THEME ISSUE

Sex-specific migration patterns of hawksbill turtles breeding at Mona Island, Puerto Rico

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ABSTRACT: Detailed post-breeding movement data is presented for hawksbill turtles tracked by satellite telemetry from Mona Island, Puerto Rico. Seven nesting females and 8 breeding males were tracked. Females traveled for 3 to 53 d to reach their foraging grounds, swimming distances of 84 to 2051 km (mean 867 km, n = 7) at average speeds of 23.5 to 38.7 km d^{-1} (n = 7). Males traveled for <1 to 22 d, covering distances of <2 to 476 km (mean 101 km, n = 8) at average speeds of 13.0 to 24.7 km d^{-1} (n = 5). One of the tracked males remained at the Mona Island breeding grounds for 11 mo before being recaptured there. The migration of 2 other male hawksbill turtles returning to Mona Island the following year from their foraging grounds was also documented. Descriptions of the foraging habitats used by these adult turtles are provided. The significant differences observed in migratory range between males and females are interpreted in an evolutionary context of food abundance predictability; an alternative hypothesis of geographic variation in mortality rates is also considered.

KEY WORDS: Hawksbill turtle · *Eretmochelys imbricata* · Migration · Mona Island · Puerto Rico

INTRODUCTION

Marine turtles have long been known to travel from their nesting beaches upon completion of breeding activities, but only in the past 10 to 15 yr have the remarkable details of these migrations become clear with the advent of satellite telemetry technology. Early marine turtle researchers speculated that hawksbill turtles *Eretmochelys imbricata* were more sedentary than other species (e.g. Carr 1952). However, flipper tag returns have indicated otherwise, and the interna-

tional movement of adult hawksbill turtles is now well documented (Miller et al. 1998, Meylan 1999). Furthermore, genetic studies indicate that juvenile hawksbill aggregations on foraging grounds are composed of mixed stock, implying that turtles must be migratory during a latter stage in life history in order to return to their breeding grounds (Bass 1999, Díaz-Fernández et al. 1999). Published satellite telemetry studies conducted with post-breeding Caribbean hawksbill turtles reveal that the foraging grounds to which these animals returned were located 85 to 451 km from their

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nesting sites and often in territories of countries distinct from those of the originating nesting beaches (Hillis-Starr et al. 2000, Horrocks et al. 2001, Troëng et al. 2005a).

Although hawksbill turtle populations in the Atlantic are currently considered depleted (Meylan 1999), the 2 largest rookeries in the Caribbean Sea, at Barbados and Mona Island, have seen strong increases in nesting activity in recent years (Beggs et al. 2007, R. P. Van Dam & C. E. Diez unpubl. data). At Mona Island, the number of recorded nests deposited on the island's beaches increased by nearly 500% from 1990 to 2006 (196 vs. 951 nests counted during comparable survey periods, R. P. Van Dam & C. E. Diez unpubl. data). During the past 15 yr, in-water surveys conducted at Mona Island have also detected increased abundance of adult male hawksbill turtles in the island's near-shore waters during the September–October peak of breeding activity (R. P. Van Dam & C. E. Diez unpubl. data). Local and regional measures—such as poaching reduction, nest protection and take limitations—appear to be contributing to the recovery of the Mona Island hawksbill population. To further understand the geographic scope of this important population, we examine here the movements of 7 female and 8 male hawksbill turtles tracked by satellite telemetry from the Mona Island breeding area (along the west coast) to their individual foraging grounds during several deployments in 1998, 2002, 2003 and 2004. Two hypotheses are presented to explain the intriguing migration patterns observed in this hawksbill population.

MATERIALS AND METHODS

This study was carried out at Mona Island, Puerto Rico (18° 05' N, 67° 56' W), an uninhabited island managed as a Natural Reserve by the Puerto Rico Department of Natural and Environmental Resources. Healthy hawksbill turtles were selected from the stock of active breeders that crawl onto the Mona Island nesting beaches (females) or were encountered in the waters immediately adjacent to these nesting beaches (males). Health criteria used were as follows: (1) all flippers were at least $\frac{3}{4}$ complete, (2) vigorous behavior, and (3) individuals did not appear emaciated or more than superficially injured. The timing of transmitter application was aimed to coincide with the September–October peak of the hawksbill breeding season on Mona Island for male turtles and post-peak for females. Active male reproductive status was inferred from evidence of recent mating events, such as superficial wounds on the neck and flippers (typically caused by biting from competing males during copulation) and soft plastrons (considered an indicator of

active reproductive status; Wibbels et al. 1991). All animals used in this study were flipper-tagged and measured (straight or curved carapace length taken from the nuchal notch to the posterior-most marginal scute tip).

