

rain is sufficiently hilly that, at all release sites but position 1 (Fig. 1), the snakes would have hills between them and the workshop. Because of the trees, visual contact with the workshop would be restricted to an area no more than 50 m in radius around the building. Therefore, for the snakes to get back to the workshop they had to rely on either an internal compass or familiarity with landmarks along the way. Since males have much larger home ranges than females (Weatherhead and Hoysak, 1989), it is possible that the male that returned to the workshop was familiar with the whole study area. However, it appears the female had maintained the same home range for many years and would only have been familiar with that area, its immediate surroundings, and the route between the home range and the hibernaculum. Therefore, her return from release sites 5 and 6 (Fig. 1) in all likelihood required true navigational ability (Able, 1980; Rodda, 1984).

It is noteworthy that two snakes showed persistent homing behavior while seven others never homed. Possibly our reliance on recapture (as opposed to tracking released snakes) caused us to underestimate the extent of their homing. Nonetheless, it seems highly unlikely that by chance, two snakes would be repeatedly recaptured at or near one location and the seven others not at all. The fact that both homing individuals were larger than the other snakes is consistent with Fraker's (1970) observation that larger *Nerodia sipedon* were more successful than smaller individuals at homing following displacement. Why size (or age) should influence either the ability or motivation to home is not clear. We can rule out reproduction because breeding occurs in mid-June and these observations were made from late May–early Aug.

The most significant aspect of the homing behavior we observed was the specificity of the location to which the two snakes homed. Even after several days in captivity, these snakes returned directly to the workshop. Since the workshop's only interest for the snakes was the availability of robin's nests, their homing behavior was apparently motivated by the association of the workshop with food. Since the snakes were always prevented from reaching a nest, their persistence in homing to the workshop continued in the absence of any positive reinforcement.

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TEMPORAL PATTERN OF NOCTURNAL EMERGENCE OF LOGGERHEAD TURTLE HATCHLINGS FROM NATURAL NESTS.—Hatchling sea turtles emerge in groups from nests on oceanic beaches and immediately move toward the sea. These temporally discrete emergence events are the culmination of a prolonged (1–4 d) escape from the nest that involves, and may require, social facilitation among siblings (Carr and Hirth, 1961). Sea turtle hatchlings emerge primarily at night

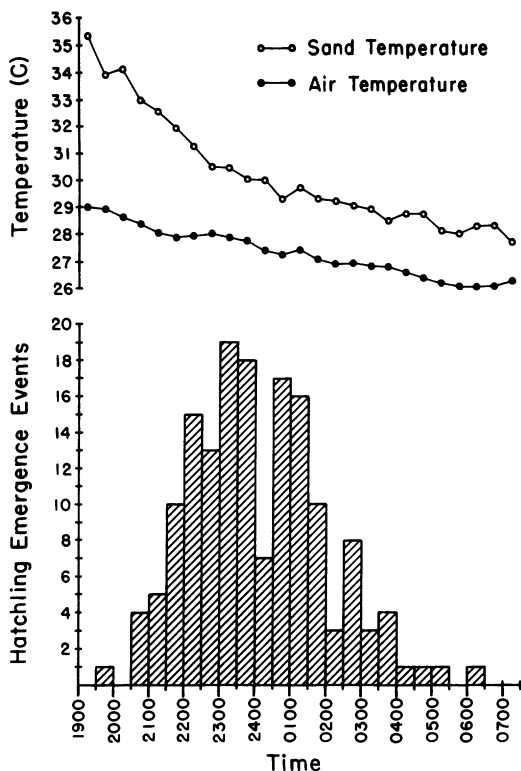


Fig. 1. Temporal distribution of loggerhead hatchling emergence events ( $n = 157$ ) from natural nests on Melbourne Beach, Florida, from 29 July–1 Sept. 1988. Mean surface sand temperatures (5 cm depth) and air temperatures are shown for the period of the study.

(Hendrickson, 1958; Bustard, 1967; Neville et al., 1988), although early morning (Chavez et al., 1968) and late afternoon (Witzell and Banner, 1980) emergences are also known. For loggerheads, these events usually involve approx. 20–120 hatchlings (Witherington, pers. observ.). Emergence events are not always independent units; 1–3 events commonly occur per nest (Witherington, 1986). The goal of this study was to describe in detail the temporal pattern exhibited by hatchling loggerhead turtles, *Caretta caretta*, emerging from natural nests.

