

Activity Patterns of Yellow-Lipped Sea Kraits (*Laticauda colubrina*) on a Fijian Island

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Yellow-lipped sea kraits (*Laticauda colubrina*) are large (to 1.5 m, 2 kg) amphibious sea-snakes that forage for eels in tropical oceans but return to land to digest their prey, slough their skins, mate, and lay eggs. During three-month field seasons in two successive years, we quantified various aspects of the behavior of sea kraits on a small island off the coast of Viti Levu, Fiji. Radiotransmitters were surgically implanted in 16 snakes, and regular surveys were conducted to quantify the times and places of various activities by nontelemetered snakes. The radio-tracked snakes spent equal amounts of time on land versus in the ocean, moving between these two habitats about once every 10 days. Their mean duration of time on land fits well with the time required for sloughing and digestion, as measured in outdoor enclosures. These snakes maintained relatively high and constant body temperatures both while on land and in the water; the only overt thermoregulation involved shade-seeking. Different age and sex groups were active in different places and at different times of day. For example, juvenile sea kraits rarely ventured far from water, whereas adults often moved well inland. The snakes moved about at night, engaged in courtship during the morning and were inactive during the afternoon. Thus, snakes were frequently found in courting groups during the morning, but most were solitary at night. Movements between land and sea generally occurred at night on gently sloping areas; movements of adult male snakes also were affected by tidal conditions and by the presence of females. Male sea kraits move about more frequently and actively on land than do females, in keeping with sex differences in locomotor performance.

ONE of the most remarkable phenomena in vertebrate phylogeny involves the invasion of novel habitat types. Many lineages have undergone such shifts, sometimes with considerable success. For example, the evolution of flight allowed birds to exploit habitats that would otherwise have been inaccessible, and the evolution of diving abilities allowed several kinds of “terrestrial” vertebrates to diversify into aquatic niches. Although the transition from terrestrial to aquatic life involves a complex suite of morphological, physiological, and behavioral adaptations, such modifications have arisen in parallel in diverse lineages of mammals (e.g., whales, seals, otters), birds (e.g., penguins, cormorants), and reptiles (e.g., iguanas, sea-snakes, sea turtles). The selective pressures acting during such major transitions are of great interest (e.g., Simpson, 1953), but evidence on the ecological context of such transitions is necessarily indirect. In most cases, the “new” environment has been occupied so successfully that links to terrestrial life have been lost. Thus, we can only speculate on the attributes of transitional forms. In a few cases, however, we can find taxa that have not fully broken their reliance upon terrestrial habitats. Studies on such amphibious species may clarify processes at

work during the evolutionary shift toward aquatic life.

Snakes offer an exceptional opportunity in this respect. At least four lineages of snakes include highly aquatic species, and each of these lineages represents an independent invasion of aquatic habitats (Heatwole, 1999). In three of these groups (hydrophiids, acrochordids, homalopsine colubrids), the species involved are recorded only rarely (or never) on land. However, the laticaudine sea snakes (often called “sea kraits”) represent a classic intermediate state. They rely entirely on aquatic prey (eels) and display a wide range of adaptations to marine life (e.g., flattened paddle-like tail, reduced belly-scales; salt-excreting glands; enlarged lung; Heatwole, 1999). However, unlike the other lineages of marine snakes, laticaudines retain an oviparous mode of reproduction and hence must return to land to lay their eggs. More important, they also return to land to mate, to digest their prey, and to slough their skins. Thus, it seems likely that many sea kraits spend a substantial proportion of their time on land (Greer, 1997).

There are substantial logistical impediments to studying sea-snakes underwater, but the terrestrial habits of sea kraits make it relatively easy

to examine their terrestrial life. These animals often occur in high densities on small isolated tropical islands (Guinea, 1986, 1994; Heatwole and Guinea, 1993). We took advantage of this opportunity to gather detailed data on the behavior of yellow-lipped sea kraits (*Laticauda colubrina*) in the Fijian islands. To do so, we used a combination of radiotelemetry and surveys. The use of radio-transmitters has revolutionized field-based studies of snakes (Fitch and Shirer, 1971; Reinert and Cundall, 1982; Reinert and Kodrich, 1982) but has rarely been applied to sea-snakes (Heatwole, 1999). The only published reference to telemetry of sea kraits consists of an anecdotal report in a popular magazine (Voris and Voris, 1995). In our study, we focussed on the snakes' relative use of marine versus terrestrial environments, to clarify the following issues: (1) How much time do sea kraits spend on land versus in the ocean, and how often do they move between these two habitats? (2) Do the snakes actively thermoregulate while on land? (3) How do a sea krait's body size and sex affect its use of the terrestrial environment? (4) Where and when do the snakes move between land and sea?

