

Non-breeding season movements of six North American Roseate Terns *Sterna dougallii* tracked with geolocators

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Abstract

Little is known of the endangered and declining western North Atlantic population of the Roseate Tern *Sterna dougallii* outside the breeding season, when most mortality probably occurs. We used geolocators to track Roseate Terns in 2007 and 2009 and retrieved six units with useful data. In the post-breeding period in July–August, all six birds staged around Cape Cod, close to the breeding site. They started southward migration from 28 August to 14 September and flew directly across the western North Atlantic Ocean to staging areas around Puerto Rico and the Dominican Republic. We identified five major areas and four minor areas in the West Indies and along the north and east coasts of South America where birds stopped over for 2–24 d during southward and northward migrations. Birds arrived at (Northern Hemisphere) wintering areas from Guyana/Suriname on the north coast of South America to eastern Brazil between 3 October and 2 November. They left wintering areas from 7–23 April and arrived back at the breeding area from 5–30 May. Although this study is based on data for only six birds, it identifies several stopover and wintering areas that should receive priority for future studies and potential conservation measures. Geolocators did not impair Roseate Terns' ability to raise young in the year the devices were attached, but lower than expected rates of return suggest that the geolocators reduced survival, and most of the birds that returned had lost body-mass and did not breed in the year of return.

Front cover photograph. Roseate Terns *Sterna dougallii*, São Gonçalo do Amarante, Ceará, Brazil, 11 September 2013. © *Ciro Albano*. This location is within the stopover area marked K on Figure 1 in the paper by Mostello *et al.* (page 6). The bird in the foreground displays the Definitive Prebasic Molt of the flight feathers, with p1–p4 (primaries numbered from the centre of the wing outwards) new, p5 missing, p6 growing, p7–p8 moderately old and p9–p10 very old. Terns have a unique pattern of moult of the flight feathers in which successive waves of moult overlap, so that the wings may have three or even four generations of feathers simultaneously. This bird was in an unusually advanced stage of moult for the date and was in area K much earlier in autumn than any of the breeding birds tracked with geolocators, so it probably had not bred in 2013 and may have been only three or even two years old (based on comments by Peter Pyle).

Introduction

The western North Atlantic population of the Roseate Tern *Sterna dougallii* breeds on nearshore islands from Québec and Nova Scotia (Canada) to New York (USA). This population declined from a peak of approximately 4,400 pairs in 2000 to 3,200 pairs in 2012–13, close to its size when it was first listed as endangered in the USA in 1987 (U.S. Fish and Wildlife Service 2010; Nisbet 2014). Although this species is intensively managed and studied at North American nesting colonies, it is poorly known outside the breeding season, when most mortality probably occurs (Nisbet 2014).

Prior knowledge of Roseate Terns was summarised by Cramp (1985), Gochfeld *et al.* (1998) and Ratcliffe *et al.* (2004). Birds from all parts of the western North Atlantic range stage around Cape Cod (41–42°N 70–72°W) in July–August before migrating south in September (Trull *et al.* 1999; Jedrey *et al.* 2010). Prior to this study, most information about migration routes, stopover locations and areas used in the (Northern Hemisphere) winter was derived from ringing recoveries (Nisbet 1984; Hays *et al.* 1997; see Discussion); one roost site in eastern Brazil has been described (Hays *et al.* 1999) and five others have been named but not described (Lima *et al.* 2005; De Luca *et al.* 2006). Subsequent to this study, Roseate Terns have been photographed at three additional locations in northern Brazil, and photographs have been posted on the web site www.wikiaves.com (see Front Cover photo).

Here, we report a study of the movements of North American Roseate Terns using geolocators. We use tracking data for six individuals to identify their dates and routes of migration, and to identify stopover and wintering areas that could be used as locations for future studies and potential conservation actions.

Methods

Fieldwork was conducted at Bird Island, Massachusetts, USA (41°40'N 70°43'W). In 2007 and 2009, we attached geolocators (MK14 and MK10, respectively, British Antarctic Survey) to Darvic leg flags (see Nisbet *et al.* 2011a for a parallel study of Common Terns *Sterna hirundo*), and placed them on ten Roseate Terns in each year. We selected birds of average or above-average body-mass for the species (mean \pm SD, 120.2 \pm 7.9 g, range = 112–147 g, vs local means of 113.1 \pm 6.5 g for females and 115.0 \pm 6.9 g for males; Palestis *et al.* 2012). Laying dates of the study birds ranged from 25 May to 7 June 2007 and 17 May to 4 June 2009, spanning the median dates (28 May 2007 and 22 May 2009) for the colony determined from regular nest checks at the time of laying. Birds were caught in treadle traps set over marked nests late in incubation; they were weighed and measured, fitted with geolocators and released within 15 min of capture.

The total mass of the assemblies (flag, geocator and adhesive) averaged 1.8 g in 2007 (1.2–1.5% of the birds' body-masses at the time of attachment) and 1.3 g (0.9–1.2% of body-mass) in 2009. In both years, we trapped each bird again 2–9 d after attaching the device, weighed it, and checked the legs for signs of injury. In 2007, we observed the birds from a hide for 1–2 h on most days for 3–6 d after attachment to look for possible adverse effects. We used the body-mass of the

second chick on day 2 of life as a predictor of its survival to fledging, and the body-masses of both chicks on day 2 as measures of the performance of each pair in feeding chicks (for details, see Nisbet *et al.* 1998, 1999). Each geocator bird was matched to a nearby control with the same clutch-size and laying date (± 4 d); control birds were studied and handled in the same way.

From 14 May to 4 July 2008 and 11 May to 12 June 2010, we searched for returning birds, intensively in areas where they had nested in the previous year and sporadically in other parts of the island and other nearby breeding colonies. Returning birds were trapped and weighed, a few μL of blood were collected for genetic sexing as described in Nisbet *et al.* (2007), and the geocator assemblies were removed.

Stored data were downloaded and decoded using British Antarctic Survey programmes BASTrak, TransEdit and BirdTracker. Geolocators had been calibrated prior to deployment for 8 d in May–June 2007 and 25–28 d in May–June 2009 at a nearby location with unobstructed views to the horizon, and were recalibrated after retrieval based on data collected during 8–12 d early in the post-breeding period while they were on the birds at the breeding site. We selected sun elevation angles to centre positions calculated for the calibration periods on the true location; in four cases where the two calibrations differed, the on-bird recalibration was used. Selected sun elevation angles ranged from -3.5° to -4.1° . Light-intensity curves were screened visually to exclude erroneous transitions due to shading by day or illumination at night.

Estimated latitudes and longitudes were mapped using BirdTracker and ArcGIS 10 (ESRI 1999–2010). For the four geolocators recalibrated in 2009, the root-mean-square (r.m.s.) deviation of the fixes from the true location in clear weather was 1.13° in latitude (113 km) and 0.74° in longitude (59 km). When weather was overcast or raining at sunrise and/or sunset (as recorded by us and/or www.wunderground.com), fixes were displaced south by up to 5.2° in latitude (520 km), and west or east by up to 1.3° in longitude (105 km). For longitude, fixes during the remainder of the year are expected to have similar precision and accuracy. Because latitudinal errors become progressively greater closer to the equinoxes and to the Equator (Ekstrom 2004), we excluded all latitude estimates within 11 d of equinoxes (although longitude estimates within these periods were reliable and were used), and relied mainly on longitude estimates to infer locations at low latitudes (10°N – 10°S) and within 12–21 d of equinoxes. We excluded 31/3,706 (0.8%) outliers (sequential records separated by > 300 km during winter, or $> 1,000$ km during migration) that we attributed to weather, shading or illumination events.

Each geocator also included an immersion sensor that detected when the device was in contact with salt water and logged contact data at 10 min intervals; immersion data are referred to briefly here but will be reported more fully elsewhere.

Location data (latitude and longitude estimates, filtered as described above) were initially analysed using Kernel Density Analysis (KDA; Worton 1995), implemented in the R package *adehabitatHR* (Calenge 2006). Data were divided prior to analysis into

either stages (breeding, southward migration, wintering, northward migration) or (for increased resolution) a series of 21-d windows initially centred on the autumn equinox and then extrapolated forward and backward to encompass the entire temporal data record except for the equinox periods. The *ad hoc* method (Worton 1989) was used to estimate appropriate spatial smoothing parameters. A temporal bivariate smoothing parameter of 60 d was used in the second analysis (in preference to estimation using Least Square Cross Validation [LSCV] usually recommended for data that may be multimodal; Worton 1989), for two reasons: (i) our data subsets were insufficiently large for computation of LSCV, (ii) data subsetting reduced the chances that multiple locations were used during the time period encompassed by the data.

