DEFORESTATION: RISK OF SEX RATIO DISTORTION IN HAWKSBILL SEA TURTLES

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Abstract. Phenotypic sex in sea turtles is determined by nest incubation temperatures, with warmer temperatures producing females and cooler temperatures producing males. The common finding of highly skewed female-biased hatchling sex ratios in sea turtle populations could have serious repercussions for the long-term survival of these species and prompted us to examine the thermal profile of a relatively pristine hawksbill nesting beach in Guadeloupe, French West Indies. Data loggers placed at nest depth revealed that temperatures in the forested areas were significantly cooler than temperatures in the more open, deforested areas. Using these temperatures as a predictor of sex ratio, we were able to assess the relative contributions of the different beach zones to the primary sex ratio: significantly more males were likely to be produced in the forested areas. Coastal forests are therefore important maleproducing areas for the hawksbill sea turtle, and this has urgent conservation implications. On Guadeloupe, as on many Caribbean islands, deforestation rates are high and show few signs of slowing, as there is continual pressure to develop beachfront areas. The destruction of coastal forest could have serious consequences both in terms of local nesting behavior and of regional demography through the effects on population sex ratios. Human alterations to nesting habitat in other reptile taxa have been shown to modify the thermal properties of nest sites in ways that can disrupt their ecology by allowing parasite transmission, increasing vulnerability to climate change, or rendering existing habitat unsuitable.

Key words: Caribbean; deforestation; Eretmochelys imbricata; hawksbill; nesting habitat; sea turtle; sex determination; sex ratio; temperature.

Introduction

Caribbean islands have long been associated with postcard images of swaying palm trees and white sandy beaches, but these do not accurately depict their natural state. Historically, beaches there were backed by denser vegetation, such as littoral woodland forest composed in large part of sea grape (Coccoloba uvifera), manchineel (Hippomane mancinella), and birch gum (Bursera simaruba) trees: exotic palm trees, from the Philippines and elsewhere, were introduced ~300 years ago (Beard 1949, Watts 1987). A transformed but idyllic tropical beach attracts substantial tourist dollars, but there are obvious disadvantages for the endemic flora and fauna. In addition to the destruction of native plant species, changes in coastal vegetation can adversely affect many resident species, as well as some that visit the coast intermittently, such as the hawksbill sea turtle (Eretmochelys imbricata; see Plate 1). The hawksbill, classified as Critically Endangered (Meylan and Donnelly 1999, but see also Mrosovsky 2000), is circumtropically distributed and inhabits waters in the Caribbean and tropical western Atlantic (Groombridge and Luxmoore 1989, Meylan 1999a, b). The females often nest in low densities and, unlike other sea turtle species, dig many of their nests in the vegetation behind the sandy beach

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(Diamond 1976, Mortimer 1982, Horrocks and Scott 1991, Kamel and Mrosovsky 2005).

Over the past decades, hawksbills have been the focus of conservation efforts, most of which have been aimed at reducing the take of turtles and their eggs. Overexploitation can cause a serious decline in population numbers, a trend that is often easily observed. However, another practice could also have serious implications for population stability: the anthropogenic alteration of primary sex ratios. Sea turtles, like some lizards and all crocodilians, have temperature-dependent sex determination, with the phenotypic sex of their embryos determined by the incubation temperature of the nest (reviewed in Wibbels 2003). In this case, high temperatures produce mostly females and low temperatures produce mostly males. The temperature that produces equal numbers of each sex when eggs are incubated under constant conditions is the pivotal temperature (Mrosovsky and Pieau 1991). Sea turtle sex ratios have been a source of great interest, in part due to the common finding of highly female-biased primary sex ratios and the related concern that global climate change may further increase feminization of hatchlings. For example, loggerhead sea turtles in Florida, Bahia, Brazil, and some parts of the Mediterranean are estimated to have sex ratios highly skewed toward females (\sim 80–90% female: Mrosovsky and Provancha 1989, Marcovaldi et al. 1997, Kaska et al. 1998, Godley et al. 2001), and

these observations have prompted a search for equally skewed male-producing beaches. The apparent absence of such areas has led to questions about whether Fisherian sex ratio theory, i.e., a 1:1 sex ratio when the parental costs of producing offspring of either sex are equal, applies to sea turtles or whether sampling error or recent changes in nesting habitat, for example, are responsible for the observed skews (Fisher 1930, Mrosovsky 1994). Additionally, since numbers of nesting females are often used as an index of population size, the observed increases may in fact be masking a potentially detrimental phenomenon: the decreased production of males.

