomadic wanderers that range over an extensive area of the Atlantic Ocean during the non-breeding season.

RESUMEN. **Distribución no reproductiva y comportamiento en alta mar del Rabijunco común originario de Bermudas (*Phaethon lepturus catesbyi*) en el Atlántico Norte**

Los movimientos y el comportamiento de muchos taxones de aves marinas durante la temporada no reproductiva permanecen todavía pobremente conocidos. Por ejemplo, aun cuando estudios realizados en los océanos Pacífico e Indico sugieren que el Rabijunco común (*Phaethon lepturus*) rara vez vuela más de unos pocos miles de kilómetros de la colonia de nidada luego de reproducir, poco se sabe sobre los movimientos y el comportamiento post reproductivos de una subespecie de Rabijunco común (*Paethon l. castebyi*) que reproduce en islas del Océano Atlántico Norte. Nuestro objetivo, entonces, fue usar geolocalizadores basados en luz para identificar los rangos de distribución y las actividades pelágicas del Rabijunco común de Bermuda durante los períodos no reproductivos en 2014–2015 ($N = 25$) y en 2015–2016 ($N = 16$). Se estimaron las ubicaciones a partir de los cambios en la intensidad de luz a lo largo del tiempo, y las actividades pelágicas fueron determinadas a partir de si los geolocalizadores adheridos a las bandas de las patas estaban mojados (i.e., aves descansando en la superficie del agua) o secos (i.e. aves volando). En 2014, las aves pasaron el verano tardío (julio-septiembre) cerca de Bermuda y las Islas Vírgenes Británicas; para mediados de septiembre, la mayoría ($N = 17$, 68%) de las aves tomaron una ruta directa y hacia el este al Mar de los Sargazos. En 2015, la mayoría de los individuos post reproductivos ($N = 15$; 94%) volaron hacia el este desde Bermuda y hacia el Mar de los Sargazos antes del final del verano. Para ambos años combinados, los rangos en otoño e invierno (octubre-febrero) se extendieron hacia el oeste tan lejos como Carolina del Norte y hacia el este tan lejos como la Dorsal Mesoatlántica. En ambos años, todas las aves fueron ubicadas entre Bermuda y las Islas Vírgenes Británicas durante la primavera (abril-mayo). Todas las aves luego volaron norte a Bermuda en ambos años, con variaciones en el momento, durante abril y mayo. También encontramos extensa superposición en los rangos de los machos y las hembras durante la temporada no reproductiva en ambos años. Durante la temporada no reproductiva, los Rabijuncos comunes pasaron el 5% de los períodos nocturnos y el 41% de los períodos diurnos en vuelo en 2014; en 2015, las aves pasaron el 8% y el 42% de los períodos nocturnos y diurnos, respectivamente, en vuelo. Los Rabijuncos pasaron más tiempo volando durante el día debido a que cazan de día, detectando las presas en vuelo por medio de la vista. En general, nuestros resultados sugieren que los Rabijuncos comunes que crían en Bermuda son diurnos, nómades errantes que se distribuyen en una extensa área del Océano Atlántico durante la temporada no reproductiva.

Key words: geolocators, migration, pelagic activities, tropical seabirds, sexual segregation

Tropicbirds (Phaethontidae) are medium-sized tropical seabirds whose year-round at-sea ranges are poorly known. White-tailed Tropicbirds (*Phaethon lepturus catesbyi*), a subspecies of the smallest (mean mass = 385 g) species, breeds on islands in the North Atlantic Ocean, including Bermuda which supports the largest (~3500 nesting pairs) population in the entire Atlantic (Lee and Walsh-McGehee 2000, Dobson and Madeiros 2009, J. L. Madeiros and M. A. Mejías, unpubl. data). In the tropics, these tropicbirds are asynchronous breeders, with some birds nesting year-round (Ramos et al. 2005, Catry et al. 2009a). In contrast, Bermudan tropicbirds, known locally as "Longtails", have a defined breeding season from March to September, with birds leaving Bermuda as late as November to unknown non-breeding areas. At-sea surveys and GLS-logger data collected in the Pacific and Indian Oceans suggest that post-breeding White-tailed Tropicbirds seldom travel more than a few thousand kilometers from nest colonies, but their movements and at-sea behavior in the Atlantic Ocean during the non-breeding season remain unexplored (Spear and Ainley 2005a, Le Corre et al. 2012).

Our objective, therefore, was to use geolocators to examine, for the first time in Atlantic waters, the distribution and pelagic activities of White-tailed Tropicbirds during the non-breeding season. Specific objectives were to: (i) identify the ranges of tagged tropicbirds during the non-breeding season, (ii) identify late-summer, fall-winter, and spring movements and core areas, (iii) determine if tropicbirds exhibit sexual segregation during the non-breeding season, and (iv) quantify diurnal and nocturnal at-sea behaviors.

Although known to travel in loose flocks a few kilometers offshore from Bermuda during the breeding season, ship sightings suggest that White-tailed Tropicbirds forage solitarily when at sea, plunge diving for fish and squid, and avoiding mixed-species flocks (Gross 1912, Catry et al. 2009c). Given their nomadic nature when far from breeding sites, we expected no pelagic segregation between non-breeding male and female tropicbirds. The diel activity patterns of this species during the non-breeding period remain uncertain. In Bermuda, tropicbirds spend morning and early afternoons feeding chicks and performing courtship flights at nest sites, with activity gradually declining in late afternoon and ceasing by nightfall (Gross 1912). If the behavior of tropicbirds during the breeding season matches their behavior during the non-breeding season, we expected greater activity by non-breeding tropicbirds during the day than at night.