After identifying important stopover and wintering regions using KDA, we examined daily longitude and latitude estimates for each bird within each region. Immersion data indicated that five of the six birds spent part or all of each night onshore and the sixth bird spent some nights onshore (based on lack of recorded contact with salt water for periods of ≥ 5 h), allowing inferences about locations from longitude data alone when geolocator estimates of latitude were uncertain.

We split the annual cycle for each bird into six stages (modified from Nisbet *et al.* 2011a): *breeding*, the period in May–July when the geolocators recorded many shading events by day while the bird was attending eggs or chicks under cover; *post-breeding*, the interval in July–September between the end of the breeding stage and departure on migration; *migration*, intervals in August–October and April–May when estimated longitudes changed by $> 1^\circ$ per day for ≥ 3 successive days, often with consistent changes in latitude; *stopovers*, intervals between bouts of migration when estimated longitudes remained constant ($\pm 1^\circ$); *wintering*, the period from the last migration in October or November until the first migration in April; *pre-breeding*, the interval from the end of the spring migration until the first shading events.

Results

Adverse effects: In the year of attachment, birds with geolocators lost body-mass at higher rates than controls, although the difference was only marginally statistically significant ($2.4 \text{ g/d} \pm 0.6 \text{ SD}$ vs $1.0 \text{ g/d} \pm 0.8 \text{ SD}$, respectively; paired Wilcoxon signed-rank test, $n = 5$, $P = 0.08$). Day 2 masses of A-chicks (geolocator: $24.5 \text{ g} \pm 3.7 \text{ SD}$, $n = 10$; control: $25.3 \text{ g} \pm 2.5 \text{ SD}$, $n = 10$) and B-chicks (geolocator: $17.6 \text{ g} \pm 4.5 \text{ SD}$, $n = 8$; control: $16.9 \text{ g} \pm 3.9 \text{ SD}$, $n = 8$) did not differ between these two groups (paired *t*-tests: A-chicks, $P = 0.47$; B-chicks, $P = 0.75$).

Geolocator birds weighed significantly less in the year of return than in the year of attachment ($107.9 \text{ g} \pm 6.9 \text{ SD}$ vs $119.6 \text{ g} \pm 6.7 \text{ SD}$; paired Wilcoxon signed-rank test, $n = 7$, $P = 0.028$) and significantly less than other Roseate Terns weighed at the same stage in the breeding cycle in the same years ($116.0 \text{ g} \pm 7.0 \text{ SD}$, $n = 280$, in 2008; $112.9 \text{ g} \pm 5.1 \text{ SD}$, $n = 80$, in 2010; Mann-Whitney test, $P < 0.01$ in each year).

We located only nine geolocator birds that returned to the breeding area, vs 16–17 expected based on population survival rates (Spendelov *et al.* 2008). There was no

significant difference in return rates for birds carrying 1.0 g geolocators in 2009 and 1.5 g units in 2007 (5/10 and 4/10 returned, respectively: Fisher Exact test, $P = 1.0$). Eight birds returned to Bird Island (one has been seen for four years at post-breeding staging sites, but has not been located at a breeding site), but one of these was seen for only a few days in May 2008. We trapped the remaining seven birds and retrieved six geolocators with useful data (two in 2008 and four in 2010, from three females and three males: Table 1). Although seven of the nine birds that returned had bred successfully in the year of attachment, only three bred at all in the year of return: two males in 2010 and a female in 2008 that paired with another female. Female-female pairs comprise about 11% of all nesting pairs at this site, but usually have much lower breeding success than female-male pairs (Nisbet & Hatch 1999), so this bird's change from having a male mate in 2007 to a female mate in 2008 represented a reduction in fitness. The other returnees spent several weeks in the nesting area courting with unmated birds and were trapped at display sites. The two males returned to the breeding site at normal dates (5 and 8 May), whereas the three non-breeders for which we have data returned at unusually late dates (15, 15 and 30 May). Two of the birds that did not breed spent 5–7 d at sea in the North Atlantic Ocean during 8–14 May after the breeders had migrated directly to the breeding area; we suspect that the behaviour of the non-breeders was abnormal. Because of this unexpected behaviour in the year of return, other aspects of the spring migration of the non-breeders may have been abnormal. However, migrations otherwise followed expected routes at appropriate dates, based on prior knowledge (Nisbet 1984, 2014; see Discussion), and were generally similar to those of Common Terns in the parallel study (Nisbet *et al.* 2011a; see Discussion), so Roseate Terns were probably affected only late in their spring migrations.

In contrast to the reduced performance of the geocator birds in the years of return relative to the years of attachment, routine monitoring of the Roseate Tern colony at Bird Island yielded no evidence of similar changes in the performance of other birds. Breeding numbers, median laying dates, mean clutch-sizes and breeding productivity were similar in all four years (authors' unpublished data). Hence, although strict comparison with controls is not possible, we attribute the reduced performance in the years of return to adverse effects of the geolocators.

Tracking results: KDA of the full tracking dataset revealed five major regions utilised by Roseate Terns (details not shown). However, KDA did not yield fine resolution within those regions and the precision of latitude estimates was low for most of the year because of proximity to the Equator (see Methods). Accordingly, we analysed longitude and latitude data separately within each of the major regions and were able to identify 11 discrete areas used for stopovers and/or wintering (Figure 1: areas A and C–L). Within each of these areas, longitude estimates for each bird varied within narrow limits, with r.m.s. deviations usually in the range 0.3° – 1.1° (30–100 km) and in no case $> 1.3^{\circ}$ (Tables 2–7). These are comparable with r.m.s. deviations of longitudes in the recalibration periods when birds are known to have been stationary (see Methods). Hence the birds were more or less stationary (at least in longitude) during most of the stopover and winter periods. In all cases latitude

