Behavioural ecology of the yellow-lipped sea krait, *Laticauda colubrina,* in the Fiji Islands

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This thesis is my own original work, except where specifically acknowledged.

Sohan Shetty
August 2000

DEDICATED TO

EVOLUTION

....the creator of these awesome beasts.

ABSTRACT

Yellow-lipped sea kraits (*Laticauda colubrina*) are large (> 1.5 m body length, 1.5 kg) amphibious snakes widely distributed throughout the Pacific region. They forage in the ocean, but frequently return to land. I captured, measured and individually marked > 1,100 sea kraits between September 1998 and December 1999, on Mabualau and Toberua Islands (Fiji). Female sea kraits grow much larger than males, and the sexes differ in head sizes even at the same snout-vent length (females have longer, wider heads). The sex differences in mean adult body length and in relative head size probably reflect a combination of evolutionary processes involving fecundity selection, sexual selection and natural selection. Female sea kraits eat much larger prey items than do conspecific males (mostly conger eels) and usually contained only a single prey item when examined. In contrast, male sea kraits eat smaller prey items (mostly moray eels) and often contain multiple prey. The sex divergence in relative head sizes may be an adaptation to this sex difference in dietary habits. Interestingly, the prey taken by female sea kraits are larger relative to the snake's head length, as well as its snout-vent length, than is the case for prey items in males.

I quantified various facets of terrestrial behaviour in the sea kraits of Mabualau. Intensive surveys and radiotelemetry were used to monitor daily activity and movement patterns of sea kraits, and to suggest causal influences on these traits. Behavioural patterns including activity levels, activity type and microhabitat use differed significantly between juvenile and adult snakes, and between adult males versus females. Juvenile sea kraits rarely ventured far from water, whereas adults moved much further. Adult snakes were generally most active at night. The movements of adult male snakes were influenced not only by the location of females, but also by tidal conditions and physical attributes of the island. Radiotelemetric monitoring of 16 adult snakes indicated that most of these animals spent relatively equal amounts of time on land and at sea, moving between the two habitats about once every ten days. In keeping with this pattern, resampling of individuals showed that they required about eight days to digest a large prey item, and about 12 days to complete the sloughing process. Radio-tracked male sea kraits maintained higher body temperatures than females throughout the day.

I collected groups of courting snakes and placed them in outdoor arenas to obtain data on courtship and mating behaviour. These behaviours observed differ substantially from published descriptions of courtship in other snake species. First, males in courting groups displayed overt courtship only rarely, remaining immobile the rest of the time. Second, males exhibited body spasms during the occasional periods of intense courtship. I did not see any overt physical interactions among rival males within courting groups, and body sizes of copulating males compared to unsuccessful suitors suggest that larger body size does not enhance mating success. The intensity of courtship behaviour differed substantially among groups. Larger females attracted more intense courtship, and significant temporal variation in courtship behaviour suggests that environmental factors or attributes of males may also influence these reproductive interactions.

I used a simple raceway to measured locomotor speeds of these snakes in water and on land. The resulting data were used to investigate two topics: (1) to what degree have adaptations to increase swimming speed (paddle-like tail, etc.) reduced terrestrial locomotor ability in sea kraits?; and (2) do a sea krait's sex and body size influence its locomotor ability in these two habitats, as might be expected from the fact that different age and sex classes of sea kraits use the marine and terrestrial environments in different ways? To estimate ancestral states for locomotor performance, I measured speeds of three species of Australian terrestrial elapid snakes that spend part of their time foraging in water. The evolutionary modifications of *Laticauda* for marine life have enhanced their swimming speeds by about 60%, but decreased their terrestrial locomotor speed by about 80%. Larger snakes moved faster than smaller individuals in absolute terms but were slower in terms of body lengths travelled per second, especially on land. Male sea kraits were faster than females (independent of the body-size effect), especially on land. Prey items in the gut reduced locomotor speeds both on land and in water. Proteroglyphous snakes may offer exceptional opportunities to study phylogenetic shifts in locomotor ability, because (1) they display multiple independent evolutionary shifts from terrestrial to aquatic habits, and (2) one proteroglyph lineage (the laticaudids) displays considerable intraspecific and interspecific diversity in terms of the degree of reliance upon land *versus* water.

Based on growth of marked snakes in my study, I can estimate the "typical" growth trajectory for Fijian sea kraits. Snakes of both sexes grow rapidly during the first year of their lives, from about 30 cm SVL at

hatching to about 55 to 65 cm SVL at 12 months of age. Male sea kraits mature at 18 months of age, and females at 30 months. In both sexes, growth rates slow dramatically after maturation. At the same body length, male sea kraits on Mabualau grew more rapidly than did those on Toberua.

Several of my results are relevant to the conservation and management of these snakes. However, the most striking of these results was the extreme site fidelity of the individually marked animals. All snakes displaced from Toberua Island and relocated to Mabualau Island rapidly returned to their "home" island. Similarly, none of the snakes from Mabualau Island were ever captured on Toberua Island. Population estimates from the mark-recapture data reveal that there were over 2,300 snakes on Mabualau. Toberua had a resident population of approximately 900 snakes. Because of the high site fidelity, human activities such as commercial harvesting of snakes, or anthropogenic modifications to island habitats, are likely to have intense but highly localised effects on sea krait populations.

ACKNOWLEDGMENTS

This project involved a fair amount of input from folks in Australia, Fiji and home, who not only offered financial and technical support, but a lot of moral support as well. I am grateful to each one of them irrespective of the magnitude of help rendered. I would like to highlight the support of a few people and organisations whose role was vital during the project.

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CHAPTER 1. GENERAL INTRODUCTION

Coral reefs in tropical oceans are among the most diverse and complex ecological assemblages on our planet, and have long been a significant focus of interest from the general public as well as from scientific researchers. In human terms, reefs are important not only as a source of recreation for tourists from developed nations, but also because the livelihood of a significant local population depends on these highly productive ecosystems. As well as contributing to biodiversity in their own right, reefs influence the faunal composition of surrounding areas: for example, reefs serve as nurseries for the young of many marine organisms.

Because coral reefs support human activities as well as providing habitats for a diverse fauna, there is obvious potential for conflict. In many areas, the increasing human population has placed so much pressure on these ecosystems that there has been substantial degradation. Clearly, we need to manage these complex ecosystems so as to ensure their long-term viability. To achieve this aim, we require information. Despite the vast amount of research conducted on coral reefs, however, there are still massive gaps in our knowledge. Even in developed countries, managers of these ecosystems frequently have to adopt the precautionary principle in their management plans.

Given the urgency of the situation, it is important to focus on identifying and maintaining ecologically important components in these ecosystems. This procedure involves identifying "keystone" and "umbrella" species and/or adopting the "top down" approach, complemented by the "bottom up" approach (Zann, 1996) to keep these ecosystems alive. The "top down" approach to conservation targets the understanding of predators in an ecosystem. The logic behind this approach is that by fulfilling the requirements of predators, a host of other organisms, as well as the habitat, will be protected.

In coral reefs, the top end of the food chain comprises a variety of taxa including sea snakes along with sharks, eels and other predatory fish. However, sea snakes have received much less scientific attention than their terrestrial counterparts. For example, Australia is home to about 38 species of sea snakes, which constitute over half of all sea snake species known to science (Heatwole, 1999). Most of these species occur in northern Australian waters and about 50% of these snakes are endemic to that region. Yet, according to the State of the Great Barrier Reef World Heritage Area report (Wachenfeld, 1998), the ecological status of sea snakes is "unknown". Currently, there are no management measures for sea snakes in this region. In fact, a lack of information means that we cannot even judge whether or not such measures are needed. Even in the Gulf of Carpentaria, where there have been a few estimates of numbers of sea snakes killed in trawl nets (Ward, 1996), the impact of this mortality is not known (Wachenfeld, 1998).

This scarcity of information is due to a combination of factors, mostly involving logistics. Most universities (and thus, herpetologists) are based in temperate climates, far from the natural range of sea snakes. Also, there are substantial difficulties in studying aquatic animals: many of the kinds of techniques and equipment used to study terrestrial reptiles are simply not feasible in the ocean. Added to this are the relatively low abundances of many species, and their highly toxic venoms.

However, one group of sea snakes do not pose as much of a threat or inconvenience to researchers. Sea snakes belonging to the family Laticaudidae are commonly referred to as sea kraits. There are four known species in this family, one of which, *Laticauda colubrina* is the focus of my research. The uniqueness of these snakes lies in two facets of their inherent characteristics: their amphibious habits and their remarkably tolerant dispositions. Although they forage in the ocean, sea kraits return to land for most other activities. They congregate on small isolated islands and thus, can be found in large numbers. Second, although these snakes are highly venomous, they are very reluctant to retaliate against humans even after considerable provocation. The atypical nature of this species makes them "research-friendly", overcoming the obstacles of rarity and high dependence on logistical support. Despite the "conveniences" offered by this species to researchers, however, the biology of sea kraits has attracted relatively little study. Although the species occurs over a wide geographic area, the only detailed studies on the ecology of *L. colubrina* have come from New Caledonia (Saint Girons, 1964) and Fiji (Pernetta, 1977; Guinea, 1981). Although these studies have contributed significantly to our understanding of the species, there are still large areas where information is either ambiguous or missing.

Sea kraits are distributed throughout along the south-east Asian coast, through Indonesia, the Philippines, New Guinea, and the Pacific Islands. They have been recorded in Australian waters but not as breeding populations (Greer, 1997). For this reason I chose to study them in Fiji, where breeding populations are known to occur. My study was designed to clarify the general biology of these animals, and also to generate baseline information that will enable managers to make confident decisions about sustainable use of resources in tropical reef systems.

Some basic attributes of the study species, such as its morphology and diet, are considered in Chapter 2. Detailed studies on the terrestrial behaviour of the sea kraits and factors affecting these behaviours are discussed in Chapters 3, 4 and 5. Lastly, in Chapter 6, I discuss aspects of the biology of sea kraits that are particularly relevant to the conservation of this species.

STUDY SITES

This study was conducted in the Fiji Islands between September 1998 and December 1999. Two islands (Toberua and Mabualau) in the Bau waters (Tailevu Province) were chosen for the study. I set up a camp on Mabualau Island and spent a total of 180 days (divided in two trips) collecting data.

Mabualau Island

Mabualau (also known as Bird Island; 17°97.119'S, 178°75.6E) lies about 6 km off the south-east coast of Viti Levu, and about 25 km from the city of Suva. It is a 4 ha, elliptical limestone islet (Plate 1) and is believed to have been a reef which formed underwater and later emerged from the ocean (Thaman, 1997). This origin explains the fact that over 70% of the island is made up of sharp coralline rock. The island rises about 5 m above sea level and is

Plate 1. Mabualau Island

surrounded by a vast expanse of reef flats. These flats extend 500 m or more all around the island. During an average low tide, at least 100 m of these intertidal reef flats are exposed.