After oviposition was completed and the turtles had begun returning to the water, females were intercepted on the nesting beach and detained in a plywood box for transmitter attachment. Male turtles were hand-captured at sea by divers and lifted onto a small boat for transmitter attachment. Transmitters applied were models ST-14 (size, $17 \times 10 \times 3.5$ cm; weight in air, 760 g) or ST-20 (size, $12 \times 6 \times 3$ cm; weight in air, 280 g) (Telonics, Mesa); some turtles were also fitted with CHP-87L or CHP-87XL sonic transmitters (Sonotronics, Tucson) (see Table 1). Prior to the attachments, turtles' carapaces were cleaned, which included removal of interfering external commensals such as barnacles. Transmitters were applied to the highest point on the carapace using silicone elastomer and resined fiberglass, following Balazs et al. (1996), modified by reinforcing the antenna base as well as by placing hydrodynamically shaped filler material along the frontal area of the transmitter to streamline the package. Turtles were held for 1 to 2 h after attaching the transmitters to allow adhesives to set, then released at the location of capture (recorded by GPS receiver). In subsequent years, whenever study animals were recaptured bearing transmitters at the Mona Island breeding grounds, we removed the devices together with any adhesive residues (for transmitter recovery dates, see Table 1).

Turtle location data was received from Service Argos. The online Satellite Tracking and Analysis Tool (Coyne & Godley 2005) was used for creating base maps and data parsing for the 2004 deployments. Turtle migration was measured primarily by examining coordinates with Argos location classes (LC) 0, 1, 2, and 3. Further detail was obtained by selectively adding data points with LC's A and B, ensuring that these locations did not imply unrealistic swim speeds (i.e. >5 km h^{-1}; Luschi et al. 1998). Navigational efficiency was calculated for each migration path as the quotient of the shortest possible in-water distance between start and end points and the turtle's actual distance traveled, as measured by telemetry.

In several instances, it was possible to visit turtle foraging habitats and attempt to precisely locate the animals fitted with transmitters by listening for sonic tag signals with a directional hydrophone (Dukane model N15A235B, St. Charles). Once the sonic tag was heard, position was recorded by GPS receiver and a visual confirmation of the turtle's presence was attempted. Foraging ground benthic habitat characteristics were noted.

RESULTS

Migration

After being fitted with transmitters, female hawksbill turtles remained from 0 to 38 d in the immediate vicinity of Mona Island (Table 1), with periods of 13 d or more indicative of subsequent return visits to the nesting beach for additional egg laying. All females then departed from the island, taking 3 to 53 d to reach their foraging ground destinations and covering distances of 84 to 2051 km (see Figs. 1a,b & 3, Table 1). Swim speeds for all females averaged 31.2 km d^{-1}. Females swimming westward, and thus aided by the prevailing surface currents, covered a mean 33.4 km d^{-1}, whereas those swimming eastwards against the current covered on average 29.5 km d^{-1}.

Turtle F3 exhibited unusual behavior during her migration. This turtle left Mona Island on 16 December 1998 in the direction of her eventual foraging grounds, but then, within several days of leaving Mona Island, she detoured towards Saona Island, Dominican Republic. This turtle then remained very near Saona, and the received locations indicated that she visited a beach on the southern coast of the island on 31 December 1998. The turtle then departed and swam west to her foraging grounds on the Rosalind Bank near Honduras (Fig. 1a).

After application of transmitters, the 8 tracked male hawksbill turtles remained near Mona island for 6 to 68 d before departing. Turtle M4 was the exception, as he did not make any measurable excursion for 11 mo (this male was then recaptured for transmitter removal less than 2 km from where he had been released). The other males swam for <1 to 22 d, covering distances of 13 to 476 km to reach their foraging ground destinations (Figs. 2a,b & 3). Three of these individuals traveled only 13 to 16 km away from their respective locations of transmitter application: to the eastern side of Mona Island (Turtle M1) and to Monito Island (Turtles M7 and M8). The furthest migrating male (M5) interrupted his trip for 13 d, staying near Saona Island where female F3 may have nested, before continuing his migration to Beata Island, along the southwest coast of the Dominican Republic.