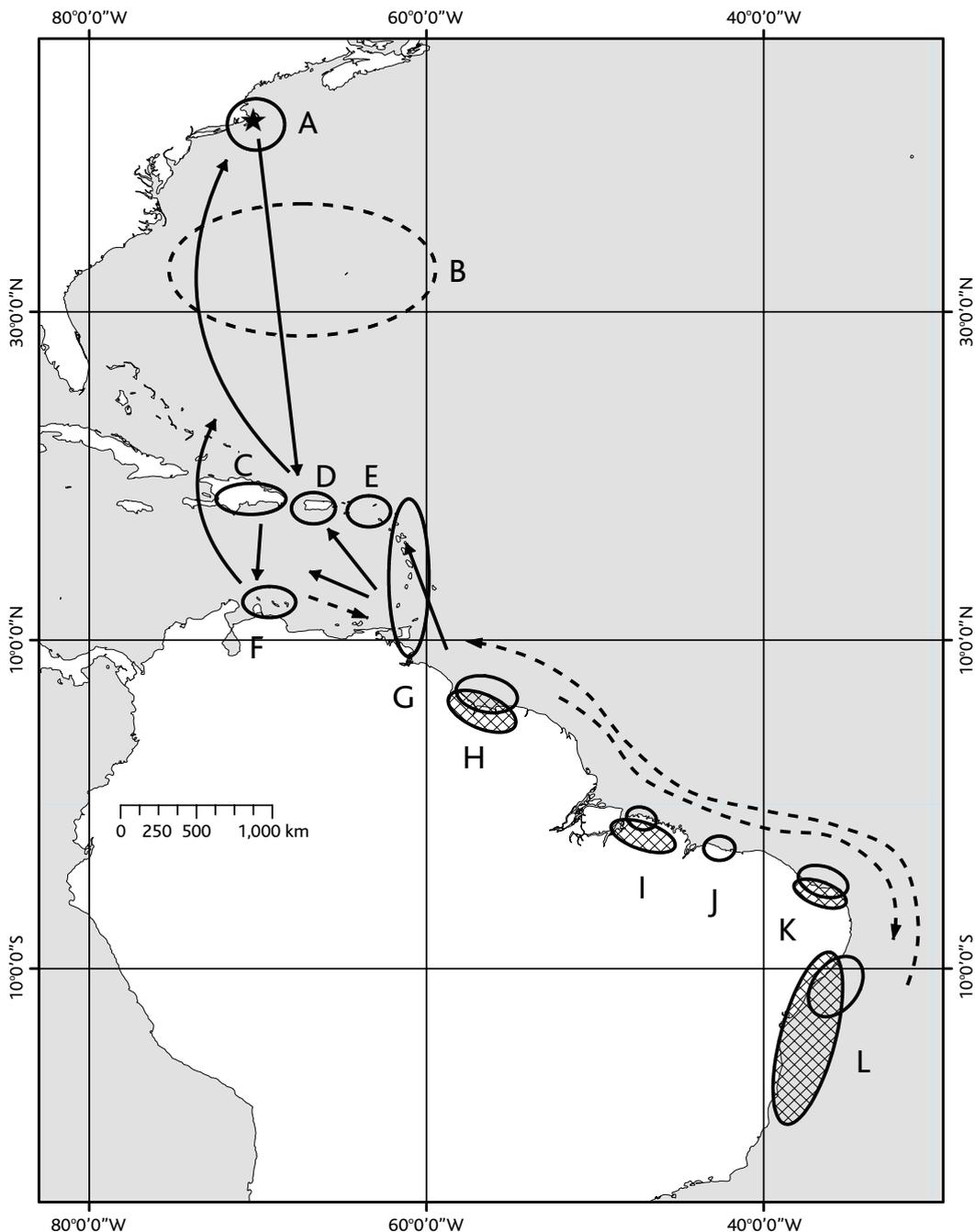


Figure 1. Winter quarters, migration routes and stopover sites of six Roseate Terns *Sterna dougallii* breeding at Bird Island, Massachusetts. Star: breeding site. Hatched areas: wintering areas. Open areas: stopover sites. Letter codes are keyed to location information and dates in Table 1. Continuous arrows: migration routes. Dashed arrows: approximate migration routes derived from longitude information only (latitudes are uncertain, so actual tracks may have been closer to shore). The outline of area B is dashed because the birds' behaviour may have been abnormal (see Results: adverse effects).

estimates were much more variable than longitude estimates (Tables 2–7), with the largest r.m.s. deviations in latitudes for dates within 12–21 d of the equinoxes. However, in many cases latitude estimates were sufficiently precise to resolve ambiguities in locations inferred from longitudes, e.g. in distinguishing between stopovers in the northeastern and southeastern Caribbean (Tables 3–4; Figure 1).

Post-breeding: Although dates of departure from the breeding site could not be determined, five of the Roseate Terns carrying geolocators were present in the post-breeding area from early or mid July until late August or early September (Table 2); the exception was one bird that re-nested and remained in the nesting area until mid August (Table 1). Although several birds showed significant changes

Table 1. Breeding dates, migration dates, stopover and wintering areas of six North American Roseate Terns *Sterna dougallii* tracked with geolocators. Capital letters refer to areas marked on Figure 1. For dates and locations within stopover areas, see Tables 2–7.

	Bird 6114 (♂)	Bird 6120 (♀)	Bird 7654 (♂) ^a	Bird 7659 (♂) ^a	Bird 7660 (♀) ^b	Bird 7877 (♀)
First chick hatched	18 Jun	24 Jun	20 Jun	26 Jul ^c	unknown ^d	22 Jun
Chick fledged (approx.)	11 Jul	17 Jul	13 Jul	— ^c	unknown ^d	15 Jul
Post-breeding ^e	27 Jun–31 Aug	1 Jul–28 Aug	26 Jun–16 Sep	2 Aug–14 Sep	13 Jul–31 Aug	3 Jul–5 Sep
Started autumn migration	31 Aug	28 Aug	uncertain	14 Sep	31 Aug	5 Sep
Autumn stopover areas	D, H, I, J	C, D, H, I, J	C, E, H	D, G, H, I	D, H, I, J	C, F
Reached South America	14 Sep	8–10 Sep	9 Oct	24 Sep–2 Oct	≤ 16 Sep	9 Sep
Reached winter quarters	25 Oct	30 Oct	19 Oct	2 Nov	3 Oct	24 Oct
Wintering areas	L → K	L → K	I	L	L	H
Days in winter quarters	159	Unknown ^f	186	161	172	179
Left winter quarters	7 Apr	Unknown ^f	20 Apr	13 Apr	20 Apr	23 Apr
Spring stopover areas	I, C, B	Unknown ^f	I, D	I	I, D	F, B
Returned to breeding site	30 May	Unknown ^f	5 May	8 May	15 May	15 May

^a Bred in the year the geolocator was retrieved.

^b Bred in a female-female pair in the year the geolocator was retrieved.

^c First nest failed; the bird re-nested and probably failed to raise a chick in the second nesting.

^d First nest failed; continued shading events to 12 July may indicate either prolonged incubation of infertile eggs or re-nesting.

^e Includes time spent tending the chicks at the colony before dispersing to the staging site.

^f Record incomplete; the geolocator failed on 13 March.

Table 2. Use by Roseate Terns *Sterna dougallii* of the major post-breeding area around Cape Cod, USA (see Figure 1: area A).

Bird	Staging period (d)	Latitude: mean ± SD (range) ^a	Longitude: mean ± SD (range) ^a
6114 (♂)	17 Jul–30 Aug (45)	39.7°N ± 2.1° (38.5°–40.9°)	70.8°W ± 0.9° (70.7°–71.0°)
6120 (♀)	20 Jul–28 Aug (40)	39.1°N ± 2.6° (36.9°–41.7°)**	71.4°W ± 1.1° (70.5°–71.8°)*
7654 (♂)	30 Jun–6 Sep (69)	40.7°N ± 2.2° (39.6°–42.2°)**	70.7°W ± 1.2° (70.0°–72.3°)**
7659 (♂)	15 Aug–13 Sep (30)	41.2°N ± 2.8° (40.2°–41.9°)**	70.5°W ± 0.8° (70.1°–70.8°)
7660 (♀)	13 Jul–28 Aug (47)	40.4°N ± 2.1° (39.6°–41.1°)	70.3°W ± 0.9° (70.0°–70.6°)
7877 (♀)	3 Jul–5 Sep (65)	39.2°N ± 2.5° (38.4°–40.1°)*	70.6°W ± 1.1° (70.1°–71.1°)

^a Range of means for 9–11 d periods. * indicates significant difference (ANOVA, $P < 0.05$); ** indicates $P < 0.01$.

in latitude and/or longitude within this period (Table 2), all birds appear to have remained within a small area around Cape Cod and the islands to the south, Martha's Vineyard and Nantucket (41–42°N 70–72°W). Mean latitude estimates were further south (39–41°N; Table 2), probably because cloudy weather causes displacement errors towards lower latitudes in summer (see Methods).

Southward migration and stopovers: See Figures 1–2. Excluding one bird with an uncertain migration date, the birds started southward (autumn) migration from the post-breeding area at various times between 28 August and 14 September. They completed trans-oceanic crossings of ~2,300 km in 1.5–2.5 d (900–1,500 km/d), arriving in the northeastern Caribbean in the vicinity of Puerto Rico and the Dominican Republic from 30 August to 17 September. After remaining in stable locations for 7–13 d (Areas C–E; Table 3), five birds moved south and east, stopping over at 1–5 additional locations in the Lesser Antilles and along the north and east coasts of South America for periods of 2–24 d. All five birds made prolonged stopovers in Suriname/Guyana and northern Brazil (Areas H–I; Tables 5–6); one remained in northern Brazil for the winter while the others continued to winter quarters in eastern Brazil (Area L; Table 7). Other stopover areas (G, J and K) were used by only 1–3 birds and for only 2–10 d (Table 1). One bird (7877) differed from all the others by stopping over for 32 d in the southeastern Caribbean (Area F; Table 4) and continuing without intermediate stopovers to winter in Suriname/Guyana (Area H; Table 5). Arrival dates in the winter quarters ranged from 3 October to 2 November, 33–63 d after departure from the post-breeding area (mean 50.2 d ± 9.9 SD). The mean travel speed, including stopovers, was 143 km/d ± 47 SD (range 96–230 km/d); the mean speed between stopovers was 290 km/d (mean 2.5° longitude per day ± 0.9 SD, n = 19).

