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Offshore Migratory Activity of Hawksbill Turtle (*Eretmochelys imbricata*) Hatchlings, I. Quantitative Analysis of Activity, with Comparisons to Green Turtles (*Chelonia mydas*)

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ABSTRACT. – **Hatchling marine turtles emerge at night from underground nests, enter the ocean, and swim offshore. Here, we measured the intensity (hours swimming) and the temporal patterning (diurnal vs. nocturnal expression) of activity shown by Malaysian (Sulu Sea) hawksbill (*Eretmochelys imbricata*) and green turtle (*Chelonia mydas*) hatchlings tethered inside pools for six days, postemergence. The results were compared to the activity shown during the same period of development by sea turtles in Florida. The two species from Malaysia showed significant differences in activity both from one another and from the Florida (leatherback, *Dermochelys coriacea*; loggerhead, *Caretta caretta*; and green turtle) species. Hawksbills were less active than the hatchlings from Florida, swimming on average $<$ 6 h/d. Hawksbills did not show a frenzy period of hyperactive swimming, typical of the first day of offshore migration by the hatchlings from Florida. Green turtles swam on average about 17 h each day during a two-day frenzy period that was one day longer than the frenzy period shown by green turtles from Florida; thereafter, activity showed a significant decline. These results suggest the two species use different strategies to avoid predators near shore. Hawksbills may hide in flotsam or remain inactive to minimize detection; whereas, green turtles may reduce their exposure time by rapid locomotion through shallow water. We conclude that the frenzy period shown by hatchlings during offshore migration is a variable trait both among marine turtle species and between green turtle populations nesting on Western Atlantic and Sulu Sea beaches.**

KEY WORDS. – **Reptilia; Testudines; Cheloniidae; migration; behavior; activity; predation**

Sea turtle hatchlings emerge at night from underground nests, crawl to the surf zone, enter the ocean, and swim out to sea (Carr and Ogren 1960; Bustard 1972). For most species, this migration marks the beginning of an oceanic phase of development (Carr 1986, 1987) that varies in duration with species (Bolten 2003a, b).

After entering the ocean, typically at night, hatchlings swim vigorously (the "frenzy"; Carr 1962). The migratory activity of loggerhead (*Caretta caretta*), leatherback (*Dermochelys coriacea*), and green turtle (*Chelonia mydas*) hatchlings from the East coast of Florida has been studied under laboratory (Wyneken and Salmon 1992) and field (loggerheads; Witherington 1995) conditions. Swimming is almost continuous over the first 24–30 h (Wyneken and Salmon 1992). Over the next two days, nocturnal (but not diurnal) activity declines; this change characterizes a transition between the frenzy and a "postfrenzy" period. By the end of day 5, postfrenzy turtles largely confine their swimming to the daylight hours. Some nocturnal activity persists; although, its expression varies with species. Loggerheads become virtually inactive; green turtles and leatherbacks swim for about 15% and 25%, respectively, of the dark period (Wyneken and Salmon 1992). Diurnal activity is probably characteristic of all three species during the early stages of their oceanic existence because they use vision to find prey and to avoid predators (Witherington 2002; Constantino and Salmon 2003; Salmon et al. 2004).

The adaptive significance of frenzy and postfrenzy activity in sea turtles is a matter of speculation because hatchling marine turtles disperse widely in the open ocean where their behavior and ecology are difficult to study. However, the similar duration of the frenzy period among loggerhead, leatherback, and green turtles in Florida led to the hypothesis that its function is similar in all three species: to escape from shallow water and the predators concentrated there (Wyneken and Salmon 1992; Stewart and Wyneken 2004; Whelan and Wyneken 2007). Support for this hypothesis comes from studies in other locations documenting that predators take many hatchlings within minutes or hours after offshore migration begins (Gyuris 1994; Pilcher et al. 2000).

Comparative studies allow behavioral ecologists to test hypotheses about relationships between natural selection and adaptation (Clutton-Brock and Harvey 1984). For example, a similar frenzy period among even distantly related ("hard-shelled" [Cheloniidae] and "leathery-shelled" [Dermochelyidae] marine turtles; Bowen and Karl 1997) species provides support for the hypothesis that predation selects for behavioral convergence in function. However, it would be premature to conclude that selection favors the same adaptations in other marine turtle populations or species, at least in the absence of additional studies.