Distance traveled was significantly different between the sexes (*t*-test, p < 0.05). Females swam on average 8.6 times as far as males from Mona Island to
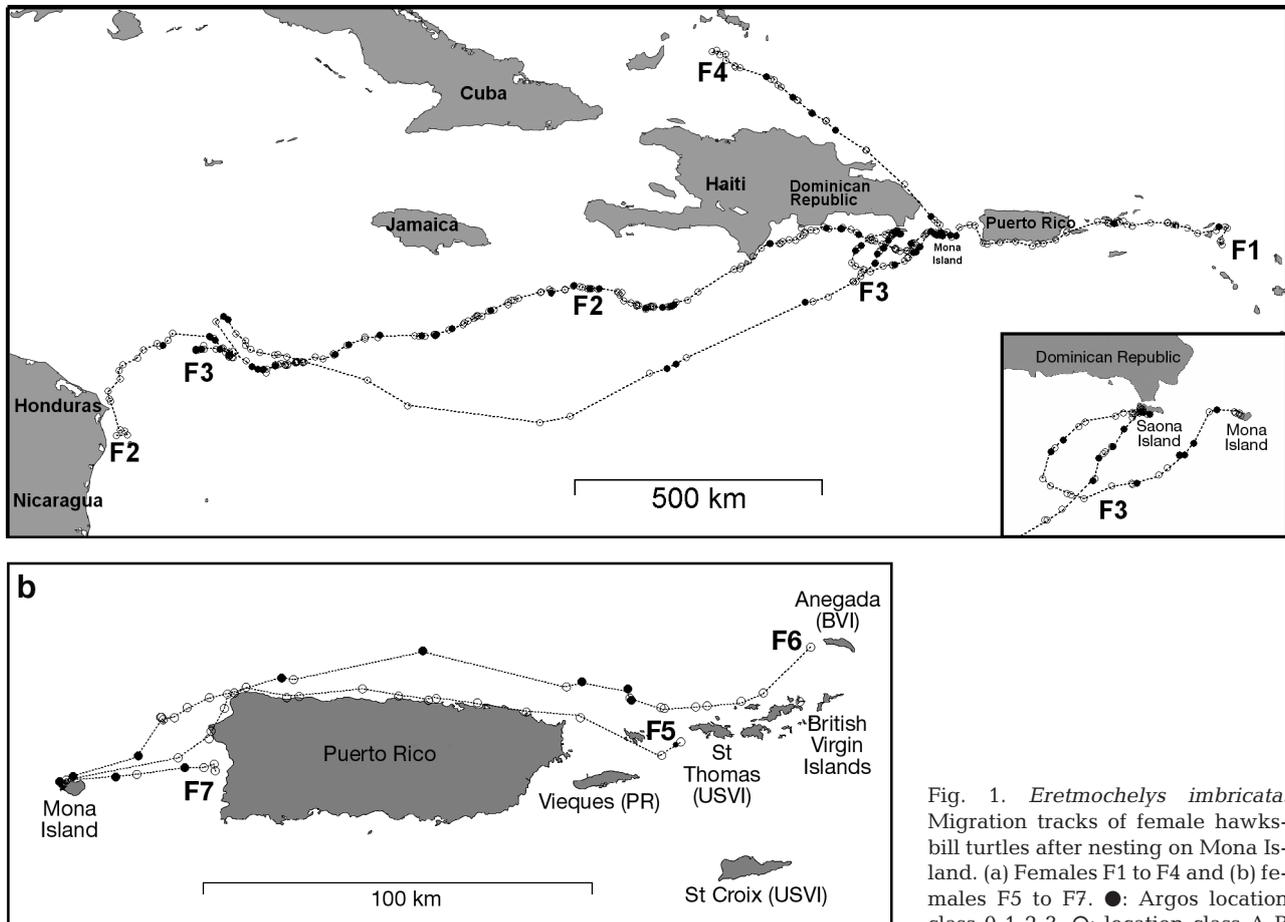

Fig. 1. *Eretmochelys imbricata.* Migration tracks of female hawksbill turtles after nesting on Mona Island. (a) Females F1 to F4 and (b) females F5 to F7. ●: Argos location class 0-1-2-3; ○: location class A-B

Table 1. *Eretmochelys imbricata*. Data from transmitter deployments on female and male hawksbill turtles at their breeding grounds on Mona Island. Size of females was converted from curved carapace length to straight carapace length (SCL) using the conversion formula in Van Dam & Diez (1998). Instrument configuration — A: Telonics ST-14; B: Telonics ST-20; C: Sonotronics CHP-L; D: Sonotronics CHP-XL. Habitat depth range determined from nautical charts, supplemented with direct observation data for the visited habitats