Table 3. Use by Roseate Terns *Sterna dougallii* of a major stopover area in the northeastern Caribbean (see Figure 1: areas C, D, E). Estimated locations include the Virgin Islands (64–65°W), Puerto Rico (65–67°W) and the Dominican Republic (68–72°W).

Bird	Stopover period (d)	Latitude: mean ± SD (range) ^a	Longitude: mean ± SD (range) ^a
6114 (♂)	1–13 Sep (13)	20.6°N ± 2.3 ^{ob}	66.2°W ± 0.6° (66.1°–66.3°)
	16–26 May (11)	19.0°N ± 1.2° (18.3°–19.6°)	71.0°W ± 0.8° (70.9°–71.1°)
6120 (♀)	31 Aug–6 Sep (7)	17.6°N ± 1.7° (17.1°–18.1°)	65.5°W ± 0.7° (65.2°–65.8°)
	7654 (♂)	19–26 Sep (8)	n/a
	27 Sep–7 Oct (11)	20.0°N ± 5.9 ^{ob}	69.8°W ± 0.8° (69.7°–69.9°)
7659 (♂)	25 Apr–2 May (8)	19.5°N ± 1.9° (18.9°–20.0°)	64.4°W ± 0.6° (64.3°–64.5°)
	7660 (♀)	17–23 Sep (7)	n/a
7660 (♀)	2–10 Sep (9)	18.0°N ± 7.2 ^{ob}	65.8°W ± 0.8° (65.2°–66.3°)** west
	30 Apr–9 May (10)	17.0°N ± 0.7° (16.7°–17.2°)	66.8°W ± 0.6° (66.7°–66.8°)
			66.6°W ± 0.7° (66.1°–67.0°)** east
			66.4°W ± 0.4° (66.4°–66.5°)

^a Means for first and second half of stopover period in each case. ** indicates significant difference (ANOVA, P < 0.01); east, west indicate direction of movement.

^b Fixes between 10 September and 2 October are excluded from the calculation. n/a, too close to the equinox for valid estimates of latitude.

Table 4. Use by one Roseate Tern *Sterna dougallii* of a major stopover area in the southeastern Caribbean (see Figure 1: area F; Figure 2F). Estimated locations include Aruba and the adjacent coast of Venezuela.

Bird	Stopover period (d)	Latitude: mean \pm SD (range) ^a	Longitude: mean \pm SD (range) ^a
7877 (♀)	9 Sep–20 Oct (32)	11.1°N \pm 2.9° (11.0°–11.2°) ^a	70.0°W \pm 0.7° (69.5°–70.3°)** west
	26 Apr–4 May (9)	8.8°N \pm 2.6° (9.0°–9.5°) ^b	70.0°W \pm 0.4° (69.8°–70.1°)

^a Range of means for three 10–11 d periods.

^b Means for first and second half of stopover period.

** indicates significant difference (ANOVA, $P < 0.01$); west indicates direction of movement.

Table 5. Use by Roseate Terns *Sterna dougallii* of a major stopover and wintering area in Suriname/Guyana (see Figure 1: area H). Most records were within a narrow range of longitudes (55.6–56.9°W), corresponding to 130 km of coast in northwest Suriname, but extending to northeast Guyana (57–58°W).

Bird	Stopover period (d)	Longitude: mean \pm SD (range) ^a
6114 (♂)	16–23 Sep (8)	57.6°W \pm 1.0° (56.9°–58.0°)
6120 (♀)	9–14 Sep (6)	56.9°W \pm 0.5° (56.6°–57.3°)* east
7654 (♂)	9–16 Sep (8)	56.8°W \pm 1.1° (56.1°–57.5°)** east
7659 (♂)	4–14 Oct (11)	56.2°W \pm 0.5° (55.9°–56.6°)** east
7660 (♀)	14–18 Sep (5)	55.6°W \pm 0.7° (55.2°–56.2°)* east
7877 (♀)	25 Oct–22 Apr (179)	56.3°W \pm 1.0° (56.1°–57.7°)***

^a Means for first and second half of stopover period in each case, except range of means for 18 ten-day periods for bird 7877.

Significant differences (ANOVA): *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; east, west indicate direction of movement. For bird 7877, mean longitude was 56.1° \pm 0.9°W except during 30 January to 15 February, when it was 57.8° \pm 0.5°W.

This area was too close to the equator for valid estimates of latitude.

Table 6. Use by Roseate Terns *Sterna dougallii* of a major stopover and wintering area in northern Brazil (see Figure 1: areas I, J). Almost all records were from a 200 km stretch of coast (46–48°W) in the states of Pará and Maranhão.

Bird	Stopover period (d)	Longitude: mean \pm SD (range) ^a
6114 (♂)	27 Sep–10 Oct (14)	46.9°W \pm 0.3° (46.8°–47.0°)
	12–30 Apr (19)	46.8°W \pm 0.9° (46.5°–47.1°)
6120 (♀)	17 Sep–10 Oct (24)	47.4°W \pm 0.4° (47.2°–47.6°)** west
7654 (♂)	19 Oct–29 Dec (72)	46.7°W \pm 0.5° (46.2°–46.7°)**
	4 Jan–19 Apr (109)	46.7°W \pm 0.9° (46.1°–47.2°)**
7659 (♂)	17–22 Oct (6)	47.1°W \pm 0.2° (47.0°–47.3°)* east
	23–30 Apr (8)	47.8°W \pm 0.6° (47.5°–48.0°)
7660 (♀)	21–27 Sep (7)	47.0°W \pm 0.7° (46.4°–47.6°)*** west
	23–25 Apr (3)	47.1°W \pm 0.6°

^a Range of means for first and second half of stopover period in each case, except range of means for 18 ten-day periods for bird 7654.

Significant differences (ANOVA): *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; east, west indicate direction of movement. Bird 7654 moved east about 300 km to longitude 43.8°W for the period 30 December to 3 January, then returned to exactly the same area it had used prior to 30 December for the rest of the winter. This area was too close to the equator for valid estimates of latitude.

Table 7. Use by Roseate Terns *Sterna dougallii* of a major wintering area in eastern Brazil (see Figure 1: areas K, L). Most records fall into two groups: around 37°W in the state of Sergipe and around 39°W in the state of Bahia. Exact locations are uncertain because the coast in this region runs NNE/SSW, but latitude estimates range along 900 km of coast (10–19°S). Bird 6120 moved to the north coast of Brazil in the state of Rio Grande do Norte late in the winter and bird 6114 probably did so, but latitude estimates were very imprecise close to the Equator and the equinox.

Bird	Stopover period (d)	Latitude: mean \pm SD (range) ^a	Longitude: mean \pm SD (range) ^a
6114 (♂)	26 Oct–12 Feb (110)	11.0°S \pm 1.9° (10.2°–12.3°)**	37.8°W \pm 1.1° (36.9°–38.5°)**
	16 Feb–1 Apr (46)	3.9°S \pm 5.2° ^c	36.1°W \pm 0.8° (36.0°–36.2°)
6120 (♀)	30 Oct–27 Feb (121)	11.9°S \pm 2.5° (11.2°–12.3°)	38.7°W \pm 0.7° (37.6°–38.9°)
	2–13 Mar ^b (12+)	4.2°S \pm 2.8° ^c	36.7°W \pm 0.6°
7659 (♂)	3 Nov–12 Apr (161)	16.7°S \pm 2.6° (15.1°–17.8°)**	38.8° \pm 0.6° (38.6°–38.9°)
7660 (♀)	4–29 Oct (26)	8.5°S \pm 4.8°	36.9°W \pm 0.5°
	30 Oct–19 Apr (172)	18.1°S \pm 2.4° (17.5°–18.6°)	39.2°W \pm 0.7° (38.9°–39.4°)

^a Range of means for periods of 23–32 d. ** indicates significant differences among monthly means (ANOVA, $P < 0.01$).

^b The geolocator stopped collecting data on 13 March, so the winter period is incomplete.

^c Records from 2–9 March only.

Wintering: One bird spent the (Northern Hemisphere) winter within a 130 km stretch of coast in Suriname/Guyana (Area H; Figure 2F; Table 5) and another within a 200 km stretch of coast in northern Brazil (Area I; Figure 2C; Table 6). The other four birds wintered primarily on the east coast of Brazil along a 900 km stretch of coast (Area L; Table 7), but precise locations are uncertain because this section of the coast runs approximately NNE/SSW. One bird spent the entire winter, and another the early part of the winter, in Alagoas and Sergipe (around 37.0°W, corresponding to 10°–12°S). Three birds spent most of the winter further south in Bahia or northern Espírito Santo (38.7°–39.2°W, corresponding to 12°–19°S), with a southern limit of about 20°S (Table 7). Periods spent in winter quarters varied from 159–186 d (Table 1).