In spite of being mostly rocky, the island is densely vegetated with about 56 species of plants, 25 of which are trees (Thaman, 1997). The vegetation is anchored around the rocks and as a result, the trees are superficially rooted and easily collapse during high winds. The island is a major rookery for sea birds such as red-footed boobies, frigate birds and noddies, and is home to a significant population of sea kraits (*Laticauda colubrina*). The island is uninhabited by humans, probably because of the lack of fresh water and its inaccessibility during low tide, but is visited fairly regularly by fishing parties.

Toberua Island

Toberua is an exotic sandy tourist resort situated 5.3 km away from Mabualau. It is about 1.5 ha in area, and rises about 2 m above sea level. It is dominated by coconut palms and has a considerable built-up area - about 20 cottages and two jetties. Like Mabualau, it also has a vast expanse of fringing reef flats which are exposed during low tide and that are also home to a significant population of sea snakes. There is a constant human presence on Toberua.

Although humans live on Toberua fulltime, and visit Mabualau frequently, there is little direct interaction between humans and snakes. In particular, local customs discourage killing snakes. There have been no reports of envenomation by the snakes on Toberua, despite frequent close encounters over many years (M. Dennis, pers. comm.). The staff regularly encounter these snakes but have learnt to ignore their presence. Soon after their arrival on Toberua, tourists are educated about the snakes by the staff. As part of their activities, the guests are taken for day trips to Mabualau Island and a staff member teaches them about the flora and fauna. Thus, human activities in my study area have probably had little direct impact on snake populations, except for perhaps, the indirect and unintentional consequence of peoples' movements and the development of the Toberua resort.

CHAPTER 2. MORPHOLOGY AND FEEDING HABITS

INTRODUCTION

Over the course of my mark-recapture study, I measured, weighed and individually marked > 1,000 sea kraits. Many of these animals also contained freshly-ingested prey items which they disgorged during handling. Thus, this component of the study generated an extensive data set on the body sizes and shapes of yellow-lipped sea kraits, and on the types and sizes of prey that they consume. In this chapter, I will describe the results from this work.

Previous studies on *Laticauda colubrina* have documented significant geographic variation in body size, extreme sexual dimorphism in mean adult body sizes and body proportions (Plate 2), and have suggested that male and female sea kraits may show intraspecific niche divergence (e.g. Saint Girons, 1964; Pernetta, 1977; Guinea, 1986; Camilleri and Shine, 1990). However, the findings of these have been based on small sample sizes, or have combined specimens from a wide geographic area. Thus, my data are the first to enable a detailed examination of such questions within a single population.

METHODS

Snakes on Mabualau Island were collected by hand at various times of the day and night, and brought to the camp site where they were processed. On

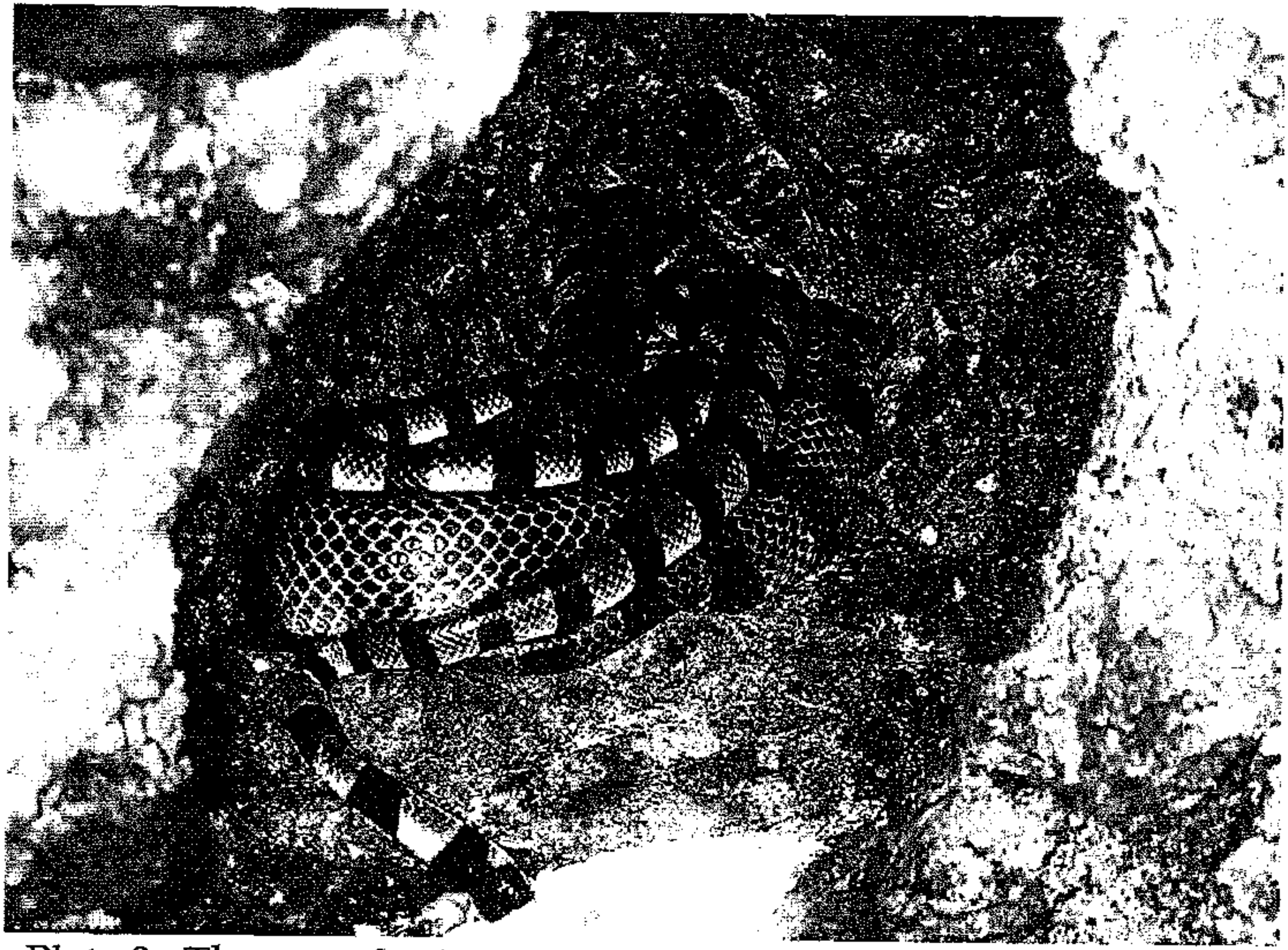


Plate 2. Three sea kraits resting in a rock crevice. Notice the difference in male (smaller) and female (larger) body sizes.

Toberua Island, snakes were collected by resident staff who would bag the snakes and deliver them to me on Mabualau Island the next day.

Morphometric measurements

Measurements of snout-vent length (SVL) and tail length (TL) were taken from every snake captured (± 1 cm). Mass (± 1 g) was determined using a Pesola spring balance. Head dimensions (length and width) were measured to the nearest millimetre using Vernier callipers. Head width (HW) was measured at the widest part of the head. Head length (HL) was measured along the jaw, from the tip of the snout to the back of the mandibular joint. Date and location of capture, sex, number of black bands around the body, presence of ectoparasites, feeding status, predation marks, and any unusual or identifying characters were also recorded. Among adult snakes, the sexes were easily identified due to marked differences in morphology. Firstly, females have much larger SVLs than males. Secondly, males have long pear-shaped, fleshy tails while females have short, thin, flat tails. Based on his dissections of Fijian *L. colubrina*, Guinea (1986) reported that males with SVL < 70 cm and females < 90 cm were juveniles. I also used these criteria, and thus classified males and females with SVLs ≥ 70 and 90 cm respectively as adults.

Individual marking

Once measured, the snakes were marked by clipping ventral scales in a combination that corresponded to a unique serial number. The numbering system involved the first 30 consecutive ventral scales starting from the anals, running towards the anterior portion of the body. The anal scale was the reference, and each consecutive scale thereafter was designated a number as follows; 0, 1, 2, 3 4,........10, then 20, 30, 40,.....100, then 200, 300, 400......1000, 2000 and 3000. Thus, for example, if a snake was to be marked # 232, the scales 200, 30 and 2 would be clipped. To aid identification when recaptured, odd numbers were used for females and even numbers for males.

Sterile surgical blades were used to clip the scales. First, I clipped half of the desired ventral scale and then continued to clip the four adjoining dorsal scales so as to form an '*L*' shaped scar along the lateral side of the body. A modified battery-operated 6 V soldering iron was then used to cauterise the clipped area. This procedure resulted in a permanent scar once the epithelial tissue regenerated (in approximately 3 weeks time).

The snakes responded very well to the marking procedure and did not exhibit any overt signs of stress. This inference is supported by the fact that recently marked individuals were observed actively courting. Additionally, because the scar was clearly visible, it allowed me to identify marked individuals without having to disturb them (i.e. lift them to check if the ventrals were clipped).

All care was taken to ensure the welfare of the animals during the entire study. Snakes were held in "breathable" bags, kept in the shade, and as far as possible were processed within a day of capture before being released.

Diet sampling

Snakes that had recently ingested prey items were easily identified by their significantly distended bodies. Nevertheless, the stomach of every snake was squeezed gently to locate prey items, and if present, these were removed by palpation (Shine, 1986; Fitch, 1987). Since these snakes feed exclusively on eels, palpation required less than one minute and caused no harm to the snake (because eels do not have any hard external protrusions). In fact, in most cases palpation was not necessary as the initial stimulation provided by handling induced the snake to regurgitate its prey voluntarily.

I recorded the number of prey items, prey species, maximum diameter of the prey and its orientation (swallowed head-first or tail-first).

RESULTS

Of the 1138 snakes I marked between October 1998 and December 1999, 810 snakes were from Mabualau Island and 328 were from Toberua Island. The combined morphometric data from these animals are summarised in Table 2.1 and Figure 2.1.

Sexual size dimorphism and differences between islands

Juveniles

Only six juveniles were captured from Toberua Island and thus the data from these animals were not used in the following analyses. Data on

Table 2.1 Sample sizes, means and standard deviations of morphological traits of all adult and juvenile snakes measured in this study. (Note: 10 snakes are not included in the analyses).