Turtle	Turtle size, SCL (cm)	Date released, instrument configuration	Pre-departure period (d)	Distance traveled (km)	Travel time (d)	Mean swim speed (km d⁻¹)	Navigational efficiency (%)	Date last location range (m)	Foraging habitat Name	Location	Depth (m)	Notes
Females												
F1	82.7	5 Nov 98, A	16	643	21	30.6	85	9 Jul 00	St Barthelemy Channel, French West Indies	18.0093°N, 62.8736°W	32–36	Transmitter recovered 13 Sep 05
F2	84.7	6 Nov 98, A	2	1940	51	38.0	84	25 May 00	Nicaragua	14.5311°N, 83.0191°W	7–20	Transmitter recovered 6 Nov 02
F3	87.2	8 Nov 98, A	38	2051	53[a]	38.7[a]	72	10 Jul 00	Rosalind Bank, Honduras	16.0562°N, 81.5511°W	42–46	Transmitter recovered 21 Sep 01
F4	87.9	20 Nov 98, A	19	611	26	23.5	90	9 Feb 00	Caicos Bank, Turks & Caicos Islands	21.2295°N, 72.0044°W	5–50	Near dropoff to water >200 m deep, transmitter recovered 21 Nov 01
F5	84.1	21 Nov 03, B	2	336	11	30.5	94	24 Jan 04	Sail Rock, US Virgin Islands	18.2760°N, 65.1030°W	15–24	Transmitter recovered 30 Oct 05
F6	88.9	8 Oct 04, B, D	13	403	14	28.8	94	4 Feb 05	Anegada, British Virgin Islands	18.7100°N, 64.4760°W	12–20	
F7	91.7	9 Oct 04, B, D	0	84	3	28.0	93	1 May 05	Puerto Rico, west coast	18.1610°N, 67.2410°W	5–25	Heard sonic tag & underwater sighting at west coast Puerto Rico 10 Apr 05
Males												
M1	77.0	12 Sep 02, A, C	68	13	1	13.0	–	8 Apr 04	Mona Island, northeast coast	18.0940°N, 67.8420°W	20–60	
M2	83.8	13 Sep 02, A, C	60	173	7	24.7	92	23 Oct 03	Puerto Rico, south-central coast	17.8300°N, 66.4700°W	20–40	Near dropoff to water >200 m deep, transmitter recovered 23 Oct 03
M3	79.3	13 Sep 02, A, C	73	54	3	18.0	100	26 Aug 03	Puerto Rico, west coast	18.0620°N, 67.4040°W	15–60	Near dropoff to water >200 m deep, transmitter recovered 26 Aug 03
M4	76.8	14 Sep 02, A, C	–	<2	–	–	–	13 Aug 03	Mona Island, southwest coast	18.0520°N, 67.9046°W	5–40	Near dropoff to water >200 m deep, transmitter recovered 14 Aug 03
M5	78.7	13 Sep 03, B, C	6	476	22[b]	21.6[b]	83	18 Dec 03	Isla Beata, Dominican Republic	17.5250°N, 71.6010°W	10–60	
M6	83.1	6 Oct 04, B, D	39	62	3	20.7	97	22 Mar 05	Puerto Rico, west coast	18.1640°N, 67.3730°W	10–60	
M7	78.5	7 Oct 04, B, D	15	14	<1	–	–	8 Jan 05	Monito Island	18.1660°N, 67.9500°W	15–60	Underwater sighting at Monito Island 28 Jan 05
M8	83.5	9 Oct 04, B, D	46	16	<1	–	–	4 Jun 05	Monito Island	18.1581°N, 67.9430°W	15–60	Heard sonic tag & surface sighting at west Mona Island 29 Aug 05

[a] Not including 9 d stop at Saona Island; [b] not including 13 d stop at Saona Island
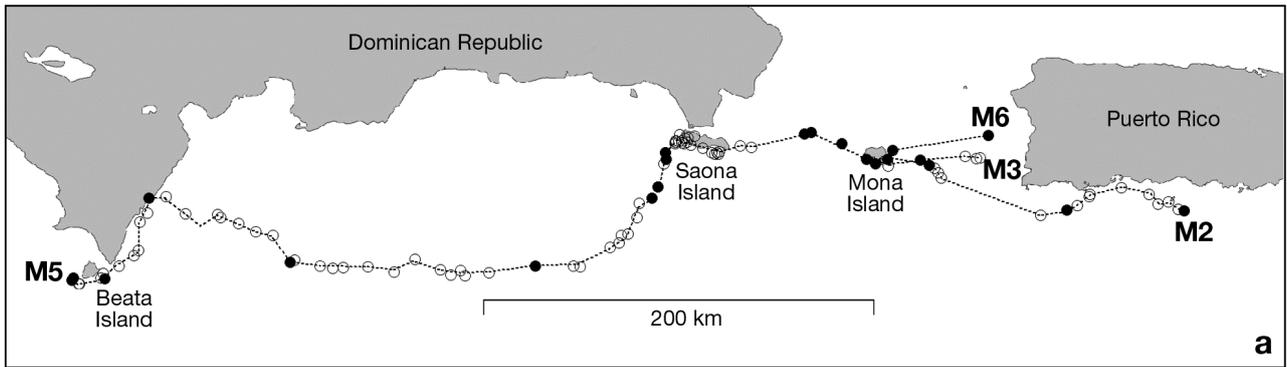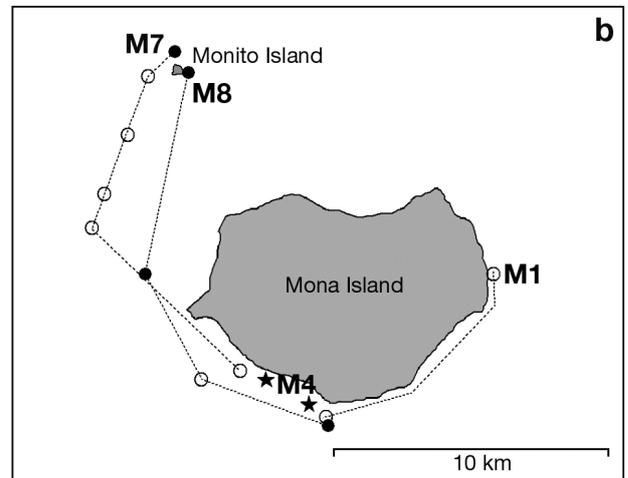
Fig. 2. *Eretmochelys imbricata*. Migration tracks of male hawksbill turtles after breeding at Mona Island. (a) Males M2, M3, M5 and M6, and (b) males M1, M4, M7 and M8. Male M4 moved <2 km during 11 mo with the satellite transmitter. ★: M4's capture and recapture location; ●: Argos location class 0-1-2-3; ○: location class A-B