Although all birds remained more or less stationary for long periods (see above), they all changed locations one or more times during the winter. Bird 7660 moved south to a new location within area L in October, and bird 7659 moved north and south several times within Area L (Table 7). Birds 6114 and 6120 moved from the east coast of Brazil (Area L) to the north coast in February (Area K; Table 7). Bird 7654 made a 5-d excursion about 300 km to the east at the end of December and then returned (Table 6, footnote). Bird 7877 moved about 180 km west to waters off northeast Guyana for 15 d in December–January (Table 5, footnote). During that

Figure 2 a–f (opposite). Migrations and winter quarters of Roseate Terns *Sterna dougallii*: A, 6114; B, 6120; C, 7654; D, 7659; E, 7660; F, 7877. Wintering and stopover areas are marked as ellipses centred on the mean locations shown in Tables 2–7, with horizontal axes equal to 1 SD in longitude; vertical axes are equal to 1 SD in latitude for areas at higher latitudes than 10°N or 10°S, but are set at an arbitrary value of 2.5° for areas at lower latitudes because geolocator estimates of latitude are uncertain near the equator. Migration routes are uncertain between 10°N or 10°S for the same reason; dashed arrows and dashed ellipses indicate movements and stopovers close to the equinox when latitudes could not be estimated.

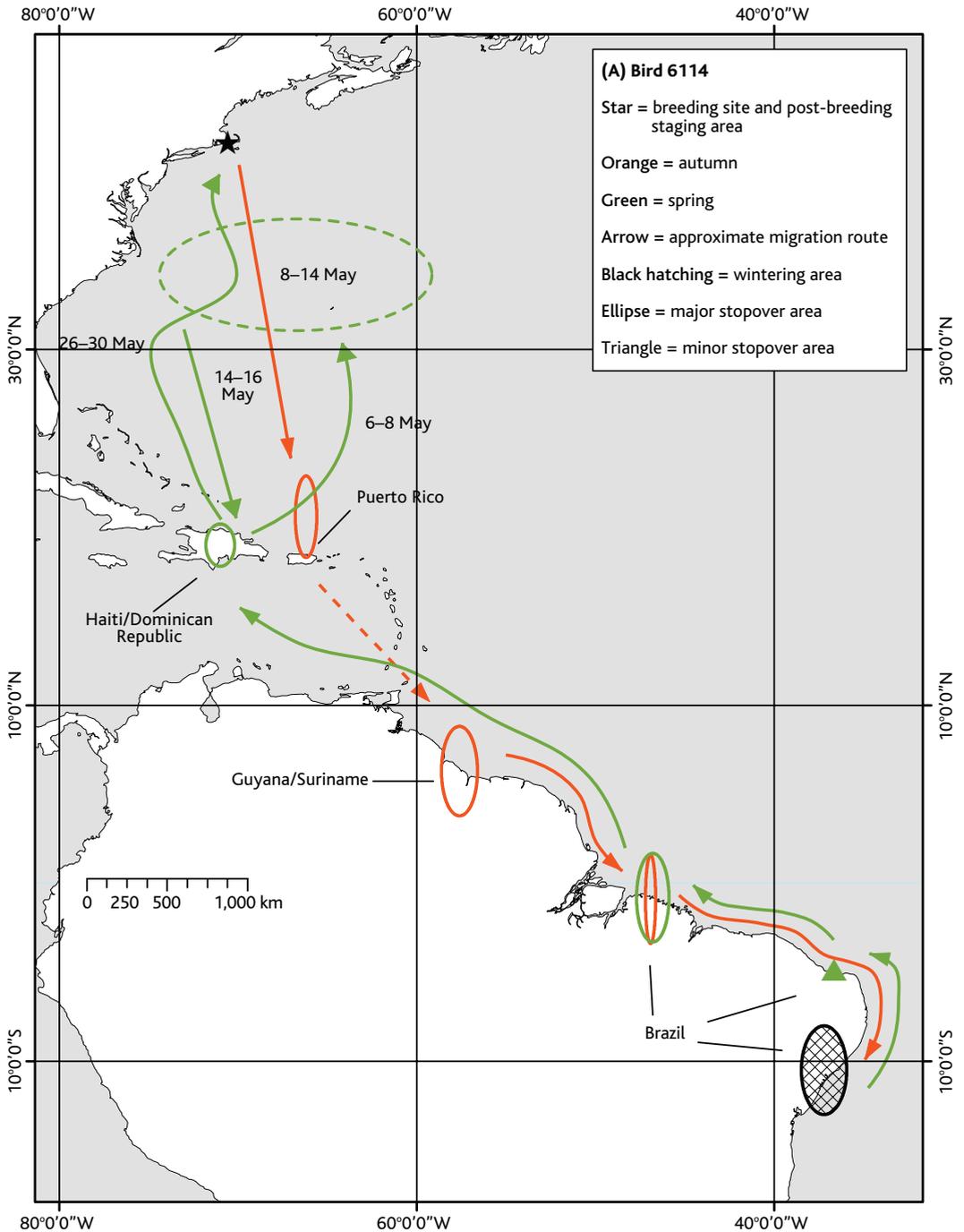


Figure 2a.

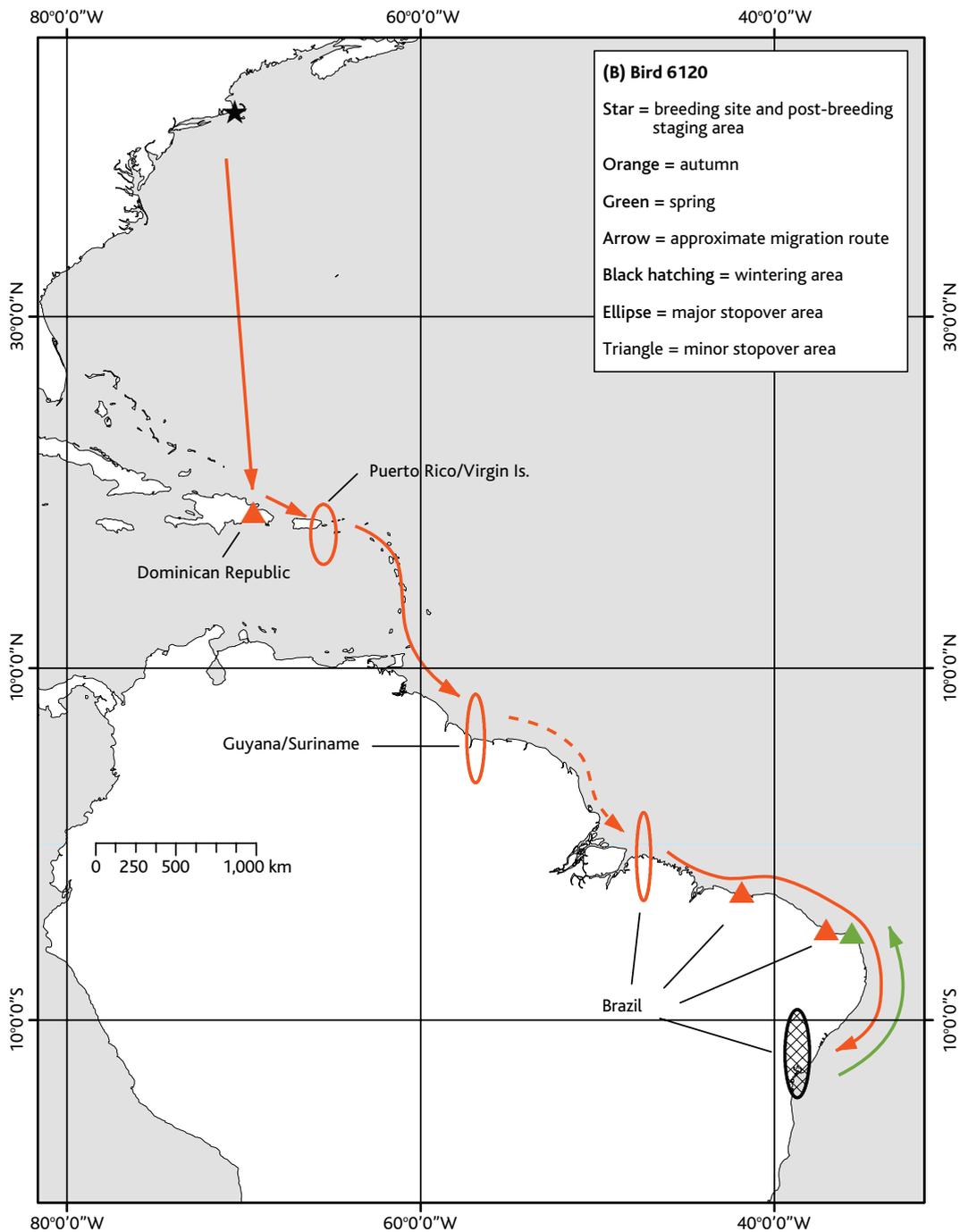


Figure 2b.