There are several reasons why hawksbill sea turtles *(Eretmochelys imbricata*), whose migratory behavior has not been previously quantified, might make interesting subjects for comparative studies. First, although they are closely related to loggerheads (Bowen and Karl 1997), they show important differences in their life-history characteristics. Loggerhead clutches rarely exceed 165 eggs (Dodd 1988); whereas, hawksbill clutches can consist of up to 200 eggs (Chan and Liew 1999; Pilcher and Ali 1999). Hawksbill hatchlings are also on average smaller (Witzell 1983; Pilcher and Ali 1999) than loggerhead hatchlings (Dodd 1988). Thus, hawksbills provide an opportunity to explore how hatchling size might affect offshore migratory behavior.

Second, qualitative differences in hatchling behavior have already been reported. Deraniyagala (1930) observed that newly emerged hawksbills in Ceylon crawled for hours on land but, when placed in water, soon become inactive. Carr and Ogren (1960) also noted that newly emerged hawksbills in Costa Rica swam less actively than did hatchling leatherbacks and green turtles, which swam incessantly under the same conditions. These reports led us to suspect that hawksbill hatchlings might differ behaviorally from other species studied to date. Those differences could provide new insights into the selection pressures shaping differences in hatchling behavior during migration.

Here, we describe migratory activity shown by hawksbills from Malaysia. Local green turtle hatchlings, studied at the same time using the same methods, served as controls that we assumed would behave much like the green turtles studied earlier in Florida by Wyneken and Salmon (1992). We found that hawksbills were indeed different from all other species. They swam for only a few hours each day and failed to show a frenzy period. Malaysian green turtles, like those in Florida, swam for many hours but, unlike the Florida turtles, showed a 2-d frenzy period. Together, these results suggest that offshore migratory activity by marine turtles varies significantly not only among species but also between geographically isolated populations of the same species.

METHODS

Study Site and Hatchling Collection. — Observations and measurements were conducted between March and July, 1999–2000 at Gulisaan Island (6°09′N, 118°03′E), one of three islands in the Turtle Islands Park located 40 km north-northeast of Sandakan (a port city in the Sabah region of Borneo; Fig. 1). Gulisaan Island contains a large confinement hatchery and staff housing but lacks other development.

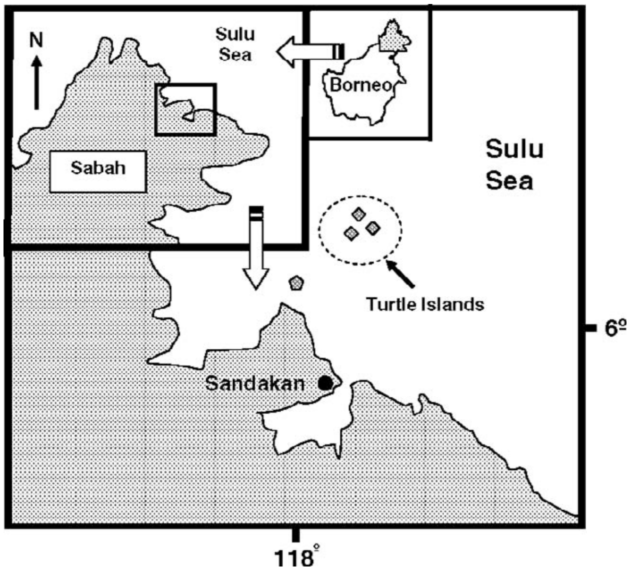

Figure 1. Map of the study area. Inset, upper right: Island of Borneo showing Saba region of Malaysia. Upper left: Sabah region in greater detail. Boxed area expanded below shows the three islands of the Turtle Islands Park, about 40 km north-northeast of the port city of Sandakan.

The activity of 40 hawksbill and 20 green turtle hatchlings was measured. All of the green turtles and 20 of the hawksbills came from hatchery nests; 20 additional hawksbills were obtained from natural nests. Each sample of 20 hatchlings consisted of six turtles from three nests and two turtles from one nest.