**Methods.**—An emergence event is defined as the movement of a group of 10 or more hatchlings from a single nest to the surf. Groups of fewer than 10 were noted as stragglers and not included in this analysis. We recorded emergence events from natural nests that had been deposited by loggerhead turtles on a 1.7 km study

beach near Melbourne Beach, Florida (28.02°N, 80.52°W). Substantial numbers of loggerhead turtles (400–700 nests  $\text{km}^{-1} \text{yr}^{-1}$ ) nest at this site (Witherington, 1986). We surveyed hatchling emergence activity from 1900–0100 (evening) and from 0100–0730 (morning). Eleven morning and 11 evening surveys were allocated randomly over a 35 d period between 29 July–1 Sept. 1988. Sunset occurred between 1945–2014 h, and sunrise occurred between 0643–0702 h during this period. Loggerhead hatchlings emerge from nests at Melbourne Beach from early July–Oct.

Field assistants conducted surveys on a small, all-terrain vehicle (ATV) towing a weighted broom (70 cm wide) between stations at either end of a 1.7 km transect every 0.5 h. The path taken was just above the recent high tide wrack. Evidence of emergence events was the presence of hatchling tracks over the previously swept path of the ATV. A red-filtered light shown at an acute angle to the swept path made recent hatchling tracks clearly visible to the rider. The time we assigned to an emergence event was the time of departure of the surveyor from the previous station. This method provided an estimate of emergence time with an error of less than  $\pm 0.5$  h. When the surveyor turned at the end of a transect, air and sand surface (depth 5 cm) temperatures were recorded using a Fluke 51 digital telethermometer. Temperatures were averaged for each half hour interval over the entire sampling period.

**Results and discussion.**—We recorded 157 hatchling emergence events between 1930–0630 h. The timing of hatchling emergence events (Fig. 1) was not significantly different from a normal distribution (Kolmogorov-Smirnov goodness of fit,  $D = 0.056$ , Pimentel and Smith, 1986) with peak activity between 2300–2400 h. Hatchling emergence times on a North Carolina beach ( $n = 51$ ) had a distribution similar to that reported here (Fig. 1), but shifted to earlier in the evening with peak activity at 2000 h (Neville et al., 1988). This shift may be a result of differences in temperature patterns, but appropriate data are not available to test this hypothesis. Loggerhead hatchlings from 19 clutches buried in individual boxes and maintained in a house trailer on Merritt Island, Florida, emerged between 1900–0200 h (Demmer, 1981).

The daily periodicity of hatchling emergence suggests strong selection against diurnal emergences. Although the upper thermal tolerance

limits have not been determined for sea turtle hatchlings, mid-afternoon sand surface temperatures (commonly as high as 55 C at Melbourne Beach) are probably sufficient for hyperthermic mortality. If hatchlings are not killed by high temperatures during diurnal emergences, the heat lowers their activity level, leaving them vulnerable to predation for a longer time (Mrosovsky, 1968). Predation is much greater on hatchlings that emerge during the day than on those that emerge at night because more predators are active and because hatchlings are more visible (Stancyk, 1982). The only predator known to take emerging hatchlings at night on Melbourne Beach is the ghost crab, *Ocyropsis quadrata*. It is apparently a minor predator; less than one hatchling was taken from each of 48 clutches (Witherington, 1986).

Hendrickson (1958), Bustard (1967) and Mrosovsky (1968) presented evidence that thermal cues are important in triggering hatchling sea turtle emergence. Mrosovsky (1968) reported that emergence in hatchling green turtles, *Chelonia mydas*, occurs at or below the threshold temperature of 28.5 C. In our study, hatchling emergence began as sand surface temperatures dropped from approx. 34 to 30 C; a rapid decrease in temperature may be an important thermal cue for the timing of emergence events (Fig. 1). Our results are similar to those of Hendrickson (1958), who reported that a temperature above 33 C deterred activity in emerging green turtle hatchlings. Research is needed to elucidate the specific thermal information used by emerging hatchlings.

Low or decreasing temperatures typically follow sunset, but prolonged rain showers during the day also may lower temperatures. Approximately 10% of the loggerhead hatchling emergence events at Melbourne Beach occur during afternoon rain showers (Witherington, 1986).

