# Report

# Phenotypically Linked Dichotomy in Sea Turtle Foraging Requires Multiple Conservation Approaches

Lucy A. Hawkes,[1] Annette C. Broderick,[1]
Michael S. Coyne,[2] Matthew H. Godfrey,[3]
Luis-Felipe Lopez-Jurado,[4] Pedro Lopez-Suarez,[4]
Sonia Elsy Merino,[5] Nuria Varo-Cruz,[4]
and Brendan J. Godley[1,*]
[1] Marine Turtle Research Group
Centre for Ecology and Conservation
School of Biosciences
University of Exeter, Cornwall Campus
Penryn TR10 9EZ
United Kingdom
[2] Marine Geospatial Ecology Lab
Nicholas School of the Environment and Earth Sciences
Duke University
A321 LSRC, Box 90328
Durham, North Carolina 27708-0328
[3] North Carolina Wildlife Resources Commission
1507 Ann Street
Beaufort, North Carolina 28516
[4] Universidad Las Palmas de Gran Canaria
Departamento de Biología
35017 Las Palmas de Gran Canaria
[5] Instituto Nacional de Desenvolvimento das Pescas
C.P. 132
Mindelo, Sao Vicente
Islas de Cabo Verde

## Summary

Marine turtles undergo dramatic ontogenic changes in body size and behavior, with the loggerhead sea turtle, *Caretta caretta*, typically switching from an initial oceanic juvenile stage to one in the neritic, where maturation is reached and breeding migrations are subsequently undertaken every 2–3 years [1–3]. Using satellite tracking, we investigated the migratory movements of adult females from one of the world's largest nesting aggregations at Cape Verde, West Africa. In direct contrast with the accepted life-history model for this species [4], results reveal two distinct adult foraging strategies that appear to be linked to body size. The larger turtles (n = 3) foraged in coastal waters, whereas smaller individuals (n = 7) foraged oceanically. The conservation implications of these findings are profound, with the population compartmentalized into habitats that may be differentially impacted by fishery threats in what is a global fishing hotspot [5]. Although the protection of discrete areas containing coastal individuals may be attainable, the more numerous pelagic individuals are widely dispersed with individuals roaming over more than half a million square kilometers. Therefore, mitigation of fisheries by-catch for sea turtles in the east Atlantic will likely require

*Correspondence: bgodley@seaturtle.org

complex and regionally tailored actions to account for this dichotomous behavior.

## Results and Discussion

We tracked ten postnesting loggerhead turtles from the Cape Verde Islands and integrated spatial movements with a range of remotely sensed oceanographic information. Data highlighted two distinct movement patterns.

Group 1—neritic turtles (n = 3; individuals a–c)—traveled southeast after the completion of nesting. Individuals a and b followed a relatively direct path down the West African coast (traveling for 35 and 50 days, straightness index 0.73 and 0.85, respectively) to foraging areas off Guinea and Sierra Leone (mean of mean displacement from release location for all turtles in this group 1253 km; Figure 1A). These turtles remained within a relatively discrete foraging area inside the 100 m isobath for the duration of the tracking project (foraging area: 112, 177, and 421 km$^2$, respectively; Figure S1 in the Supplemental Data available online). Mean ocean depth at filtered locations was 60 m, 26 m, and 59 m for locations received from turtles a, b, and c, respectively. With more than 89% of locations received from these individuals in water <100 m deep (range 1–3511 m), it is likely that these turtles foraged benthically. Dive-profile data collected by the transmitter on individual c demonstrated long dives to the seafloor (approximately 60 m water depth; Figures 2A and 2B).