METHODS

GLS logger programming. We captured White-tailed Tropicbirds at nine breeding sites in Bermuda (32°31′N, 64°75′W) from 2014 to 2016 (Fig. 1). Prior to deployment of geolocators (1 g; C-65 Migrate Tec Intigeo, Migrate Technology Ltd: Cambridge, UK; hereafter, GLS loggers), we activated six random GLS loggers and zip-tied them to a low shrub with no leaves on Nonsuch Island (G on Fig. 1) for 31 days in 2014 for open-sky calibration (Lisovski et al. 2012). Each GLS logger measured the light regimes at this site, producing a single elevation angle. Following the calibration period, we took the average of the sun elevation angles from the six GLS loggers to use as the reference sun angle for any recaptured birds in both years (Lisovski et al. 2012). We set all GLS loggers on "mode 6", allowing them to estimate geographic location based on changes in light intensity across time, and to record periods of saltwater immersion every 30 sec. Saltwater immersion values ranged from 0 (completely dry) to 20 (completely saturated) and were saved at 10-min intervals each day.

GLS logger deployment and retrieval. We captured 30 tropicbirds in both 2014 and 2015 ($N = 60$) and avoided re-sampling

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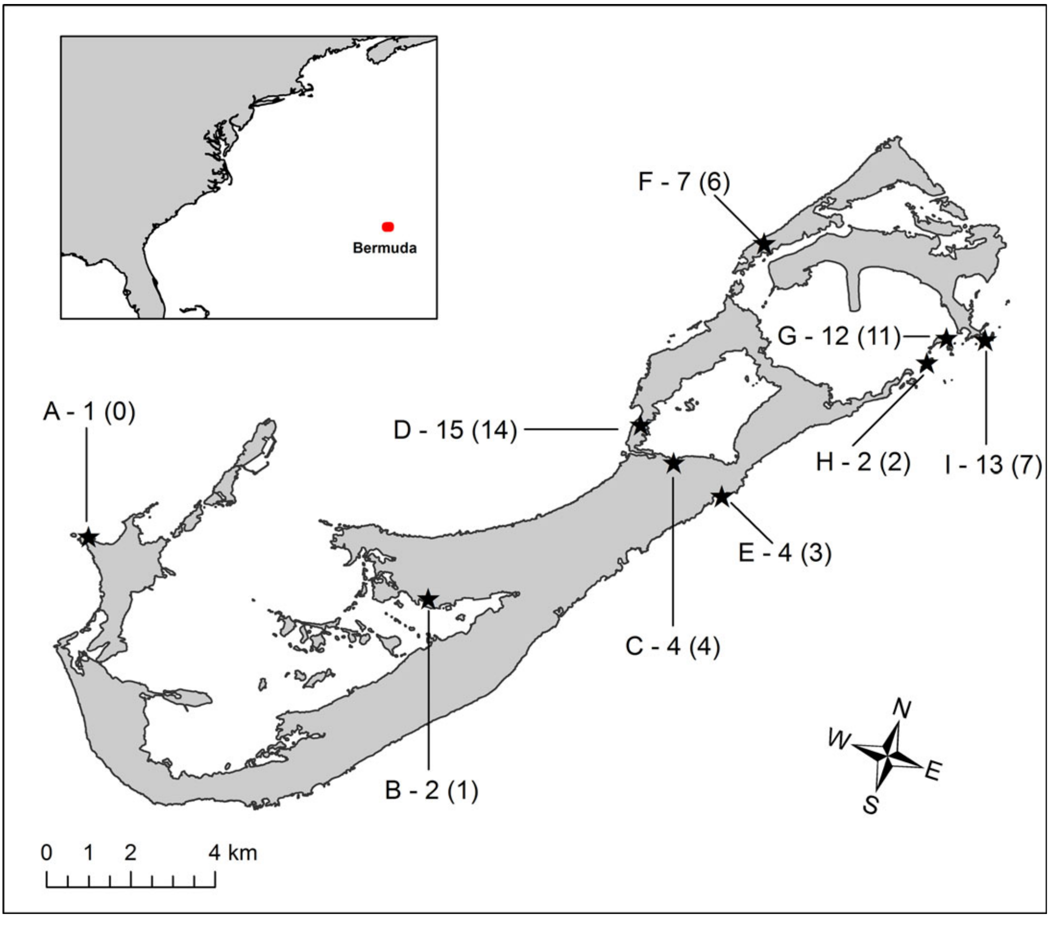

Fig. 1. Sites where White-tailed Tropicbirds were captured and fitted with GLS loggers across Bermuda in 2014 and 2015. (A) Daniel's Head, (B) Bay House, (C) Bermuda Aquarium, (D) Shelly Bay, (E) Spittal Pond, (F) Ferry Reach, (G) Nonsuch Island, (H) Horn Rock, and (I) Cooper's Island. Numbers represent the number of tagged and recaptured (in parentheses) birds at each site.

individuals; GLS loggers were deployed from July to August and during May in 2014 and 2015. We captured birds by removing them from nest cavities by their bills and placing them in a cotton weighing bag, where they remained for the following procedures. Captured adults were at various breeding stages, including sitting in cavities with no egg or chick, incubating an egg, or brooding a chick. We recorded mass with a 500-g Pesola spring scale ($\pm$ 1 g). We banded adults with a unique identification incoloy metal band (0.5 g) on their right leg and with a plastic Darvic band equipped with a single GLS logger (< 0.5% of adult body mass) on the left leg. We secured GLS loggers to the Darvic band with a small zip tie, with excess zip tie being cut, and moderate application of quick-dry two-part marine epoxy (Amazing GOOP, Eclectic, Eugene, OR). We kept birds in the weighing bag until the marine epoxy was dry. GLS loggers plus band weighed ~2 g.

