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Satellite-tracking of female loggerhead turtles highlights fidelity behavior in northeastern Brazil

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ABSTRACT: We studied inter- and postnesting movements in the major loggerhead *Caretta caretta* nesting population in Brazil. Ten breeding females were satellite-tracked from nesting grounds in the state of Bahia, northeastern Brazil, for up to 1284 d. Eight females stayed in the nesting area after deployment, showing fidelity between internesting home ranges and nesting locations, even at a local scale. During postnesting movements, all of the turtles migrated to the northern coast of Brazil to individual foraging areas on the continental shelf. Distances between nesting and foraging areas reached up to 2400 km, and migration lasted from 28 to 47 d. Five females were tracked during subsequent breeding migrations to the nesting area at different remigration intervals of 2 or 3 yr. Females were also tracked during a second postnesting migration back to foraging areas, and these showed strong fidelity to foraging grounds. Movements to and from foraging grounds occurred along the shelf, clearly delineating a migratory corridor. The northern coast of Brazil, specifically the coast of the state of Ceará, is an important foraging ground for loggerheads nesting along the northern coast of Bahia.

KEY WORDS: Satellite-tracking · Caretta caretta · Internesting · Postnesting · Migration · Brazil

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INTRODUCTION

Loggerhead *Caretta caretta* migrations from nesting to feeding areas are known from early tag-recapture studies (Bustard & Limpus 1971, Meylan 1982). More recently, satellite telemetry and the integrated use of GPS have revealed new possibilities of studying important aspects of habitat use by sea turtles (Godley et al. 2008).

The first satellite telemetry studies focused on postnesting loggerheads (Stoneburner 1982, Timko & Kolz 1982). Since then, the increase in the use of this tool has been continuous, with the development of new equipment and deployment procedures (Godley et al. 2008). Several behavioral aspects have been revealed, for different populations and in diverse developmental stages (e.g. Polovina et al. 2004).

Information on internesting movements can be derived from tag-recapture studies (Tucker et al. 1996, Limpus & Limpus 2001), direct observation (Limpus & Reed 1985), sonic and radio telemetry (Hopkins & Murphy 1981, Hopkins-Murphy et al. 2003) and satellite telemetry (Stoneburner 1982, Godley et al. 2003a,b, Zbinden et al. 2007, Tucker 2009, 2010). Long-term tag-recapture (Limpus & Limpus 2003) and satellite telemetry studies (Hawkes et al. 2007, Girard et al. 2009) have delineated foraging areas. Loggerhead fidelity to foraging grounds is inferred from early tag-recapture studies (Hughes 1982, Limpus et al. 1992); however, the main limitations of this methodology include tag loss and biases in the likelihood of recapture and reporting. Although flipper tags enable the tracking of individuals over long periods, no information is available regarding the intervening route and habitat preferences (Godley et al. 2008). In contrast, satellite telemetry studies provide significant information regarding each study individual, yet few telemetry studies are available to corroborate previous findings.

The northern coast of the state of Bahia comprises the main loggerhead nesting area in Brazil (Marcovaldi & Marcovaldi 1999, Marcovaldi & Chaloupka 2007). Over 28 yr of tag-recapture data have delineated the reproductive biology and provided important information on inter- and postnesting movements (Marcovaldi & Laurent 1996, Marcovaldi et al. 2000). However, habitat use during internesting, the location of foraging areas and the migratory behavior between nesting and foraging grounds remain unknown. Delimitation of high-use areas is extremely important to understand important aspects of loggerheads' foraging ecology and to mitigate potential anthropogenic impacts (Zbinden et al. 2007, Hays 2008). The present study aimed to evaluate inter- and postnesting movements on the major loggerhead nesting colony in Brazil.

MATERIALS AND METHODS

The nesting ground on the northern coast of the state of Bahia, northeastern Brazil (around 13°S, Fig. 1), comprises the main loggerhead nesting site in Latin America (Marcovaldi & Chaloupka 2007). The Brazilian National Sea Turtle Conservation and Research Program–Projeto TAMAR/ICMBio maintains 4 field stations in Bahia that protect a 215 km coast, divided into 1 km sectors (Fig. 1). See Marcovaldi & Laurent (1996) and Marcovaldi & Marcovaldi (1999) for details on the study area.