When sea turtle hatchlings emerge on beaches with artificial lighting, they often become disoriented and move away from the ocean toward the light source (McFarlane, 1963). The great number and high mortality of disoriented hatchlings in Florida have prompted some municipalities to designate time periods during which beach lighting is prohibited. These ordinances usually allow beach lighting up to a specific time (often 2300 h). Our data indicate that beach lighting during the early evening may still disorient substantial numbers of hatchlings (Fig. 1). For example, lighting allowed until 2300 h will affect approx. 31% of the hatch-

lings emerging on a given night. To be effective, beach lighting restrictions on sea turtle nesting beaches should include the entire period of darkness.

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**GEOGRAPHIC VARIATION IN SCALE AND SKELETAL ANOMALIES OF TIGER SNAKES (ELAPIDAE: *NOTECHIS SCUTATUS-ATER* COMPLEX) IN SOUTHERN AUSTRALIA.**—Anomalous scutellation and skeletal deformities commonly occur in snakes (Cunningham, 1937; King, 1959) and are usually reported for single individuals (King, 1959; Clark and Callison, 1967) or as low frequency phenomena in natural populations (Martof, 1954; Rossman, 1963; Peters, 1969). Gross skeletal and scale abnormalities have been induced experimentally in embryos by subjecting viviparous, gravid snakes to temperatures higher or lower than those preferred during gestation (Fox, 1948; Fox et al., 1961; Osgood, 1978). Recently, Arnold (1988) presented heritability estimates for ventral and subcaudal scale numbers in snakes and discussed the effects of environmental temperature and maternal thermoregulatory behavior on variation in these characters.

These authors indicated an equally important genetic component to the appearance of such anomalies. Some studies noted moderately high frequencies of anomalous ventral scales, apparently in small or isolated populations (Barton, 1956; Peters, 1969; Plummer, 1980). Barton (1956) reported the presence of ventral scale anomalies in 19.5% of specimens from geographically restricted populations of the short-headed garter snake, *Thamnophis brachystoma*. Plummer (1980) found that low frequencies (15%) of anomalous ventral scales in a local population of rough green snakes, *Ophiodrys aestivus*, were not necessarily indicative of underlying skeletal deformities, as reported by King

(1959), and were probably not so extreme as to be selectively disadvantageous. The constancy of anomaly type and location (i.e., near the anal region) led Plummer (1980) to favor a genetic rather than environmental cause.

During a mark-recapture study of viviparous tiger snakes (*Notechis scutatus-ater* complex) in southern Australia and offshore islands (Schwaner, 1985, 1989; Schwaner and Sarre, 1988, 1990), I observed scale and skeletal anomalies occurring in very high frequencies. Here I compare patterns of anomalies among conspecific populations with measures of environmental and genetic variation.

*Materials and methods.*—A total of 2043 tiger snakes was examined from 16 localities: two mainland areas—Western Australia (WAS) and southeastern South Australia (SAS); two large islands—Tasmania (TAS) and Kangaroo Id. (KAI); and 12 small islands—Hareby Id. (HAR), Roxby Id. (ROX), Reevesby Id. (REE) of the Sir Joseph Banks Ids. in Spencer Gulf, Hopkins Id. (HOP) and Goat Id. (GOT) off the coast of Eyre Peninsula, East (EFI) and West (WFI) Franklin Id. in the Nuyts Archipelago, four islets (475-478) in Pelican Lagoon of Kangaroo Id., and Mt. Chappell Id. (CHP) in Bass Strait. Mainland, KAI, and TAS samples contained (134) live snakes (examined, marked, and released), and (233) preserved specimens from the collections of the South Australian Museum (Adelaide), Western Australian Museum (Perth), Queen Victoria Museum and Art Gallery (Launceston) and Tasmanian Museum and Art Gallery (Hobart). At the other locations, observations were based on live snakes only.

Peters' (1969) descriptions of six types of ventral scale anomalies were used to categorize anomalous ventral and subcaudal scales. Anomalous head scales and deformities of the back and tail bones were noted and a peculiar ventral scale anomaly was also recorded. Means, SD and coefficients of variation (i.e.,  $CV = SD \times 100 / \text{Mean}$ ) for counts of ventral scales (method of Dowling, 1951) were calculated separately for males and females.

Proportions of the total number of snakes that had one or more scale or skeletal anomalies, and CV for counts of ventral scales, were compared (using the Spearman Rank Correlation Coefficient,  $r_s$ ) with heterozygosity estimates (HE) per population to determine whether a relationship between the two parameters exists. Nei's (1978) unbiased heterozygosities