After processing, we returned adults to nest cavities and placed a towel in the cavity entrance for 5 min to prevent immediate fleeing and give birds time to calm down. We briefly checked adults immediately after towel removal. From April to June 2015 and 2016, we revisited all nest sites weekly to remove GLS loggers from recaptured birds. All recaptured birds were weighed as described above. In addition, we collected eight to 10 flank feathers from each recaptured adult and placed samples in paper envelopes and refrigerated them until they were analyzed for genetic sex determination (Fridolfsson and Ellegren 1999) at the Genomics and Proteomics Facility at Memorial University of Newfoundland. Total handling time for captured and recaptured tropicbirds was 8–10 min.

GLS logger analysis and mapping. To view raw light data from recovered GLS loggers, we imported and viewed each day as light curves using IntiProc v2.0 Geolocation Processing Software from Migrate Technology. We then used the "auto-mark up" command in IntiProc to estimate sunrise and sunset events for each light curve. Deep, abrupt dips in light curves were likely caused by birds spending long periods in nest cavities. Therefore, approximate departure dates (i.e., start of the non-breeding period) of birds whose nesting fate were unknown were determined by identifying the last date birds exhibited nest-cavity shading in their light curves. For birds whose nesting fates were known, departure dates were estimated using our nest-monitoring data.

Light curves where sunrise and sunset events were disrupted (i.e., irregular rather than a smooth curve) by cloud cover were identified and removed. We used −7.3° as our sun elevation angle based on our averaged calibration data. We further validated this elevation angle by looking at the distributions of birds around Bermuda during the entire breeding season using IntiProc. To account for the natural latitudinal error associated with GLS loggers, we smoothed validated non-breeding data twice by taking the average of the previous, current, and subsequent positions (Phillips et al. 2004a, Fifield et al. 2014). To avoid potential positional errors, fixed start positions (departure date and return date) for each bird were not smoothed (Phillips et al. 2004a). Our tropicbird movement data were erratic between 16 September and 19 October and between 20 February and 9 April (i.e., fall and spring equinoxes, respectively) so these time periods were excluded from our dataset. The earliest sightings of returning White-tailed Tropicbirds in Bermuda are from mid-February through March so the return dates of tagged birds coincided with the spring equinox where data are unreliable. Although we observed much crevice-shading among light curves in March, corresponding to spring sightings in Bermuda, GLS data for one bird showed crevice-shading post-equinox in April when it was located close to Puerto Rico and the British Virgin Islands south of Bermuda. This suggests that some birds may visit crevices on other islands in the Caribbean. Without reliable latitudinal data during the equinox, and because Bermuda and Puerto Rico are at similar longitudes, we could not confidently determine which island birds were visiting during the spring equinox.

Tropicbirds in nest cavities with neither eggs nor chicks when recaptured were considered to be non-breeding adults and, for these birds, the day of recapture was considered the end of the non-breeding period. For tropicbirds incubating eggs when recaptured, we estimated the approximate date of egg laying using the hatch date in combination with evidence of crevice-shading to determine the approximate end to their non-breeding periods.

After IntiProc analysis, tracking data collected during the non-breeding period were imported into ArcGIS (ESRI, v.10.3.1: Redlands, CA). Data were projected using the Transverse Mercator Complex projection (Projected Coordinate system: WGS_1984_Complex_UTM_Zone_21N). We generated kernel densities representing the non-breeding locations with Geospatial Modelling Environment (GME) (v. 0.7.4.0; Beyer 2015). In GME, we used a raster resolution of 40 km for all kernel densities. We are aware that 50 km is commonly used for seabird geolocation studies (Phillips et al. 2005, Raine et al. 2013, Hedd et al. 2014). However, we used a 40-km cell size strictly for visualizing tropicbird distribution; we did not include any environmental layers in our GIS analysis. In addition, 40 km seemed like an appropriate compromise between considering the spatial error of GLS loggers and capturing key concentration areas. We then used GME to calculate 30, 50, 70, and 90% contours for each kernel density, with 50% contours representing "core" areas. We generated kernel densities for the following periods for 2014–2015 and 2015–2016: (i) entire non-breeding period (July to May), (ii) late summer (July to mid-September), (iii) fall-winter (late October to mid-February), and (iv) spring (April and May). We chose these seasonal break points to have finer-grained resolution of post-breeding movements, an approach also used in other tracking studies of seabirds (Lorentsen and May 2012, Reiertsen et al. 2014). Lastly, we generated 50% contours representing core ranges of male and female tropicbirds across the non-breeding season.

To quantify pelagic activities, we manually restored sunrise and sunset events associated with the breeding season in IntiProc. We then imported the immersion data for each bird into R v2.12.1, where we categorized each 24-h period into day and night periods. We calculated the approximate duration of day and night for each day from the light-curve data. We then used the plot function in R v2.12.1 (R Development Core Team 2010) to graph the average amount of time all birds were dry during the breeding and non-breeding periods. To avoid overestimation of dry periods during the breeding season, we removed sunrise and sunset events where birds were clearly inside nest cavities.

Statistical analysis. We used paired *t*-tests to compare the mean body mass of White-tailed Tropicbirds when first captured and when recaptured within years. We then used independent *t*-tests to determine if the proportion of time birds were wet and dry during day and night periods differed between the sexes across the non-breeding period within years. All *t*-tests were two-tailed, and results were considered significant if $P < 0.05$. All statistical tests were run in R v2.12.1 (R Development Core Team 2010).

RESULTS

Retrieval details and body condition. In 2015, we recaptured 25 of 30 breeding birds (83%) fitted with GLS loggers in 2014. In 2016, we recaptured 23 of 30 birds (76%) tagged in 2015. In total, all 25 loggers recovered in 2015 and 16 of 23 loggers (70%) in 2016 recorded data until birds were recaptured, providing movement data for 41 tropicbirds ($N = 24$ males and 17 females). Birds were lighter when GLS loggers were first deployed than when recaptured in both 2014–2015 ($t_{21} = -2.2$, $P = 0.04$) and 2015–2016 ($t_{22} = -7.6$, $P < 0.001$).