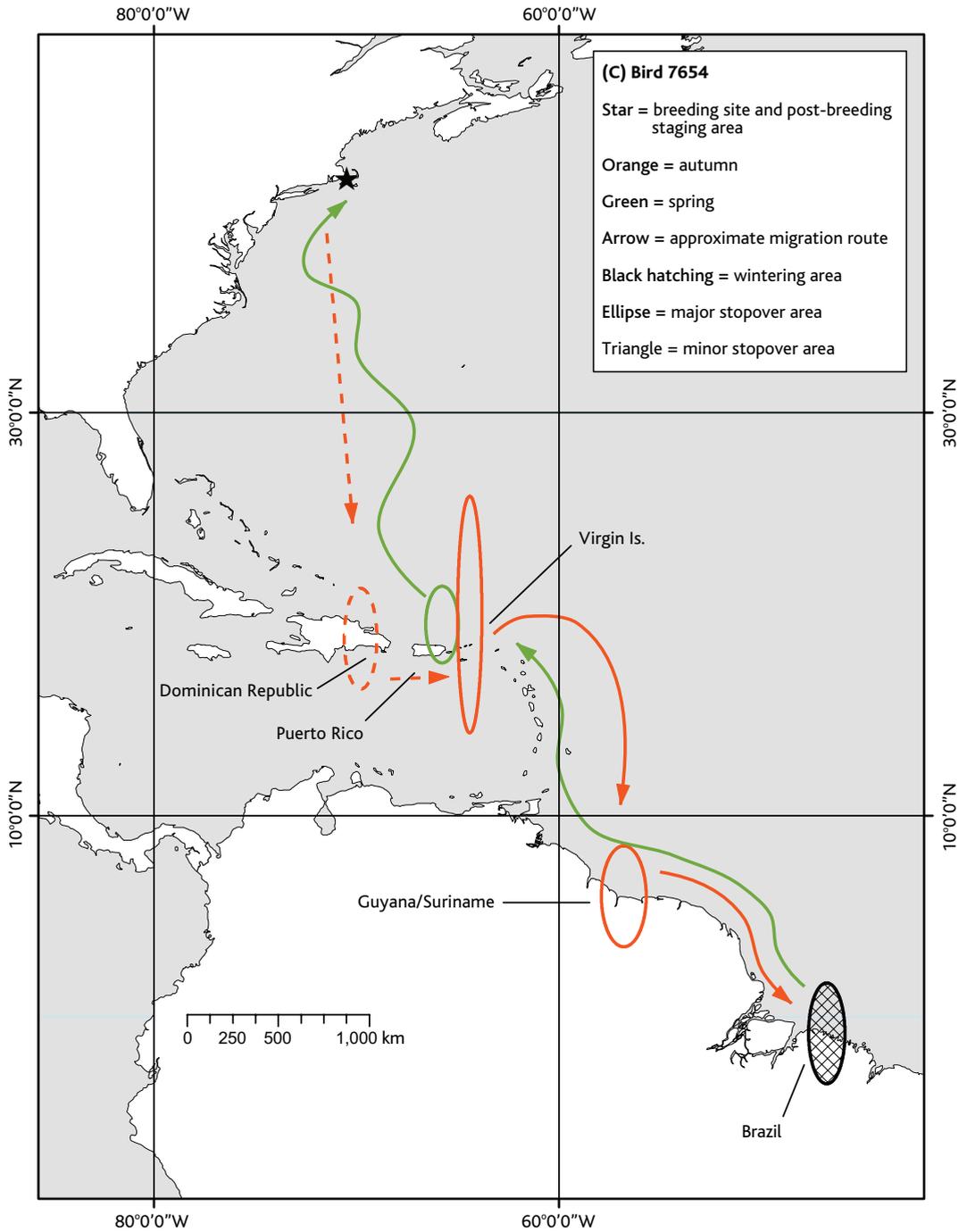


Figure 2c.

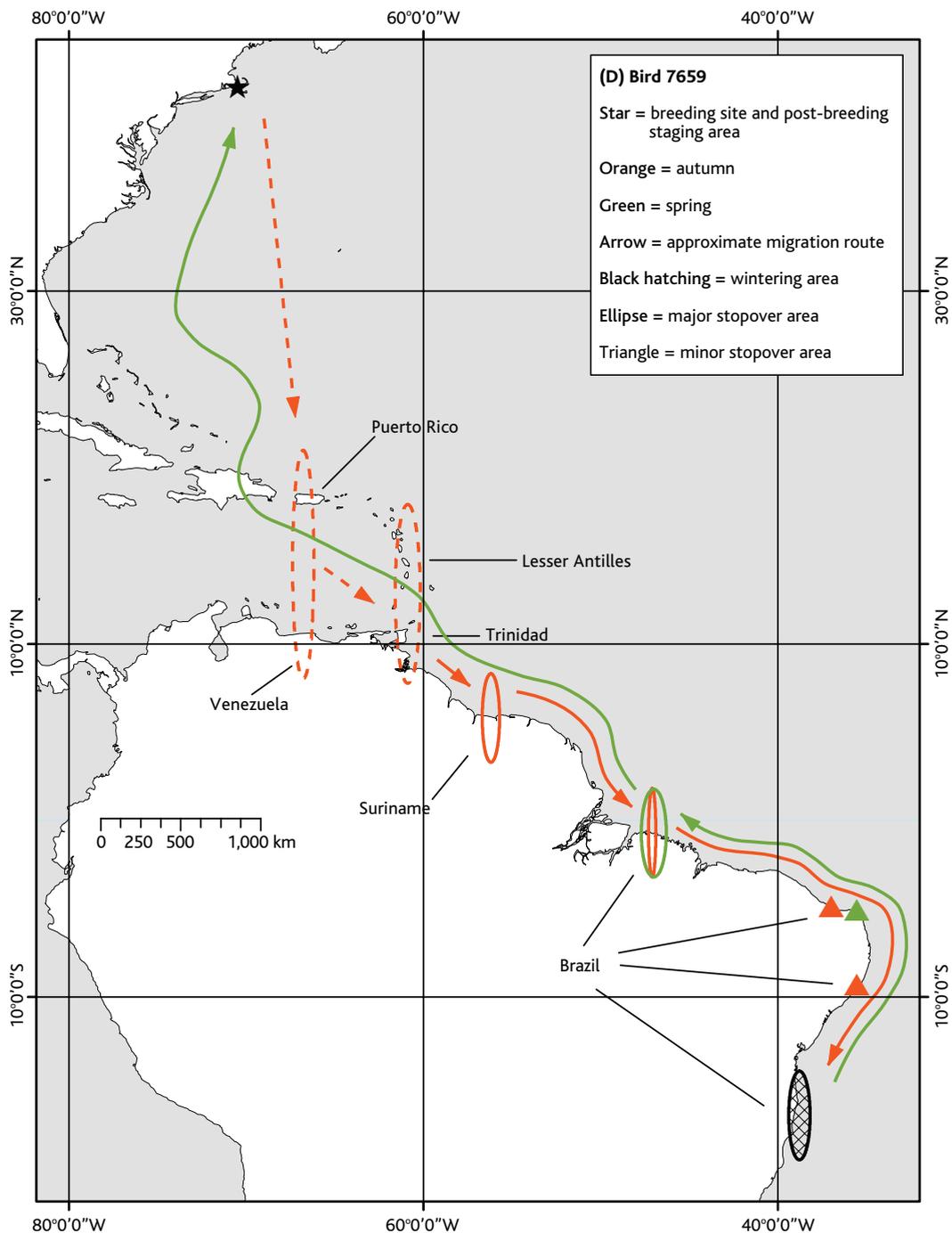


Figure 2d.