Ten loggerhead females were equipped with satellite transmitters (KiwiSat 101, Sirtrack) from January 25 to March 5, 2006, during the second half of the nesting season. Transmitters were attached using a 2-part epoxy resin (Tubolit MEP-301) and covered with a layer of antifouling paint. The units were powered by 2 D-size lithium batteries (0.5 W output), and were duty cycled to work 24 h on, during the first 30 d, and 24 h on/48 h off thereafter. Transmissions were processed via ARGOS location system (http://argosinc. com) for location information, surface temperature at the time of transmission, battery voltage and number and duration of transmissions.

Five satellite transmitters were deployed on Busca Vida and Jauá beaches (Kilometers 21 to 27), and 5 on Praia do Forte and Imbassaí beaches (Kilometers 69 to 77) (Fig. 1, Table 1).

Each turtle was measured with flexible plastic tape over the curve carapace length (CCL) and tagged with inconel tags on each front flipper (National Band and Tag Co.). Other data, such as date, time, location and tissue samples, were collected according to TAMAR's standardized protocols (Marcovaldi & Marcovaldi 1999).

Location data provided by ARGOS were analyzed using the Satellite Tracking and Analysis Tool (STAT; Coyne & Godley 2005) program from seaturtle.org. The most accurate positions (Location Classes [LC] 3, 2, 1 and A; see Hays et al. 2001) were used to reconstruct routes and calculate distances. LC Z, B and 0 and speeds >5 km h^{-1} were excluded from analysis.

Geographic information systems software (ArcGis 9.1, ESRI) was used to map turtle movements and calculate high-use areas and movement pathways.

Postnesting migrations were considered completed when movement was no longer directed for at least 3



Fig. 1. Caretta caretta. Location of the nesting area in northeastern Brazil

| Turtle | Length (CCL; cm) | Deployment location | Deployment date in 2006 (dd/mm) | Days tracked | Min. distance traveled (km) |
|--------|---------------------|------------------------|---------------------------------------|-----------------|--------------------------------|
| L1 | 107 | Busca Vida | 25/01 | 593 | 7129 |
| L2 | 99 | Busca Vida | 27/01 | 897 | 6902 |
| L3 | 102 | Praia do Forte | 31/01 | 1284 | 13911 |
| L4 | 100 | Praia do Forte | 03/02 | 1250 | 17681 |
| L5 | 101.5 | Jauá | 14/02 | 426 | 5132 |
| L6 | 100 | Busca Vida | 15/02 | 565 | 5442 |
| L7 | 103 | Imbassaí | 18/02 | 1109 | 12430 |
| L8 | 101 | Praia do Forte | 21/02 | 1249 | 7539 |
| L9 | 101.5 | Busca Vida | 21/02 | 504 | 7127 |
| L10 | 101 | Praia do Forte | 05/03 | 826 | 8680 |

Table 1. *Caretta caretta*. Deployment information, tracking period and minimum distance traveled for each tracked loggerhead. CCL: curved carapace length

consecutive days (Zbinden et al. 2008). Foraging areas were identified as those areas where turtles showed restricted movements (multidirectional and back-tracked over previous tracks) following postnesting migrations, which continued until the transmitters stopped sending information or until turtles engaged new return migrations (Troeng et al. 2005). To define important habitats for each turtle, we calculated fixed kernel home ranges using Hawth's analysis tools for ArcGIS (Beyer 2004). Using kernel home-range estimates (KHRE) 50% utilization distributions (UD), we delineated individual and joined core habitatuse areas; h factor was 0.05, calculated following Silverman (1986).

RESULTS

Internesting movements

Turtles were tracked for 426 to 1284 d (mean: 870 d; Table 1). Location data showed that 2 turtles left the nesting beaches immediately after deployment, while 8 stayed for 12 to 66 d (mean: 33.6 d) and displayed subsequent internesting behavior prior to departure. Maximum distance between successive nesting events of a single female varied from 1 to 41 km (mean: 8.8 km; Table 2).