reach their foraging grounds. Overall, navigational efficiency correlated inversely with the distance traveled ($r = -0.67$, $p < 0.05$); however, males and females exhibited no significant differences in navigational efficiency (*t*-test, $p > 0.05$).

The return migration from their foraging grounds to Mona Island was documented by satellite telemetry for 2 of the male hawksbill turtles: M2 and M3 (Fig. 4). Approaching Mona Island, turtle M3 overshot to the north by some 20 km, then corrected course after swimming a loop, resulting in a relatively low navigational efficiency of 47%. M2 and M3 returned to Mona Island after spending 311 and 233 d, respectively, on their foraging grounds along the south and southwest

coast of Puerto Rico and took 7 and 5 d, respectively, to make the return trip. A third male hawksbill (M8) had returned to the breeding grounds at west Mona Island by 29 August 2005, where the animal's sonic tag was heard and his presence visually confirmed. The last
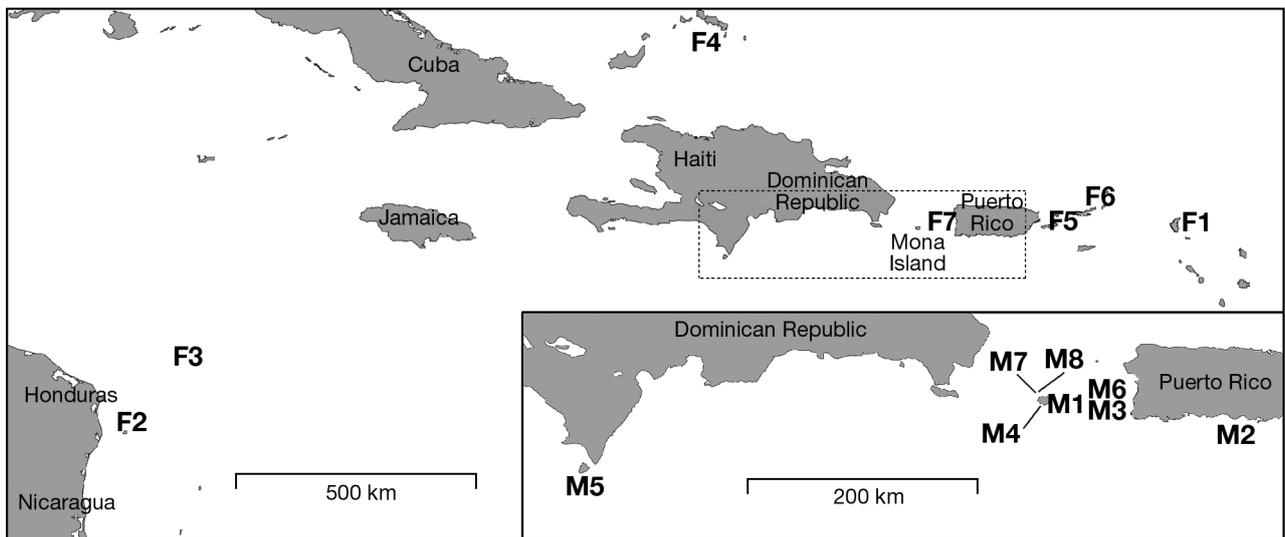