	Data from Mabualau and Toberua Islands combined								
	Adult Males			Adult Females			Juveniles		
	N	mean	SD	N	mean	SD	N	mean	SD
snout-vent length (cm)	588	82.2	4.6	273	114.6	10.2	267	49.9	10.2
tail length (cm)	588	12.4	1.1	273	11.9	1.2	267	6.1	1.4
head length (mm)	588	23.7	1.6	273	34.8	4.1	267	17.1	2.4
head width (mm)	588	13.6	1.1	273	22.2	2.9	267	9.4	1.7
no. of bands	580	31.7	1.8	271	29.7	1.8	265	30.9	2
mass (g)	588	229.1	39.4	275	655.6	231.8	267	60.6	53.3

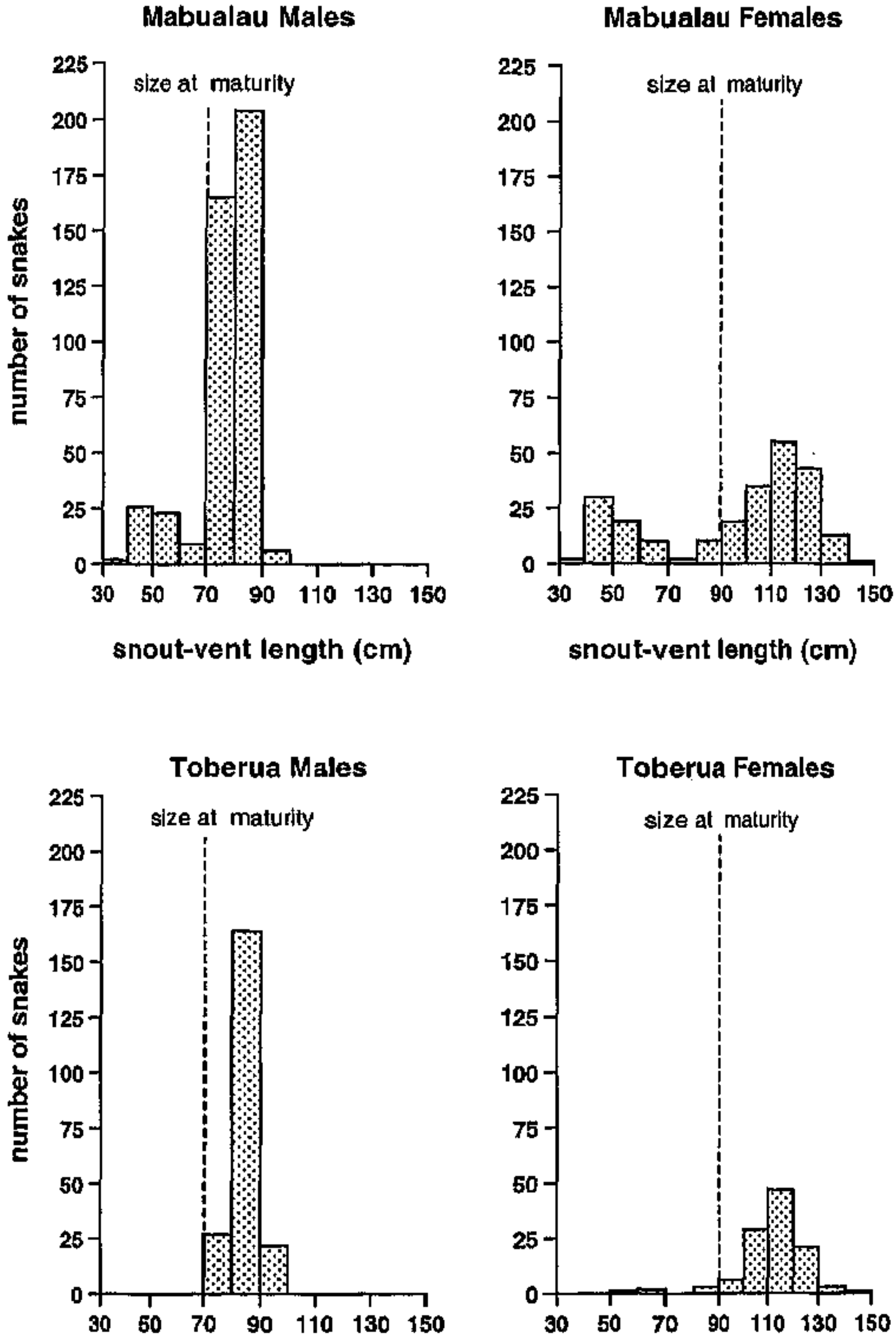


Figure 2.1 Frequency distribution of snakes in various size classes, as a function of sex and island of origin.

juveniles obtained from Mabualau Island, and the mean difference in morphological traits between male and female juveniles, are presented in Table 2.2. Although the small sample size of juveniles from Toberua Island prevented any between-island comparisons, analysis of the juveniles from Mabualau Island yielded some interesting results.

Among Mabualau juveniles, significant differences were observed between the sexes (Fig. 2.2). Although SVLs were similar, juvenile females had shorter tails ($F_{1,265} = 81.45$, $P < 0.0001$) and fewer bands ($F_{1,265} = 81.02$, $P < 0.0001$). Juvenile males, on the other hand, had significantly smaller heads (head length: $F_{1,265} = 18.61$, $P < 0.0001$; head width: $F_{1,265} = 12.26$, $P = 0.0005$) than did females.

Adults

Laticauda colubrina are known to be sexually dimorphic (Guinea, 1986) and the results of my study support this finding. Males and females differed significantly in all of the five morphological traits that were measured (i.e. SVL, TL, head length, head width and number of bands). Interestingly, the morphological traits of adults of each sex also differed significantly between islands. The descriptive statistics for these data and mean differences are presented in Table 2.3. Male snakes from Toberua Island were significantly larger with respect to body size (SVL and TL) and head size (head length and width) than the male snakes from Mabualau Island. In contrast, females did not differ significantly in body sizes between the two islands, although Mabualau females did have significantly larger heads (Table 2.3).

Table 2.2 Mean values for body sizes and morphological traits of juvenile *Laticauda colubrina,* with mean difference between males and females and a test for the statistical significance of this sexual dimorphism.

	Data for juvenile snakes from Mabualau Island							
	Juvenile Males			**Juvenile Females**			**Mean Difference between sexes**	
	N	**mean**	**SD**	**N**	**mean**	**SD**	**mean diff.**	**P-value**
snout-vent length (cm)	131	49.4	8.2	138	50.9	12.4	-1.6	0.2
tail length (cm)	131	6.8	1.3	138	5.4	1.2	+1.4	<0.0001
head length (mm)	131	16.5	1.7	138	17.8	2.9	-1.3	<0.0001
head width (mm)	131	9.0	1.2	138	9.8	2.1	-0.7	0.0004
no. of bands	129	31.9	1.7	138	29.9	1.8	+1.9	<0.0001
mass (g)	131	55.9	30.4	136	65.0	68.3	9.1	0.2

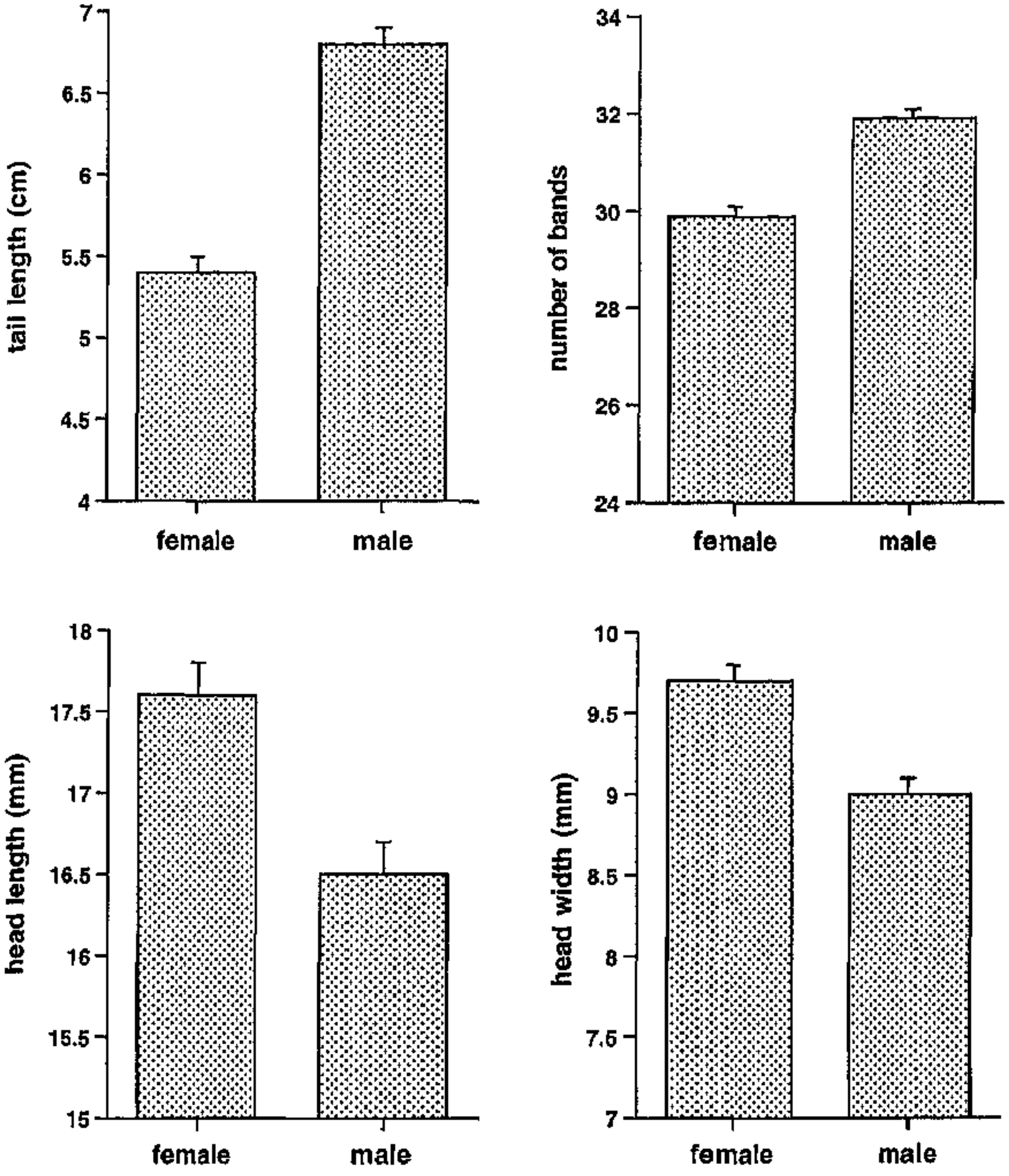


Figure 2.2 Sexual size dimorphism in juvenile snakes from Mabualau Island. Males have significantly longer tails and more bands than females, whereas females have significantly larger heads than males.

Table 2.3 Sample sizes, means and standard deviations of morphological traits of adult sea kraits from each island and mean differences in these traits between islands. Statistical results of two-factor ANOVA with effects of sex, island and the interaction effect of sex and island are also shown. (Note that the degrees of freedom are $F_{1, 859}$ for all tests).