MATERIALS AND METHODS

Study species.—Yellow-lipped sea kraits (*L. colubrina*) are large black-and-white banded proteroglyphous snakes. Their phylogenetic origin remains unclear, but sea kraits evolved aquatic habits independently of the other main sea-snake lineage, the hydrophiids (McDowell, 1987; Keogh et al. 1998). In our study area, female *L. colubrina* grow to 150 cm snout-vent length (SVL) and 1800 g, whereas males do not exceed 100 cm and 600 g (Shetty, 2000). This species is widely distributed through islands of the tropical Pacific (Cogger, 1975). Their ecology on Fiji has been described by Pernetta (1977) and Guinea (1986, 1994; Heatwole and Guinea, 1993). The most detailed analyses of activity patterns were conducted for a New Caledonian population by Saint Girons (1964).

Study site.—Mabualau (17°58'S, 178°46'E) lies 6 km off the southeast coast of Viti Levu, about 25 km from Suva. It is a small (4 ha) elliptical, limestone islet with a maximum height of 5 m above sea level and is surrounded by shallow reef flats. Mabualau (also known as "Bird Island") is uninhabited by humans apart from occasional fishing parties, and there is little anthropogenic modification of the native vegetation. In each of two successive years (1998 and 1999), we camped on Mabualau for three-

month periods from September to December/January. This time of the year is slightly warmer (mean daily air temperature in Suva = 26.5 C in December vs 24.5 C in June: Fiji Meteorological Service, <http://www.met.gov.fj/climate.htm>) and wetter (mean monthly precipitation = 263 mm in December vs 164 mm in June; Schneider, 1996) than most other months, and it coincides with the main mating period for *L. colubrina* in this area (Guinea, 1986).

Radiotelemetry.—We used 3.4 g (21 × 13 × 7 mm case size; 150 mm whip-antenna) temperature-sensitive radio transmitters (Holohil Systems, Canada; model PD-2T; 150 mHz) with a battery life of 35 weeks at 30 C. These constituted < 2% of snake body mass. A hand-held H-frame antenna attached to a Telonics Scanner-Receiver and Digital Processor were used to track the radio signals. Snakes in terrestrial locations provided strong radio-signals, but the signal disappeared completely when the snakes entered salt-water. We took advantage of this fact to quantify the duration of time that telemetered snakes spent on land versus in the ocean.

Brietal Sodium (Methohexitone Sodium; 5 mg/kg) was injected subcutaneously to anaesthetise the snake. The transmitter plus antenna was inserted into the abdominal cavity via a 30 mm incision in the abdominal region, at the ninth band from the tip of the tail on the left-hand side of the snake. The incision was closed using a synthetic absorbable suture, dusted with an antibiotic powder and sprayed with a moisture-vapor-permeable dressing. The snakes were kept in captivity for a further 24–48 h before release. Of the 16 individuals implanted with transmitters (eight of each sex), 15 (seven males and eight females) provided useful information.

After release, the snakes were monitored (present/absent) at least once a day by scanning for all 16 frequencies from elevated sites on Mabualau Island. Because the signal could not be detected from underwater (see above), a lack of signal suggested that the snake was at sea. To use the absence of signal as an indication that the snake was in the ocean, we need to be sure that signals could be received from snakes anywhere on Mabualau, even if they were hidden deep underground. We checked signal reception comprehensively at the beginning of the study, and obtained clear signals from every site in which we placed transmitters. Similarly, our inference that "missing" snakes were in the ocean would be in error if the snakes hauled out on some other island. We checked all potential resting-sites within 10 km of Mabualau and never found signals from these snakes.

Thus, we infer (although we cannot be absolutely certain) that telemetered snakes not present on Mabualau were in the ocean rather than on some other island or coral outcrop. Pulse-interval readings allowed us to estimate body temperatures of the snakes from previously determined calibration equations.