Fig. 3. *Eretmochelys imbricata*. Foraging ground locations of 7 female (F1 to F7) and 8 male (M1 to M8) hawksbill turtles tracked after breeding at Mona Island, Puerto Rico
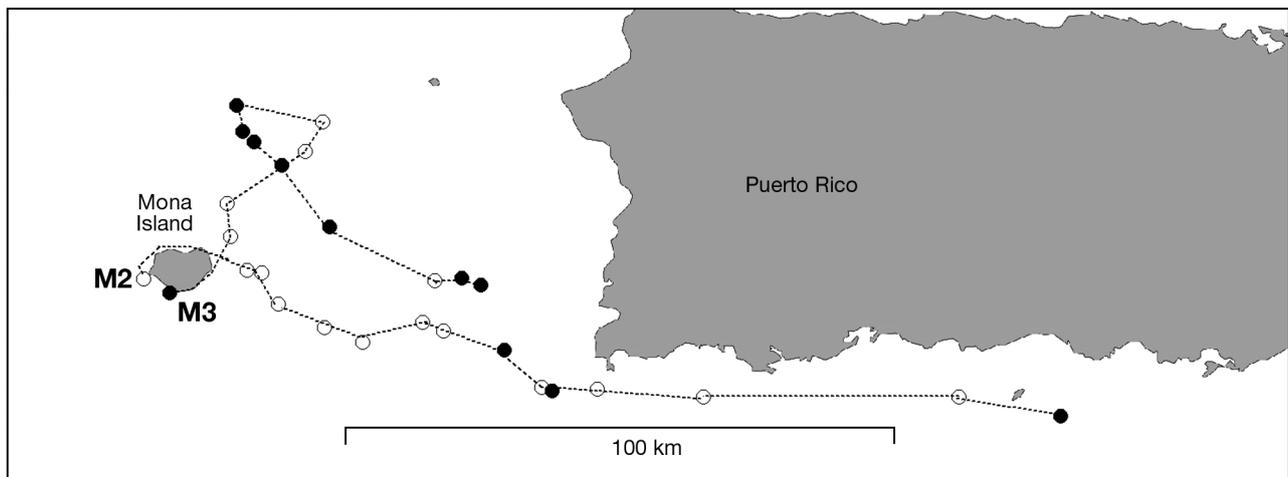
Fig. 4. *Eretmochelys imbricata*. Return migration tracks of 2 male hawksbill turtles from their foraging grounds to the Mona Island breeding area. ●: Argos location class 0-1-2-3; ○: location class A-B

good quality Argos location that was received placed the male close to Monito Island on 4 June 2005, therefore, after his arrival there on 22 October 2004, he spent between 225 and 311 d on that foraging ground.

Foraging habitat descriptions

We visited 4 foraging habitats <100 km from the breeding area and used by 5 tracked turtles (4 males and 1 female): Monito Island (males M7 and M8), northeast Mona Island (male M1), southwest Mona Island (male M4), and west Puerto Rico (female F7).

Monito Island is a limestone rock standing in waters 15 to 40 m deep, surrounded by boulders to ca. 100 m distance from the island's cliffs, with a rubble seafloor extending further out at depths of 35 to 60 m. The cave-pocketed cliffs and boulders are covered with diverse corals, sponges and algae. On the seafloor, sponges *Xestospongia muta* and *Geodia neptuni* are prominent, with the latter frequently exhibiting bite marks attributable to feeding by subadult and adult hawksbill turtles (see Van Dam & Diez 1997 for photographs of such bite marks).

The northeast coast of Mona Island is geologically similar to the shore of Monito Island. This area used by Turtle M1 consists of a vertical limestone cliff face extending to 20 to 30 m depth and many large boulders strewn out to ca. 150 m distance from the island, beyond which a rubble seafloor extends gradually to depths of about 60 m. *Xestospongia muta* is the most prominent sponge growing on both the boulders and rubble seafloor.

The southwest coast foraging habitat of Mona Island is immediately adjacent to heavily used nesting beaches and consists of a sandy ledge 5 to 20 m deep inter-

spersed with coral reef patches and punctuated by a vertical dropoff extending to 100 to 200 m depth. Prominent sponges include *Xestospongia muta* and *Geodia neptuni*, with the latter frequently exhibiting hawksbill turtle bite marks.

The foraging habitat of female Turtle F7 off the central western Puerto Rico coast appears relatively atypical, consisting of a pebble-bottom seafloor at 10 to 25 m depth with no prominent sponges apparent. When we located and followed this animal by sonic tracking, she moved to a shallower (5 to 10 m) area with a sandy bottom and sparse coral, seagrass and algae cover, again without any visibly prominent sponge fauna.

DISCUSSION

Migrations of post-breeding hawksbill turtles have been documented through flipper tag returns and via satellite telemetry from several other rookeries in the Caribbean Sea. Flipper tag records have revealed the migratory capability of Caribbean hawksbill turtles, with reported displacement distances of up to 1963 km in a dataset consisting nearly entirely of adult females (Meylan 1999). Relatively few published accounts exist of hawksbill turtles tracked long distances by telemetry in the Caribbean. These accounts report small sample sizes and none include tracking of breeding males, which limits the scope of comparisons that can be made. Nesting hawksbill turtles have been tracked by satellite telemetry from Barbados (Horrocks et al. 2001, n = 4), Tortuguero, Costa Rica (Troëng et al. 2005a, n = 2), and St Croix, US Virgin Islands (Hillis et al. 2000, n = 2). The females from these 3 rookeries migrated up to 500 km to their foraging grounds.

