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Migratory and reproductive movements of male leatherback turtles (*Dermochelys coriacea*)

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Abstract The biology of the endangered leatherback turtle (*Dermochelys coriacea*) at sea is poorly understood. As research has been almost exclusively limited to studies of nesting females, the movements of male turtles and the timing and location of mating activity have remained unknown. We report on the first deployments of satellite tags on male leatherbacks. Male migration to and residency in waters adjacent low-latitude nesting beaches in the western Atlantic suggest that this is where mating occurs, and return migration to these areas reveals male fidelity for breeding sites. Rate of travel decreased markedly after arriving in coastal breeding areas, where males remained for up to 96 days before assuming northward migrations. The initiation of these northward migrations coincided with peak nesting activity in adjacent nesting colonies. Data from satellite-linked time-depth recorders attached to two males revealed diel dive patterns in breeding areas and marked differences in diving behaviour between migratory and breeding periods in one turtle. When male turtles were in waters adjacent nesting colonies, their movements differed from those reported for nesting females, with females ranging farther from shore. Our results suggest that male leatherbacks may be vulnerable to entanglement in coastal fishing gear in waters adjacent nesting beaches.

Introduction

Research on the behaviour of leatherback turtles, *Dermochelys coriacea*, has previously focused on the movements of adult females, because they nest on tropical and subtropical beaches and are, therefore, readily available for study. The interesting behaviour of turtles in tropical waters has been studied through the use of electronic archival tags (Eckert et al. 1989, 1996; Southwood et al. 1999; Eckert 2002) and radio telemetry (Eckert 2002). The post-nesting movements of turtles have been revealed using both satellite telemetry (Morreale et al. 1996; Hughes et al. 1998; Luschi et al. 2003; Ferraroli et al. 2004; Hays et al. 2004a, 2004b) and the recovery of conventional flipper tags (Pritchard 1976; Girondot and Fretey 1996; James 2004). These studies have shown that female turtles disperse broadly after nesting and frequently journey to northern waters. In contrast, the behaviour of male leatherbacks has been difficult to study, as males never come ashore and there are formidable challenges associated with locating and humanely capturing this species at sea. Field research in eastern Canada has recently provided access to leatherbacks at sea, including males, to investigate broad movement patterns (James et al. 2005). However, the spatial and temporal distribution of males is still not well understood.

A lack of data on the movements of males and only rare reports of leatherbacks mating (Carr and Carr 1986; Godfrey and Barreto 1998) have led to contrasting hypotheses about when and where leatherbacks mate. Lazell (1980) speculated that mating occurs in waters adjacent nesting beaches. This is consistent with what is known about the breeding behaviour of other sea turtles (Limpus 1993; Plotkin et al. 1996; Frick et al. 2000). However, Pritchard (1982) suggested that a paucity of observations of copulation in the vicinity of nesting beaches indicated that leatherbacks do not mate in these areas, and Eckert and Eckert (1988) proposed that females mate prior to entering tropical waters, based on

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the rate of tropical barnacle (*Chonchoderma virgatum*) colonization on turtles nesting at St. Croix (U.S. Virgin Islands). If mating does not occur in waters adjacent nesting beaches, male turtles from temperate foraging grounds might be expected not to travel to these areas. To test this hypothesis, we used satellite telemetry to study the movements of male leatherbacks encountered in waters off eastern Canada.

Materials and methods

Fieldwork occurred in two areas off the coast of Nova Scotia. The first area (approximately 47°N, 60°W) includes the northeast portion of the Scotian Shelf and encompasses waters adjacent the Laurentian Channel, a deepwater trench (>400 m) that runs between Cape Breton Island and Newfoundland. The second area (approximately 44°N, 64°W) is larger and is located off the southwest shore of mainland Nova Scotia, including waters inshore from the shelf break.

Turtles were located in these areas with the assistance of the Nova Scotia Leatherback Turtle Working Group, a network of commercial fishers and tour boat operators who voluntarily report sightings of leatherbacks to assist with research on this species (Martin and James 2005).

Turtles were captured while foraging on jellyfish using a breakaway hoop net operated from either an 8.5-m or 10.5-m commercial fishing boat equipped with a stern ramp. Each turtle was moved up the ramp onto a raised platform where it was measured and sampled for DNA using a skin biopsy punch (6 mm, Acuderm, Ft. Lauderdale, FL, USA). Sex of male turtles was readily confirmed by the presence of an elongated tail with a cloacal vent distant from the tip of the caudal peduncle. Monel tags (style no. 49, National Band and Tag Company, Newport, KY, USA) were applied to the rear flippers and a passive integrated transponder (AVID, Calgary, AB, Canada) was implanted in the right shoulder muscle. A satellite-linked transmitter was attached to the carapace using a harness made of polypropylene webbing and polyvinyl tubing, which incorporates corrodible links to ensure release (modified after Eckert 2002). Transmitters included Kiwisats (Sirtrack, Havelock North, New Zealand), Spot 3s (Wildlife Computers, Redmond, WA, USA), and an ST-10 (Telonics Inc., Mesa, AZ, USA). Satellite-linked time-depth recorders (SLTDRs) were also deployed (SDR-SSC3, Wildlife Computers, Redmond, WA, USA).