Environmental temperatures.—At the same time that we monitored body temperatures of the radio-tracked sea kraits, we measured operative temperatures every 30 min using six Hobo XT Temperature Data Loggers (Onset Computer Corporation, Massachusetts). The tip of each probe was placed inside a hollow copper model 150 mm in length and 10 mm in diameter. We placed two data loggers in each of three types of site: with full exposure to the sun's rays (to record maximum temperatures available to snakes), in total shade (under rocks, to record minimum temperatures available to snakes) and under water (at 1 m depth). Thermal regimes inside these models provide an approximation of the body temperatures that sea kraits would experience if they remained for long enough under the same conditions to achieve thermal equilibrium (Peterson et al., 1993).

Habitat and activity.—We conducted a survey between October 1998 and January 1999 to quantify general activity patterns of sea kraits. To do this, we walked two 200-m transects along the length of Mabualau: one inland transect parallel to (and 20 m away from) the cliffs that form the edge of the island, and one "edge" transect along the boundary of the island. The transects were always sampled in rapid succession. The surveys were distributed evenly across four time periods (0400–1200 h, 1200–1800 h, 1800–2200 h and 2200–0400 h), although the time periods were unequal in duration for logistical reasons. We counted all snakes within 10 m either side of the transect, and recorded their location, sex and age class, group size, activity, and whether the snake was sloughing. Most snakes lay out in clear view, and were very easy to see. However, other snakes were curled in small crevices within the coralline rock, or hidden under vegetation. Thus, our counts undoubtedly underestimate total snake numbers. On average, each 200-m transect took 15 min to walk.

Movement between the land and the sea.—In the second field season (September to December 1999), we conducted another survey to quantify the times and places that the snakes moved between terrestrial and aquatic environments. At each of six sites along the edge of Mabualau

Island, we selected two adjacent areas: one with steep cliffs and another with a more gentle slope. We recorded the number, age class (adult or juvenile), sex, and direction of movement (landward or seaward) of snakes entering and leaving the island within a 5-m radius from a fixed point at the center of each observation area. These sites were monitored on 25 nights, always at 2000 h but at different tide levels (classified as 0–2, > 2–4, and > 4 h from high tide). We collected equal numbers of samples in each of these categories. It took 30–45 min to complete each survey, although time spent at each site did not exceed 5 min.

Duration of sloughing and digestion.—Two of the reasons that sea kraits come ashore are to digest their prey and to slough (Guinea, 1986; Heatwole and Guinea, 1993; Heatwole, 1999). Thus, it is of interest to know how much time these activities require, compared to the average duration of time that snakes spend on the island between successive trips to the ocean. To determine the time taken for the snakes to digest prey and slough, we captured snakes and kept them in outdoor arenas until they had either digested their prey, or shed their skins. Snakes that had recently fed were easily recognizable by their distended stomachs. Such animals were always located near the edge of the island; their locomotor capacities were severely reduced by the presence of a prey item (Shine and Shetty, 2001). We collected such snakes and transferred them to outdoor enclosures (open-topped nylon bags 1 × 1 × 1 m) in the shade. The snake's stomach was palpated daily until we could no longer detect the prey item. The snake was then released. The same procedure was followed for snakes found in the early stages of sloughing, as evidenced by their opaque white epidermis. Given that animals containing prey or about to slough usually remain in the same place day after day (pers. obs.), most of the animals that we collected had probably eaten, or commenced the sloughing cycle, only shortly before they were collected. Thus, our data should provide a realistic estimate of the amount of time taken for these activities.

RESULTS

Radiotelemetry.—Radio-transmitters were surgically implanted into snakes in two sessions, a few weeks apart. Thus, some snakes were monitored for 80 days and others for 55 days. Between November 1998 and January 1999, we determined the amount of time that each of these animals spent on land and (we assumed) in the sea. The