	Mabualau Island						Toberua Island						Mean difference between Mabualau and Toberua islands				Statistical tests - Effects of:					
	adult males			adult females			adult males			adult females			adult males		adult females		Sex		Island		Sex*Island	
	N	mean	SD	N	mean	SD	N	mean	SD	N	mean	SD	mean diff.	P-value	mean diff.	P-value	F	P	F	P	F	P
snout-vent length (cm)	373	80.6	4.1	168	114.3	11.3	215	84.8	4.1	107	114.6	9.3	-4.2	<0.0001	0.1	0.95	3781.8	<0.0001	19.2	<0.0001	14.3	0.0002
tail length (cm)	373	12.2	0.9	168	11.9	1.3	215	12.6	1.3	107	11.8	1.2	-0.4	<0.0001	0.1	0.7	48.7	<0.0001	4.3	0.04	6.0	0.01
head length (mm)	373	23.4	1.6	168	35.1	4.5	215	24.1	1.6	107	34.1	3.5	-0.7	<0.0001	1.1	0.04	2909.1	<0.0001	0.4	0.6	16.9	<0.0001
head width (mm)	373	13.4	1.0	168	22.4	3.2	215	13.9	1.2	107	21.7	2.7	-0.5	<0.0001	0.8	0.03	3383.0	<0.0001	0.7	0.4	16.5	<0.0001
no. of bands	370	31.6	1.8	166	29.6	1.8	210	31.7	1.8	107	29.7	1.8	-0.1	0.71	-0.1	0.8	215.7	<0.0001	0.3	0.6	0.01	0.9
mass (g)	370	220.6	36.6	168	672.6	239.1	212	243.5	40.1	107	628.5	218.4	-22.9	< 0.0001	43.9	0.13	1722.0	<0.0001	1.04	0.3	11.1	0.0009

A visual comparison of the frequency distributions of snakes in 10 cm interval categories (Fig. 2.1) shows a greater number of males with snout-vent lengths between 70-80 cm on Mabualau Island compared to the same size class on Toberua Island.

Because of these differences, it was necessary to look at the effects of sex and island on morphological traits simultaneously. A two-factor ANOVA with sex and island as the factors and each of the five morphological traits as dependent variables revealed significant interactions between the factors for four traits (Table 2.3).

Sex differences in morphological traits relative to SVL

The analyses above show significant main effects of sex and source population (island) on morphology, as well as significant interactions between these two factors. To clarify these sources of variation, I conducted further analyses which removed the confounding effect of body size on the other morphological traits, i.e. tail length, head size and number of bands. For these analyses, I excluded data from snakes > 105 cm, in order to ensure body size overlap of males and females. Because sex and island had a significant influence on morphology (see above and Table 2.3), these effects were also taken into consideration.

The first step was to ask if male and female snakes (and snakes from the two islands) differed from each other in morphology after the effects of body-size had been removed. To answer this question, two-factor ANCOVAs were conducted, with sex and island as the factors, SVL as the covariate, and the remaining morphological traits (tail length, number of bands, head length, head width and mass) as dependent variables. The results are presented below.

Tail length

Sex of the snake and SVL had significant main effects ($F_{1,626} = 775.6$, $P < 0.0001$ for sex and $F_{1,626} = 440.7$, $P < 0.0001$ for SVL). Males had tails that were on average 1.9 cm longer than female tails ($P < 0.0001$; Fig. 2.3). There was also a significant difference in tail length between Mabualau and Toberua Islands, with a mean difference of 0.5 cm ($P < 0.0001$).

Hence, at the same body length, males had longer tails than females on both islands, but this difference between the sexes was slightly greater on Toberua Island than on Mabualau (Fig. 2.4).

Number of bands

There were no significant interactions between sex, island and SVL. Only sex had a significant influence on band number ($F_{1,626} = 16.7$, $P < 0.0001$). The mean difference in number of bands between males and females was 2.1 ($P < 0.0001$; Fig. 2.3), indicating that at the same body size, males had about two more bands around the body than females. This difference was consistent on both islands.

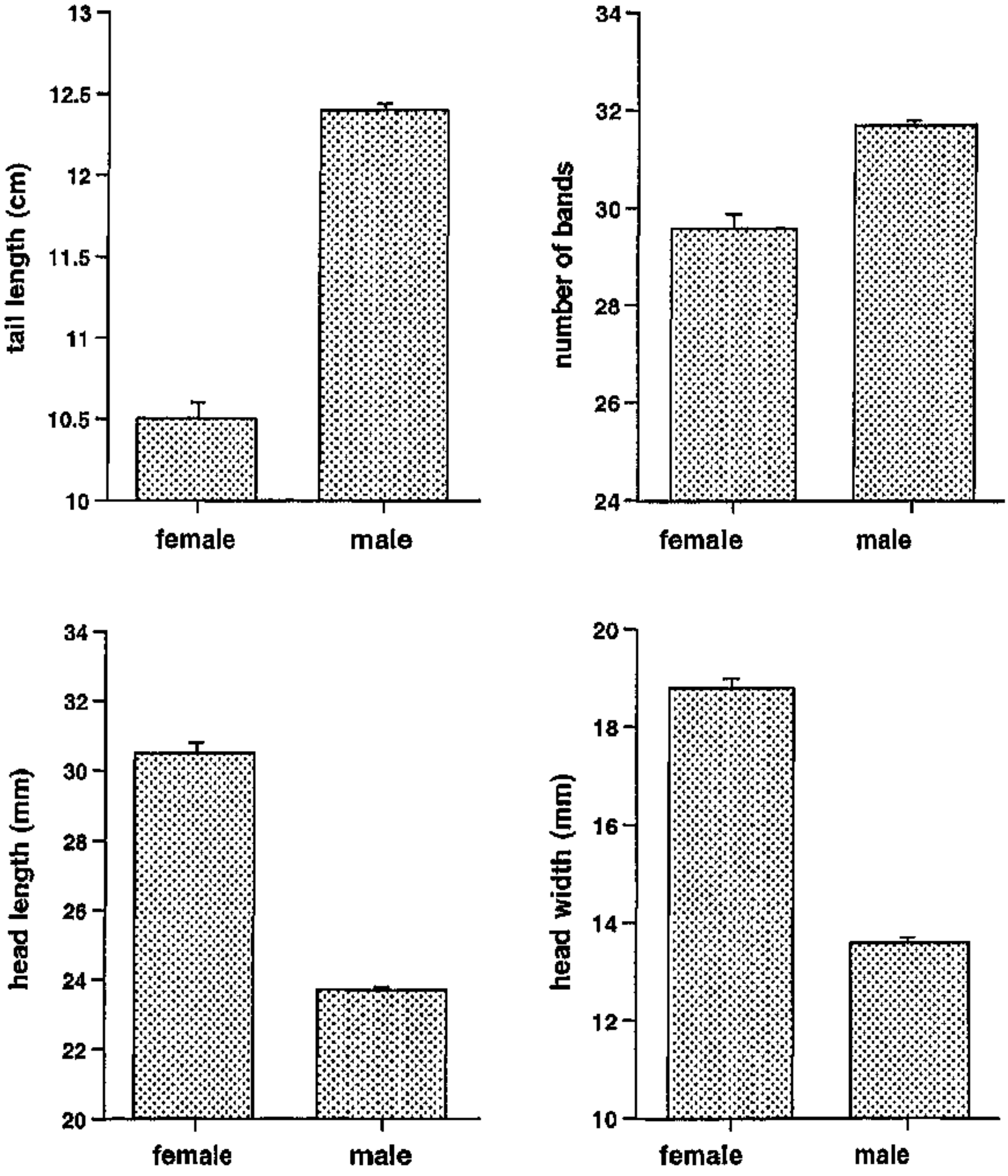


Figure 2.3 Sexual size dimorphism in adult snakes from Toberua and Mabualau Islands (combined). The patterns are similar to those of juvenile snakes. Males have significantly longer tails and more bands than females, whereas females have larger heads than males.