Non-breeding distribution. Departure dates of tropicbirds from breeding sites ranged from 4 July to 8 September in 2014 and from 29 June to 9 September in 2015. During the non-breeding period (July to May) of 2014–2015, tropicbirds were distributed widely across the North Atlantic Ocean (Fig. 2A). The non-breeding range of birds with GLS loggers extended north to the Grand Banks of Newfoundland, east to the mid-Atlantic Ridge, south to the British Virgin Islands, and west to between Bermuda and North Carolina. Core areas (50% kernels) were concentrated around Bermuda and north of the British Virgin Islands, between Bermuda and the mid-Atlantic Ridge (this boundary hereafter the Sargasso Sea), and the mid-Atlantic Ridge.

In 2015–2016, the non-breeding range of tropicbirds was similar, extending from North Carolina to the west and to waters between Bermuda and the British Virgin Islands to the south (Fig. 2B). Core areas included the Sargasso Sea and waters just south of the Georges Banks.

During the late-summer period (July to mid-September) of 2014, core areas were near Bermuda, the area between Bermuda and the British Virgin Islands, and the Sargasso Sea (Fig. 2C). Fourteen of 25 birds ranged from Bermuda to the Sargasso Sea. Eleven other birds wandered between Bermuda and the British Virgin Islands, five of which returned to Bermuda, and one stopped between Bermuda and the British Virgin Islands. By mid-September, 17 (68%) birds, 16 directly from Bermuda and one between Bermuda and the British Virgin Islands flew east into the Sargasso Sea, with two birds reaching the mid-Atlantic Ridge. During this same period, five (20%) birds remained in the Caribbean Sea and three in Bermuda. In late summer 2015, core tropicbird areas were near Bermuda and in the Sargasso Sea (Fig. 2D). Fifteen of 16 birds (94%) ranged from Bermuda to the Sargasso Sea, and spent most of late summer in the Sargasso Sea. By the end of the late-summer period, nine (56%) birds were in the Sargasso Sea and six (38%) reached the mid-Atlantic Ridge. The last bird spent the entire late-summer period in waters between Bermuda and Turks and Caicos.