Nesting hawksbill turtles tracked in other ocean basins, such as from Hawaii and the Seychelles, similarly migrated only a few hundred kilometers to their foraging grounds (Ellis et al. 2000, Mortimer & Balazs 2000). The female turtles tracked in our study tended to travel greater distances and swim faster than those tracked from Barbados and Costa Rica; however, they are not exceptional in light of the displacements documented from flipper tag recapture results for Caribbean hawksbill turtles (Meylan 1999).

The behaviors of female F3 and male M5 are noteworthy. After leaving Mona Island, both swam ca. 100 km to Saona Island, Dominican Republic, where they remained 9 and 22 d, respectively, probably to breed there. Whether through navigational error or on purpose, any breeding activity on Saona Island by animals belonging to the Mona Island population represents colonizing behavior and illustrates the geographic scope of this process for hawksbill turtles. On Saona Island, an estimated 56 hawksbill nests were laid in 2006 (J. Tomás & Y. M. León unpubl. data), and about half of these nests are thought to have been poached. More effective nest and turtle protection measures on Saona Island are important, to protect occasionally visiting Mona Island hawksbill turtles and to re-establish the island as an important Caribbean hawksbill rookery.

Females F2 and F3 were tracked to the vast array of shallow banks that extends from the east coasts of both Honduras and Nicaragua halfway to Jamaica. This continental shelf area was already known to be of prime importance for foraging green turtles (*Chelonia mydas*; Carr et al. 1978), but our results, taken together with other recent telemetry studies with nesting turtles from the Cayman Islands and Costa Rica, further highlight the importance of the area as foraging grounds for other marine turtle species as well. Blumenthal et al. (2006) tracked 3 nesting loggerhead turtles *Caretta caretta* from the Cayman Islands to the Nicaraguan section of the shelf (and 1 green turtle to the Gorda Bank, Honduras). Similarly, 2 hawksbill turtles (Troëng et al. 2005a) and 9 green turtles (Troëng et al. 2005b) were tracked from the nesting beach at Tortuguero, Costa Rica, to their foraging grounds on this Honduran/Nicaraguan bank. The ongoing turtle fisheries on the Nicaraguan coast, where annually a minimum of 11 000 green turtles are caught (Lagueux 1998), is believed to affect the Tortuguero green turtle rookery to the point of potential unsustainability (Campbell & Lagueux 2005). Whereas green turtles are specifically targeted by Nicaraguan fishermen, hawksbill and loggerhead turtles are mostly taken incidentally, i.e. when caught by lobster divers or in net sets (Bräutigam & Eckert 2006). The combined telemetry studies from 3 different countries further emphasize the importance

of efforts to limit the impact that the turtle fisheries in Nicaragua are having on green, hawksbill and loggerhead turtle populations throughout the Caribbean region.

To our knowledge, the present study is the first to report on the migratory behavior of male hawksbill turtles. Other published studies of male marine turtles include olive *Lepidochelys olivacea* and Kemp's ridley *L. kempii*, green, loggerhead, and leatherback *Dermochelys coriacea* turtles (Beavers & Cassano 1996, Plotkin et al. 1996, Sakamoto et al. 1997, Balazs & Ellis 2000, Hays et al. 2001, James et al. 2005, Shaver et al. 2005). Only in the Kemp's ridley turtle study did several of the tracked males remain near the breeding area (Shaver et al. 2005), similar to the behavior of the Mona male hawksbill turtles. With caveats, Shaver et al. (2005) interpreted male Kemp's ridley turtle behavior in terms of maximizing reproductive fitness, suggesting that food availability might allow a large proportion of males to remain resident on the breeding grounds without exceeding carrying capacity. Similarly, at Mona Island and, particularly nearby Monito Island, sponges preyed upon by large hawksbill turtles are abundant (R. P. Van Dam & C. E. Diez unpubl. data). The elevated somatic growth rates exhibited by hawksbills resident at Monito Island are attributed to high prey abundance (Diez & Van Dam 2002), indicating food availability is certainly not a limiting factor for turtles foraging in the area.

With Caribbean hawksbill turtles primarily spongivorous (Meylan 1988, Van Dam & Diez 1997, León & Bjorndal 2002), high turtle population densities must have exerted a level of control over prey sponge species to a far greater degree than is perceived at present. The migratory behavior of hawksbill turtles therefore evolved under very different circumstances than those we now observe. Millions of hawksbill turtles probably inhabited the Caribbean Sea up until even historic times (Jackson 1997), and such high turtle densities likely created strong intraspecific competition for food resources. Neritic habitats adjacent to hawksbill breeding grounds on islands in the Caribbean are often only narrow fringes delimited by seafloor dropoffs to depths inaccessible to hawksbill turtles. Whereas diving in adult hawksbills has been documented to 192 m depth, benthic foraging is generally restricted to depths of 100 m or less (R. P. Van Dam & C. E. Diez unpubl. data). Consequently, the extent of the available foraging habitat around many Caribbean breeding grounds is limited, creating the potential for extreme competition for food resources should turtles pursue opportunistic strategies of trying to forage nearby their breeding grounds.