Turtles were released promptly after satellite tag attachment (usually within 30 min) and their subsequent movements were monitored via the Argos satellite network. Location of the turtle, location class (LC, an index of positional accuracy), and the corresponding date and time were provided daily via e-mail. Argos calculates locations from transmissions received during a sa-

tellite pass and categorizes them by LC. Locations designated as LC 3, LC 2, LC 1, or LC 0 are classified as within 150 m, >150–350 m, >350–1,000 m, or >1,000 m, respectively, of the tag's true position. Locations classified as "A" and "B" are not categorized for positional accuracy by Argos; however, LC A locations have recently been shown to be as accurate as LC 1 locations and more accurate than LC 0 locations (Hays et al. 2001; Vincent et al. 2002).

An analysis has shown that less than 1% of rates of travel for leatherbacks calculated using only LC 1–3 positions exceed 5 km/h (James et al. 2005), which closely agrees with data published on leatherback sea turtle swim speeds (Eckert 2002). Therefore, we filtered positions of poorer reported quality (e.g. LC A, LC B, LC 0) based on a maximum rate of travel of 5 km/h. To maximize positional certainty, we calculated rates of travel (distance/time) between consecutive surface locations (LC 1, 2, 3, and A) that were a minimum of 2 h apart.

SLTDRs reported data on diving behaviour during 6-h periods (four per day: 20:00–01:59, 02:00–07:59, 08:00–13:59, 14:00–19:59; Atlantic Standard Time) in histogram format. SLTDRs specifically recorded the proportion of each 6-h period spent in 14 user-specified depth ranges (time at depth) and the number of dives (>4m, turtle E; >6m, turtle F) with durations that fell within 14 user-specified ranges. These data were compared to corresponding rates of travel associated with turtle migration and residency in different areas. Surface time data from two SLTDRs were also analyzed. In this case, "surface time" values represented the fraction of time in each 6-h period when the depth sensor read less than 2 m (turtle E) or 3 m (turtle F). Diel changes in diving behaviour and surface time were investigated by comparing data collected during periods 20:00–01:59 (night) and 08:00–13:59 (day).

To compare the timing of male leatherback residency in tropical waters to nesting activity on nearby beaches, we considered turtle E and turtle H, as these turtles restricted their movements to waters off relatively large colonies for which there is detailed information on the temporal distribution of nesting.

Results

Satellite tags were deployed on 11 male leatherback turtles captured off the coast of Cape Breton Island ($n=6$) and mainland Nova Scotia ($n=5$) in the summers of 1999 to 2003. All turtles eventually assumed southward migrations from temperate foraging areas, with tags on eight turtles (Table 1) transmitting long enough to reveal southerly destinations (Fig. 1). Two of these animals journeyed to pelagic areas off the coast of South America before swimming northwest (Fig. 1a, g). The remaining six turtles migrated to waters adjacent nesting beaches; four to the Lesser

Antilles (Fig. 1b–d, f), one to Trinidad (Fig. 1e), and one to Panama (Fig. 1h). Migration to waters adjacent nesting beaches was direct: once turtles assumed their southward migration, their rate of travel did not decrease until they arrived in nearshore waters (Fig. 2).

Turtles did not generally follow common paths on their southward and northward migrations, and even individual turtles utilised different routes while journeying to and from northern waters. However, the tracklines south for turtles C and D, tagged in the same area within 25 h of each other, were remarkably similar (Fig. 1c, d). While utilising northern coastal waters, these turtles were generally <10 km apart and they simultaneously departed the continental shelf and started migrating south at the beginning of November (Table 1). Both turtles then swam to the Lesser Antilles. Turtle C occupied waters between the islands of Grenada, Los Testigos (Venezuela), and Tobago for only 3 weeks (5–23 February 2002) before heading north again (Fig. 1c). However, turtle D restricted his movements to waters adjacent a string of islands, bordered by St. Lucia to the north and Grenada to the south, for 3 months (15 January to 17 April 2002) before transmissions ceased (Fig. 3). During this time, the turtle remained in waters on the eastern side of the islands (where most nesting occurs), only briefly venturing into the Caribbean Sea in the area between St. Lucia and St. Vincent. Turtle D's tag resumed transmitting 6 months later (11 October to 10 December 2002) in shelf waters of the mid-Atlantic Bight (40.8°N, 70.6°W) where he had resided for a part of the previous summer. Remarkably, transmissions from this tag resumed for a second time in late March 2003, placing turtle D in the same region of the Lesser Antilles he had occupied during the previous winter (Fig. 3). The intermittent performance of turtle D's transmitter may have reflected periodic epibiont fouling of the saltwater switch, a conductivity sensor that suppresses transmissions when the tag is submerged.

While four male leatherbacks ranged broadly in the vicinity of nesting beaches and inhabited waters off

nesting beaches on multiple islands (Fig. 1b–d, f), two turtles (turtles E and H) restricted their movements to relatively small areas off specific nesting colonies. Turtle E swam to waters off Trinidad, where he remained resident for 44 days in a nearshore area (approximately 50 km²) off the northeast tip of the island (Fig. 4) before returning to coastal waters off Atlantic Canada (Fig. 1e). In the following year, this turtle returned to the same site off Trinidad at the same time (last week of February; Fig. 4). Turtle H was the only male to venture to a Western Caribbean nesting colony, swimming to waters off the Bocas del Toro Archipelago in Panama where he resided for 96 days (Fig. 5) before assuming a northward journey.