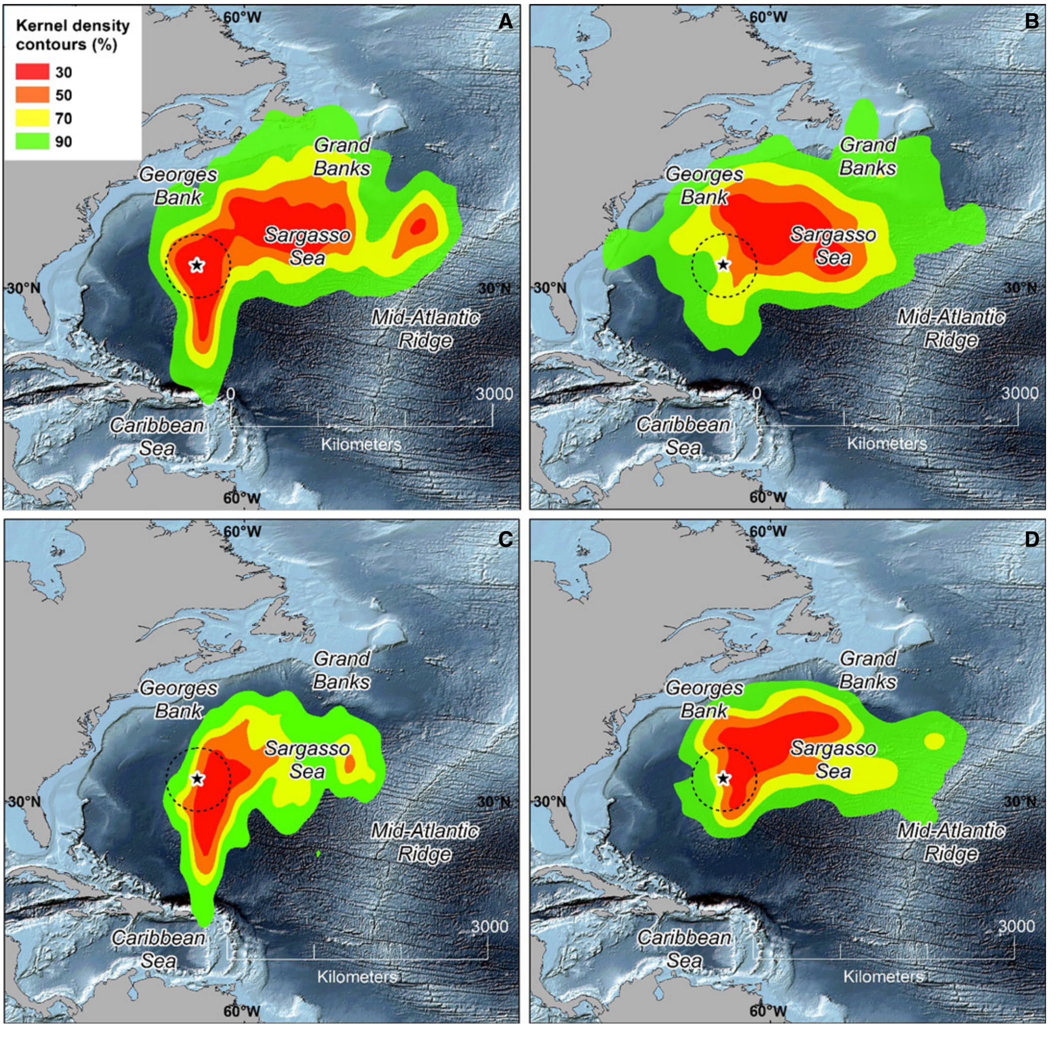

Fig. 2. Pelagic distribution of White-tailed Tropicbirds (2014–2015, $N = 25$; 2015–2016, $N = 16$) from Bermuda (indicated by stars) during the non-breeding period (i.e., from departure to approximate return; A and B), late-summer period (C and D), fall-winter period (E and F), and spring period (G and H) and by sex for the entire non-breeding period (I and J). Bermudan waters (i.e., Bermuda's exclusive economic zone, or EEZ) are indicated on maps by dashed circles with a radius of 370.4 km. Colors indicate the relative concentration of tropicbirds during specific periods, with areas of greatest use shown in red, expanding outward to areas used least shown in green. Tropicbird distributions in 2014–2015 and 2015–2016 are shown in the left and right columns, respectively. Sea-floor layer downloaded from www.NaturalEarthData.com.

During the fall and winter period (late October to mid-February) of 2014, core areas were concentrated around Bermuda, the Sargasso Sea, and the mid-Atlantic Ridge (Fig. 2E). Prior to this, 19 of 25 tropicbirds (76%) were foraging along the southern Grand Banks of Newfoundland between late October and mid-November, but then flew rapidly southward, dispersing into the above core areas. Eight (32%) birds wintered in the Sargasso Sea and the mid-Atlantic Ridge, five (20%) ranged from the Sargasso Sea to Bermuda, and two (8%) birds spent most of winter near Bermuda. Eight (32%) other tropicbirds largely used the Sargasso Sea, and one spent the period from mid-October to

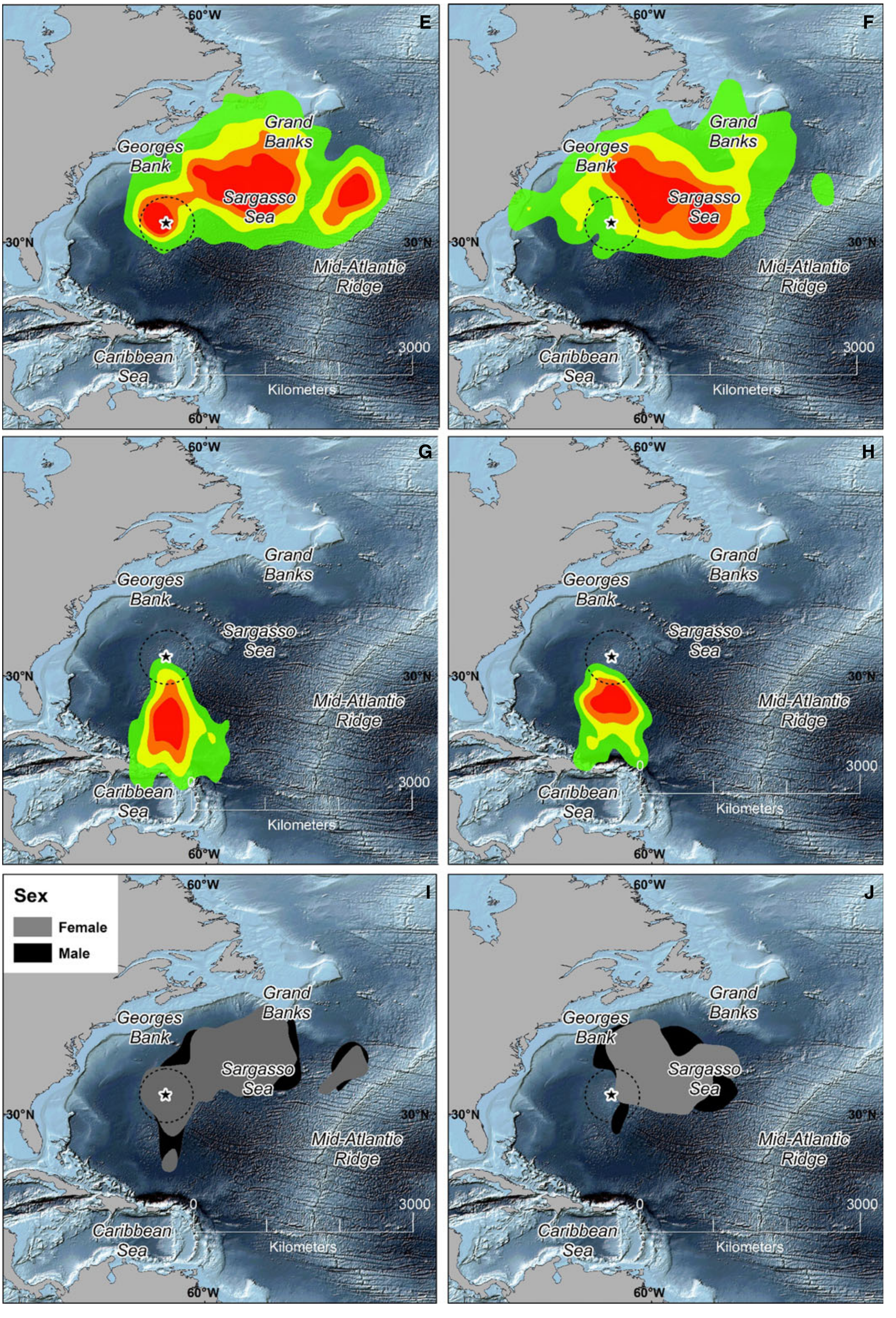

Fig. 2. Continued

late December just south of the Nova Scotian shelf before flying south to the Sargasso Sea where it spent the rest of the winter period. The last bird spent parts of December and January along the coast of North Carolina, then flew to the southern George's Banks in early February, before ending its winter period near Bermuda.