Hatchlings were collected either at night as they emerged from their nests or during the late afternoon by carefully removing them from the sand above the egg chamber (without disturbing the remaining hatchlings) on the day they would emerge. All turtles were weighed (using a digital balance; ± 0.01 g). Hatchlings collected in the afternoon were placed in covered Styrofoam® boxes at ambient (shaded) air temperatures until dark. Stored under those conditions, within minutes, the turtles became and remained inactive.

Recording System. — Activity was measured as each turtle swam inside one of six round fiberglass outdoor tanks (2.0 m dia × 50 cm deep) filled to a depth of 35–40 cm with unfiltered sea water. The tanks were aligned in a single row under a shelter provided by an open, rectangular wood frame covered with shade cloth to minimize water heating. Opaque polyvinyl sheets attached to the frame sides provided additional shade during the day and shielded the tanks from stray lighting at night. Water temperatures inside the tanks fluctuated over time between 25° and 29°C.

Each turtle's movements were confined to the tank's central area by a tether (a 20–25 cm length of monofilament fishing line), which prevented contact between the turtle and the tank side or bottom but allowed each hatchling to swim unimpeded in any direction. One end of the line was tied around the turtle's shell behind the front flippers; the other end was attached to a copper spring switch contained within a PVC pipe and centered directly above the tank. When the turtle swam, its force closed the switch contacts and completed a 1.5–v DC circuit to an electric clock. When the turtle was inactive, the contacts separated to turn off the clock. Switch and clock operation were checked frequently each day to assure system integrity.

Each turtle's activity was recorded for six days, beginning at midnight following its capture. Activity was measured as the accumulated minutes of clock time during the 12 h of daylight (between sunrise and sunset) and darkness.

Beginning on day 4, the turtles were offered small pieces of fish or squid at different times during the day. Excess food was removed from the tank shortly after feeding ceased.

At the end of each 6-d observation period, hatchlings were taken 1–2 km offshore during the early evening hours, and released.

Statistical Analysis. — Student's *t*-tests (Zar 1999) were used to determine whether hawkbills from hatchery and natural nests differed significantly in mass. Swimming activity by each species was summed and averaged as time (hours and corresponding minutes) active during each of the six days of observations and during the diurnal and nocturnal portions of each day. For hawksbills, a chi-square (goodness-of-fit) test (Siegel and Castillan 1988) was used to determine whether activity differed between hatchlings obtained from hatchery and natural nests. The observed value for each group was the mean duration (in min) of daily activity over six days; the expected value was average of activity shown by both groups. These data were then cast in a 2 × 2 contingency table (1 df).

A goodness-of-fit chi-square test was also used to determine whether, in each species, ratios of diurnal and nocturnal activity differed significantly from equality. The observed value was the average duration of activity during each photophase over six days; the expected value for each photophase was half of the total to the two averages.

Activity across the six observation days was analyzed within each species to determine whether changes (during each day and during its diurnal and nocturnal phase) showed significant differences from an average value. This hypothesis was tested using a 2 × 6 chi-square contingency in which the observed values were the daily means, and the expected value was the average of the daily means.

Activity patterns were compared between species using two sample chi-square tests cast in a 2 × 2 table (Siegel and Castillan 1988). These were used to compare ratios of 1) mean activity to mean inactivity, and 2) mean nocturnal to mean diurnal activity.

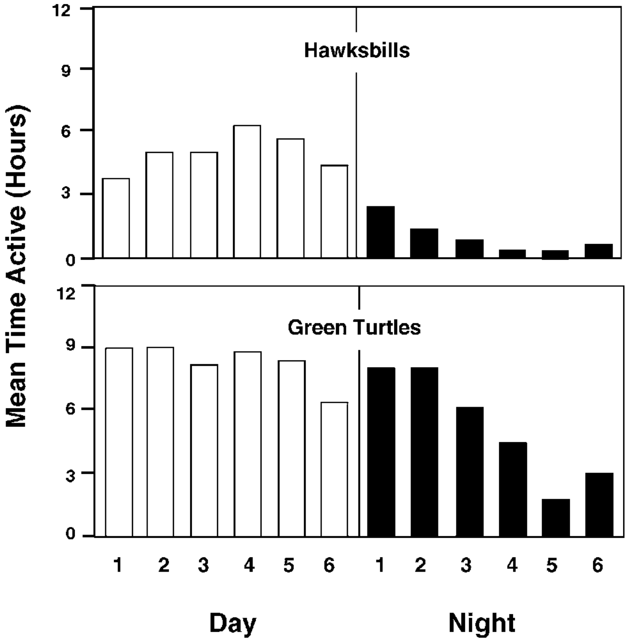

Figure 2. Mean hours of swimming activity by hawksbills ($n = 40$ hatchlings) and green turtles ($n = 20$ hatchlings) during the first six days of migratory (offshore swimming) locomotion in enclosed pools. Open bars, activity during the day; solid bars, activity at night.