Excluding the 2 turtles that departed immediately, emergences inferred from Argos location data suggest that 1 female nested 5 times, 2 nested 4 times, 2 nested 3 times and 3 nested twice, including nesting on the deployment date (Table 2).

Maximum perpendicular distance from the coastline during internesting movements varied from 12.1 to 26.4 km (mean: 19.6 km); individual-at-sea areas ranged from 36 to 1392 km² (mean: 559 km²) (Table 2). Turtles mostly remained over the continental shelf,

with 72% of location signals received in waters <50 m deep (Fig. 2).

KHREs of 50 and 25% UD for all turtles showed 2 separated internesting areas (<50 km apart), located in waters adjacent to the 2 main nesting aggregations, Busca Vida and Praia do Forte (Fig. 3). During the internesting period, turtles concentrated their movements in waters adjacent to the main nesting beaches where they were originally tagged, except for a single female that moved among the 2 areas.

Five females were tracked from foraging areas for a subsequent season after 2 (L7, L8, L10) and 3 (L3, L4) nesting years. Return migrations from

foraging grounds began in October or early November, lasting from 27 to 66 d (Table 3).

Turtles returned to the breeding ground where they were originally tagged (i.e. Praia do Forte). Kernelestimated home ranges partially overlapped in all cases (Fig. 4). Turtle L4 moved among the 2 areas (i.e. Praia do Forte and Busca Vida beaches) in both nesting seasons and showed fragmented kernel-estimated use of internesting habitat (Fig. 4). Turtle L10 departed from the nesting beach right after tag deployment, so no information is available for comparison of internesting movements during the first season.

Remigrant turtles remained in the nesting grounds for between 83 and 105 d (Table 3), while the same 4 turtles tracked during the first nesting season stayed in the area from 12 to 44 d after deployment.

Postnesting movements

Females migrated for a mean of 27 d (range: 0 to 66 d) to foraging grounds located on the northern coast of Brazil. Eight females remained on the coast of the state of Ceará, one in the state of Maranhão and one was situated in the state of Pará (Fig. 5). Movements between nesting and foraging grounds occurred along the coast, mainly in waters between 25 and 50 m depth (Figs. 2 & 5), with sporadic and short excursions to deeper waters. Three females started migrations by moving into deeper waters for 5 to 7 d, but returned to the shelf later. The minimum travel distances between nesting and foraging areas varied from 1309 to 2439 km (mean: 1695 km), and the mean migration period was 37 d (range: 28 to 47 d), at a mean travel rate of 45.8 km d^{-1} (or 1.9 km h^{-1}).

Postnesting migrations of the 5 remigrant turtles lasted from 30 to 39 d. All of the females returned to the same foraging ground off the coast of Ceará.

| Turtle | Record date in 2006 (dd/mm) | Record location (coastal km) | Distance from previous landing (km) | Time interval between consecutive records (d) | Maximum interval (km; d) | Internesting area (km²) | Maximum distance from coast (km) |
|--------|-------------------------------------------|------------------------------------|-------------------------------------------|-----------------------------------------------------|--------------------------------|----------------------------|----------------------------------------|
| L1 | 25/01 08/02 | 24 23 | _ 1 | _ 15 | (1; 15) | 36 | 12.1 |
| L2 | 27/01 | 21 | _ | _ | _ | _ | _ |
| L3 | 31/01 14/02 | 71 77 | - 6 | _ 14 | (6; 14) | 386 | 17.2 |
| L4 | 03/02 17/02 03/03 18/03 | 71 72 31 70 | - 1 41 39 | - 14 14 15 | (39; 43) | 1392 | 21.7 |
| L5 | 14/02 02/03 20/03 21/04 | 27 22 21 28 | - 5 1 7 | - 16 18 32 | (7; 66) | 609 | 21.6 |
| L6 | 15/02 01/03 15/03 | 21 24 33 | - 3 9 | - 14 14 | (13; 28) | 718 | 18.1 |
| L7 | 18/02 02/03 17/03 | 77 71 72 | - 6 1 | - 12 15 | (5; 27) | 632 | 16.2 |
| L8 | 21/02 05/03 | 69 68 | - 1 | - 12 | (1; 12) | 306 | 26.4 |
| L9 | 22/02 10/03 27/03 10/04 26/04 | 24 21 12 27 31 | - 3 9 15 4 | - 16 17 14 16 | (19; 63) | 390 | 23.5 |
| L10 | 05/03 | 69 | _ | _ | _ | _ | _ |

 Table 2. Caretta caretta. Nesting activity information recorded for the loggerheads tagged at the nesting site in the state of Bahia.