During the fall and winter of 2015, the core area included the Sargasso Sea and waters south of the Georges Banks (Fig. 2F). Between late October and mid-November, 10 of 16 birds (63%) were foraging in the southern Grand Banks of Newfoundland before flying south to core wintering areas by December. The Sargasso Sea was used by 13 of 16 wintering birds (81%). Six (38%) tropicbirds wintered in the Sargasso Sea and south of the Georges Banks, and two (13%) primarily in the Sargasso Sea. Four (25%) birds wintered in the Sargasso Sea and the mid-Atlantic Ridge, and two wintered mostly along the coasts of North Carolina before flying eastward to Bermuda, and to the Sargasso Sea by the end of winter. The remaining two birds spent half of their fall and winter period in the core area (i.e., one in the Sargasso Sea, and the other south of the George's Banks) and the other half in Bermudan waters.

During the spring periods, we were unable to determine the movements of six birds in both years because our nest-monitoring data suggested that they began breeding during the equinox period. During the spring period (April–May) of 2015, all tropicbirds were located in a core area between Bermuda and the British Virgin Islands (Fig. 2G). Sixteen of 19 birds (84%) spent most of the spring period there. During early and mid-April, 11 tropicbirds were in the Caribbean Sea, near Hispaniola, Puerto Rico, and the British Virgin Islands. The onset of a movement north to Bermuda began by mid-April, with 12 individuals arriving in Bermuda before the end of April. The seven remaining birds stayed in the spring core area, flying north to Bermuda in May. During spring 2016, all tropicbirds were in the area between Bermuda and the British Virgin Islands (Fig. 2H). Eight (80%) of 10 birds spent most of the spring in this core area. Five tropicbirds were located near Puerto Rico, Hispaniola, and the British Virgin Islands through early and mid-April. Nine birds flew north, back to nest sites by the end of April; the last individual flew north from the core area to Bermuda in late May.

Distribution of males and females. We recaptured 14 males and 11 females in 2015 and 10 males and six females in 2016. In 2014–2015, core areas during the non-breeding period for both sexes were concentrated in Bermuda, the Sargasso Sea, and the mid-Atlantic Ridge; ranges of males and females overlapped extensively (Fig. 2I). In 2015–2016, core areas of males and females were concentrated largely in the same areas of the Sargasso Sea and south of the Georges Banks (Fig. 2J).

At-sea activity patterns. During the 2014 and 2015 breeding seasons, birds spent a greater percentage of their time dry during both day and night periods (Fig. 3A, B). In both years, the start of the non-breeding season was marked by a sharp decline in the percentage of time birds were dry, particularly at night (Fig. 3A, B). This trend persisted throughout the non-breeding periods, with the breeding seasons of both 2015 and 2016 beginning with an abrupt increase in time birds spent dry during the day and night (Fig. 3A, B).

In 2014, non-breeding males and females did not differ in time spent wet during either the day ($t_{18} = 1.4$, $P = 0.18$) or night ($t_{22} = 1.5$, $P = 0.15$). Similarly, non-breeding males and females did not differ in time spent wet during the day ($t_{13} = 0.02$, $P = 0.97$) or night ($t_8 = -1.0$, $P = 0.33$) in 2015. During the non-breeding periods of both 2014 and 2015, tropicbirds (males and females combined) flew more during the day than night (Fig. 3A, B). However, during the non-breeding period in 2014, tropicbirds spent more time on the water (59% of time; mean = 7 h) than in flight (41%; 5 h) during the day. During the non-breeding period in 2015, tropicbirds also spent more time on the water (58%; 7 h) than flying (42%; 5 h) during the day. All non-breeding birds spent most of the night periods on the water in both 2014 (95%; 11 h) and 2015 (92%; 10.5 h) (Fig. 3A, B).

DISCUSSION

We recaptured most White-tailed Tropicbirds with GLS loggers attached during the previous breeding season in both 2015 (83%) and 2016 (76%). The high nest-site fidelity

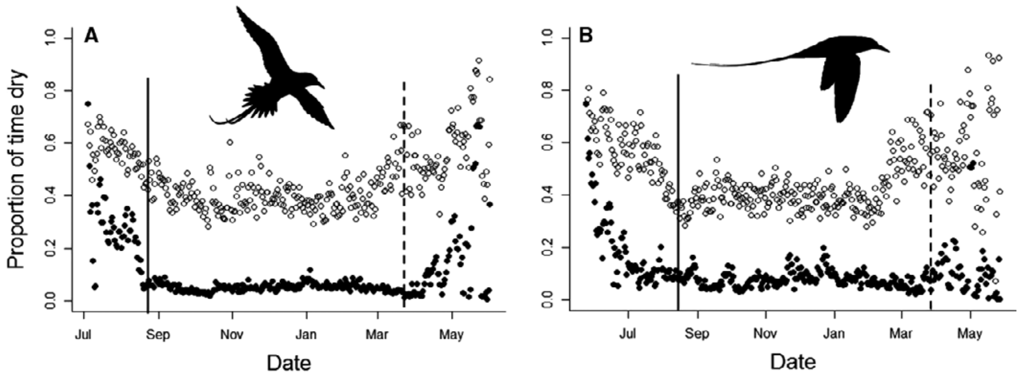

Fig. 3. Average proportion of time White-tailed Tropicbirds were dry during day (hollow circles) and night (dark circles) periods during the breeding and non-breeding periods of (A) 2014 ($N = 25$) and (B) 2015 ($N = 16$). The approximate start and end of the non-breeding period are denoted with solid and dashed lines, respectively. During both years, the average percent time that birds were dry during day and night periods declined during the non-breeding period, and steadily increased during the following breeding period.

of Bermudan White-tailed Tropicbirds, whose nest cavities limited escape possibilities, contributed to our high recapture rates. Birds we failed to recapture ($N = 5$ in 2015; $N = 7$ in 2016) were not observed and may have died during the non-breeding period. In support of this possibility, the survival rate of White-tailed Tropicbirds on Aride Island was 0.81 (Catry et al. 2009a), a percentage similar to our recovery rates. Alternatively, birds that were not recaptured may have used different nest cavities. For example, in 2015, we recaptured one adult in a nest cavity located a few meters from the one it used in 2014.