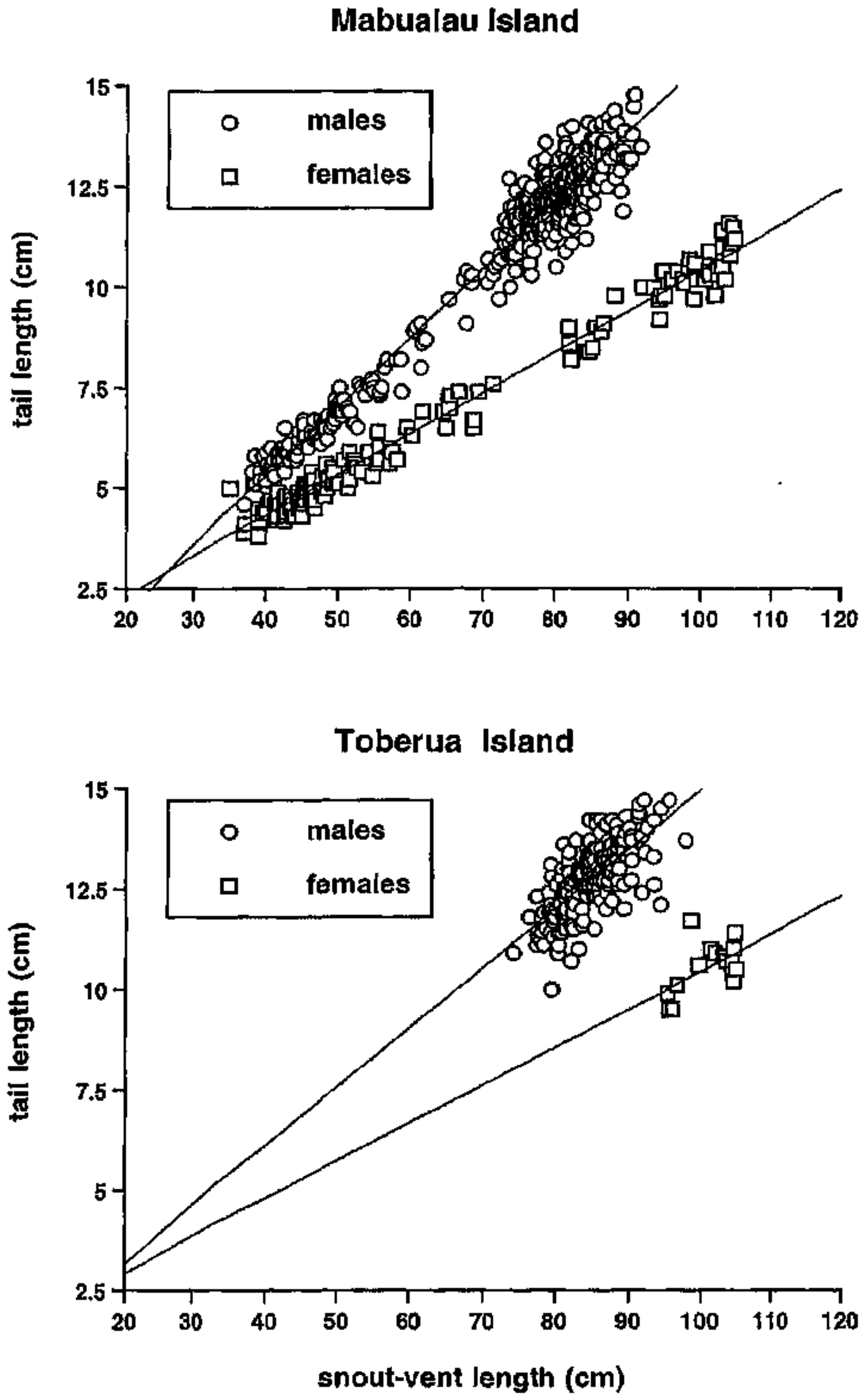


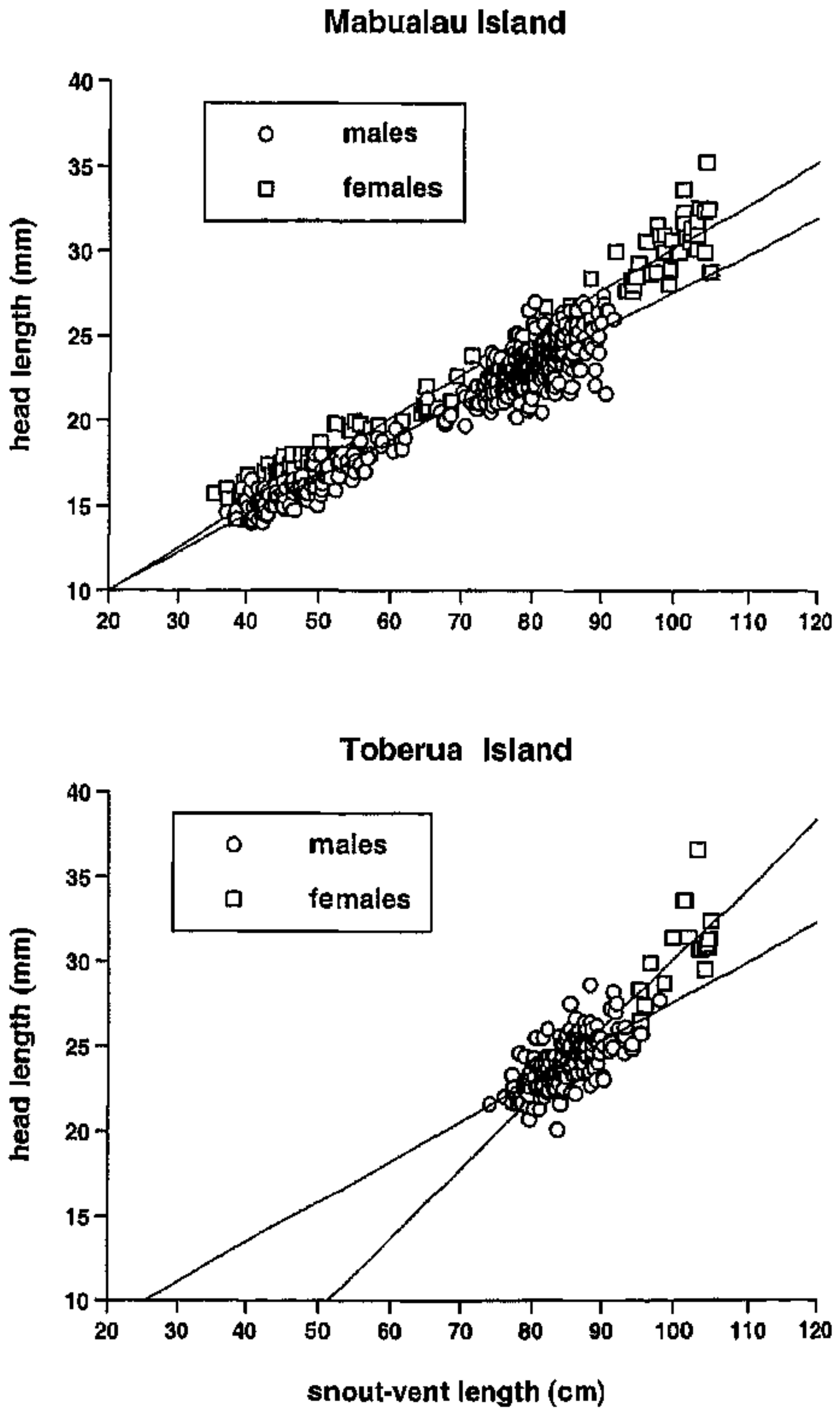
Figure 2.4 Tail length relative to snout-vent length in male and female sea kraits from Toberua and Mabualau Islands. Data restricted to snakes < 105 cm snout-vent length, to ensure overlap between the sexes.

Head size

A significant interaction term was encountered between sex and SVL for both head length ($F_{1,623} = 6.3$, $P = 0.01$) and head width ($F_{1,623} = 4.2$, $P = 0.04$). That is, the rate at which a snakes' head dimensions increased with body length was lower in male sea kraits than in females. The mean difference between female and male head length was 6.8 mm ($P < 0.0001$; Fig. 2.3) and for head width was 5.2 mm ($P < 0.0001$; Fig. 2.3). Like tail length, head sizes of males and females also differed between Mabualau and Toberua Islands (mean difference for head length = 0.5 mm, $P < 0.0001$, and mean difference for head width = 0.3 mm, $P < 0.0001$). At similar body lengths, females had much larger heads than males on both islands (Fig. 2.5; Lack of juveniles at Toberua Island do not make this relationship clear in Fig 2.5). The head shapes of males and females from the two islands are compared in Figure 2.6.

Body mass

Female sea kraits not only have shorter tails, fewer bands and larger heads than conspecific males at the same body length, they are also less heavy-bodied. This sex difference is apparent from a two-factor ANCOVA using sex and island of origin as the factors, SVL as the covariate and *ln* body mass as the dependent variable. I restricted the data set to ensure body-length overlap of males and females (SVL < 105 cm). The analysis showed a significant interaction term between SVL and island of origin ($F_{1,907} = 42.8$, $P < 0.0001$). At the same SVL male sea kraits were more heavy-bodied than



Mabualau Island

Toberua Island

Figure 2.5 Head length relative to snout-vent length in male and female sea kraits from Toberua and Mabualau Islands. Data restricted to snakes < 105 cm snout-vent length, to ensure overlap between the sexes.

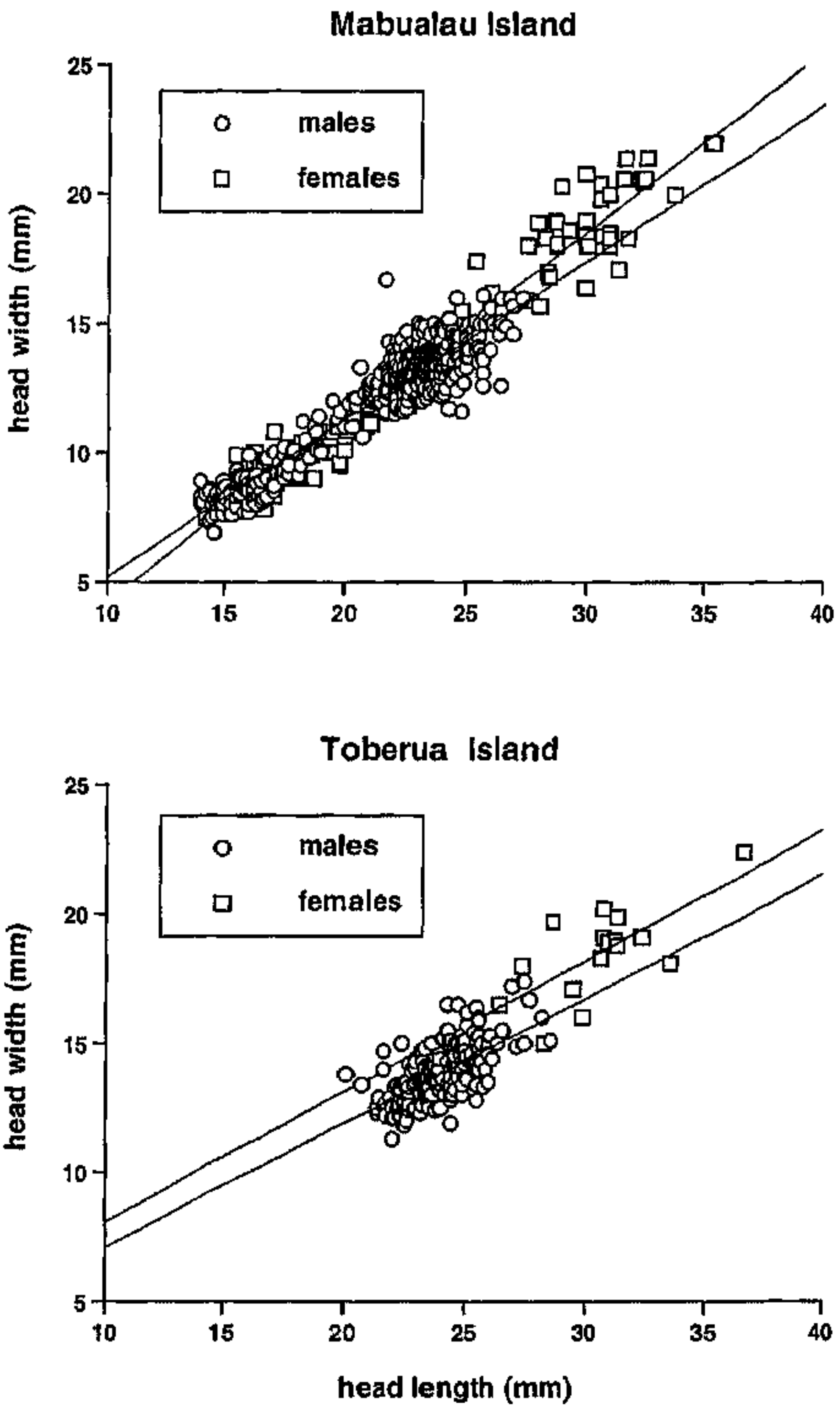


Figure 2.6 Relative head shape (width relative to length) in male and female sea kraits from Toberua and Mabualau Islands. Data restricted to snakes with snout-vent length < 105 cm to ensure overlap between sexes.

conspecific females, and snakes on Toberua Island were heavier than snakes on Mabualau (Fig. 2.7).

Ectoparasites and wounds

While collecting data on morphology (in 1998), I found ticks (*Ambylomma nitidum)* on 19% of all the animals collected for the study. The proportion of snakes that were infested differed significantly among adult females, males and juveniles (76 of 273 adult females = 27.9%; 86 of 587 adult males = 14.7%; 30 of 144 juveniles = 20.8%; $\chi^2 = 21.30$, 2 df, $P < 0.0001$).

I also recorded presence of scars on the body of the snakes. These scars resembled bite marks and were presumably inflicted by eels (from the distinct "V"shaped teeth marks) while foraging. Healed wounds, "bob-tails" and damage to eyes were all scored as scars. Such scars were recorded in 8.8% of the snakes examined. The proportion of snakes that bore scars also differed significantly among adult females, males and juveniles (30 of 273 adult females = 11%; 53 of 587 adult males = 9.03%; 5 of 144 juveniles = 3.5%; $\chi^2 = 6.8$, 2 df, $P = 0.03$).

From my surveys (in 1999), I found 69 individuals (7.3% of the total sample) that had gone into a moult. Of these snakes, 71% were females, 24.5% were males and the remaining 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, $P < 0.0001$).