Hawksbill sex ratios have been less extensively studied but data from populations in Antigua and Brazil exist. It was estimated that hatchling sex ratios were highly female-biased in Brazil (Godfrey et al. 1999), but in Antigua a more balanced sex ratio was inferred (Mrosovsky et al. 1992). The beach at Pasture Bay, Antigua, has been monitored since 1987, and habitat alterations have been documented (Hoyle and Richardson 1993). The beach used to be backed by a thick mangrove forest and coastal shrubs, but now much of the native vegetation has been cleared; there is little littoral woodland remaining and, in fact, sand temperatures are not significantly different between sunny and shaded areas (Mrosovsky et al. 1992, McIntosh et al. 2003, Glen and Mrosovsky 2004).

Therefore, we felt it important to determine the thermal profile of a relatively unaltered hawksbill beach, and Trois Ilets on Marie-Galante, Guadeloupe, is one such beach. This area hosts a regionally important nesting population of hawksbills whose numbers appear to be increasing, possibly as a result of the ban on the use of turtles and turtle products implemented by the French Government in 1991 (Chevalier and Lartiges 2001). The main nesting beach is still backed by a tract of coastal woodland forest and is one of the few stretches of coastline on Marie-Galante that has remained fairly untouched. Unfortunately, as is the case on many Caribbean islands, increasing pressure to develop the beachfront currently threatens this area. Our aim was to learn whether the presence of the forest affected the temperatures of hawksbill nesting areas and consequently, whether deforestation might have detrimental effects on the sex ratio of this already-threatened species.

METHODS

Study site

Trois Ilets beach (including a section called Folle Anse) is located on the western coast of Marie-Galante, a small island 40 km southeast of the island of Guadeloupe itself (see Plate 1). The beach is 3.3 km long and ranges from 1 to 9 m in width and is backed by forest, except for some open areas toward the southern end where sheds have been installed for public use. The forest is ~30 m wide and is composed mainly of sea grape, manchineel, and catalpa (*Catalpa* sp.) trees. Tidal

variations along the beach are negligible except during storms, which typically occur between August and October. The main nesting season appears to be between May and October, with a peak in July.

Sand temperature transects

Hobo Water Temp Pro data loggers (Onset Computer, Bourne, Massachusetts, USA) were deployed on 28 May 2002 and removed on 24 August 2003. They were deployed again on 6 June 2004 and removed on 10 October 2004. They were buried at two sand depths (30 and 60 cm) along five transects, each separated by ~500 m. Along the transects, they were placed in the following beach zones: forest (completely surrounded by trees), forest border (near the forest but not completely surrounded), and low-lying vegetation (presence of grass or beach creepers), except in one transect where the data loggers were buried in the open sand instead of the low-lying vegetation. This was done over three nesting seasons (2002, 2003, and 2004) to determine the thermal profile of the beach.

Prior to data logger placement, the depth of 15 nests was measured, defined as the distance between the surface of the sand and the bottom of the nest. The mean depth was 47.0 ± 2.3 cm, suggesting that most eggs were not incubated at depths shallower than 30 cm. Nest depths are similar to those found in other hawksbill populations (mean = 43.4 cm [Carr et al. 1966]; mean = 43.2 cm [Limpus et al. 1983]; mean = 45.5 cm [Mrosovsky et al. 1992]).

The data loggers had a resolution of 0.01°C and were guaranteed to fall within an accuracy range of $\pm 0.18^{\circ}\text{C}$, but were rechecked prior to use. They were immersed in an ice bath, and the temperatures were compared to that of a Sybron/Taylor Hg thermometer (Taylor Instruments Division, Sybron Corporation, Arden, North Carolina, USA). This thermometer had certified calibration against platinum resistance thermometers that had in turn been calibrated by the U.S. National Bureau of Standards. The temperatures deviated from that of the Hg thermometer by a maximum of $\pm 0.12^{\circ}\text{C}$. Upon removal, they were checked using the same method. The largest difference between the two calibrations was $\pm 0.15^{\circ}\text{C}$.

The temperature readings were taken every 6 h and then averaged to give a mean daily temperature for each data logger (site). All temperature groupings were calculated separately for each data logger depth and for each year. The following terminology is used: (1) mean daily zone temperature is the mean of the mean daily temperatures for data loggers (sites) in that particular zone (n=4 or 5 sites per zone, except for n=1 in the open sand zone); (2) mean seasonal site temperature is the mean of the mean daily temperatures for a particular site throughout the nesting season (e.g., 28 May to 23 November 2002; n=180 d); (3) mean seasonal zone temperature is the mean of the mean seasonal site temperatures within a particular beach zone.