We found that the mass of White-tailed Tropicbirds when recaptured was greater than that when tagged in both years. Other investigators have also reported that tracking devices did not cause seabirds to lose body mass (Adams et al. 2009, Nisbet et al. 2011). Although seabirds carrying tracking devices may experience reduced flight efficiency (Passos et al. 2010) and have lower colony attendance (Söhle et al. 2000), the high return rates of tagged tropicbirds in our study, plus the increase in mass, suggest that the small GLS loggers had minimal negative effects.

During the late-summer period (July to mid-September), distribution patterns of non-breeding tropicbirds in our study differed slightly in 2014 and 2015. In both years, birds ranged from Bermuda to the mid-Atlantic Ridge. Some post-breeding birds wandered between Bermuda and the British Virgin Islands, supporting the hypothesis that Bermudan tropicbirds migrate directly to the Caribbean after breeding (Amos 1991). In 2014, 11 post-breeding tropicbirds flew to the Caribbean, five of which returned to Bermuda before the end of the late-summer period. However, the most common flyway, used mainly by post-breeding birds near Bermuda, in both years, was a strong eastern departure from the island to the Sargasso Sea, which we interpret as the typical departure route of Bermudan tropicbirds. The one exception was a bird in 2014 that took an eastward route to the Sargasso Sea from waters between Bermuda and the British Virgin Islands. This eastward movement of birds from Bermuda by mid-September may indicate a decline in prey availability in Bermudan waters, such as the Caribbean reef squid (*Sepioteuthis sepioidea*), Atlantic flying fish (*Exocoetidae* spp.), and pufferfish (Tetraodontidae) (M. A. Mejías, unpubl. data).

During the fall and winter (late October to mid-February) of 2014, White-tailed Tropicbirds in our study exhibited considerable variation in their distributions, with some found near Bermuda, the Sargasso Sea, and the mid-Atlantic Ridge. Bermuda Petrels (*Pterodroma cahow*) have a similar distribution during their non-breeding period (Madeiros et al. 2013). In the case of Bermudan tropicbirds, the full extent of their non-breeding ranges was similar in both years. Despite White-tailed Tropicbirds being viewed largely as a tropical species, many individuals from our subtropical Bermuda population were located in the southern Grand Banks of Newfoundland from late October to mid-November in both 2014 and 2015. The Grand Banks is a nutrient-rich zone, with significant nutrient upwelling that supports large numbers of fish and squid (Anderson and Gardner 1986, Montevecchi and Myers 1995). These fish and squid densities, in turn, support an estimated 40 million seabirds annually (Montevecchi and Tuck 1987, Lock et al. 1994, Hedd et al. 2011).

Other investigators have also reported sightings of tropicbirds near Newfoundland. For example, a Red-billed Tropicbird (*Phaethon aethereus*) was observed on the Newfoundland Banks in 1876 (Mactavish 2005). Similarly, in 2006, a carcass of a White-tailed Tropicbird was found in St. John's, Newfoundland, in mid-September 2006 after a tropical storm (Mactavish 2007). The presence of tropicbirds off the coast of Newfoundland is likely explained by the warm subtropical waters of the Gulf Steam that run from the southern tip of Florida to eastern Newfoundland. Our observation of many Bermudan tropicbirds on the Grand Banks during both years of our study suggests that this is an important foraging area for this species in the fall. Although their prey in these waters remain unknown, possibilities include Atlantic saury (*Scomberesox saurus*) and northern shortfin squid (*Illex illecebrosus*) (Hurley 1980, Dudnik et al. 1981, Perez 1994). Both of these species can be as small as 20 cm and are found near the surface, traits favoring plunge diving by foraging tropicbirds (Squires 1957, Dudnik et al. 1981, Wigley 1982). Time spent on the Grand Banks by tropicbirds appears to be constrained by temperature. In both years of our study, all birds flew south from the Grand Banks by mid-November, coinciding with the cooling of the area by the Labrador Current (Han et al. 2010).

Bermuda is seemingly void of tropicbirds during the winter months, but our results indicate that a few spend much of the non-breeding season within Bermuda's exclusive economic zone, albeit far offshore. In 2014, two tropicbirds spent most of the fall and winter period in Bermudan waters, coinciding with rare onshore sightings of this species in December and January (J. L. Madeiros, unpubl. data). This also matches the distribution of White-tailed Tropicbirds in the Indian Ocean, where geolocators revealed that some post-breeders remained among their breeding colony in the Seychelles (Le Corre et al. 2012). A likely reason why most tropicbirds did not winter near Bermuda is because weather conditions typically deteriorate during the winter. Being subtropical, Bermudan winters are dominated by strong gales and heavy rains with few calm days, conditions that contrast with those during the breeding season (Diamond 1975, Phillips 1987, Amos 1991).