Behaviour in waters off nesting beaches was characterized by slower rates of travel than that associated with long-distance movement (Fig. 2, Fig. 6a, b). Diving behaviour varied between two turtles equipped with SLTDRs. After arriving in nearshore waters off Trinidad, turtle E's diving behaviour changed markedly. Dive duration decreased, and more time was spent at shallower depths (Fig. 6c, e). In contrast, arrival in waters off the nesting beaches was not punctuated by similar changes in the diving behaviour of turtle F (Fig. 6d, f).

A diel pattern in surface activity during the breeding period was observed in turtle E and turtle F. Turtle E spent more time near the surface (water depth < 2 m) during the day than during the night (day mean = 21.23%, SD = 11.04%; night mean = 16.23%, SD = 6.47%; $P = 0.058$, Wilcoxon rank-sum test). This difference was more pronounced in turtle F (day mean = 65.94%, SD = 25.97%; night mean = 14.06%, SD = 4.52%; $P = 0.029$, Wilcoxon rank-sum test).

Turtle E exhibited distinct diel changes in diving behaviour in the vicinity of the nesting beaches. Diving was shallower during the night than during the day ($P < 0.05$, t test), with a high proportion of time spent during the day at or near the ocean floor (24–50 m, Fig. 7a). This same pattern was not observed in turtle F. While this male did spend more time diving to depths > 12 m during the night versus during the day, a large

Table 1 Summary information for eight male leatherback turtles equipped with satellite tags off Nova Scotia, Canada. *CCL* Curved carapace length; *Location* location-only satellite tag; *SLTDR* satellite-linked time-depth recorder; *N.S.* waters off mainland Nova Scotia; *C.B.I.* waters off Cape Breton Island.

Turtle ID	CCL (cm)	AVID microchip ID	Instrument	Area tagged	Date instrument deployed	Start of southward migration	Duration of tracking (days)
A	152.9	021-537-019	Location	C.B.I.	25 August 2000	21 October 2000	235
B	144.3	021-358-795	Location	C.B.I.	27 August 2000	21 October 2000	247
C	143.8	021-079-837	Location	N.S.	13 August 2001	1 November 2001	276
D	155.7	None	Location	N.S.	14 August 2001	1 November 2001 26 November 2002	615
E	168.5	None	SLTDR	N.S.	19 July 2003	7 October 2003 24 October 2004	600
F	152.9	021-832-882	SLTDR	C.B.I.	3 September 2001	14 September 2001	145
G	140.0	021-587-338	Location	N.S.	12 August 2003	12 August 2003	250
H	154.0	020-859-314	Location	C.B.I.	26 August 2003	18 October 2003	290

proportion of time was spent in waters <12 m during the day (Fig. 7b).

A comparison of when turtle E was resident off Trinidad (29 February to 12 April 2004) relative to the seasonal distribution of nesting activity on Matura Beach, one of the island's largest nesting centres,

revealed that this male arrived in coastal waters at the very start of the nesting season and departed prior to peak nesting (Fig. 8a). A similar pattern was observed in turtle H, a male that was resident in waters off Panama in 2004. Leatherbacks nesting in Panama are considered part of a larger colony that includes the index beach of Gandoca in adjacent Costa Rica (Chacón et al. 1996; Chacón 1999; Troëng et al. 2004). Turtle H arrived in his residency area in late January, prior to the start of the 2004 nesting season at Gandoca Beach, and departed on 1 May, around the time of peak nesting activity (Fig. 8b).

Discussion and conclusions

Although Pritchard (1982) suggested that leatherbacks do not mate in the vicinity of nesting beaches and Eckert and Eckert (1988) proposed that mating occurs prior to, or during migration to nesting areas, the results presented here suggest that mating does occur near Caribbean nesting colonies, and that many male turtles migrate directly to breeding areas from temperate foraging grounds.

Courtship behaviour in loggerhead turtles (*Caretta caretta*) has been observed during aerial surveys conducted off the coast of Georgia and Florida, states that support large nesting populations of this species (Frick et al. 2000). If similar aerial surveys were conducted to correspond with peak abundance of leatherbacks in waters adjacent their nesting beaches, it is possible that copulation in this species would be observed more regularly.