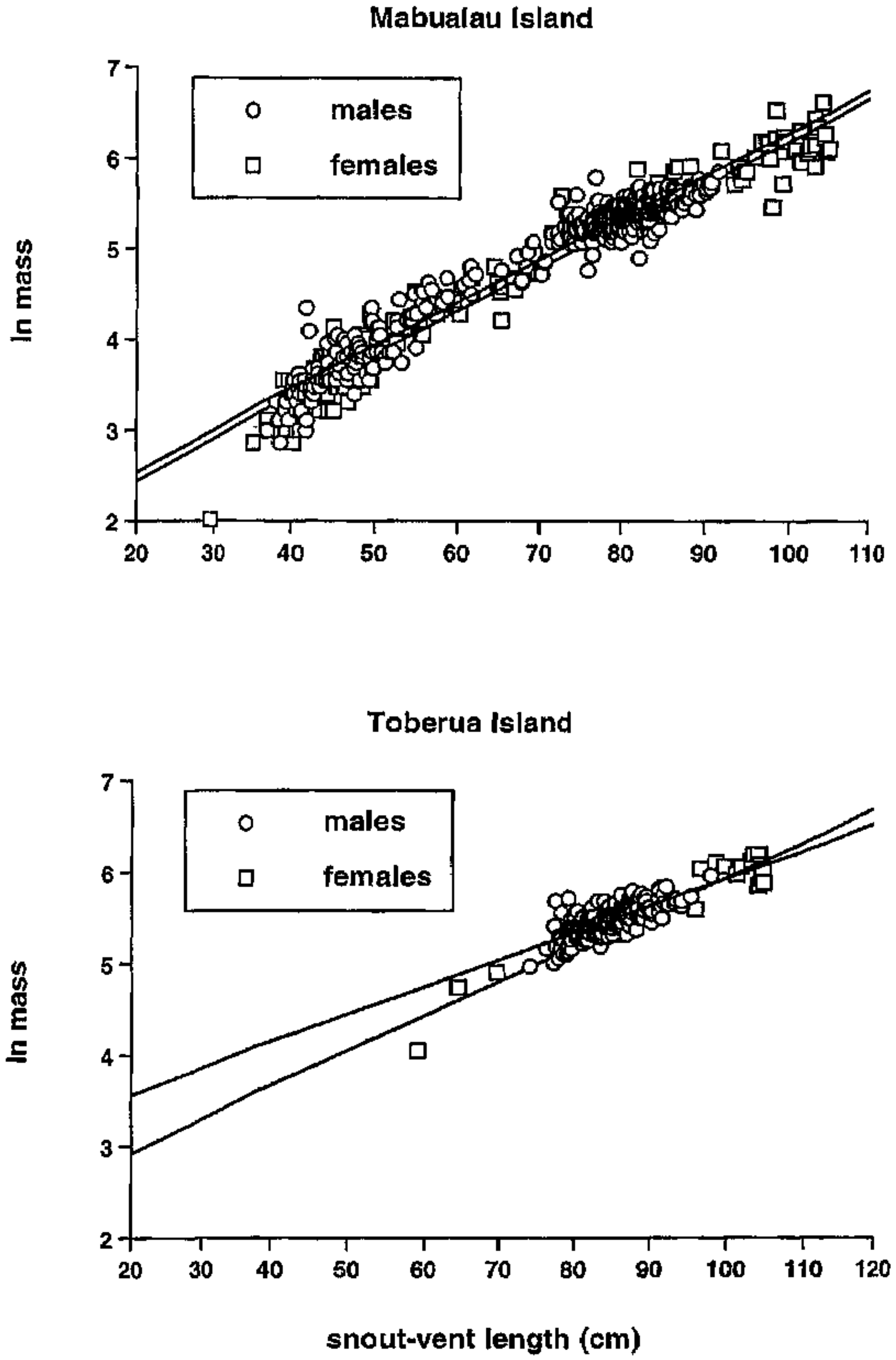


Figure 2.7 Relative body mass (*ln* mass compared to SVL) in male and female sea kraits from Toberua and Mabualau Islands. Data are restricted to snakes with snout-vent length < 105 cm to ensure overlap between the sexes.

Feeding habits

Sea kraits in this study fed exclusively on eels (Plate 3). All of the prey items that I palpated from *L. colubrina* were eels belonging to two families: the Muraenidae (Moray eels) and the Congridae (Conger eels). Of the 116 snakes that were examined for the orientation of prey items, 64% had consumed prey head-first and the remaining 36% had consumed prey tail-first.

Dietary differences between adult and juvenile snakes

In general, the size of eels consumed was proportional to the size of the snake. Adult and juvenile snakes differed significantly with respect to the relative numbers of Moray and Conger eels that they ingested ($\chi^2 = 25.48$, 1 df, $P < 0.0001$). Conger eels were found more often in adult snakes, while gut contents of juvenile snakes were comprised mostly of Moray eels (Fig. 2.8).

Dietary differences between male and female snakes

Similarly, there were significant differences in the composition of diet between male and female sea kraits ($\chi^2 = 60.57$, 1 df, $P < 0.0001$), with more Conger eels being eaten by females and higher numbers of Morays being consumed by males (Fig. 2.9).

Hence, both body size and sex appear to influence a sea krait's diet. Because both of these factors are themselves linked (because of sex

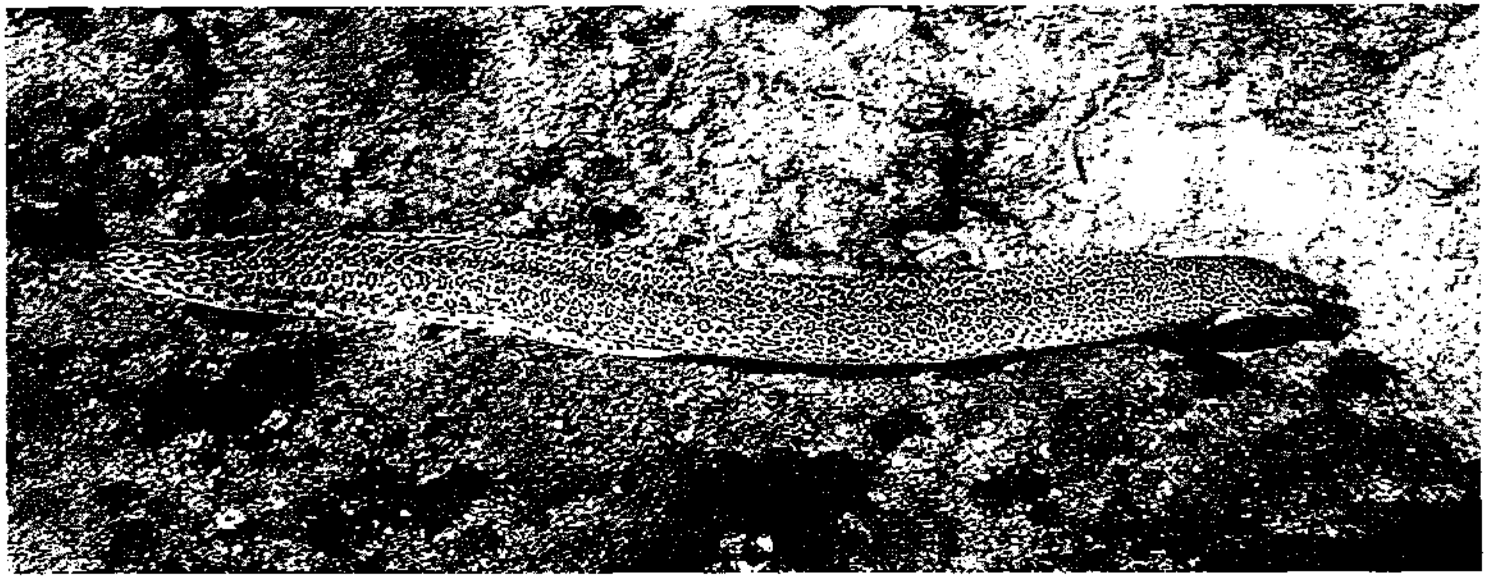


Plate 3. A Moray eel.

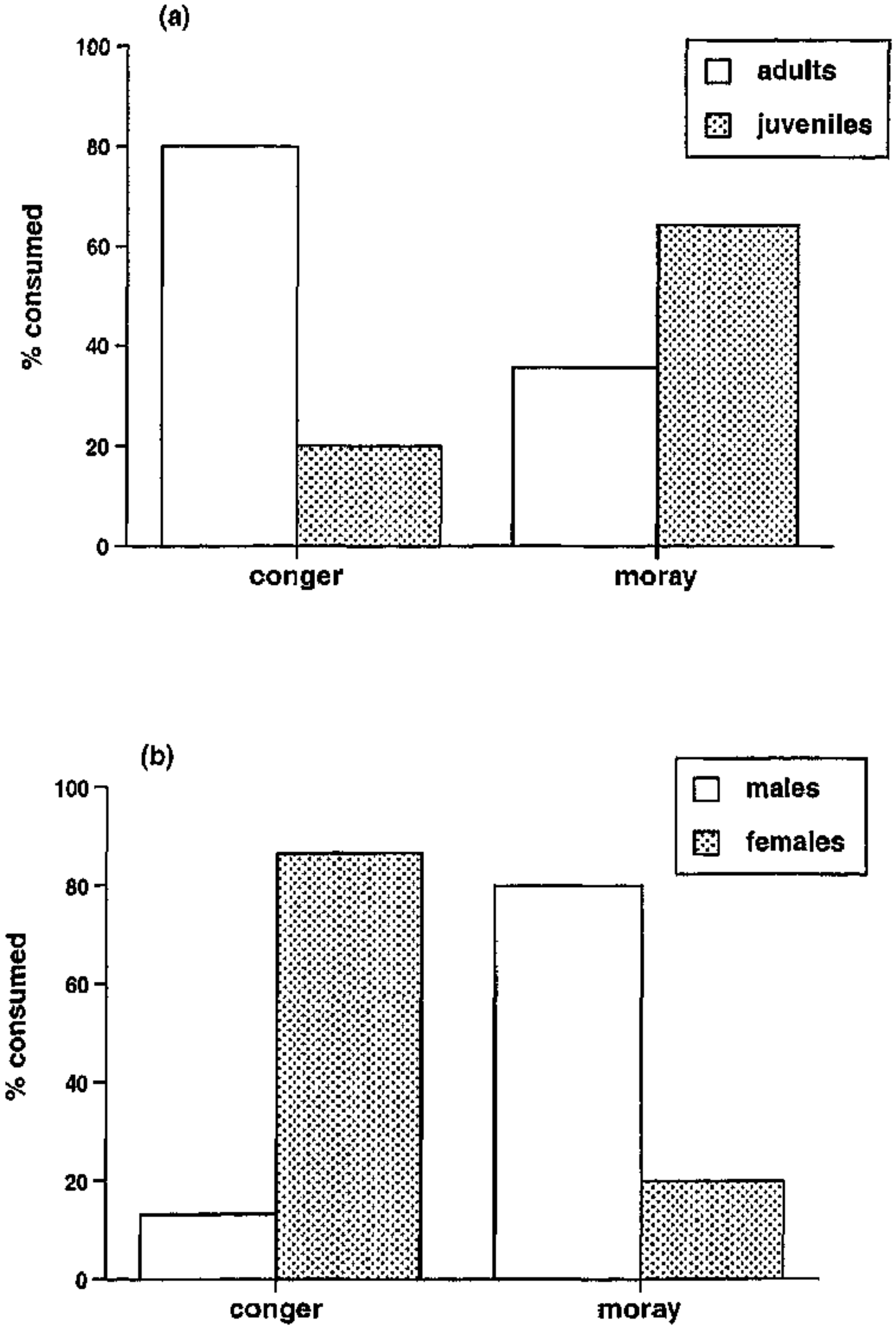


Figure 2.8 Proportion of diet composed of Conger and Moray eels in (a) adult and juvenile sea kraits and (b) male and female sea kraits.