PLATE 1. Female hawksbill turtle nesting in the low-lying vegetation at Trois Ilets beach, Marie-Galante, Guadeloupe. Photo credit: S. Kamel

Comparisons between forested and deforested areas

In 2004, to more accurately assess the effects of deforestation on sand temperature, data loggers were placed in two forest zones and in two adjoining deforested areas. We also placed loggers on Feuillière, a beach where palm trees are currently the only vegetation. Feuillière is located along the southeast coast of Marie-Galante ~12 km from Trois Ilets.

Nest locations

The beach zone (forest, forest border, low-lying vegetation, or open sand) in which nests were laid was recorded during nightly patrols between 28 May 2002 and 12 September 2002. Nests were assigned to one of these categories. Only nest locations from 2002 were used to estimate the primary sex ratio because data from the 2003 and 2004 seasons were incomplete. However, we included temperatures from all three years to demonstrate that 2002 was not a thermally atypical year.

Incubation durations and sex ratio

Incubation duration was calculated as the number of days between the night a nest was laid and the night the

hatchlings emerged. Nests were all laid between 10 June and 11 July (n=19). From these nests, we estimated the mean incubation duration for clutches laid in each of the four beach zones. The value for nests laid in the low-lying vegetation zone was also used for nests in the open sand zone because there were no incubation durations available for nests laid in the latter zone. Once the mean incubation duration for each zone was calculated, we estimated the thermosensitive period for sexual differentiation, which occurs during the middle third of incubation (Yntema and Mrosovsky 1982, Desvages et al. 1993). The zone-specific values (number of days) for the thermosensitive period were used as an estimate for all the nests within a particular beach zone.

Based on the mean of the mean daily zone temperatures during the thermosensitive period, we then approximated the sex ratio for each nest observed during the 2002 nesting season (n=185) using the pivotal temperature obtained for hawksbills in Antigua (Mrosovsky et al. 1992). If the mean temperature was within 0.05°C of the pivotal (29.2°C), the clutch was scored as half male and half female. If it was greater than 0.05°C from the pivotal, the clutch was scored as all female, and if it was less than 0.05°C from the pivotal,

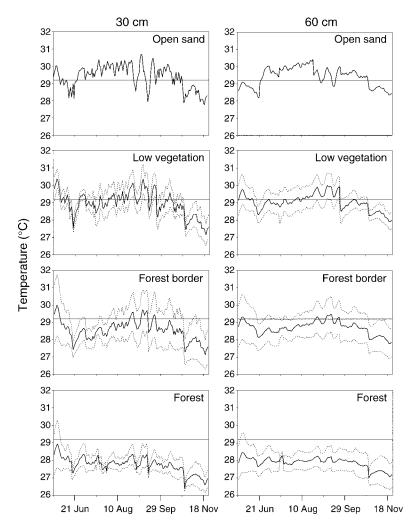


Fig. 1. Daily temperatures (mean \pm sp) over the 2002 nesting season from data loggers placed at two depths on Trois Ilets beach, Marie-Galante, Guadeloupe. Day 1 is 28 May 2002, and day 180 is 23 November 2002. Temperature data were grouped by beach zone, and each data point represents the mean daily zone temperature. The thin horizontal lines indicate the pivotal temperature for Antigua (see Mrosovsky et al. 1992).

the clutch was scored as all male. We also recalculated the sex ratio estimates for each clutch after adding 1°C to the mean temperature during the thermosensitive period to allow for potential metabolic heating of the egg mass (Glen and Mrosovsky 2004).

Data analyses

A two-factor ANOVA was used to compare sand temperatures between depths and among years for each beach zone and to compare temperatures among beach zones in all years. A single-factor ANOVA was used to

Table 1. Mean seasonal zone temperatures (°C) with 95% confidence intervals over three nesting seasons.