Group 2—oceanic turtles (n = 7; individuals d–j)—initially headed eastward from Cape Verde, generally toward mainland Africa. Their subsequent movements were not typically directed to one specific foraging area (mean straightness index 0.33 ± 0.38, standard deviation [SD]), and they traveled extensively over a wide range from 10.5° to 19.1°N and 16.4° to 25.0°W (Figure 1B). They did not appear to be seeking a specific location; rather, they were likely foraging while traveling in the oceanic environment with mean distance covered on a weekly basis (with filtered data) ranging from 111 to 205 km (mean of means 160 ± 33 km). These large-scale movements were mostly restricted to the territorial waters of Mauritania and Senegal, but also included waters of The Gambia, Guinea, and Guinea Bissau (mean of mean displacement from release location for all turtles: 415 km ± 118 km, range 177–544 km). Water depth at the filtered locations for these turtles ranged from 3–5005 m with more than 98% of locations centered in water deeper than 500 m. Information collected by the transmitter on individual d demonstrated that this turtle was making short, shallow dives in deep oceanic waters, suggesting that this group of animals forages epipelagically (Figures 2C and 2D). Comparison of the wandering movements of these turtles with ocean surface-current data (Movie S1) shows clear correspondence between turtle movement and current speed and direction, suggesting that movements are at least in part driven by local surface currents. We also propose that the turtles
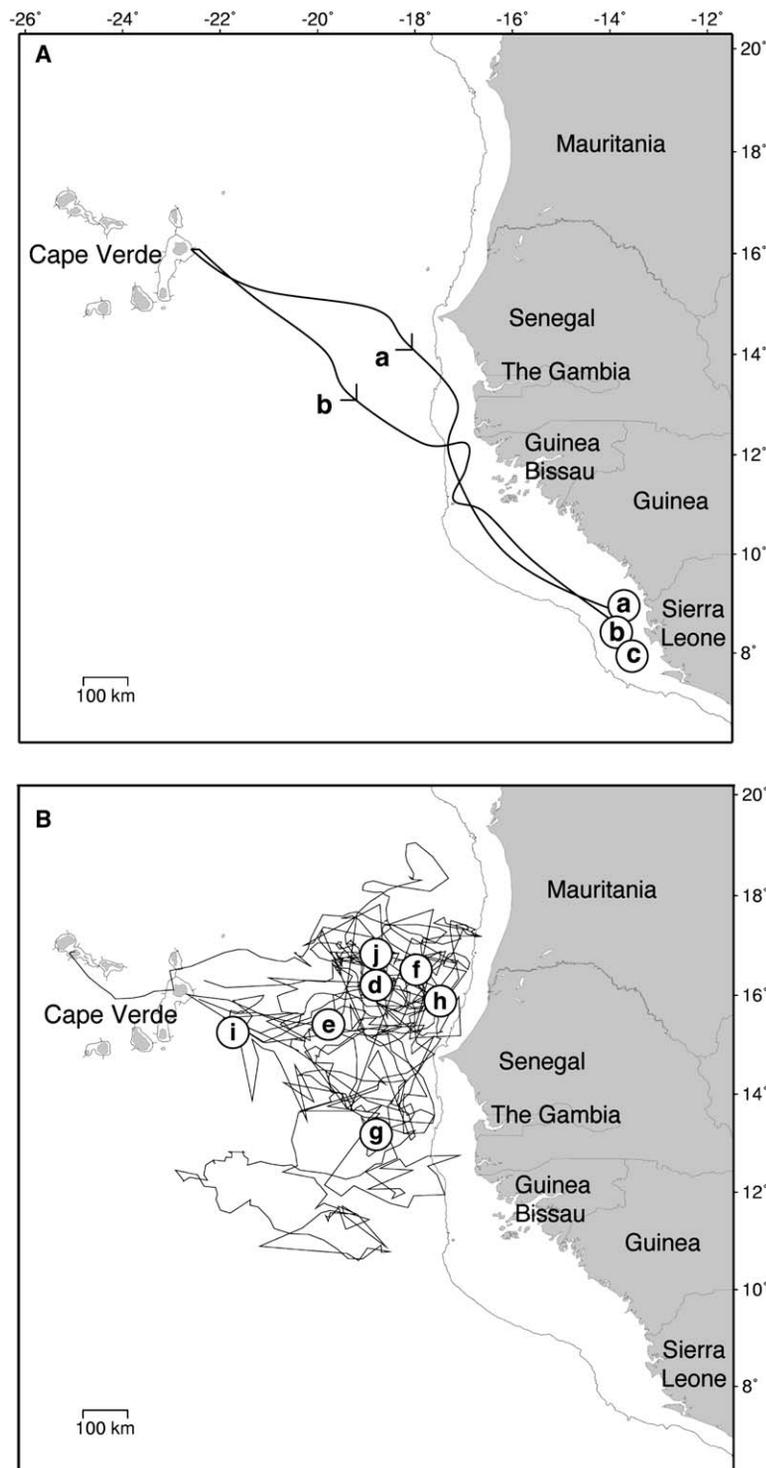
Figure 1. Migratory Patterns and Foraging Areas of Postnesting Loggerhead Turtles

Patterns of movement of the two groups are remarkably different.

(A) Migratory route and foraging areas of group 1 turtles (a–c) to the coast of Guinea and Sierra Leone. Note that for individual c, too few transmissions were received on migration to allow accurate reconstruction of the route, but reliable transmissions resumed in the foraging area.