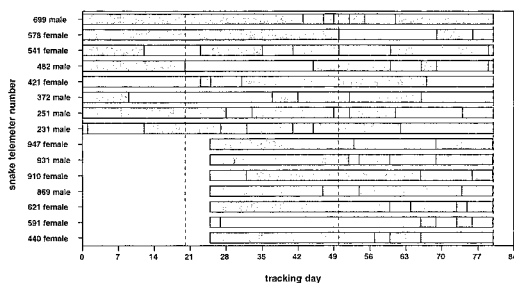


Fig. 1. The number of days spent on land (dark blocks) and in the sea (light blocks) by radio-tracked sea kraits. Note that some snakes were implanted with transmitters 25 days earlier than others.

radio-tracked snakes spent an average of 22.8 days on the island before moving into the sea and presumably were recovering from surgery over this period. Thereafter, all of the radio-tracked snakes spent approximately equal amounts of time in the ocean versus on land, moving between the two habitats once every week or two (Fig. 1). The average duration of time spent by snakes in one habitat, before returning to the other, was 10.8 days in the case of females and 9.8 days in the case of males. The two sexes did not differ significantly in this respect ($t = 0.61$, 13 df, $P = 0.60$) nor in the relative amounts of time they spent on land versus at sea ($t = 0.51$, 28 df, $P = 0.61$) nor in the number of times that radio-tracked snakes shifted from one habitat to another over the course of our study ($t = -1.85$, 13 df, $P = 0.09$).

Operative temperatures and snake body temperatures.—The thermal data loggers quantified the range of operative temperatures available to snakes on Mabualau during our radio-tracking study. Copper models in full sunlight heated to > 35 C, whereas temperatures inside models in full shade remained lower (< 28 C) and more stable (Fig. 2). Thermal maxima inside full-sun models were not attained until the afternoon. Water temperatures were generally higher than shaded land temperatures, and exhibited only minor fluctuations (Fig. 2). Mean body temperatures of telemetered snakes in terrestrial habitats were intermediate between those of the water and shaded habitats on land. Male snakes were hotter than females, with mean body temperatures averaging 28.4 C in males and 27.7 C in females (comparing hourly means with a paired t -test: $t = 2.6$, 12 df, $P = 0.03$). There was little diurnal variation in sea krait temperatures, despite the substantial diel thermal variation inside physical models exposed to full sunlight (Fig. 2).

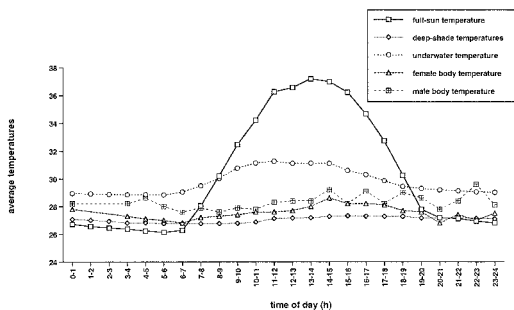


Fig. 2. Diurnal variation in body temperatures of radio-tracked sea kraits, and in associated operative temperatures, on Mabualau Island. These data refer only to periods when the snakes were on land rather than at sea.

Habitat and activity.—The relative numbers of adult males, adult females and juveniles encountered varied significantly among the four time periods ($\chi^2 = 37.15$, 6 df, $P < 0.0001$). Many juveniles were encountered in the afternoon, whereas adult males were more often seen late at night and adult females were mostly seen in the morning (Fig. 3). When the data were split by location, this temporal shift in relative numbers was significant only for the edge transect ($\chi^2 = 30.34$, 6 df, $P < 0.0001$; inland transect $\chi^2 = 6.9$, 6 df, $P = 0.30$). Very few juvenile snakes were seen inland (4, vs 44 on the edge), although total numbers of snakes seen on the two transects were almost identical (470 vs 475). Adult sex ratios also differed between the two transects ($\chi^2 = 74.2$, 1 df, $P = 0.0001$), with more females inland (ratio M:F = 0.87:1, $\chi^2 = 2.2$, 1 df, $P = 0.14$) and more males on the edge (M:F = 1:1.97, $\chi^2 = 46.1$, 1 df, $P = 0.0001$).