 Maximum interval: maximum distance and time period between first and last records. -: no data

Foraging area movements

All 10 females were tracked to a foraging ground. Five ceased transmissions before leaving these forag-



Fig. 2. *Caretta caretta*. Proportion of locations (n = 3654) in relation to bathymetry of the 10 loggerheads tracked from Bahia, during the different phases of the migratory cycle

ing areas after periods lasting from 313 to 860 d (mean: 524 d). The 5 remaining turtles left the foraging area for a second nesting season after intervals ranging from 534 to 932 d (mean: 700 d).

KHRE 50 % UD ranged from 545 to 1501 km² (mean: 889 km²; Table 3) and showed that all individual core foraging areas were usually located in waters between 25 and 50 m deep (Figs. 2 & 6). Sea bed substrate was medium-coarse sand and gravel (Dias et al. 2004).

Turtles that returned to foraging areas after a second nesting season showed core foraging areas that overlapped with previous ones, with the exception of turtle L10, which limited its movements to <15 km north of the previous areas (Fig. 6). There was no significant relationship between remigration interval and body size.



Fig. 3. Caretta caretta. Internesting movements and kernel-estimated homerange utilization distributions (KHRE) of 8 loggerheads satellite-tracked from nesting grounds in Bahia, Brazil

DISCUSSION

Tracking durations are among the longest reported for satellite-tracked loggerhead studies to date (see Table 4). This indeed allowed us to reveal individual foraging areas and track several turtles through an entire remigration interval for the first time.

Loggerhead females typically remain within the vicinity of the nesting beach during the internesting period (Stoneburner 1982, Sakamoto et al. 1990, Hays et al. 2001, Godley et al. 2003a, 2008), with alongshore instead of offshore movements (Tucker et al. 1996, Hopkins-Murphy et al. 2003). Turtles tracked in the present study showed similar movements; furthermore, except for 1 single female (L4), which moved between the 2 tagging sites, turtles from different beaches did not exchange sites, as evidenced by kernel distribution analysis, remaining very close to the deployment area. Interestingly, turtles that returned for a second nesting season, 2 or 3 yr after the first, occupied similar-sized home range areas which partially overlapped with those of the first season.

Unfortunately, little information is available in the literature quantifying the size of internesting habitats (Table 4). Stoneburner (1982) reported that tracked females entered estuarine waters behind nesting areas following nesting and left these areas after 1 to 3 d, but did not provide information on the entire size of the area used.

Turtles tracked for consecutive breeding seasons (L3, L4, L7 and L8) showed a strong fidelity to nesting

grounds, considering the overall scale of migrations from and to foraging areas. However, some factors must be taken into account for comparisons of internesting habitat use in successive breeding seasons. First of all, the transmission duty cycle was different in the 2 tracked nesting seasons; thus, fewer locations were available in the second one. Furthermore, for 2 turtles (L3 and L8), the large intervals between satellite locations prevented the determination of arrival date at the nesting sites.

Migrations to foraging areas start immediately after the last clutch has been laid (Stoneburner 1982, Tucker et al. 1996, Griffin 2002, Plotkin & Spotila 2002), and are typically nearshore (Papi et al. 1997, Luschi et al. 2006, Hawkes et al. 2007), even if a shorter deep-sea pathway is available (Blumenthal et al. 2006). There are, however, reports of adult loggerheads foraging in oceanic environments (e.g. Hatase et al. 2002,

Hawkes et al. 2006). Papi et al. (1997) reported that 1 of 4 tracked loggerheads stopped at a resting area during postnesting migration along the western Indian coast, before heading to the foraging area. Lemke et al. (2003) also reported that 1 turtle tracked settled on a sea mount offshore in the southwestern Atlantic. With the exception of one of the females that made a short excursion off the shelf, all the turtles tracked in our study migrated nearshore, directly towards their foraging areas.