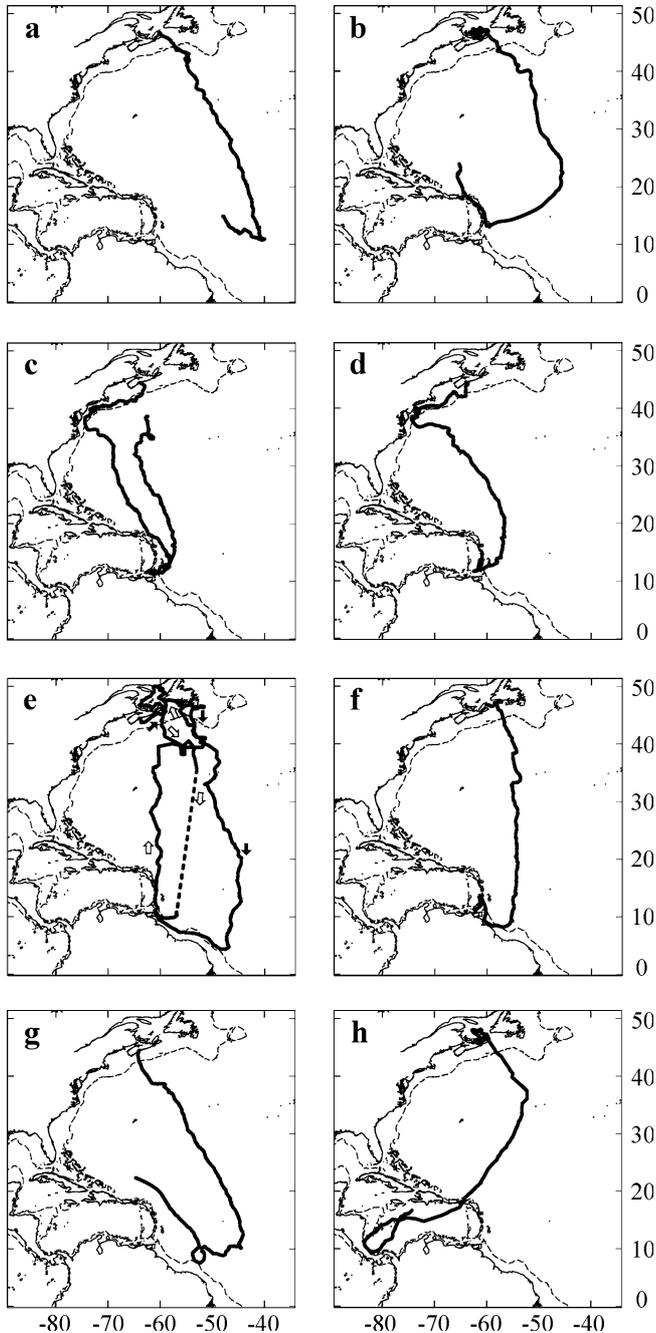


Fig. 1 Movements of eight male leatherback turtles (turtles A–H, panels a–h) satellite tagged off Nova Scotia, Canada. Dashed lines represent 1,000 m depth contour. Turtle E: dotted line corresponds to segment of track for which no positions were received; solid arrows indicate direction of travel in 2003; open arrows indicate direction of travel in 2004 and 2005. Tracks of turtles C and E from James et al. (2005); track of turtle E updated to 10 March 2005

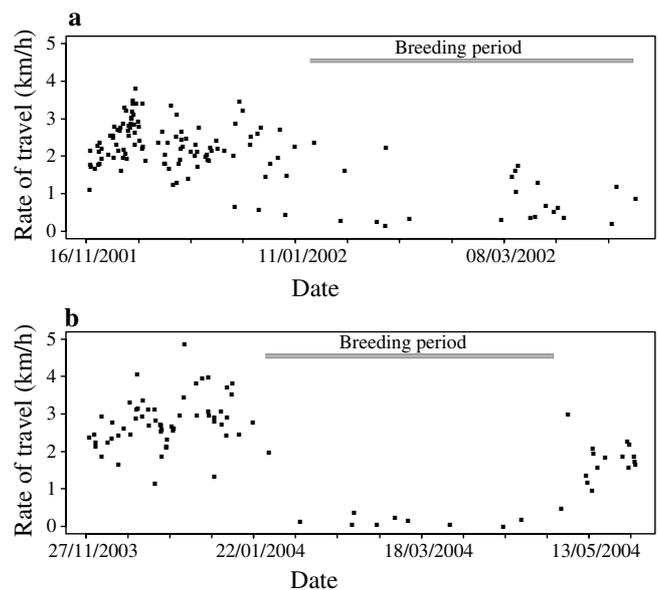


Fig. 2 Representative plots of rates of travel for male leatherback turtles during migration and while resident in breeding areas. a Turtle D. b Turtle H. Calculations of rate of travel begin 2 months before arrival in breeding area

It does seem strange, however, that more reports of mating by leatherbacks near large nesting colonies such as Trinidad and Panama have not been recorded. This may reflect that most observations of mating are probably made by fishers who are unlikely to report or formally document their observations. This appears to be the case in Trinidad, where one of us (S.A.E.) has interviewed fishers and confirmed that mating is occasionally observed off the north and east coasts of the island. Infrequent reports of mating may also reflect a true scarcity of observations. While studies of mating in most species of sea turtle have been limited to surface observations (e.g. Frick et al. 2000; Godley et al. 2002), underwater studies of green turtles (*Chelonia mydas*) have shown that copulation also regularly takes place on the ocean floor (Booth and Peters 1972). Behavioural data from turtle E raise the possibility that this may also be the case for leatherbacks, at least off those nesting areas where water depths are relatively shallow. While resident off Trinidad, turtle E spent much of his time during the day at or near the bottom (Fig. 7a), where the water depth was generally < 50 m (Fig. 4).