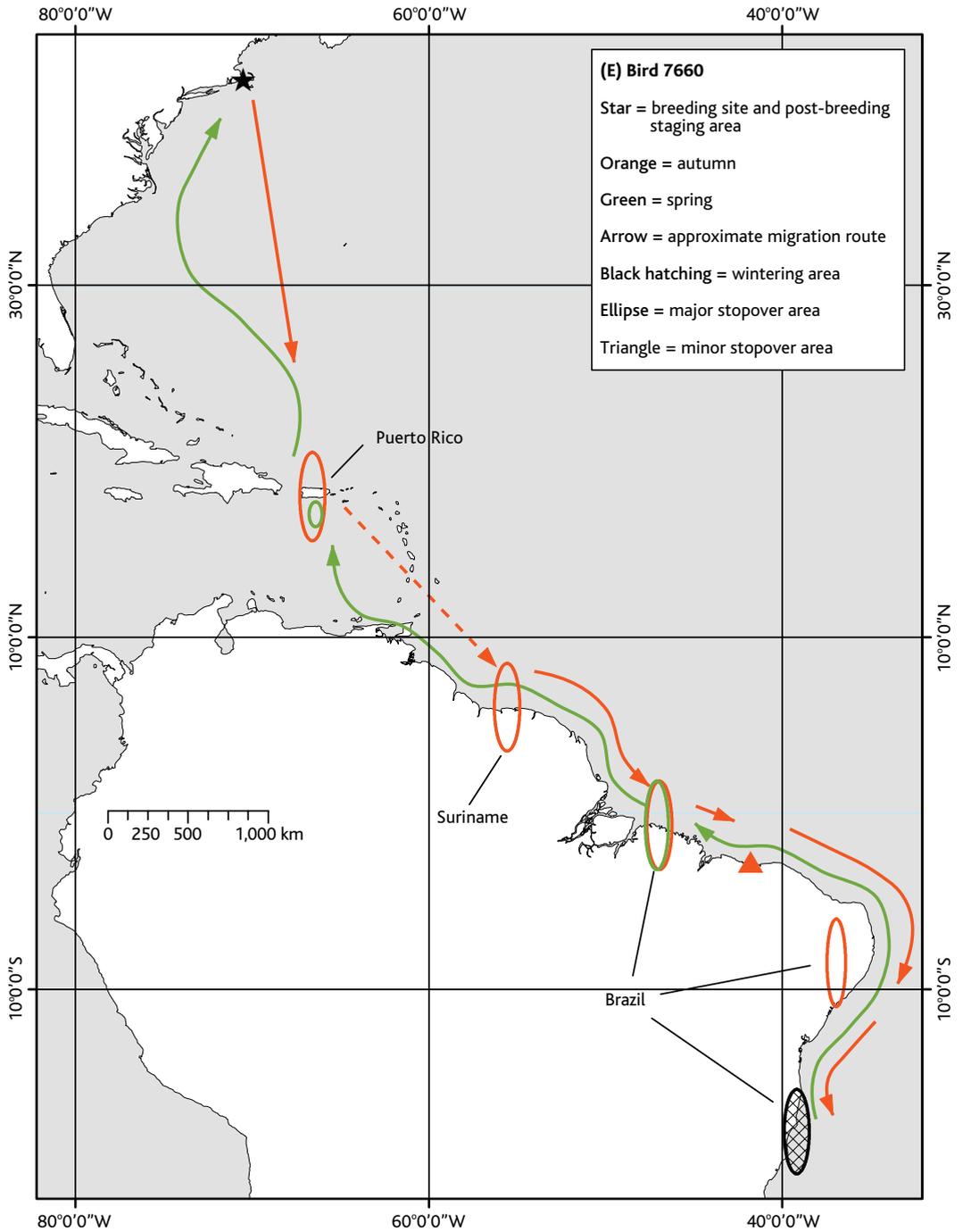


Figure 2e.

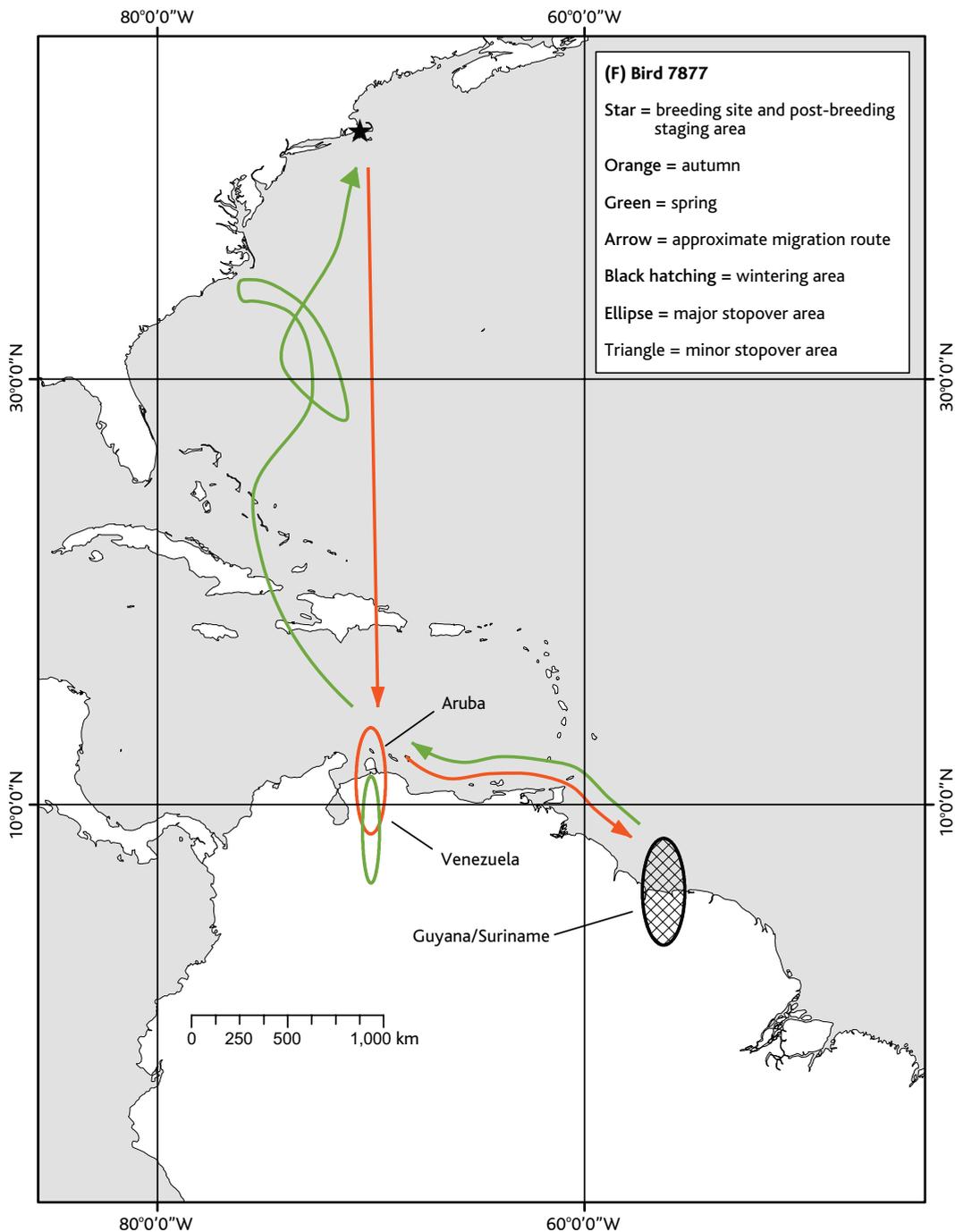


Figure 2f.

period the immersion sensor indicated that it spent less time resting on the sea at night than earlier or later, and the light sensor recorded many illumination events at night, suggesting that it was then attending fishing boats with bright lights.