(B) Routes of group 2. For both graphics, labeled circles mark the endpoint of each migratory route. The 500 m isobath is marked.

were occasionally amending their positions in and between local surface currents, allowing them to remain within the highly productive waters off West Africa throughout the tracking study. There is notable individual variation within the oceanic foraging pattern, likely largely driven by the stochastic nature of the oceanic environment.

Although sample size in this study was limited, the major findings, based on long-term tracking data, suggest a clear dichotomy in behavior for adult turtles

from Cape Verde. In the study animals, body size correlated markedly with foraging mode, with group 1 turtles (foraging neritically) being significantly larger than turtles from group 2 (foraging oceanically; Mann Whitney $U_{1,9} = 0.00$, $p < 0.05$, Figure 3). The West African region over which the study animals dispersed is a hotspot of primary productivity within the tropical Atlantic (Figure S2), and we extracted data for chlorophyll $\alpha$ levels to see whether the behavioral differences between the two groups were linked to local differences

**A**

## Neritic
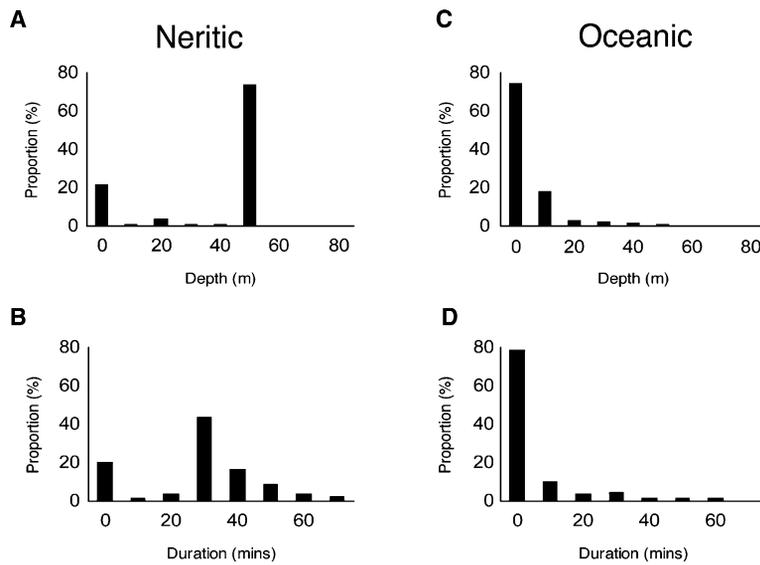


**C**

## Oceanic



**B**



**D**



Figure 2. Contrasting Dive Patterns of Neritic and Pelagic Turtles

Neritic turtles make long, deep foraging dives whereas oceanic turtles make short, shallow dives to feed in the epipelagic zone. Frequency distribution of (A) maximum depth per dive (44.5 ± 21.9 m) and (B) dive duration (34.6 ± 18.5 min) for neritic individual c (n = 245 dives) and (C) maximum depth per dive (8.9 ± 9.7 meters) and (D) dive duration (7.9 ± 12.9 min) for oceanic individual d (n = 791 dives) are shown.

in resource availability or quality. The coastal foraging areas used by neritic turtles showed significantly higher primary productivity than those used by oceanic turtles (Mann Whitney $U_{1,8} = 1$, $p < 0.05$). Water temperatures experienced were not significantly different between the two groups (Mann Whitney $U_{1,9} = 2$, $p = 0.07$).

In the generally accepted life-history model for the loggerhead turtle, hatchlings leave their natal beach and enter the sea, traveling to oceanic habitats and foraging on small, floating items such as *Sargassum*, molluscs, cnidarians, and crustacea [4, 6]. When juveniles reach sizes between 40 and 60 cm carapace length, they begin to recruit to the neritic zone close to their natal area [1, 7] while other individuals remain in the oceanic habitat or shuttle between the two [3]. The age of juvenile loggerheads at this ontogenetic switch is thought to be approximately 14 years [8]. At sexual maturity (circa 30 years [8]), adult turtles will switch from subadult to adult neritic foraging habitats, feeding mainly on large benthic slow-moving or sessile organisms [1, 9]. These adult neritic foraging habitats have been widely

identified for nesting populations in the Atlantic [1, 9], Pacific [10, 11], and Indian Oceans [12] and the Mediterranean Sea [13, 14]. Thereafter, adults exhibit philopatry, shuttling between natal breeding areas and their neritic foraging areas [2, 4].