Foraging grounds are generally located 100s (Godley et al. 2003a) or 1000s (Limpus et al. 1992, Papi et al. 1997) of kilometers away from nesting beaches. Limpus et al. (1992) reported mean migration distances of 564 to 1028 km, based on tag-recapture data. Limpus & Limpus (2001) reported migrations of >1600 km between nesting and foraging grounds. Our results fit this long-distance pattern (range: 1309 to 2439 km). Our study also documented swimming speeds similar to those noted in previous studies of loggerheads migrating to neritic foraging areas (Zbinden et al. 2008).

In the northwestern Atlantic, turtles from the same nesting population showed different migration patterns, which could be related to different settlement locations after the oceanic developmental period (Hawkes et al. 2007).

Two subpopulations of Brazilian loggerheads exist throughout the region, the southern stock nesting at Rio de Janeiro and Espirito Santo and the northern stock nesting at Bahia and Sergipe (Reis et al. 2009). While the southern stock turtles dispersed both north niv

| ground location Ceará Ceará | 6 | Migration for. grounds (d) (d) 28 37 29 40 47 47 47 36 36 42 36 36 33 42 33 34 33 | $ \begin{array}{ ccccccccccccccccccccccccccccccccccc$ | Residency (d) 550 ^a 860 ^{a,b} 932 906 ^e 313 ^a 500 ^a 534 559 3399 ^a 576 | Area (km ²) 50% KHRE 545 1501 1237 734 | Distance from coast (range in km) 15.4–42.2 23.6–64.5 | Migration to nest. grounds (d) (| Arrival nest. area (dd/mm/yy) | period (d) | Departure nest. area (dd/mm/vv) | Migration for. grounds (d) | Residency (d) (| y Area Dist (km ²) 50% from | Dictor |
|--------------------------------------|--------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------|----------------------------------------------------------------------|-------------------------------------------------------------------|---------------------------------------------------------|-------------------------------------|---------------------------------------------------------------|---------------------------------------|----------------------------------------------------------------|--------------------|--------------------------------------------|---------------------------|
| Ceará Ceará Ceará | 1595 1525 1499 | 237 237 36 36 37 37 38 36 39 42 34 34 34 34 34 34 34 34 34 34 34 34 34 | 09/03/06 05/03/06 17/03/06 09/05/06 07/06/06 16/03/06 13/04/06 07/06/06 07/06/06 08/04/06 08/04/06 08/04/06 | 550 ^a 860 ^{a,b} 932 906 ^c 534 559 313 ^a 576 576 | 545 1501 1237 734 | 15.4–42.2 23.6–64.5 | | | | 177 | | | KHRE | from coast (range; km) |
| Ceará Ceará | 1525 1499 | 37 37 36 36 36 36 36 36 36 37 37 37 37 37 37 37 37 37 37 37 37 37 | 05/03/06 17/03/06 09/05/06 07/06/06 16/03/06 13/04/06 07/06/06 08/04/06 08/04/06 08/04/06 08/04/06 08/04/06 13/04/06 08/04/06 08/04/06 08/04/06 08/04/06 | 860 ^{a.b} 932 906° 513ª 559 334 559 399 ^a 576 | 1501 1237 734 | 23.6-64.5 | | | | | | | | |
| Ceará | 1499 | 29 40 42 36 34 36 34 | 17/03/06 09/05/06 07/06/06 16/03/06 29/04/06 13/04/06 07/06/06 08/04/06 08/04/06 08/04/06 13/04/06 08/04/06 13/04/06 08/04/06 13/04/06 08/04/06 1 /05/06 1 /06 1 /07/06 1 /07/06 1 /07/06 1 /07/06 1 /07/06 1 /06 1 /06 1 /06 1 /07/06 1 /07/06 1 /07/06 1 /06 1 /07 1 | 932 906° 313ª 534 559 399ª 399ª 576 | 1237 734 526 | | | | | | | | | |