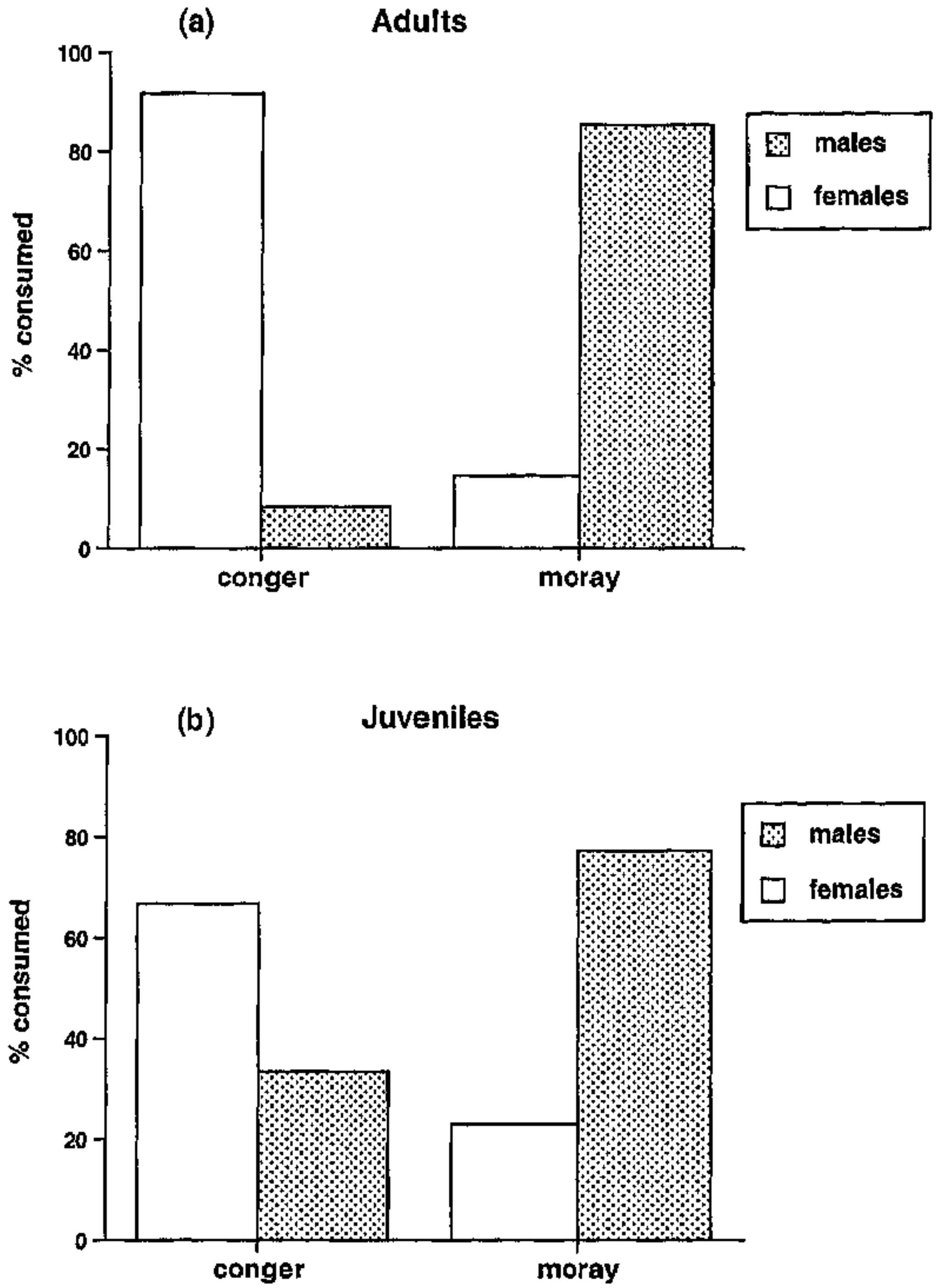


Figure 2.9 Proportion of diet composed of Conger and Moray eels, in each sex, within **(a)** adult and **(b)** juvenile size classes.

differences in body size), I looked at the effects of sex on dietary habits within adult and juvenile snakes separately.

Sex differences in diet among adult and juvenile snakes

Contingency-table analyses revealed significant effects of sex on the dietary composition of both adult ($\chi^2 = 45.51$, 1 df, $P < 0.0001$) and juvenile ($\chi^2 = 7.65$, 1 df, $P = 0.0057$) sea kraits. These sex differences were similar in both age classes of snakes: Conger eels were consumed more often by females while males consumed more Moray eels (Fig. 2.9).

Prey size

Data on the size (diameter) of prey items recovered from stomach contents of all snakes in this study are presented in Figure 2.10. Prey size is plausibly affected by both size and sex of the snake (Fig. 2.11); females have larger bodies and heads than males (see above) and may forage in different habitats (Pernetta, 1977). To investigate whether there were any differences in the size of prey ingested by male and female sea kraits, the data were limited to snakes with SVL < 105 cm so as to ensure size overlap between the sexes. A one-factor heterogeneity of slopes test was conducted with prey size as the dependent variable, sex as the factor and snout-vent length as the covariate. The analysis revealed that prey size was significantly affected by the interaction between sex and body size ($F_{1,116} = 12.29$, $P = 0.0006$). That is, females ate larger eels than males at the same body size, and the rate at which prey size increased with a snake's SVL was greater in females than in males (Fig. 2.12). I then repeated the analyses using head length rather than

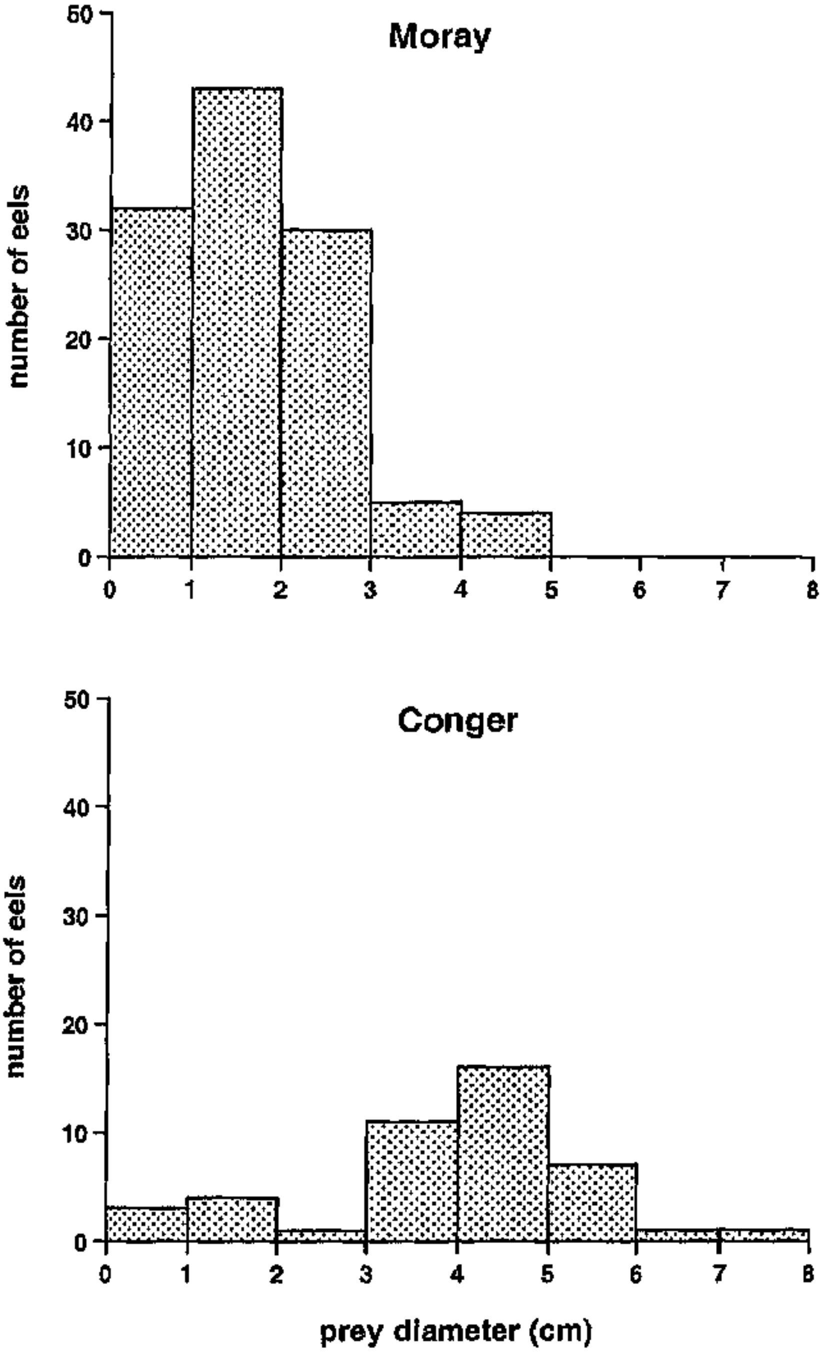


Figure 2.10 Numbers of Moray and Conger eels of different size classes (diameter) consumed by sea kraits.