Chi-square tests require the use of whole numbers (Siegel and Castillan 1988). Therefore, comparisons were done using minutes of activity rather than hours and their fractions (e.g., 384 min substituted for 6.4 h). In all statistical tests, null hypotheses of no differences between groups were rejected when probabilities were ≤ 0.01.

RESULTS

There were no statistical differences in mass between the hawksbills obtained from hatchery and natural nests (mean ± SD: 11.52 ± 0.62 g [hatchery]; 11.84 ± 1.08 g [natural]; $t = 1.1438$, $p = 0.26$, df = 38).

Hawksbills from hatchery nests were more active (6.12 h/d) than hatchlings from natural nests (5.45 h/d). However, those differences were not statistically distinguishable from expected equivalence (5.8 h/d; $\chi^2 = 1.15$, $p = 0.28$). Therefore, the two data sets were pooled (Fig. 2).

Over the six days of observations, hawksbills were significantly more active during the day (mean of 5.0 h/d) than at night (0.7 h/d; Table 1). Diurnal activity gradually increased from 3.7 h on day 1 to 6.2 h on day 4 then declined (Fig. 2). Nocturnal activity was highest (2.2 h) on night 1 and then declined over subsequent evenings (Fig. 2). These changes in activity resulted in significant departures from an average (6-d) mean during each photophase (Table 1). Variation in total (nocturnal + diurnal) activity ranged between 5.3 h (on day 6) and 6.5 h

Table 1. Intraspecific comparisons of swimming activity shown by the two species. See the text for further details.

		Hawksbills		Green turtles	
Null hypothesis	df	χ^2	$p \leq$	χ^2	$p \leq$
Diurnal = nocturnal activity	1	113.0	0.0001	24.2	0.0001
Diurnal activity constant	5	21.5	0.0001	24.2	0.0001
Nocturnal activity constant	5	95.1	0.0001	267.0	0.0001
Total activity constant	5	9.0	0.20	163.0	0.001

(on day 4; Fig. 2). This observed variation did not differ statistically from an expected average (5.8 h; Table 1).

Over the six days of observations, green turtles were also significantly more active during the day (8.5 h) than at night (5.2 h; Table 1). Diurnal activity ranged narrowly between 8.7 and 9.2 h/d during the first 5 days of observations before declining to 6.5 h on day 6 (Fig. 2). Nocturnal activity was highest during the first two evenings (7.9 and 8.0 h) and then declined during the later evenings (Fig. 2). This variation in activity over the six days of observations departed significantly from the daily average for each photophase (Table 1). Total activity varied between 9.3 h (day 6) and 17 h (days 1 and 2; Fig. 2). This variation was also a statistically significant departure from the daily average (Table 1).

Over six days, green turtles were on average active for 13.7 h/d and inactive 10.3 h/d. This ratio differed significantly from the hawksbill ratio (5.7 h active and 18.3 inactive; $\chi^2 = 332$, $p < 0.0001$). Although both species were more active during the day than at night, in green turtles, those ratios (8.5:5.2 h) more closely approximated equality than those shown by hawksbills (5.0:0.7 h; $\chi^2 = 75.2$, $p < 0.001$).

DISCUSSION

Constraints. — Our results show clear differences in migratory activity between Malaysian hawksbills and sympatric green turtles, both in terms of intensity (hours swimming) and temporal pattern (diurnal vs. nocturnal expression). Because identical procedures were used to quantify those differences, direct comparisons can be used to substantiate hypotheses regarding similarities and differences between those species.

However, direct comparisons between Malaysian and Florida green turtles cannot be made because methodological differences confound the two studies. The Florida turtles were observed in a laboratory setting where light and temperature were controlled. This study was done in the field where those conditions varied. Different systems, perhaps with different sensitivities, were used to translate the turtles' swimming movements into time active. Absolute differences in swimming activity during the postfrenzy period, when the turtles are diurnally active, may have occurred because day length in subtropical Florida is longer than day length in tropical Malaysia.