It is apparent that the life history of adult loggerhead turtles from Cape Verde differs markedly from this model. Epipelagic foraging has been recorded for adult female loggerheads in Japan [15], where there is a similar dichotomy in body size and foraging strategy. However, routine epipelagic foraging in an adult loggerhead population has not been reported before in the Atlantic. It has been speculated that in the western Atlantic, loggerhead sea turtles recruit to the neritic zone by the time they have reached 64 cm in order to maximize growth rates relative to the oceanic zone [4]. However, we have recorded turtles of up to 86.5 cm foraging oceanically with 91% of nesting turtles in this population being this size or smaller. Although this study includes a limited number of animals, smaller body size linked to oceanic foraging suggests that this behavior may be exhibited
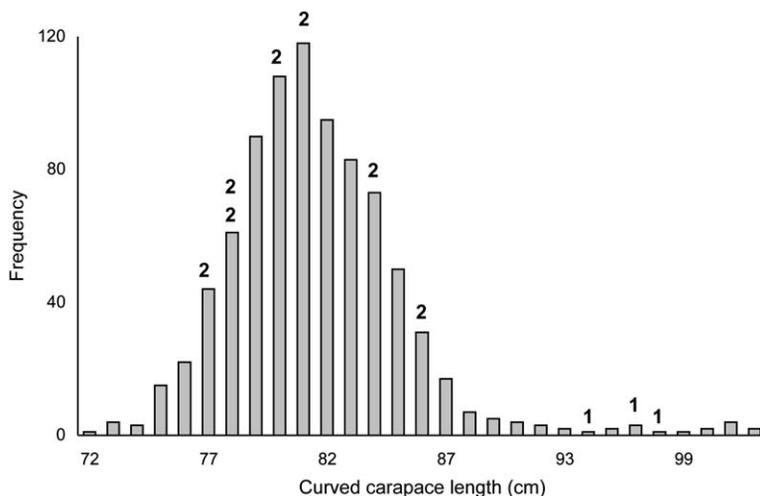


Figure 3. Length-Frequency Histogram of the Cape Verde Loggerhead Turtle Population

The nesting population at Cape Verde exhibits a broad range of body sizes. Frequency histogram showing carapace lengths (curved carapace length, CCL) recorded for turtles nesting at Boavista, Cape Verde, in 2004. Sizes of individuals from group 1 (neritic foraging) and group 2 (oceanic foraging) are indicated by the numbers 1 and 2, respectively.

by the majority of adults in the Cape Verde population. Interestingly, both records of oceanic foraging in adults of this species have come from insular nesting populations, and it is possible that similarities in productivity and surface currents, or other factors, account for this unusual behavior. The absolute range and limits of sizes over which these two adult strategies occur remain undefined. It is possible that oceanic foraging turtles are not able to invest as much energy into growth as turtles inhabiting coastal areas because they do not experience the high quality and abundance of prey available in the neritic. Or perhaps at a threshold carapace size, smaller oceanic turtles become large enough to capably exploit the neritic of West Africa and undergo an ontogenetic shift to coastal waters. Although growth rates have not been established for this population, other conspecific populations show little to no growth upon reaching reproductive maturity [16], suggesting that any shift between the two groups observed (oceanic and neritic) would be unlikely.

This unusual behavioral dichotomy is of particular interest, both from fundamental and applied perspectives. Intraspecific variation in body size has an important influence on life-history characteristics in many other species [17] and can lead to segregation of behavioral strategies, e.g., flying ability in albatrosses [18], migratory distance in elephant seals [19], and diving ability in marine iguanas [20]. Body size is positively correlated with fecundity in marine turtles [21] and also limits diving capacity (e.g., for foraging) in a variety of air-breathing marine animals. Larger divers exhibit better capacity for oxygen storage, lower metabolic rate, and less inertia and drag relative to smaller divers, and they are less limited in dive duration [22, 23]. For those individuals carrying dive-logging transmitters, the larger, neritic turtle in this study performed significantly deeper (Mann Whitney $U_{1,1627}$ = 107,991, p < 0.01, Figure 2) and longer (Mann Whitney $U_{1,1626}$ = 103,115, p < 0.01, Figure 2) dives than the smaller oceanic turtle.

There are higher levels of primary productivity in the coastal zone relative to oceanic waters in this study. Thus, animals foraging in the neritic likely experience more abundant and reliable food sources than oceanically foraging animals. Where they have been studied, turtles foraging benthically (i.e., in the neritic) normally feed on prey such as arthropods, decapods, gastropod molluscs, and other benthic invertebrates [6], whereas turtles foraging oceanically probably feed on epipelagic prey [24]. The fact that oceanic turtles tracked in this study moved in and out of the neritic zone at Mauritania and Senegal without stopping to forage in shallower waters is suggestive of selective pressures acting to keep the turtles in the oceanic zone. This could include factors such as smaller turtles lacking the ability to exploit coastal resources because of reduced diving capacity, increased predation risk, or reduced intraspecific competitive ability.