The survey also detected spatial and temporal shifts in activity patterns. For adult female snakes, the proportion of animals moving versus resting did not vary significantly with time of day on the edge transect (dividing the day into four periods: $\chi^2 = 5.37$, 3 df, $P = 0.15$) but did so along the inland transect ($\chi^2 = 8.59$, 3 df, $P = 0.035$). However, in both areas, females were more often recorded as moving in the late-night period and resting in the morning (Fig. 4). For adult males, the relative numbers of snakes involved in moving, resting, or courting varied significantly with time of day on both transects (edge of the island: $\chi^2 = 25.38$, 6 df, $P = 0.0003$; inland: $\chi^2 = 31.02$, 6 df, $P < 0.0001$; Fig. 4). Adult male sea kraits were generally recorded moving late at night, courting in the morning, and resting in the afternoon. No significant differences were detected in juvenile activity pat-

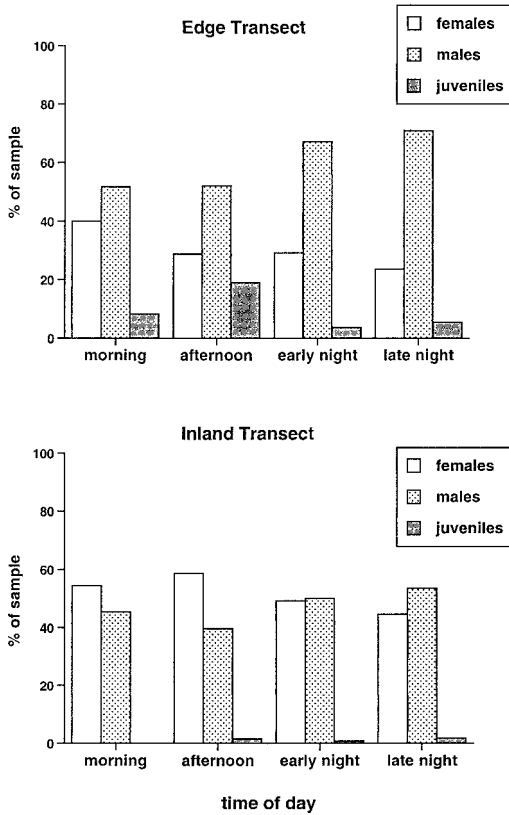


Fig. 3. Occurrence of sea kraits along two transects on Mabualau Island, at different times of the day and night. One transect ran along the edge of the island, whereas the other was parallel to the first but 20 m inland. Data are shown separately for adult females, adult males, and juveniles (sexes combined).

terms with time of day, possibly reflecting the low sample size.

Overall, snakes were often seen in courting groups (i.e., at least one male and one female) in the mornings, whereas most snakes seen at night were solitary. This temporal shift was statistically significant ($\chi^2 = 21.72$, 3 df, $P < 0.0001$). Although the temporal shift in the incidence of courting groups was stronger along the island's edge ($\chi^2 = 19.11$, 3 df, $P = 0.0003$) than inland ($\chi^2 = 7.07$, 3 df, $P = 0.06$), both areas exhibited the same pattern (Fig. 5).

Of 69 individuals (7.3% of the total sample) that were sloughing, 71% were females, 24.5% were males and 4.5% were juveniles. Thus, the proportion of snakes that were recorded in moult differed among these groups (49 of 394 adult females = 12.4%; 17 of 486 adult males = 3.4%; 3 of 45 juveniles = 6.3%; $\chi^2 = 26.86$, 2 df, $P < 0.0001$).

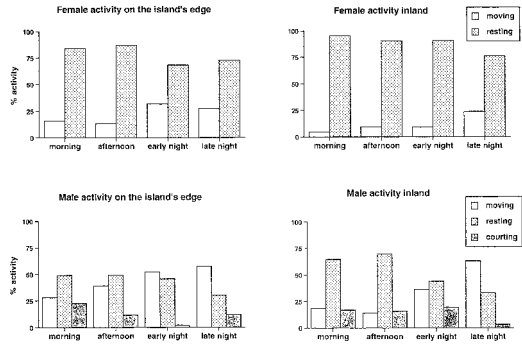


Fig. 4. Activities recorded for adult sea kraits during our surveys on Mabualau Island. Data are shown separately for females (left-hand graphs) and males (right-hand graphs), and for data from a transect along the edge of the island (upper graphs), and 20 m inland (lower graphs).