Turtle E's choice of residence area in nearshore waters off Trinidad deserves special mention. Trinidad supports one of the five largest leatherback nesting colonies in the Atlantic, with an estimated population of 1,800–2,000 females (Eckert 2001). Therefore, waters off the island represent a logical area for male turtles to seek mating opportunities, as encounter rates with females

will be relatively high. Moreover, turtle E's highly localized movements off Trinidad are readily explained, as they were limited to an area off Golera Point (Fig. 4) that constitutes the epicentre of interesting habitat for female turtles from the island's largest nesting beaches (S.A. Eckert, unpublished data). It is likely that breeding ranges of many other males incorporate these waters, as females are concentrated here during the nesting season. Turtle H's localized movements off the Bocas del Toro Archipelago (Fig. 5), which constitutes part of the fourth-largest leatherback nesting colony in the world (Troëng et al. 2004), provide a comparable example. In contrast, mating opportunities may be relatively scarce for males returning to waters adjacent smaller nesting colonies. Therefore, to maximize mating success, these males may have to range more broadly during the breeding season to find mates than those returning to waters off large nesting colonies. This is precisely the pattern we observed among the four males that migrated to waters off beaches in the Lesser Antilles (turtles B–D, F), where individual nesting populations number in the tens, rather than hundreds or thousands of animals. Rather than positioning themselves off specific islands, as was the case with turtle E and turtle H, the breeding ranges of these males appeared to include waters off several islands (e.g. Fig. 3), where they likely take advantage of mating opportunities with females from different nesting populations.

The four turtles that utilized waters near islands in the Lesser Antilles (turtles B–D, F) may also have been attempting to secure mating opportunities not only with those females using local nesting beaches, but also with females entering the Caribbean Sea en route to insular Caribbean nesting beaches. Therefore, some breeding ranges may facilitate mating with turtles from both proximate and distant colonies.

Male fidelity to courtship areas has been documented in other species of sea turtle (Limpus 1993); however, without detailed information on the movements of male leatherbacks spanning multiple breeding seasons, it is not possible to determine if males have long-term fidelity for particular breeding sites, or if they simply opportunistically seek mates over a broad geographic area. Our results are consistent with fidelity to specific breeding destinations. This suggestion is supported by the migration of several turtles through shelf waters off large nesting colonies, en route to more distant breeding sites. For example, in 2004, turtle E maintained a high rate of travel while swimming through waters off French Guiana and Suriname, countries that support the largest nesting colony in the world (Spotila et al. 1996), and did not stop until he reached coastal Trinidad (Fig. 6a). Similarly, turtle H rapidly transited between the U.S. and British Virgin Islands, both of which host nesting populations of leatherbacks (Boulon et al. 1996; Hasting 2003), while entering the Caribbean Sea en route to the Bocas del Toro archipelago in Panama (Fig. 5). Again, his rapid movement through these potential breeding sites demonstrates that he did not seek mating

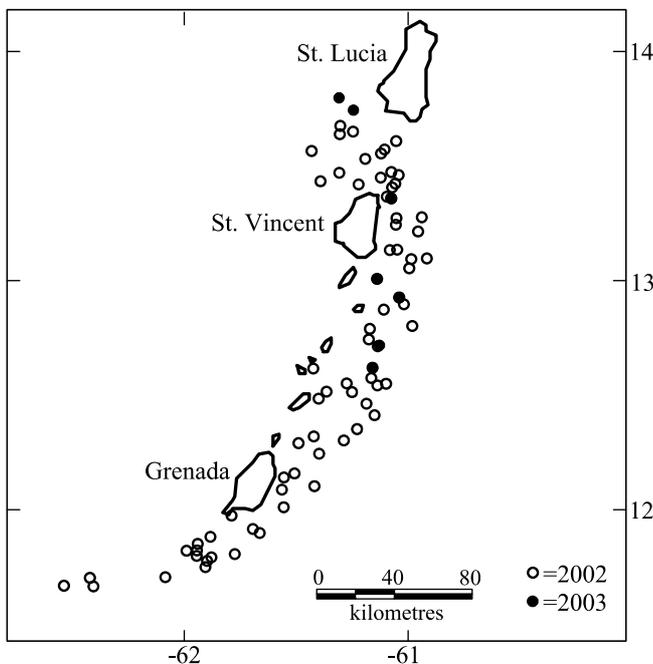


Fig. 3 Male leatherback turtle fidelity for a breeding area adjacent nesting beaches in the Lesser Antilles (turtle D). *Open circles* are positions of turtle D from 12 January to 11 April 2002, when satellite tag transmissions ceased. *Solid circles* are positions from 25 March 2003, when transmissions resumed, to 20 April 2003, when transmissions ceased

Fig. 4 Remigration of a male leatherback to a coastal breeding area off Trinidad (turtle E). *Solid circles* are positions from 2004; *open circles* are positions from 2005; *arrows* show direction of travel. *Inset* shows locations of turtle while resident off the island from 28 February to 12 April 2004 and 26 February to 10 March 2005 (when track was last updated)