| | | 40 36 36 36 34 3 | 09/05/06 07/06/06 16/03/06 29/04/06 13/04/06 07/06/06 08/04/06 08/04/06 08/04/06 13 008/04/06 to ceased tr? | 906° 313ª 500ª 534 539 399ª 576 | 734 | 27.6 - 58.1 | 34 | 07/11/08 | 83^{d} | I | I | 102^{a} | 1017 | 28.7 - 60.8 |
| Ceará | 1530 | 47 36 36 36 36 36 | 07/06/06 16/03/06 29/04/06 13/04/06 07/06/06 08/04/06 to ceased treased | 313 ^a 500 ^a 534 399 ^a 399 ^a | 202 | 39.3-67.9 | 49 | 19/12/08 | 06 | 19/03/09 | 39 | 71^{a} | 1777 | 45.2-99.8 |
| Maranhão | | 36 36 34 34 | 16/03/06 29/04/06 13/04/06 07/06/06 08/04/06 to ceased tra 008 and $27 \neq$ | 500 ^a 534 559 399 ^a 576 | 020 | 108.4 - 144.3 | | | | | | | | |
| Ceará | | 42 36 34 | 29/04/06 13/04/06 07/06/06 08/04/06 to ceased tra 008 and 27 <i>k</i> | 534 559 399 ^a 576 | 972 | 40.8 - 73.5 | | | | | | | | |
| Ceará | 1555 | 36 42 34 | 13/04/06 07/06/06 08/04/06 to ceased tre 008 and 27 # | 559 399ª 576 | 1080 | 13.9 - 46 | 66 | 20/12/07 | 93 | 22/03/08 | 30 | 316^{a} | 1074 | 11 - 44 |
| Ceará | 1534 | 42 34 | 07/06/06 08/04/06 to ceased tre 008 and 27 ∉ | 399ª 576 | 854 | 28.9-59 | 51 | 14/12/07 | I | I | I | $507^{a,e}$ | 426 | 42.7-61.4 |
| Pará | 2439 | 34 | 08/04/06 to ceased tro 008 and 27 ₽ | 576 | 667 | 34.4 - 61.7 | | | | | | | | |
| Ceará | 1309 | | to ceased tra 008 and 27 ≙ | an emiceione. | 663 | 26.3 - 52.4 | 27 | 11/11/07 | 105 | 24/02/08 | 33 | 66^{a} | 1248 | 30.2-63.7 |
| Deplo | Deployment location | tion | ι. | Tracked turtles (n) | Tracking period (d) | Mean tracking period (d) | Internesting home range (mean) (km ²) | | Foraging home range (km²) (range; <i>mean</i> ; n) | Distanc nesting grounds | Distance between nesting and feeding grounds (range; km) | | Source | |
| North | Northwestern Atlantic (USA) | antic (USA) | | 8 | 1 - 34 | 6 | na | | na | | na | Stone | Stoneburner (1982) | 32) |
| South | western Ind | Southwestern Indian (South Africa) | frica) | 4 | na | na | na | | na | 54. | 545 - 930 | Papi e | Papi et al. (1997) | |
| North | Northwestern Atlantic (USA) | antic (USA) | | 5 | 101 - 163 | $138^{\rm a}$ | na | | na | | na | Plotki | Plotkin & Spotila (2002) | (2002) |
| Medit | Mediterranean (Cyprus) | (Syprus) | | 2 | 60 - 82 | 71 | na | | na | 22 | 227 - 320 | Godle | Godley et al. (2003a) | 03a) |
| North | Northwestern Atlantic (USA) | antic (USA) | | 4 | 27 - 132 | 81^{a} | na | | na | | na | Dodd | Dodd & Byles (2003) | 03) |
| South | Southwestern Atlantic (Brazil) | antic (Brazil) | | 8 | na-301 | na | na | 570-27 | 570-2700; 757; 3 | | na | Lemk | Lemke et al. (2003) |)3) |
| Carib | bean Atlant. | Caribbean Atlantic (Cayman Islands) | slands) | Э | 379 - 1000 | 685 | na | | na | 48. | 485-791 | Blume | Blumenthal et al. (2006) | . (2006) |
| Easter | rn Atlantic (| Eastern Atlantic (Cape Verde) | | 10 | 57 - 566 | 249^{a} | na | 112-4 | 112-421; 237; 3 | | na (mean: 1253) | Hawk | Hawkes et al. (2006) | (90c |
| North | Northwestern Atlantic (USA) | antic (USA) | | 12 | na | 428 | na | 17.5 - 95. 33.6 - 207 | 17.5–95.4; <i>51.9</i> ; 5 w 33.6–207.2; <i>97.7</i> ; 5 f | | 330–752 w 576–895 | Hawk | Hawkes et al. (2007) | (±00 |
| Medit | Mediterranean (Cyprus) | vprus) | | 10 | 59 - 1356 | 322 | na | 55 | $55-331^{b}$ | | na | Brode | Broderick et al. (2007) | 2007) |
| North | Northwest Atlantic (USA) | ir (USA) | | 23 | 7-1415 | 2.16 | na | | еu | | na | Mansi | Mansfield et al. (2009) | 16006 |
| | | Conthracton Atlantic (Dari) | | 04 | CT#T_/ | 017 | 2 2 2 2 | 2 4 2 | 5 1 5 0 1 5 0 1 | 001 | 1000 0120 | Turner I | Duccont stude | (0007 |