Movement between the land and the sea.—Our data on movement were analyzed separately for each sex, using ANOVA to examine the effects of site, slope, and tide on the numbers of landward and seaward movements by snakes. For adult females, only one factor (slope) had a significant

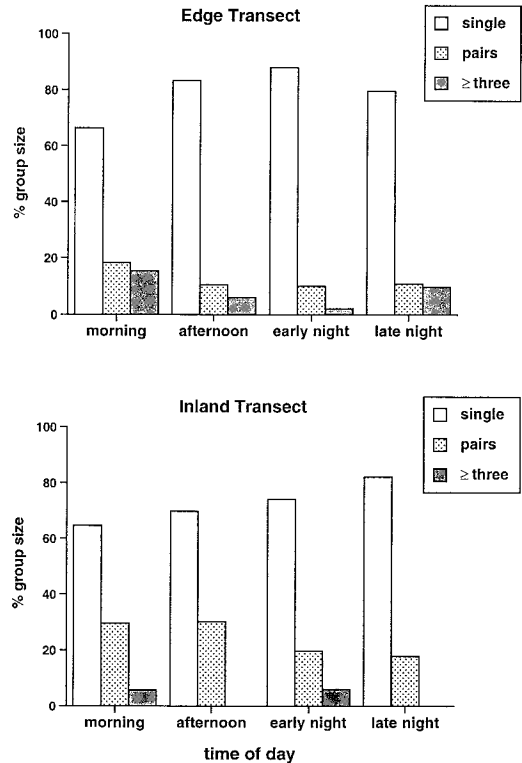


Fig. 5. Occurrence of aggregations of sea kraits along two transects on Mabualau Island, at different times of the day and night.

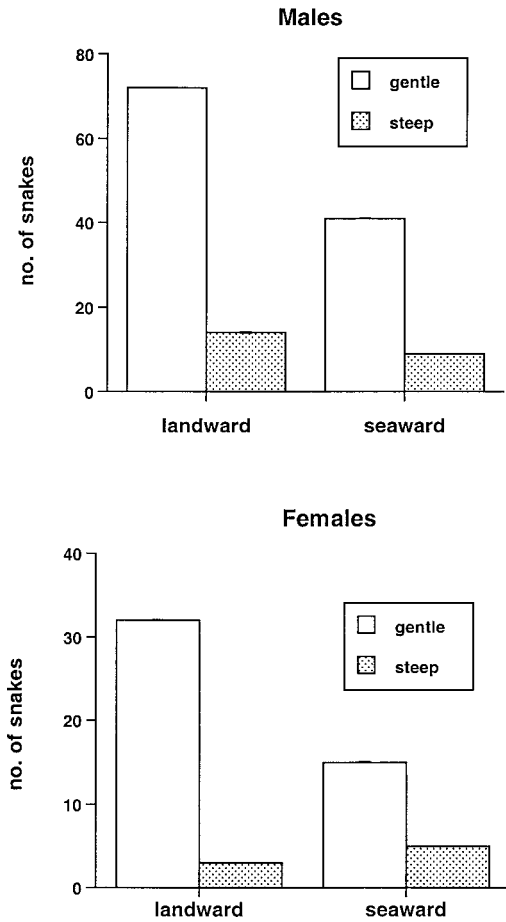


Fig. 6. The numbers of sea kraits encountered in steeply sloping versus gently sloping areas of shoreline on Mabualau Island. The data are further divided by sex and by whether the snake was moving from the sea to the land or from the land to the sea.

main effect on the number of snakes moving in either direction (landward: $F_{1,292} = 26.70$, $P < 0.0001$; seaward: $F_{1,292} = 5.80$, $P = 0.02$). The snakes selected gentle slopes to move between habitats (Fig. 6). Movement patterns of females were not influenced by tidal conditions, nor did they differ significantly among sites. In contrast, a similar analysis for adult male snakes revealed a more complex picture. During the mating season, male sea kraits frequently pursue females, courting them vigorously whenever the female stops moving (Guinea, 1986; Saint Girons, 1964). Thus, movement patterns of males may be influenced by the presence of females, as well as by factors such as weather and local topography. For this reason, we incorporated female movements (total number moving per observation site and period) as a covariate in a

two-factor ANCOVA with site and slope as the factors. This analysis revealed that the numbers of adult male sea kraits seen differed significantly among sites ($F_{5,292} = 4.60$, $P = 0.0005$), was higher on areas of gentle slope than steep slope ($F_{1,292} = 16.60$, $P < 0.0001$), and was higher when many females were present (covariate $F_{1,292} = 20.20$, $P < 0.0001$). Overall then, movement of male sea kraits was influenced by at least three factors: the site where they were observed, the slope at each site, and the movement of females.