	2002 nesting season (28 May to 23 November)				2003 nesting season (28 May to 23 August)			
	30-cm depth		60-cm depth		30-cm depth		60-cm depth	
Beach zone (no. sites)	Mean	95% ci	Mean	95% сі	Mean	95% ci	Mean	95% ci
Low-lying vegetation (4) Forest border (5) Forest (5)	28.94 28.55 27.78	28.1–29.8 27.1–29.9 27.1–28.4	29.03 28.70 27.92	28.4–29.7 27.4–30.0 27.1–27.9	29.43 28.58 28.12	28.0–30.88 27.4–9.7 26.8–29.5	29.32 28.73 28.13	28.3 - 30.3 $27.4 - 30.1$ $26.6 - 29.7$

Note: Temperatures are categorized by data logger depth and beach zone.

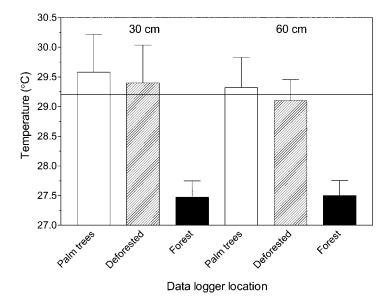


Fig. 2. Seasonal zone temperatures (mean + sp) over the 2004 nesting season (7 June–14 September) from data loggers placed in the forest and in deforested areas on Trois Ilets. Data loggers were also placed on Feuillière beach, where palm trees are the only vegetation. The thin horizontal line indicates the pivotal temperature for Antigua. At 30 cm, temperatures were 29.58° \pm 0.64°C, 29.38° \pm 0.48°C, and 27.45° \pm 0.15°C; at 60 cm, 29.32° \pm 0.51°C, 29.10° \pm 0.27°C, and 27.50° \pm 0.19°C for palm tree, deforested, and forested areas, respectively.

compare incubation durations among zones and to compare temperatures in the forested and deforested areas. Analyses were done using Statistica version 6.1 (StatSoft, Tulsa, Oklahoma, USA), and data are expressed as mean ± sp.

RESULTS

Nest distributions

Most turtles preferred nesting in areas with at least some vegetation: 8.6% of nests were placed in the open sand zone and 91.4% of nests were placed in vegetated areas (in low-lying vegetation, 33.0%; in forest border, 38.9%; and in forest, 19.5%). The distribution of nests (n=185) peaked in July. No systematic trends in nest placement among zones were apparent over the season (P>0.05; data not shown). The lower nesting density at the tail ends of the distribution suggests that the main portion of the nesting season was monitored.

Table 1. Extended.

2004 nesting season (7 June to 9 October)						
30-0	cm depth	60-cm depth				
Mean	95% сі	Mean	95% сі			
28.99 28.53 27.92	28.9 - 29.1 28.2 - 28.9 27.8 - 28.1	28.87 28.28 27.54	28.8 - 29.0 27.9 - 28.7 25.7 - 29.4			

Sand temperature

Between depths.—Sand temperatures at both data logger depths varied over the three nesting seasons (for 2002 see Fig. 1). The mean seasonal zone temperatures for the open sand in 2002 were 29.43° ± 0.63°C and $29.43^{\circ} \pm 0.54^{\circ}$ C for 30-cm and 60-cm depths, respectively. The mean seasonal temperatures for the other beach zones in all years are shown in Table 1. There were no significant differences in mean daily zone temperatures between depths in the low-lying vegetation or in the forest border, but there was a significant difference between depths in the forest. There was also a significant effect of year in all cases and a significant depth × year interaction, except in the low-lying vegetation (two-factor ANOVA for each zone; [a] lowlying vegetation, effect of depth, $F_{1,840} = 1$, P = 0.34; effect of year, $F_{2,840} = 35$, P < 0.0001; interaction, $F_{1,840}$ = 3, P = 0.051; [b] forest border, effect of depth, $F_{1,840} =$ 0, P = 0.89; effect of year, $F_{2,840} = 11$, P < 0.0001; interaction, $F_{1,840} = 12$, P < 0.0001; [c] forest, effect of depth, $F_{1,840} = 8$, P = 0.004; effect of year, $F_{2,840} = 47$, P< 0.0001; interaction, $F_{1,840} = 26$, P < 0.0001). The mean temperature difference between depths was only $0.2^{\circ} \pm 0.25^{\circ}$ C with one depth not being consistently warmer or cooler than the other, so the significance values obtained were probably a result of the large number of temperature readings at each site.

Among zones.—Mean seasonal zone temperatures differed significantly among the three beach zones at both depths but not among years (two-factor ANOVA; [a] 30-cm depth, effect of zone, $F_{2,33} = 15.47$, P < 0.0001;

Table 2. Sex ratio estimates for hawksbill clutches (n = 185 clutches) in 2002, grouped by the beach zone in which they were laid.