Although the two populations cannot be compared in terms of absolute time spent swimming, comparisons can be made between how each population apportions activity between the frenzy and postfrenzy period. That behavioral "decision" is less likely to be directly determined by conditions in the external environment and more likely to be a function of endogenous factors, known to differ among spatially distinct populations of many migratory insects, fishes, and birds (Dingle 1996). On that basis, we hypothesize below that those differences among hatchlings are probably adaptations that function to promote their survival under the ecological conditions unique to each location.

Variation in Hatchling Migratory Behavior. — Hawksbill hatchlings, like those of other marine turtles, usually emerge from their nests at night, immediately crawl to the surf zone, and swim offshore (Witzell 1983). However, as this study shows, the intensity of their swimming activity is abbreviated compared to local green turtles (Fig. 2) and compared to all the species studied in Florida (Wyneken and Salmon 1992).

Hawksbills also failed to show a frenzy period, characterized in other species by continuous locomotion during the day and night, and heightened levels of locomotion compared to the postfrenzy period (Wyneken and Salmon 1992). In hawksbills, there was no change in total activity across days (Table 1). This situation occurred because, when there was an increase in mean diurnal activity across days, it was often accompanied by a decrease in mean nocturnal activity and vice versa (Fig. 2).

Malaysian green turtles in this study were used to provide a baseline for comparisons to the hawksbills. They served that purpose but, in addition, showed differences from the Florida green turtles studied earlier by Wyneken and Salmon (1992). Florida green turtles showed a one-day frenzy period of elevated swimming activity; whereas, in Malaysian green turtles the frenzy period lasted for two days (Fig. 2).

Ecology and Variation in Hatchling Migration. — What factors shape differences in the timing and duration of offshore migration by marine turtle hatchlings? Recent studies point to interesting correlations between ecology and behavior both between populations and among species.

Ecological factors may have selected for the differences in frenzy period duration shown by Malaysian and Florida green turtle hatchlings. Malaysian hatchlings often negotiate extensive areas of shallow reefs before they can reach the relative safety of deep water. In the tropical Pacific, these reefs can host high concentrations of predators that can take a majority of the hatchlings within an hour or two after they enter the sea (Gyuris 1994; Pilcher et al. 2000). High intensities of locomotor activity over a 2-d period may enable the turtles to minimize their exposure time to these predators.

Hatchlings swimming away from the southeast coast of Florida typically cross few reefs as they head toward deep water. Those that they do encounter are narrow structures that probably harbor fewer predators. In many locations, reefs are absent altogether, and the turtles swim over an open sand bottom. Predation rates for Florida green turtles are unknown, but for loggerheads swimming in the same locations, rates in shallow water are low (Stewart and Wyneken 2004; Whelan and Wyneken 2007).

Loggerhead hatchlings migrating offshore from nesting beaches on the southwest coast of Florida devote more time to postfrenzy locomotion than do hatchlings from the southeast coast (Madrak et al. 2007). Southwest coast hatchlings must traverse a broader region of shallow water (the extensive eastern continental shelf of the Gulf of Mexico) than turtles swimming offshore on the east coast. In addition, southwest coast hatchlings must swim farther (~ 200 km) to locate the Loop Current in the Gulf of Mexico than do the east coast turtles, which swim 5–90 km (depending upon nesting beach latitude) to locate the Gulf Stream. Entrainment within both currents may ultimately be essential for transport of hatchlings to nursery habitats located in the eastern Atlantic (Bolten 2003a, b).

Australian flatbacks (*Natator depressus*) represent yet another behavioral motif (Wyneken et al. 1997). Posthatchlings lack an oceanic phase of development, and most of the turtles remain in Australian shelf waters (Walker and Parmenter 1990; Walker 1994) where it is likely that they are continually exposed to high concentrations of predators. Flatback hatchlings are large and aggressive (pers. obs.). Under laboratory conditions, hatchlings are continuously active for two days and show only a slight decline ($< 7\%$) in activity during days 3 and 4 (Wyneken et al. 1997). Periods of inactivity are short and irregular, perhaps because the turtles must remain continuously vigilant to survive encounters with predators.