A more detailed analysis of landward movements by adult male snakes revealed significant interactions between the factors site and slope ($F_{5,281} = 2.50$, $P = 0.03$) and one of the factors (slope) and the covariate (tide; $F_{1,281} = 12.0$, $P = 0.0006$). Therefore, we looked at the effects of tide and site on each slope separately by using an ANCOVA (with site as the factor and tide as the covariate). The results revealed significant main effects of site and tide on the movement of males but only on gentle slopes (site: $F_{5,143} = 2.40$, $P = 0.04$; tide: $F_{1,143} = 13.80$, $P = 0.0003$). Hence, the number of adult male sea kraits moving was affected by tide and differed between steep versus gentle slopes and also differed among sites of similar slope. Landward movements of adult male sea kraits were more frequent when the tide was high, on gentle slopes rather than steep slopes, and at some sites rather than at others (Fig. 6).

Analysis of the data on seaward movements by adult male snakes did not reveal significant interactions between any of the factors (site and slope) and the covariate (tide). Site and slope had significant main effects (site: $F_{5,292} = 2.30$, $P = 0.04$; slope: $F_{1,292} = 25.70$, $P < 0.0001$), whereas tide had no significant effect on the number of male snakes moving out to sea ($F_{1,292} = 1.80$, $P = 0.20$). Hence, more adult males left the island at gentle slopes rather than steep slopes and more left the island from some sites than from others.

Duration of sloughing and digestion.—Our enclosure data revealed that snakes required approximately 12 days to slough their skins (mean values and range: for seven adult males, 12.6, 5–24 days; for 12 adult females, 11.2, 7–13; for 19 juveniles, 11.7, 5–24). Digestion was a slightly quicker process (for 3 adult males, 8.7, 6–10 days; for 23 adult females, 7.7, 3–11; for 26 juveniles, 7.8, 3–11). Thus, adult males and females did not differ significantly in the duration of either of these activities (digestion: $t = 0.8$, 24 df, $P = 0.40$; sloughing: $t = 0.7$, 17 df, $P = 0.50$).

DISCUSSION

Laticaudine sea-snakes provide an opportunity to examine the ways in which amphibious species use aquatic versus terrestrial habitats. Various lineages of snakes have clearly moved between these two habitat types over evolutionary time. Indeed, such a transition may have played an important role in the evolutionary origin of snakes (Lee and Caldwell, 1998; but see Greene and Cundall, 2000). Although the large terrestrial congregations and tolerant disposition of sea kraits make them particularly well suited to behavioral studies, this opportunity has rarely been exploited. There is considerable potential for comparative analyses in this respect, because anecdotal reports suggest a substantial diversity within the genus *Laticauda* in terms of their degree of reliance on terrestrial habitats (e.g., Tu et al., 1990). Although *L. colubrina* can (and does) move rapidly on the ground, some other *Laticauda* species rarely leave the water (e.g., *L. crockeri*; Cogger et al., 1987).

Our radiotelemetric studies indicate that yellow-lipped sea kraits are truly amphibious animals. The snakes that we radio-tracked spent approximately equal amounts of time in the ocean as on land. Lading et al. (1991) estimated that *L. colubrina* spend only about 30% of their time on land, based on surveys of the proportion of marked snakes that could be located on land at any given time. In our experience, some snakes in terrestrial locations on Mabualau were so well hidden that they were essentially impossible to see. Thus, survey data may underestimate terrestrial activity. Saint Girons (1964) speculated that female *L. colubrina* may spend more time at sea than do males, and that snakes move between the land and the ocean on a relatively long timescale (weeks rather than days). More terrestrial habits in male than female *L. colubrina* were also inferred by Pernetta (1977) and Lading et al. (1991), based on sex ratios among snakes sampled on the islands. However, Shetty and Prasad (1996) came to the opposite conclusion from their studies in the Andaman islands; these authors estimated that females spent an average of about six days on land and males about four days. Our study at Mabualau revealed movements between land and sea about every 10 days in both sexes.