During the breeding season, a female hawksbill turtle will typically lay 4 to 5 nests of 155 eggs each

(Richardson et al. 1999). With a mass of 20 to 27 g per egg (Witzell 1983), she thus sheds approximately 12 to 21 kg in egg biomass alone. Furthermore, female hawksbill turtles tend not to feed while breeding (R. P. Van Dam & C. E. Diez pers. obs.), a behavior that is likely related to the internal volume constraints of hard-shelled turtle bodies and the volume that maturing eggs occupy therein. Therefore, upon completion of the reproductive season, female hawksbill turtles have substantially depleted their energy reserves and need to locate food to recover from this deficit. By adopting a strategy of migrating back to a foraging habitat with predictably abundant food resources— even if located hundreds or even thousands of kilometers away—females avoid potential failure in attempting to find sufficient food in nearby locations. Once on their foraging grounds, they can then spend 2 to 5 yr restoring their energy reserves before embarking on their next trip back to the nesting beach.

Males face much lesser energetic burdens of reproduction. Although this study demonstrates that most male hawksbill turtles do migrate to some extent, and thus incur energetic costs of swimming, once they arrive on the breeding grounds males can replenish their reserves by feeding there (R. P. Van Dam & C. E. Diez pers. obs.). The much smaller energetic deficits experienced by breeding males therefore may allow them to pursue more opportunistic foraging strategies. However, the limited extent of available neritic habitat around islands such as Mona Island still makes a strategy of migration away from the breeding grounds a sound one for most individuals in order to reduce foraging competition. Males may also choose to move away from the breeding grounds to avoid male–male territorial fighting (R. P. Van Dam & C. E. Diez unpubl. data). Given that many male hawksbill turtles travel to the breeding area every year (this study, R. P. Van Dam & C. E. Diez unpubl. data), the swimming cost of migration may impose a relatively larger annual burden on energy budgets of males as compared to females, thus providing greater adaptational incentive for males to establish themselves on high quality foraging habitats closer to the breeding grounds. A possible test for the hypothesis that the difference in the extent of migration by male and female hawksbill turtles is related to the proximity of predictably abundant food resources would be to track both sexes from rookeries with an ample foraging habitat nearby, such as those fringed by a wide continental shelf, for example at the Yucatán Peninsula, Mexico.

An alternative explanation for the difference observed in migration patterns from Mona Island between male and female hawksbill turtles lies in the timing of this study in relation to improving turtle survival rates on foraging grounds in the Caribbean, and Puerto Rico

in particular. Between 1998, when we first deployed transmitters on Mona Island hawksbill turtles, and 2002 to 2004, when we continued this tracking study, the number of nests recorded on the nesting beaches of Mona Island rose by ca. 70 % (from 503 nests to 817–926 nests, R. P. Van Dam & C. E. Diez unpubl. data) reflecting a strong and sustained increase of this population. We attribute this increase to higher survival rates brought about by conservation actions taken locally and regionally, and to the important turtle take reductions implemented by Cuba in 1990 to 1994 (Carillo et al. 1999). Turtles utilizing safer foraging grounds and/or following migratory pathways with less mortality risk will gradually comprise a greater proportion of the turtle population, in what could be termed a geographical survivorship effect. With the observed strong expansion of the Mona Island hawksbill population during the years over which this tracking study was conducted, turtles recruiting to the breeding population from areas where conditions for survival have been improving would therefore have been more likely to become participants during the latter years of our study. Indeed, the 3 females tracked in 2003 and 2004 were all untagged when encountered on the nesting beach, suggesting that they may all have been new recruits to the breeding population. These females moved only 84 to 403 km from Mona Island towards their foraging grounds, compared with migration distances of 611 to 2051 km for the 4 females tracked in 1998 (Table 1).

Male hawksbill turtles were only tracked during 2002 to 2004, so that the same geographical survivorship effect may have influenced the limited migration range observed in these animals. All participating males were also untagged when captured for this study. Seven of the 8 tracked males reside year-round in Puerto Rico waters, where they are protected from capture with increasing effectiveness through enforcement of state and federal laws.

Turtles venturing west from Mona Island towards the Dominican Republic or east towards the British Virgin Islands and beyond may face higher human-induced mortality rates. Those turtles that manage to evade capture at sea are therefore concentrated in habitats where mortality is low, even if these may not be ecologically optimal. We conclude, therefore, that the range of the observed migrations for male and female hawksbill turtles breeding on Mona Island is the result of a confluence of, potentially competing, ecological factors and artificial geographical variation in survivorship.

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