Hawksbill and Green Turtle Hatchlings: Alternative Solutions to Predator Avoidance? — Worldwide, there is broad overlap between the present geographic distribution of nesting beaches used by green turtles and hawksbills. Both species nest primarily on continental shores and remote island beaches located in the tropics (hawksbills: reviewed by Witzell 1983; Miller 1994; National Marine Fisheries Service and U.S. Fish and Wildlife Service 1998; Meylan 1999; green turtles: reviewed by Hirth 1997). Some, although not all, of these beaches are bordered by coral reefs that provide habitats or refuge for an array of turtle predators (jacks, *Caranx* sp.; reef sharks, *Carcharinus* sp.; barracuda, *Sphyrraena* sp.; grouper, *Epinephelus* sp.; snook, *Centropomus* sp.; tarpon, *Megalops* sp.; several genera of wrasses; snappers, *Lutjanus* sp.; and squid, *Dorytheuthis* sp*., Sepioteuthis* sp.]; Stancyk 1982; Gyuris 1994; Wyneken et al. 1997; Pilcher 1999).

Predation rates on hatchlings after they enter the sea can be high (Bustard 1972, 1979; Richardson and Richardson 1982; Stancyk 1982; Gyuris 1994; Pilcher et al. 2000). The highest risks are associated with nesting beaches adjacent to reefs, both for green turtles (Gyuris 1994; Pilcher et al. 2000) and for loggerheads (Wyneken et al. 1997; Whelan and Wyneken 2007), where most of the turtles are taken. A number of predatory fishes are known to take hawksbill hatchlings (Witzell 1983) whose small size may make them particularly vulnerable. Unfortunately, there is only one study quantifying predation rates on this species (6.9% during the first 20 min of migration; Harewood and Horrocks 2008).

Our results (Fig. 2) suggest that hawksbill and green turtle hatchlings have evolved different strategies for avoiding predators. Green turtles produce streamlined hatchlings that are relatively large, powerful swimmers. The turtles appear behaviorally adapted to reduce the duration of their vulnerability by rapid movement through shallow water. This “sprinter” strategy (Wyneken 1997) may be supplemented by counter shading to reduce detection by predators from below.

We postulate that hawksbills avoid predators through a combination of mimicry (resemblance to dead leaves and other flotsam on the water surface), crypsis (resemblance to background, such as floating algal mats), and inactivity. Inactivity is especially appropriate since many fishes are visual predators, attracted to prey by movement (Gyuris 1994; Helfman et al. 1997). Inactivity, when coupled with either mimicry or crypsis, is an effective mechanism used by both predators and prey to avoid detection in marine and in terrestrial communities (e.g., Edmunds 1974; Feder and Lauder 1986; Hacker and Madin 1991). For small hatchlings like hawksbills, such a strategy may be especially effective while the turtles pass through relatively shallow, predator-rich waters. The low level of activity during day 1, followed by an increase later (Fig. 2), might reflect a change in the probability of encountering predators once the hatchlings reach deeper water.

Hawksbill hatchlings resemble loggerheads in appearance (variably dark and medium brown coloration on carapace and plastron) and in behavior (drifting inactively in open water), prompting the suggestion that both species may, at least in the Atlantic, seek out and rest within floating algal mats concentrated in drift lines (National Marine Fisheries Service and U.S. Fish and Wildlife Service 1998). Experiments in outdoor pools revealed that hawksbill posthatchlings (~ 30 d postemergence) rest on mats of flotsam (Mellgren et al. 2003). Juvenile hawksbills have been found on *Sargassum* mats in the Gulf of Mexico (Witherington and Hirama 2006). The whereabouts of young hawksbills in the Pacific, where weed lines are less common, is unknown.

Thus, differences in offshore migratory activity between hawksbill and green turtle hatchlings lead us to hypothesize that different strategies are used by the two species to avoid detection by predators. The lower levels of swimming activity shown by hawksbills also suggest that they could rely more than green turtles upon tidal and wind-generated surface currents for offshore transport. Observations and experiments are now required to determine whether hawksbill hatchlings in the field behave as they do in tanks, whether immobility reduces predation rates, and whether hawksbill migratory behavior and survival varies at different locations, depending upon ecological conditions.

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