The presence of different migratory strategies for turtles tracked from Cape Verde has significant implications for conservation of the population at large. First, there appear to be at least two demographic units that should be considered as part of any monitoring and conservation efforts. Second, the major threat to sea turtles in West Africa comes from direct and indirect take in both artisanal and commercial fisheries [5, 25, 26] with different fisheries operating in coastal and oceanic waters. This complicates conservation efforts, especially when one considers the geographic scales involved. Larger reproductive turtles observed in this study remained in relatively discrete foraging areas off the coast of Guinea and Sierra Leone. Our results suggest that a larger proportion of the important adult reproductive population are oceanic, foraging in the waters from Mauritania to Guinea Bissau, and also in international waters (total foraging area for oceanic turtles in this study was greater than half a million square kilometres). Finally, given the range demonstrated thus far, conservation of this population necessitates international cooperative efforts in seven African states (Cape Verde, Mauritania, Senegal, The Gambia, Guinea Bissau, Guinea, and Sierra Leone). In addition, the waters of the eastern central Atlantic represent a hotspot for pelagic longline fisheries [5], with the majority of the fishing fleet from China, Equatorial Guinea, and several Central American countries (e.g., Belize, Honduras, and Panama). The problems inherent in implementing and enforcing measures to reduce or eliminate by-catch are obvious. Widespread use of "flags of convenience" throughout the region, whereby vessel owners register in foreign nations to exploit more relaxed vessel registration standards, labor laws, and conservation regulations, complicates matters further. Conservation priorities should focus on less harmful gear types and increased coverage of observer and training programs.

Knowledge of marine vertebrates lags behind that of many other groups, hindering their management and conservation [27]. This study has underlined how satellite tagging can quickly facilitate tremendous insights into the range, routes, and foraging behavior of marine turtles. We have uncovered what appears to be a fundamental dichotomy in life-history strategy of Atlantic loggerhead turtles that has only been previously described in Japan [15] and never before in the Atlantic Ocean. Our findings hold profound conservation ramifications with regard to population monitoring and fisheries-impact mitigation.

### Experimental Procedures

Transmitter attachment was carried out according to previously tested methods [28], and spatial movement data were automatically downloaded, interpreted and analyzed with the Satellite Tracking and Analysis Tool (STAT; [29]), where they were also integrated with sea surface-current, bathymetry, and chlorophyll data. Transmitters were Sirtrack Kiwisat model 101's (n = 6, individuals a, b, e, and h–j), Telonics model ST-14's (n = 2, individuals f and g), and dive-recording Sea Mammal Research Unit 9000× Satellite Relay Data Loggers (n = 2, individuals c and d; for more details, see Table S1). Individuals a, b, and d–i were tracked after the nesting season of 2004, and individuals c and j were tracked in 2005. Transmitters gave locations for 57 to 566 days (mean 249 days, ± 153 SD). All location data were filtered with STAT before analysis (retained locations were those that resulted in speeds of <5 km/hr$^{-1}$ and >5° turning angle). Only one data point per 24 hr was used to reduce the effects of serial autocorrelation within the data. Data from the inter-nesting period were excluded from analyses. Straightness index was calculated as the ratio of the straight line distance between the release location and last transmitted location over the total distance traveled. Foraging areas were calculated with data from location classes 3, 2, and 1 by using Hawth's Analysis Tools for ArcGIS (http://www.spatialecology.com/htools/) and ArcGIS 9.0 to generate

minimum convex polygons. Sea surface-current (geostrophic velocity vector) data were obtained from AVISO (http://www.aviso. oceanobs.com/html/donnees/tools/citations_uk.html). Bathymetric data were sampled from the General Bathymetric Chart of the Oceans (GEBCO 1-Minute Global Bathymetry Grid, http://www.bodc. ac.uk/projects/international/gebco/gebco_digital_atlas). Chlorophyll data were sampled in a similar fashion from NASA's Ocean Color project MODIS satellite-based sensor (http://oceancolor. gsfc.nasa.gov/). Morphometric data for turtles (curved carapace length [30]) were taken as part of an ongoing nesting-beach monitoring project.

### Supplemental Data

Supplemental Data include one movie, two figures, and one table and are available with this article online at: http://www.current-biology. com/cgi/content/full/16/10/990/DC1/.

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