The 10-day cycle of moving between land and water fits well with the average duration of sloughing (12 days) and digestion (eight days). In turn, these data are consistent with a report that sloughing required nine to 13 days in captive *L. colubrina* (Franklin, 1977). The propor-

tion of individuals that were either sloughing (12.4%) or recently fed (4.1%; Shetty, 2000) was much higher among adult female sea kraits than among males (3.4% and 0.6%, respectively). Presumably, sloughing and digestion are major reasons for adult female sea kraits to return to land. The same is true, to a slightly lesser degree, for juvenile snakes (6.3%, 4.2%). In contrast, adult males spend much of their time in courtship and may remain on the island (at least during the breeding season) for this reason instead.

Because different age/sex classes use terrestrial habitats for different functions (above), they are distributed differently in time and space. Juvenile sea kraits move about on land less than do adults, and so are less likely to be found further from the water (and hence, were virtually absent from our "inland" transect, unlike the other two groups). Similarly, the numbers of male snakes entering and leaving the water were significantly associated with the numbers of females seen at the same time and the same place. Observation indicated a strong causal link, with many males actively courting these females.

The radiotelemetric monitoring of snakes also allowed us to evaluate whether or not they displayed any overt thermoregulatory behavior. The answer is that they do but only to avoid overheating. The thermal environment is a benevolent one in which high, stable body temperatures are relatively easy to maintain. The only problem for a sea krait on land is that operative temperatures become dangerously high in the afternoon (Fig. 2). In response, the snakes cease their activities (especially, courtship) and retire to shaded areas at this time. In consequence, their body temperatures remain relatively constant through the day. Sea kraits may resemble many other tropical reptiles in that their thermoregulatory behaviour involves avoidance of high rather than low temperatures (Shine and Madsen, 1996).

The higher body temperatures of male than female sea kraits reflect sex differences in location and behaviour. Males are more active, and often are located in higher, drier areas where evaporation has less impact on thermal regimes. One of the most intriguing results from our study is the fact that the two sexes use habitats in different ways and for different functions. The same is true of the aquatic habitat: female sea kraits feed on large deepwater eels, whereas males take smaller shallow-water species (Pernetta, 1977; Shetty, 2000). Thus, males move about further in terrestrial habitats, but less in aquatic habitats, than do females. Per-

formance trials reveal a corresponding sex difference in locomotor ability: males crawl on land faster than females, but females can swim faster than males (Shine and Shetty, 2001). Several interspecific comparisons of locomotor performance have suggested that species are best able to move about in the kinds of habitat that they most frequently use (e.g., Losos, 1990). However, we are not aware of any previous case where two sexes within the same species have been shown to differ both in their usage of two different habitat types and in their relative locomotor performance under those two conditions.

In their review of activity patterns in snakes, Gibbons and Semlitsch (1987) concluded that many studies had detected significantly nonrandom patterns of activity, but the actual causes for such patterns remained elusive in almost all cases. Many of our results are readily interpretable in the light of challenges facing these amphibious animals. For example, the restriction of juveniles to aquatic and edge habitats may reflect their greater vulnerability to predators or to overheating (Guinea, 1986). The same may be true of the general tendency for sea kraits of all age and sex classes to move about mostly at night. The selection of gently sloping areas to move between land and water is also not surprising: these snakes are buffeted about by waves as they try to move across this boundary and are often thrown against sharp coralline rock. Especially if they contain large prey items, they experience substantial difficulty in making the transition. Moving at high tide has the advantage that the snake does not have to crawl across a wide area of exposed coral between the land and the deeper water (Pernetta, 1977).

Laticaudine sea-snakes are well suited to studies of the type that we have conducted. They are extraordinarily abundant in suitable habitats, and their bright colour pattern makes them easy to see (and thus, to survey). Although they are highly venomous, they are remarkably tolerant of human interference. Their large body size simplifies the logistical problems of surgical insertion of radio-transmitters. Given the wide geographical distribution of laticaudines, and interspecific differences in the degree to which they use terrestrial habitats, there is an obvious potential for comparative studies. Indeed, the sea kraits may offer a uniquely powerful opportunity to explore the ways in which ecological and behavioral traits become modified in the course of a major phylogenetic transition from terrestrial to aquatic life.

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