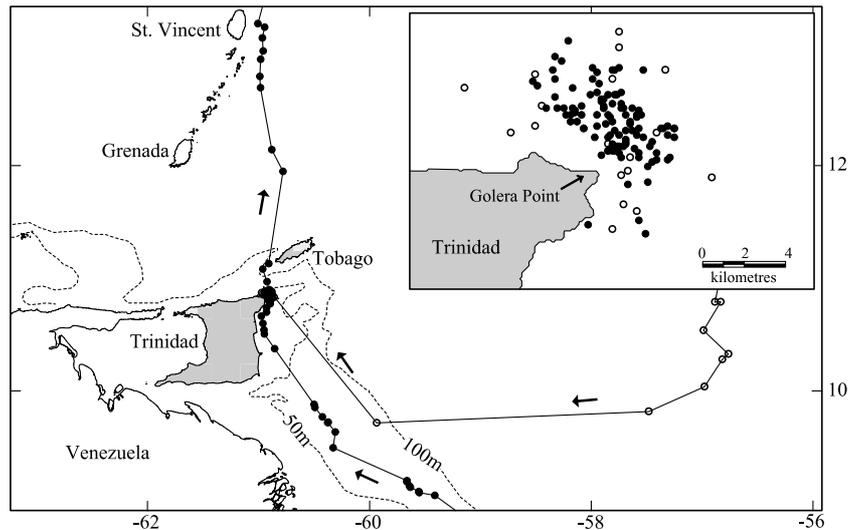
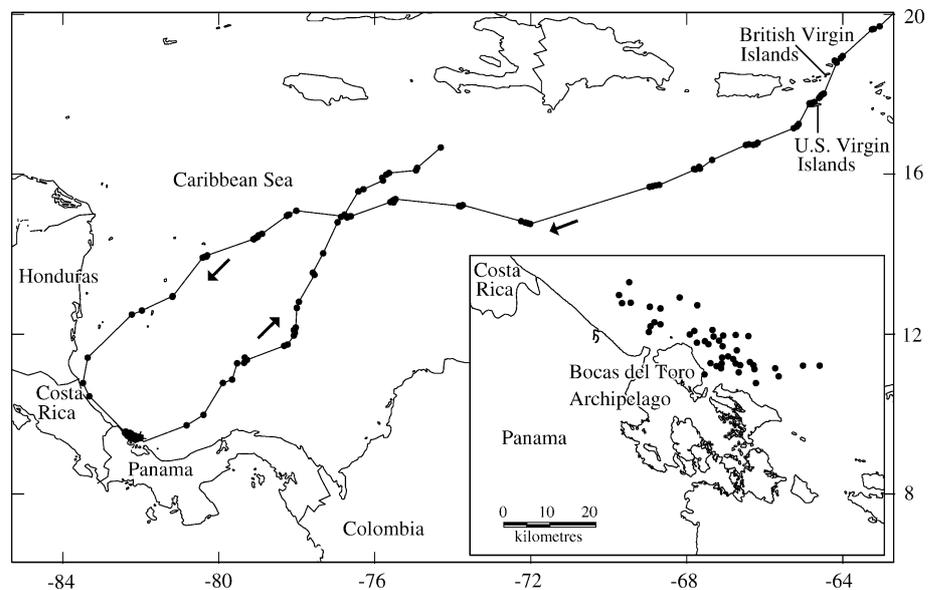


Fig. 5 Male leatherback migration to and departure from coastal waters off the Bocas del Toro Archipelago in Panama (turtle H). *Arrows* show direction of travel. *Inset* shows positions of turtle while resident in the area from 26 January to 1 May 2004



opportunities there, but instead was destined for an alternative breeding area.

The most convincing evidence for male leatherback fidelity for specific breeding areas comes from long-term telemetry data from two turtles. Our 20-month tracking of turtle D revealed return movements to a breeding range encompassing waters adjacent nesting beaches in the Lesser Antilles (Fig. 3). Moreover, turtle E, tracked for a similar duration, remigrated to the same area off Golera Point, Trinidad, in 2 consecutive years (Fig. 4). These results indicate that some male leatherbacks that forage in temperate waters of the northwest Atlantic return to breeding areas annually. This is consistent with males migrating more frequently to breeding grounds than females, a pattern that has been reported for other sea turtle species (Limpus 1993). However, the tracks of turtles A and G suggest that if mating activity is limited to waters adjacent nesting beaches, not all males may

breed every year. A return to breeding areas every 2–3 years would parallel the remigration interval between nesting seasons for most female Atlantic leatherbacks (Boulon et al. 1996).

In the absence of conclusive genetic results, it is not known whether male leatherbacks exhibit philopatry to breeding areas in the vicinity of natal beaches; however, such behaviour is likely, as it has been reported in other species of sea turtle (FitzSimmons et al. 1997) and would be consistent with regional homing exhibited by nesting females.

Diving data from turtle E and turtle F reveal variability in male behaviour at breeding sites. During the day, turtle E, occupying shallow (maximum depth < 80 m) nearshore waters, spent much of his time at or near the bottom (Fig. 7a), whereas turtle F, occupying deeper waters (maximum depth 200 m), spent more time at depths ≤ 12 m (Fig. 7b). Dive duration also varied