Beach zone	Male clutches	Female clutches	Equal sex clutches	Sex ratio (% female)	Sex ratio (% female) with +1°C for metabolic heating†
Open sand	0	16	0	100	100
Low-lying vegetation	31	24	6	44	100
Forest border	61	0	11	8	100
Forest	36	0	0	0	0

Note: The mean of the daily zone temperatures during the middle third of incubation was determined and was used to assign sex.

effect of year, $F_{2,33} = 1.23$, P = 0.31; interaction, $F_{4,33} = 0.36$, P = 0.84; [b] 60-cm depth, effect of zone, $F_{2,33} = 16.07$, P < 0.0001; effect of year, $F_{2,33} = 2.17$, P = 0.13; interaction, $F_{4,33} = 0.18$, P = 0.95). In all cases, the forest zone was markedly cooler than the other zones (Table 1).

In 2004, temperatures were significantly different between forested and deforested areas, with forest temperatures almost 2°C cooler than the corresponding open sand areas (one-factor ANOVA; [a] 30-cm depth, $F_{2,98} = 401.5$, P < 0.0001, Bonferroni post hoc test, P < 0.001; [b] 60-cm depth, $F_{2,98} = 665.9$, P < 0.001, Bonferroni post hoc test, P < 0.001; Fig. 2). There was no significant difference between temperatures in the deforested areas at Trois Ilets and at Feuillière, indicating that palm trees do not provide sufficient amounts of shade needed to lower sand temperatures (Bonferroni post hoc test, P > 0.05 for both depths).

Incubation durations and sex ratios

The nests were categorized by beach zone and were used to estimate the mean incubation duration for each zone (low-lying vegetation, 58 ± 0.92 d, n = 10; forest border, 61 ± 1.87 d, n = 5; forest, 65 ± 2.5 d, n = 4). From this, zone-specific thermosensitive periods were estimated: forest, days 23–44; forest border, days 21–40; low-lying vegetation, days 20–38; and open sand, days 20–38. Nests laid in the forest had significantly longer incubation durations than nests laid in the other beach zones (ANOVA, $F_{2,17} = 32.28$, P < 0.0001; Bonferroni post hoc test, P < 0.01 for all comparisons).

The sex ratios of each clutch were approximated and were grouped by beach zone (Table 2). This indicates that nests laid in the forest are likely to be male producing, much more so than those nests laid in more open areas. This result holds true even after 1°C was added to the mean daily temperature during the middle third of incubation.

DISCUSSION

Trois Ilets is a nearly pristine hawksbill nesting beach, with littoral forest remaining intact for much of its

length (Fig. 3). Our results demonstrate that substrate temperatures at nest depth generally decrease as one moves further inland, with the forest zone being markedly cooler than other beach zones, a result seen over the course of three nesting seasons. This is consistent with the differences in incubation duration among the beach zones, with nests in the cooler forest zone having longer durations than those elsewhere. Cooler temperatures will result in embryos differentiating into males, and vegetation cover has been shown to correlate well with sex ratio in other turtle species (Vogt and Bull 1984, Janzen 1994a).

The exact number of males produced in various areas will depend on several factors, including the pivotal temperature and the amount of metabolic warming of the egg mass. Metabolic warming means that sand temperatures may underestimate the production of females, but only to the extent that it overlaps the thermosensitive period. There are few and mostly imprecise studies on the thermosensitive period in sea turtles (Yntema and Mrosovsky 1982, Desvages et al. 1993, Hewavisenthi and Parmenter 2001) and none in hawksbills. If, despite this lack of information, we allow 1°C for metabolic warming we find, of course, that the overall percentage of males decreases. However, the importance of the forest zone as a maleproducing area becomes more pronounced relative to other zones, which would produce virtually all females (Table 2).

The existence of a male-producing habitat becomes especially important in the context of the female-biased sex ratios for hawksbills elsewhere in the Caribbean and western Atlantic. In the U.S. Virgin Islands, a sample of 494 hatchlings found dead in 51 nests were sexed, and the hatchlings from 49 of those 51 nests were females (Wibbels et al. 1999). In Antigua, the latest work points to hatchling production being female biased (Glen and Mrosovsky 2004); earlier work suggesting the contrary was based on temperature data from years unrepresentative of the current situation (Mrosovsky et al. 1992). In Bahia, Brazil, the short incubation durations of hawksbill nests lead to estimates of hatchling sex

[†] Sex ratio was also calculated after adding 1°C to the mean daily temperature during the thermosensitive period to account for potential metabolic heating.