268

(50% KHRE) 1209 - 2439na

^aCalculated from published data; ^bwinter and summer areas, respectively



Fig. 4. Caretta caretta. Kernel-estimated home-range utilization 50% distributions of 4 tracked loggerheads (L3, >L4, L7, L8) showing their first (red) and second (blue) internesting areas



Fig. 5. Caretta caretta. Postnesting movements of 10 loggerheads satellite-tracked from nesting grounds in northern Bahia, Brazil. State abbreviations — PA: Pará; MA: Maranhão;
PI: Piauí; CE: Ceará; RN: Rio Grande do Norte; PB: Paraíba; PE: Pernambuco; AL: Alagoas; SE: Sergipe; BA: Bahia



Fig. 6. *Caretta caretta*. Kernel-estimated home-range utilization 50% distributions of feeding areas of the 5 tracked loggerheads following their first (solid perimeter) and second (broken perimeter) postnesting migration. State abbreviations—PI: Piauí; CE: Ceará; RN: Rio Grande do Norte

and south from the nesting area (Lemke et al. 2003), the northern stock turtles traveled to common foraging areas in northern Brazil. Although we observed a distinctive migratory behavior among the 2 stocks, limited tracking duration of individuals from the southern stock (Espírito Santo) and tag recoveries from adult females found stranded in Uruguay from both loggerhead subpopulations (Almeida et al. 2000, Laporta & Lopez 2003) prevent definitive conclusions on migration patterns.

A seasonal shuttling between foraging and wintering grounds has been observed in several populations from temperate regions as an attempt to avoid lethally cold winter temperatures (Broderick et al. 2007, Hawkes et al. 2007, Zbinden et al. 2008). Following postnesting migrations, females tracked in the present study arrived at foraging grounds and remained within restricted areas until subsequent nesting migrations. Foraging grounds located along the tropical northern coast of Brazil exhibit minimal water temperature variations (27 to 29°C; Freire & Cavalcanti 1998) during the year and are thus suitable for loggerheads on a yearround basis.

All the loggerheads tracked during the present study remained at their foraging grounds until subsequent reproductive migrations, in a similar manner to other nesting populations (Luschi et al. 2006, Broderick et al. 2007, Zbinden et al. 2008). These results differ from the results on loggerheads nesting at Cape Verde and Japan, where the turtles used both coastal and oceanic foraging areas, and the body size of the individuals correlated markedly with the foraging mode. Turtles foraging neritically were significantly larger than turtles foraging oceanically (Hatase et al. 2002, Hawkes et al. 2006). It seems that the neritic foraging strategy maintained over a long period of time by Brazilian loggerheads leads to the relatively large body size of the population (102.8 ± 0.04 cm CCL, Marcovaldi & Laurent 1996; 103 cm, Marcovaldi & Chaloupka 2007).