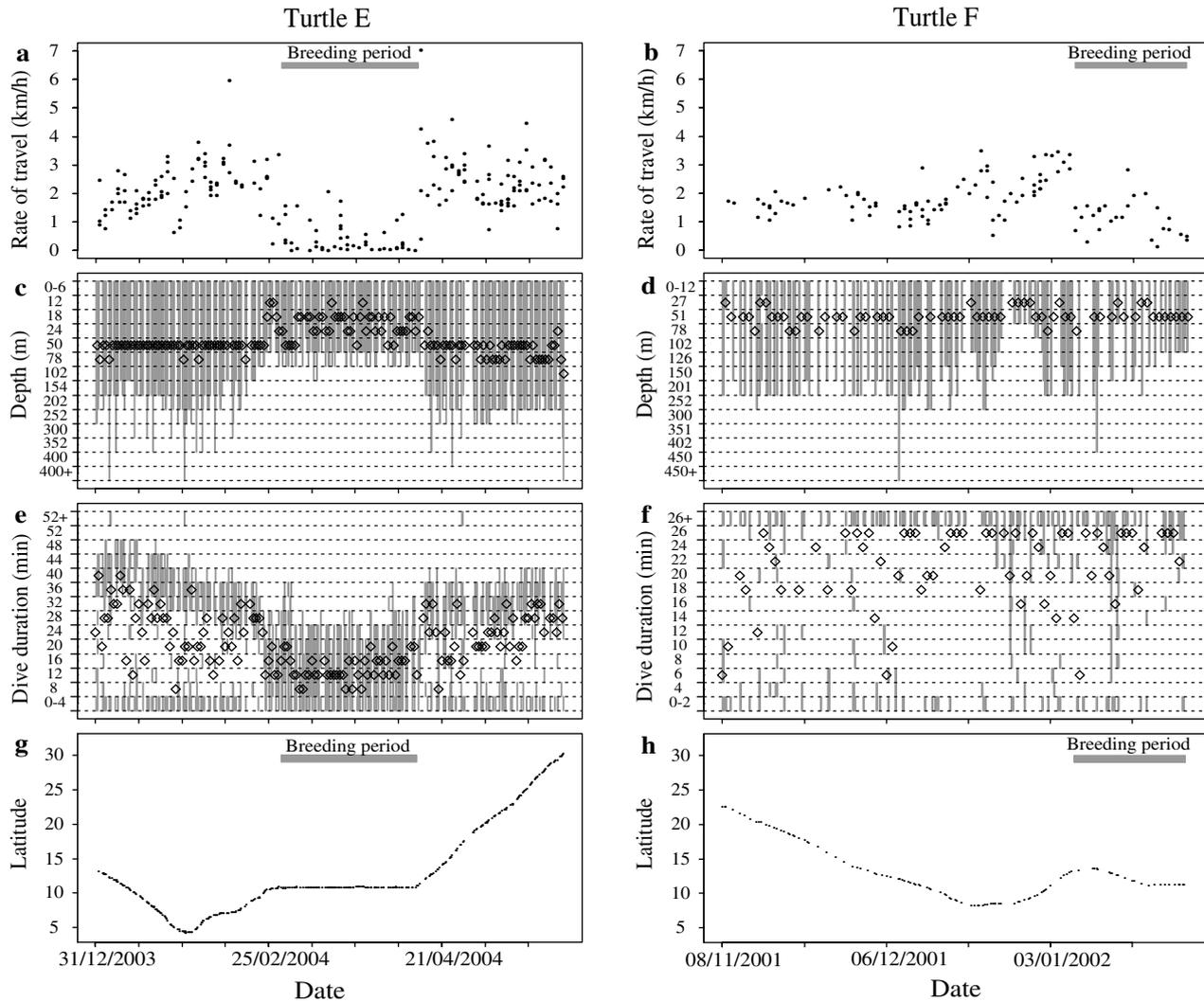


Fig. 6 Behaviour of turtles E (left column) and F (right column) during migration and while resident in breeding areas in tropical waters. **a, b** Rate of travel. **c, d** Dive depth. The vertical bars represent the depth range sampled over 6-h periods for which data were received. The deeper limits of 14 depth ranges are identified on the left-hand axis. Diamonds show midpoint of depth range in which daily mean falls. **e, f** Distribution of dive durations (per 6-h sample). Vertical bars indicate the range for each 6-h period for which data were received. The upper limits of 14 dive duration ranges are identified on the left-hand axis. Diamonds show midpoint of duration range in which daily mean falls. **g, h** Latitudinal movement

between the two males, with turtle E (Fig. 6e) completing much shorter dives than turtle F (Fig. 6f) in the vicinity of the nesting beaches. Much of this variability may reflect that these animals were occupying areas characterized by differences in bathymetry, prevailing currents, proximity to nesting beaches, and so forth. Bathymetry has been shown to strongly influence the diving behaviour of female leatherbacks, with turtles in the shallow South China Sea routinely diving near the bottom, while turtles off St. Croix (U.S. Virgin Islands) undertake much deeper dives with virtually no bottom time (Eckert et al. 1996).

Our results show that male leatherbacks E and H arrived in waters adjacent nesting colonies before the nesting season began (Fig. 8a, b). This is probably a behavioural adaptation to increase reproductive fitness as males arriving in breeding areas early will maximize their potential for mating with multiple females before their first clutches of eggs are laid. The males in this study also departed breeding areas around the time of peak nesting activity on nearby beaches. This pattern has been observed in other species of sea turtle (Plotkin et al. 1996) and likely reflects a decrease in the number of opportunities for successful mating, as females of some species will reject the advances of males after they have started nesting (Booth and Peters 1972). Moreover, while mating was not observed in this study, the timing of male arrival and departure from residency areas relative to nesting activity on nearby beaches does correspond with the temporal distribution of mating reported for other sea turtles species (Booth and Peters 1972; Godley et al. 2002).