Northward migration and staging: See Figures 1–2. The five birds for which we obtained data for the northward (spring) migration left their wintering areas between 7 and 23 April. All birds stopped at fewer locations than they had during autumn migration, and spring migration was completed more quickly ($28.0 \text{ d} \pm 14.6 \text{ SD}$, range 15–53). Mean travel speed (from leaving the wintering site to arriving in the breeding area) was $270 \text{ km/d} (\pm 100 \text{ SD}, \text{ range } 136\text{--}400)$. Along the north coast of South America, estimated travel speeds between stopovers were also much higher in spring (mean $4.7^\circ \text{ longitude/d} \pm 0.7 \text{ SD}$, about 540 km/d , $n = 7$) than in autumn (ANOVA, $F_{1,24} = 24.5$, $P < 0.001$). The four birds that wintered in eastern Brazil flew round the northeast corner of Brazil (35°W) on both migrations and did not cross overland.

The main stopover areas in spring were northern Brazil (area I; 3 birds; Table 6) and the northeastern Caribbean (areas C and E; 3 birds; Table 3). Spring migration paths between the West Indies and the breeding area fell to the west of the autumn migration paths for four of five birds for which both spring and autumn migration data were retrieved. However, none of these birds appeared to have flown on a straight path, as they did in autumn (Figures 2A and 2D–F). Two birds meandered for 5–7 days in mid-May in expanses of ocean bounded by $28\text{--}34^\circ\text{N } 71\text{--}75^\circ\text{W}$ and $31\text{--}36^\circ\text{N } 59\text{--}73^\circ\text{W}$ (area B on Figure 1; Figures 2A and 2F). One then moved north to the breeding area (Figure 2F), while the other moved back to the northeastern Caribbean, where it spent 11 more days before travelling to the breeding area (Figure 2A).

Pre-breeding: Estimated locations in the pre-breeding stage were in the same range as during the post-breeding stage.

Discussion

Limitations of geolocator data: Previous information on migrations of western North Atlantic Roseate Terns was derived largely from ringing recoveries (Nisbet 1984). In that study, > 95% of recoveries were east of 75°W : in the West Indies from Hispaniola to Trinidad, and along the north and east coasts of South America from Venezuela to Brazil. Our findings conform to that general picture, but add much new information, especially on the timing of migrations and the locations of stopover and wintering areas. However, our data (like those of many other geolocator studies) have two major limitations. First, we have data for only six birds, severely limiting the statistical analyses that could be conducted and precluding any inferences about the population as a whole. Even within our sample of six birds, there was considerable variability in migratory behaviour (Table 1, Figure 2), so it is very unlikely that we recorded the full range of locations used by the population. Second, geolocator fixes have low precision, especially for estimates of latitude close to the Equator, where our birds spent much of the year. Hence, for example, we could track the birds' movements along the north coast of South America in spring and autumn on a

precise day-to-day basis, but we do not know how far offshore they may have travelled (dashed arrows on Figure 1). Although we could derive fairly precise estimates of mean longitude during periods when the birds were stationary (Tables 2–7), estimates of latitude were much more uncertain (ellipses on Figure 2).

Stopover areas: After leaving the breeding area and staging around Cape Cod, all of our six birds migrated directly to the northeastern Caribbean between Hispaniola and the Virgin Islands (areas C–E on Figure 1), where they stopped over for varying lengths of time; most of our birds stopped over in the same area in spring. Hence these areas appear to be important for this vulnerable population, particularly during autumn migration. We identified seven other stopover areas in the Caribbean and on the South American coast; three of the latter were also used in winter (Figure 1). Although our findings were based on data for only six birds, areas A, C–E, H and I were used by most or all of the Roseate Terns that passed through them and hence can probably be designated as significant staging areas.

Comparison with Common Terns: Our findings for Roseate Terns are generally similar to those for Common Terns in a parallel study (Nisbet *et al.* 2011a, b, and unpublished data), but show some noteworthy differences. Common Terns wintered over a larger area than Roseate Terns, from NW Venezuela (11°N 70°W) to NE Argentina (37°S 57°W), extending along > 8,000 km of coastline vs < 4,000 km for Roseates. Like Roseate Terns, Common Terns staged around Cape Cod (Area A on Figure 1) in July–August, and then migrated directly across the western North Atlantic Ocean to the West Indies, but they started these crossings over a longer period, from 1 August to 5 October (Nisbet *et al.* 2011b). The stopover areas C, D, F, H, I and K used by Roseate Terns (Figure 1) were also used by Common Terns, although none of them was used by more than half the Common Terns we studied. In spring, Common Terns returned more rapidly than Roseates. Unlike Roseate Terns, some Common Terns suffered substantial adverse effects in the year the geolocators were attached, but a higher proportion returned (13/20 vs 9/20) and all the Common Terns that returned bred successfully (13/13 vs 2/9).

Wintering areas: The wintering locations of Roseate Terns in our study extended along the north and east coasts of South America from 6°N 57°W to approximately 20°S 40°W, slightly extending the southernmost sight record (18°S; Hays *et al.* 1997; a moribund bird was recently recovered at 21°S; Castro Tavares *et al.* 2013). The wintering areas in Guyana/Suriname and Pará/Maranhão, Brazil, are located within the highly productive North Brazil Shelf Large Marine Ecosystem (LME; Heileman 2009–2013a), which receives significant inputs of nutrients from the Amazon River. The thermal and salinity fronts resulting from the outflows of the Amazon and Orinoco rivers are important areas of biodiversity that may be attractive to terns because of localised high food availability. The wintering areas in northeastern and eastern Brazil are located within the moderately productive East Brazil Shelf LME (Heileman 2009–2013b), a generally oligotrophic region except for localised areas of upwelling. Highest biomass and plankton densities are found in eastern Brazil along the southern continental shelf and in the Abrolhos Bank region

(15°–22°S; Susini-Ribeiro 1999; Susini-Ribeiro *et al.* 2013). These latitudes overlap with a portion of the main wintering area of the Roseate Terns in this study (10°–19°S; area L on Figure 1) and suggest that prey from the Abrolhos Bank, which extends to 220 km offshore, may be important for wintering Roseate Terns.

Implications for conservation: Hitherto, the lack of information on the distribution, ecology and causes of mortality of Roseate Terns in non-breeding areas has made it difficult or impossible to devise conservation measures. This study has identified five staging and wintering areas (A, C–E, H, I and L on Figure 1) that were used by most or all of our small group of Roseate Terns. We suggest that these areas should now have high priority for focused field investigations. Area A is heavily used for human recreation and a study of the effects of human disturbance is under way (Jedrey *et al.* 2010; J. Spindelw & K. Parsons pers. comm.). On the north and east coasts of South America, environmental threats include severe over-exploitation of fisheries; coastal and offshore oil and gas exploration, exploitation, and shipping; pollution from development, industry, agriculture and maritime transport; destruction of mangroves; degradation of coral reefs; and coastal development for human recreation and building of vacation homes (De Luca *et al.* 2006; Chatwin 2007; Heileman 2009–2013a, b; S. Hecker pers. comm.). However, any causal relationships between these potential threats and actual effects on waterbirds, including Roseate Terns, are unknown and need further study.

Adverse effects: The effects of geolocators on Roseate Terns that we identified demonstrate the necessity of proceeding at a small scale with new studies that require attachment of devices to birds, and monitoring them intensively after attachment for adverse effects. Although the geolocators that we used weighed \leq 1.5% of the Roseate Terns' body-mass, the unexpectedly low return rate (45%) of study birds, delayed return, substantial loss of body-mass and failure of most returnees to obtain mates of the opposite sex indicate that the geolocators compromised both survival and the fitness of the birds that did survive. However, the effects were not permanent, because at least two of the birds that did not obtain mates in the year of return are known to have obtained mates and bred in subsequent years after removal of the geolocators (J. Spindelw and authors' unpublished data). We recommend that geolocators should not be used again on Roseate Terns until (i) devices that are much lighter and/or have less drag become available; (ii) there is high confidence that returning birds can be located and trapped, even if they do not breed; and (iii) a small pilot study has been conducted to test for adverse effects of the smaller devices. More generally, we recommend that researchers should consider carefully the conservation value of the data potentially to be gained when scaling and implementing new studies involving the attachment of devices to birds, particularly those on vulnerable species (see Bridge *et al.* 2013). Despite substantial adverse effects and the probable loss of several individuals, our study yielded much new information that should be useful in designing new field studies directed towards future conservation measures.

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