Fig. 3. Vegetation profile at Trois Ilets beach (top) and at Feuillière beach (bottom), a popular tourist spot. Many beaches on Marie-Galante currently resemble the latter.

ratios between 91% and 98% female (Godfrey et al. 1999). The sex ratio from the Cuban harvest of 2818 subadult and adult hawksbills in 1985 and 1986 was 77% female (Carrillo et al. 1998). There may be sex differences in catch rate, but, at the least, this large data set does not contradict the impression that hawksbills are producing predominantly females in this region (but see Diez and van Dam [2003] for an exception).

Until it is better understood why frequency-dependent pressures have not favored a greater production of the rarer sex as theory would suggest (Fisher 1930), it would seem wise with these already apparently highly femaleskewed populations to pay extra attention to preserving male-producing areas. Unfortunately, both global and local forces are diminishing the chances of producing sufficient numbers of males. Globally the greenhouse effect is a serious problem, and in Guadeloupe ambient sand temperatures are already close to the pivotal level for hawksbills (Fig. 1). In nearby Antigua, air temperatures, which correlate with sand temperatures, have risen by 0.7°C over the last 35 years (Glen and Mrosovsky 2004). Even a 1°–2°C rise in air temperatures is likely to result in considerable changes to the sex ratio (Janzen 1994b).

At present, local rather than global pressures are more immediate threats to maintaining demographically appropriate sex ratios. In many parts of the Caribbean, trees and vegetation have been cleared to make room for housing and beach types that attract tourists or to create landscapes aesthetically pleasing for residents. In Barbados, following colonization in 1627, most of the forest was cleared over the next 30 years to make way for crops; coastal forest has mostly disappeared (Watts 1987). Beaches on the west and south coasts of Barbados are now largely lined with houses and hotels interspersed with trees, except in the few locations where coastal woodlands remain (J. Horrocks, personal communication). In Bahia, there is a tendency for the denser types of vegetation such as clumps of sea grape to have been replaced by more open areas planted with coconut palms (Johnson and Nair 1984). In Antigua, the loss of maritime vegetation and shade has reduced hawksbill nesting habitat at Jumby Bay (Hoyle and Richardson 1993, McIntosh et al. 2003); recently, however, beach gardens of native vegetation have been planted to increase the amount of suitable nesting habitat (Muenz and Andrews 2003). In Guadeloupe, the forest is starting to be thinned out by the creation of clearings for sheds at the south end of the beach and is beginning to be reduced in extent at the north end.

Deforestation can impact other reptile species as well. Forest clearing for power lines in Australia has altered the thermal distributional limits of montane lizards. Their ability to exploit higher elevations can now affect their demographic structure through new competitive interactions or by increasing connectivity among subpopulations (Shine et al. 2002). Human alterations to nesting habitat have been shown to modify the thermal properties of nest sites in many taxa, which can disrupt their ecology by allowing parasite transmission, increasing vulnerability to climate change, or rendering existing habitat unsuitable (Madsen 1984, Congdon and Gatten 1989, Janzen 1994*b*, Shine et al. 2002).

With these considerations in mind, we urge that natural beach vegetation be preserved on marine turtle nesting beaches as much as possible. This is especially important for the hawksbill turtle, which preferentially selects vegetated and shaded places for egg-laying (Diamond 1976, Mortimer 1982, Limpus et al. 1983, Horrocks and Scott 1991). Palm trees provide insufficient shade, and sand temperatures are similar to those in treeless areas. Nesting beaches per se may still remain, giving the illusion of the preservation of critical habitat, but systematic destruction of forested areas could be catastrophic for hawksbill demography and continued survival. Given that there is strong nest site fidelity, both to specific beaches and to specific beach zones, it is unknown what effects the destruction of a particular microhabitat will have on nesting behavior as well. Even if turtles no longer return to Trois Ilets post-deforestation, this type of beach is disappearing throughout the Caribbean. Given that the forested zone at Trois Ilets is one of the few places in the Caribbean so far identified as having thermal characteristics favoring male production, we urge that special attention be devoted to preserving this habitat, both for more study and as a precautionary measure to mitigate the effects of global warming. In species whose sexual differentiation depends on the temperature of the embryos, it may be insufficient to limit the take of turtles or their eggs if appropriate thermal habitat is not also preserved.

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