As foraging opportunities for sea turtles may be very limited in breeding areas and energy expenditure by males during the breeding period is high (Jessop et al. 2004), a rapid return to productive foraging areas

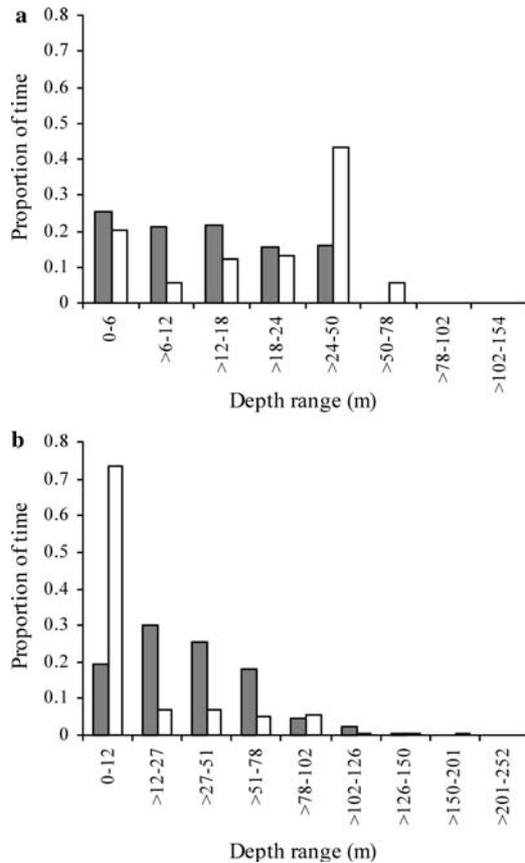


Fig. 7 Diel dive patterns of male leatherback turtles during residency periods off nesting beaches: mean proportion of time spent in different depth ranges. *Solid bars* show behaviour at night (20:00–01:59 local time) and *open bars* show behaviour during the day (08:00–13:59 local time). **a** Turtle E, 28 February to 12 April 2004. **b** Turtle F, 7–26 January 2002

following mating is probably important. This suggestion is supported by the tracking data from the males in this study. In all cases, departure from the breeding area was followed by a northward migration (Fig. 1), characterized by rates of travel higher than those recorded in breeding areas (e.g. Figs. 2b, 6a).

During the interesting interval, female leatherbacks from Caribbean nesting colonies range broadly from their nesting sites (Eckert et al. 1989; Keinath and Musick 1993; Eckert 2002). By contrast, some of the males we tracked remained in relatively small areas near nesting beaches throughout the breeding period. It may be possible that female leatherbacks move farther offshore to avoid continual pursuit from concentrations of males seeking mating opportunities in nearshore waters.

Entanglement in fishing gear in waters adjacent nesting beaches has recently been identified as an important source of mortality for leatherbacks (Chevalier 2001; Lee Lum 2003). While sex ratios of entangled turtles are not currently available, in addition to mature females, male leatherbacks may be vulnerable to entanglement in these areas, as they appear mainly to restrict their movements during the breeding period to nearshore waters, where fishing effort is highest.

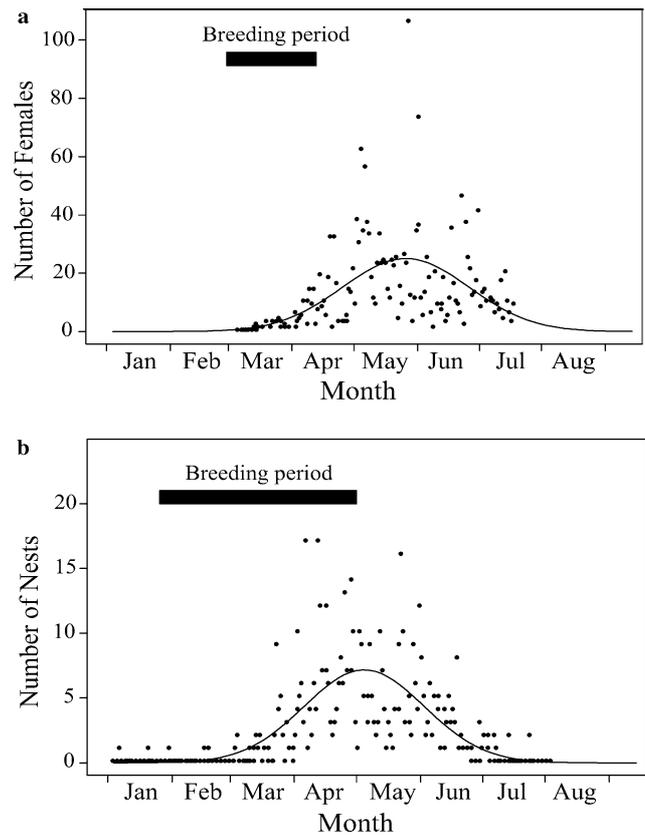


Fig. 8 Timing of male leatherback residency in waters off nesting beaches relative to the temporal distribution of nesting. *Solid bars* indicate residency period. **a** Turtle E. *Solid circles* represent number of females encountered each night from 2 March to 17 July 2004 at Matura Beach, Trinidad. Line fit for normal distribution by least squares after log transformation. **b** Turtle H. *Solid circles* represent nest counts from nightly surveys conducted from 1 January to 3 August 2004 at Gandoca Beach, Costa Rica (D. Chacón, unpublished data). Line fit for normal distribution by least squares after log transformation

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