Little is known about the extent of individual foraging areas (Table 4). Hawkes et al. (2006) reported foraging areas ranging from 112 to 421 km², using minimum convex polygons. The same procedure was employed by Broderick et al. (2007) to calculate winter and summer home ranges for 3 loggerheads, ranging from 55 (winter) to 331 km² (summer). Loggerhead foraging areas are typically small in size, on the order of 10s of square kilometers (Schroeder et al. 2003). However, calculated foraging areas for loggerheads from the Bahia coast were larger than those reported previously for other areas (see Table 4). Long-term tracking provided sufficient information to delineate the core foraging area exploited by the turtles during their entire residency (i.e. 2 and 3 nesting years) with more accuracy than was possible in previous studies. In addition, loggerheads are omnivorous and generally forage on benthic organisms such as mollusks, crustaceans and coelenterates in neritic habitats (Hatase et al. 2002); thus, as food resources become depleted, turtles may move among a few preferred foraging sites to utilize a larger foraging area (Schroeder et al. 2003). This may be an explanation for the larger size of foraging areas observed during extended residency. However, the longer tracking period, as well as differences in the methods used in area delimitations, may have led to the larger areas recorded compared to other studies (Table 4). Further studies will address prey availability and habitat characterization of loggerhead foraging grounds to better understand these findings.

Differences in remigration intervals are known to occur from long-term mark-recapture studies. Schroeder et al. (2003) summarize the observed remigration rates obtained from different studies around the world. Our study was the first satellite telemetry study to document such varying intervals. Turtles tagged at the same nesting ground migrated to the same foraging area and traveled back to the nesting site at different intervals (2 and 3 nesting years). Differences in observed remigration intervals within sea turtle populations can be assigned to several causes: mortality, variations in the quality of forage and inherent methodological limitations (e.g. flipper tagging) (Limpus & Nicholls 1988, Schroeder et al. 2003). Further analyses are underway to explore these results in more detail in terms of oceanography and resource availability.

Broderick et al. (2007) tracked 2 loggerhead females during consecutive postnesting migrations to foraging areas in the Mediterranean, where turtles exhibited high levels of fidelity to migratory routes, foraging areas and wintering sites. However, turtles were recaptured at the nesting beach after an interval of 2 to 3 yr and tracked for a second migration; thus, information about the complete residency period at foraging areas and prenesting migration routes was limited. After a second postnesting migration, turtles tracked in the present study returned to the same foraging area, indicating strong philopatry to specific foraging areas, as previously noted by Broderick et al. (2007). Furthermore, our migration data demonstrated fidelity to internesting areas after subsequent nesting seasons, as well as migratory routes from nesting to foraging areas and vice versa.

CONSERVATION IMPLICATIONS

The northern coast of Brazil has previously been identified as an important foraging ground for green turtles *Chelonia mydas* (Koch et al. 1969, Meylan et al. 1990, Luschi et al. 1998, Godley et al. 2003b), especially the Ceará coast (Lima & Troëng 2001, Naro-Maciel et al. 2007). Our findings demonstrate the importance of these foraging grounds for loggerheads breeding on the coast of Bahia as well. Satellite telemetry was an efficient tool for defining both migratory pathways and the extent of internesting and foraging areas of the tracked turtles.

The 10 tracked loggerheads used distinct areas during internesting periods, related to their tagging site; movements between nesting and foraging areas comprised >1500 km, along the coast of 10 Brazilian states. This behavior exposes the turtles to different impacts depending on habitat and jurisdiction (e.g. different fisheries and respective time closures, varying licensing criteria in different states) and highlights the need for integrated and complementary actions along the entire delineated migratory corridor. Noteworthy is the fact that the nesting and foraging areas for adult females from the same population are located within a single country. This provides a good starting point for ensuring the long-term protection of this relevant part of the turtle's life cycle, since national policies and conservation measures are already established.

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