The Sargasso Sea, an area bordered by currents and so-named because of the presence of floating mats of *Sargassum* seaweed (Trott et al. 2010), supported the greatest number of wintering tropicbirds during both years of our study. In addition to being crucial habitat for juvenile turtles and a diverse assemblage of invertebrates, *Sargassum* seaweed serves as spawning substrate for Atlantic flyingfish an important food source for tropicbirds (Adams 1960, Dooley 1972, Sterrer 1992, Mansfield et al. 2014). The influx of tropicbirds to the Sargasso Sea was apparent by mid-November, after many birds flew there from the Grand Banks in both years of our study. Similarly, Haney (1986) reported more than 50% of White-tailed Tropicbird sightings off the eastern coast of Florida occurred over *Sargassum* patches where they were foraging.

Our fall and winter kernel analysis did not capture the extreme movements displayed by some birds. Across both years, nine tropicbirds were located in the Labrador Sea in late October, including three birds just south of Greenland, before all birds left the Labrador Sea and flew south by November. Although latitudinal error of the geolocators could explain these extreme northern distributions, the removal of equinox periods followed by smoothing reduced the likelihood of such errors. Alternatively, strong weather systems could have forced these birds further north. However, tropicbirds were still in the Grand Banks several weeks after Hurricane Gonzalo, which first passed over Bermuda on 18 October 2014 and passed the Avalon

Peninsula of Newfoundland several days later. Therefore, our data suggests that the presence of tropicbirds in Newfoundland waters was not entirely storm dependent. The greatest longitudinal distance moved by a White-tailed Tropicbird in our study was by one that flew east in late November 2014, stopping west of the Azores and ~2500 km from Bermuda. Previously, Monticelli and Aalto (2012) reported a rare sighting of a White-tailed Tropicbird in the Azores in late October.

During the spring (April–May) of 2015 and 2016, all non-breeding White-tailed Tropicbirds were located between Bermuda and the British Virgin Islands, demonstrating a more localized core area that contrasts with their more extensive movements during the winter. The aggregation of tropicbirds in this core area could coincide with when they become more social as the breeding season approaches. Alternatively, this area may be a productive, pre-breeding foraging area (Catry et al. 2009b). Our data also confirm that the ranges of Bermudan tropicbirds and Caribbean tropicbirds overlap. For both years combined, 16 White-tailed Tropicbirds in our study spent the early to mid-spring period near the British Virgin Islands and Puerto Rico, the latter island supporting 200–300 nesting pairs of White-tailed Tropicbirds (Lee and Walsh-McGehee 2000). We also found abrupt changes in the light data for one bird, indicating cavity shading, during the time it was located close to Puerto Rico and the British Virgin Islands in early April. This suggests Bermudan tropicbirds may enter cavities or crevices while in the Caribbean, possibly following resident tropicbirds to their nest sites, a behavior also observed at breeding sites in Bermuda, where prospecting adults enter cavities belonging to established pairs. (M. A. Mejías, unpubl. data).

As expected, we found no evidence of pelagic segregation by non-breeding male and female White-tailed Tropicbirds. Both males and females were located in Bermudan waters, the area between Bermuda and the British Virgin Islands, the Sargasso Sea, and the mid-Atlantic Ridge in 2014, and in the Sargasso Sea and waters south of the Georges Banks in 2015. Although nothing is known about the possibility of sexual segregation among either tropicbirds or ecologically similar seabirds, such segregation has been reported among species in the order Procellariiformes. For example, sexual segregation during the non-breeding period has been reported for Wandering Albatrosses (*Diomedea exulans*), Grey-headed Albatrosses (*Thalassarche chrysostoma*), Black-browed Albatrosses (*Thalassarche melanophris*), and Northern Giant Petrels (Xavier et al. 2004, Phillips et al. 2004b, González-Solís et al. 2007). These species exhibit moderate-to-extreme sexual size dimorphism, allowing one sex to exploit prey in specific areas more effectively than the other sex. In contrast, male and female White-tailed Tropicbirds are similar in size, minimizing the likelihood of behavioral dominance by one sex, and hunt solitarily, minimizing the likelihood of competition for resources by male and female tropicbirds (Catry et al. 2009c, J. L. Madeiros, unpubl. data).

The pelagic activities of White-tailed Tropicbirds differed between the breeding and non-breeding periods in 2014 and 2015. In both years, breeding birds spent a greater percentage of time dry during both the day and night. This was expected because nesting birds regularly visit nest sites. In contrast, non-breeding seasons began with an abrupt and consistent trend of birds spending less time dry during both day and night. In addition, White-tailed Tropicbirds in our study flew more during the day than night during the non-breeding period. The limited time spent flying during the night by White-tailed Tropicbirds in our study was not surprising because tropicbirds hunt by day, detecting prey on the wing by sight rather than by use of olfactory cues like nocturnal seabirds (Nevitt 1999). In both years, non-breeding tropicbirds spent an average of 5 h in daily flight. We interpret these long dry periods as time spent foraging in areas where prey are patchily distributed in nutrient-poor tropical and subtropical waters, especially when traveling between rafts of *Sargassum* seaweed (Russel-Hunter 1970, Flint 1991). Although non-breeding tropicbirds in our study spent more time flying during the day than at night, they still spent a greater proportion of day periods resting on the water. Similarly, Spear and Ainley (2005b) found that White-tailed Tropicbirds in the Pacific spent most of the day resting on the water. In both years, all tropicbirds spent most night periods on the water, confirming for the first time that tropicbirds roost on the water at night.

Our results show that the fall and winter (October–February) ranges of White-tailed Tropicbirds extended as far west as North Carolina and as far east as the mid-Atlantic Ridge. The range of post-breeding birds from Bermuda also overlapped that of Caribbean tropicbirds during the late summer and spring. Despite variation in movements among individuals, males and females largely shared the same non-breeding areas. Overall, our results suggest that White-tailed Tropicbirds that breed in Bermuda range over an extensive area of the Atlantic Ocean during the non-breeding season.

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