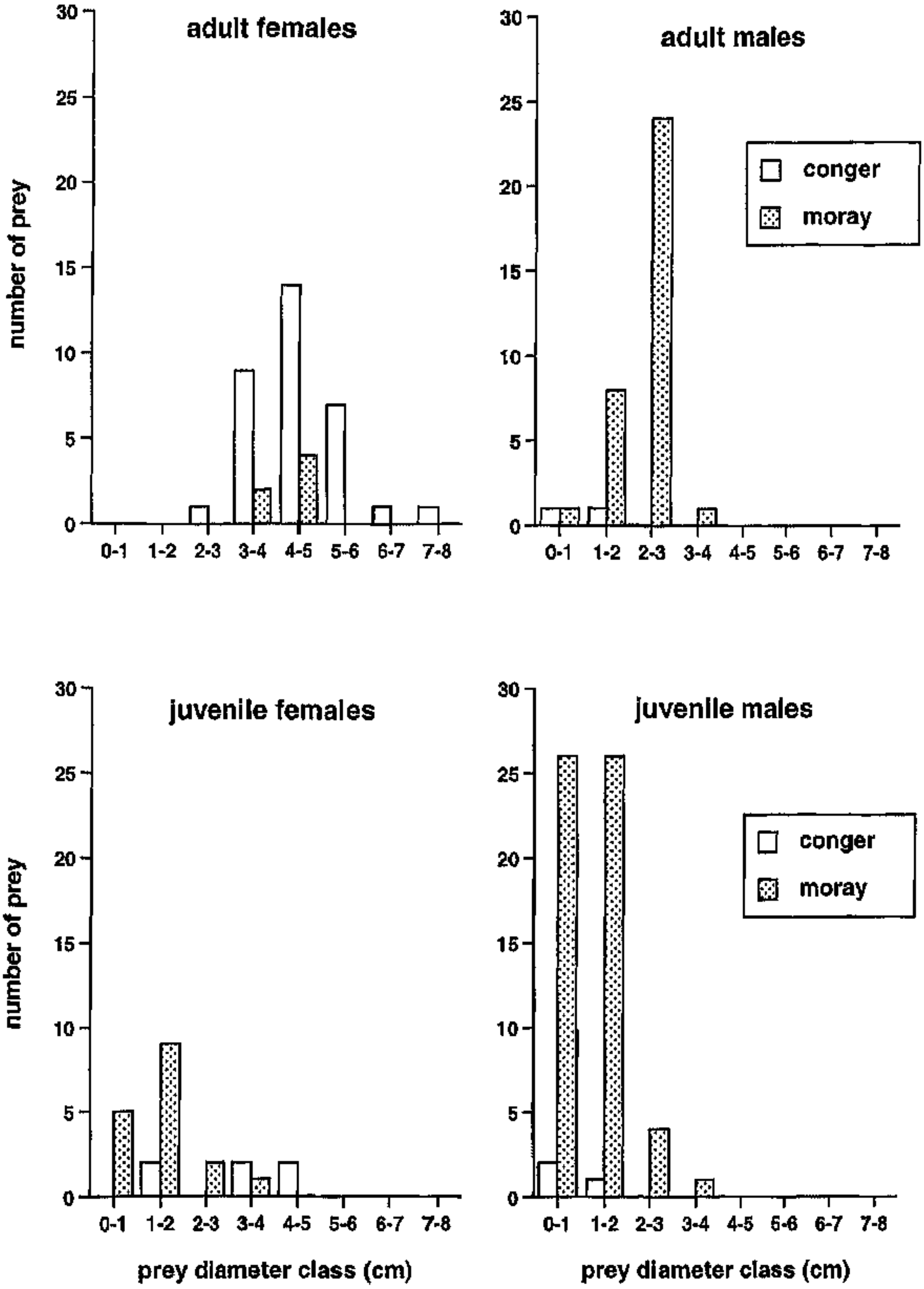


Figure 2.11 Distributions of prey sizes among adult and juvenile snakes.

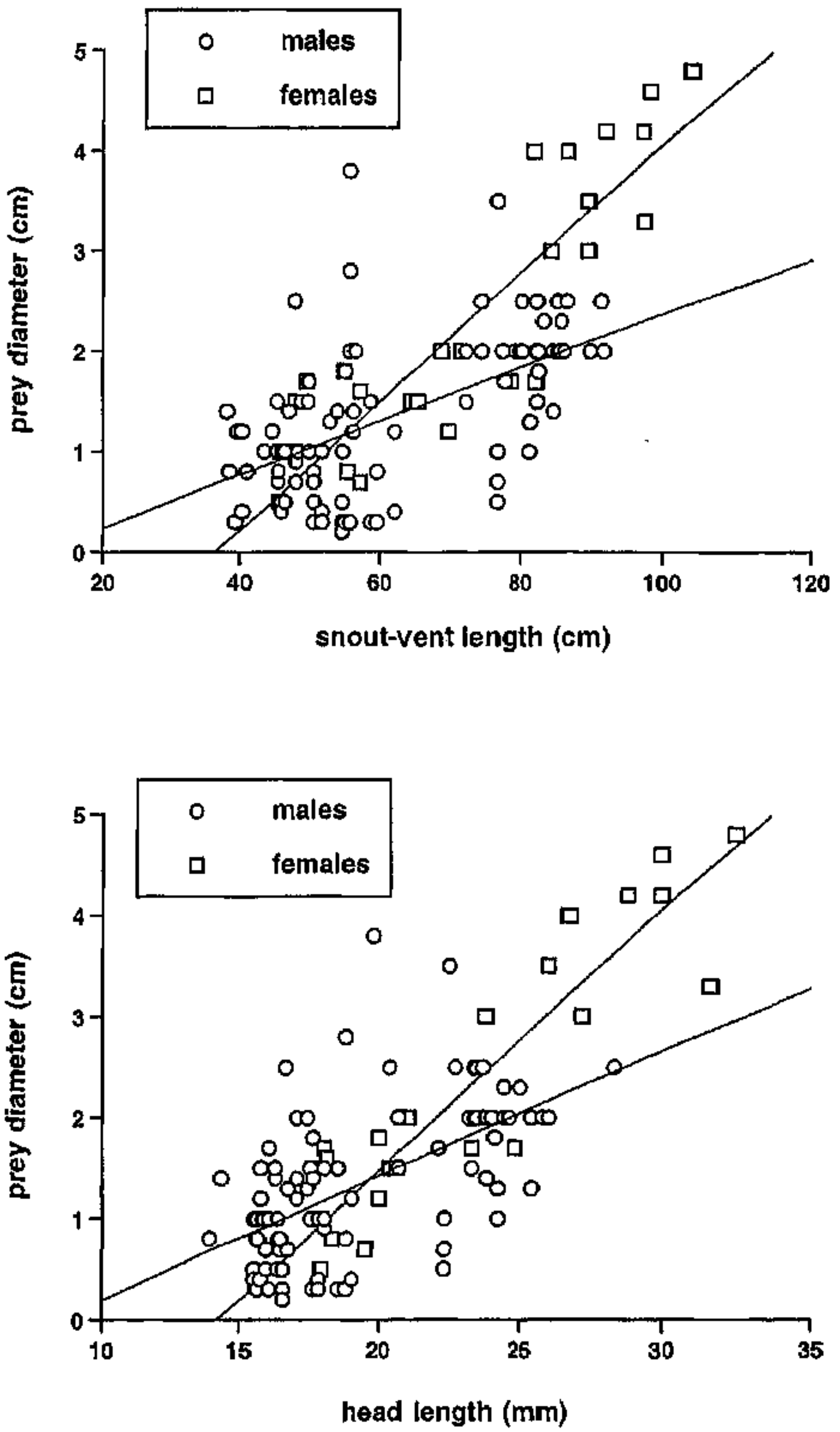


Figure 2.12 The relationship between prey size and snake body length (SVL) or head size (length) in male and female sea kraits.

SVL as the covariate. As before, I restricted the data set to ensure overlap between the sexes. The interaction between sex and head length was significant ($F_{1,116} = 14.26$, $P = 0.0003$). Thus, prey size increased with a snake's head length more rapidly in females than in males (Fig. 2.12).

The overall result is that female sea kraits eat larger prey items than males. This sex difference is partly due to the larger body size and relative head size of females compared to males. However, the heterogeneity of slopes test (above) shows that such morphological differences do not fully explain the divergence in prey sizes.

Prey numbers

There was a significant difference in the number of prey items found in snakes of different sex and size classes ($\chi^2 = 18.48$, 9 df, $P = 0.03$). All of the adult female sea kraits examined had only one prey item in their gut, whereas multiple smaller prey items were commonly recorded in adult male and juvenile snakes (Fig. 2.13).

DISCUSSION

My study has provided much larger sample sizes than those available from previous research on *L. colubrina*, and hence I have been able to examine several issues in more detail (and with more robust empirical evidence) than was previously possible. Most of my results concur with conclusions from previous studies, and thus, allow me to test some of the speculations from

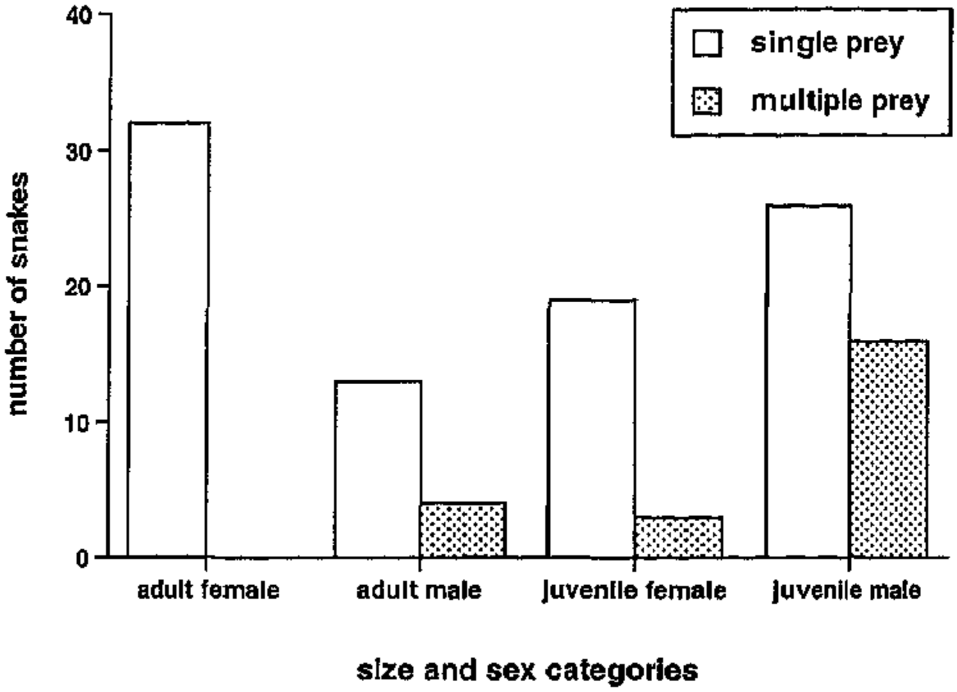


Figure 2.13 Number of snakes (adults and juveniles of each sex) containing single *versus* multiple prey items.

earlier research. In the following discussion, I will first focus on geographic variation within the species throughout its range, and then consider the topic of sexual differences in morphology and diet.

Geographic variation

Several researchers have suggested that *L. colubrina* may show interesting patterns of geographic variation in morphological traits (Pernetta, 1977; Guinea, 1986; Bhaskar, 1996). Based on published studies plus my own research, I have collated information on the mean body sizes of adult *L. colubrina* at several locations throughout its range (Table 2.4). Although geographic variation is apparent from this compilation, comparisons are problematic because of small sample sizes from some areas, compounded by differences in the methods used to conduct these studies. For example, studies by two different researchers conducted in the same general region (Pernetta, 1977; Guinea, 1986) or even on the same island (Bhaskar, 1996; Shetty and Sivasundar, 1998) produced rather different estimates of basic variables such as mean body sizes of adult specimens of each sex (Table 2.4). Some of this variation may have been generated by methodological inconsistencies (i.e. it is notoriously difficult to obtain reliable measures of the body length of live snakes: Fitch, 1987). Variation in body sizes can also occur depending on the time of the year when the study was conducted. For example, it is possible that nesting females differ in seasonal availability, and hence that they were more strongly represented in some samples than in others.

Table 2.4 Mean body sizes of adult *Laticauda colubrina* from studies conducted in the past along with measures from the present study. Note that snout-vent lengths are not free from measurement biases as some studies report post mortem measures of SVL while others measured live snakes.

Locality	Adult Males			Adult Females			Authority
	N	Mean	SE/ Range	N	Mean	SE / Range	
Mabualau Island, Fiji	*373*	*80.6*	*0.2*	*168*	*114.3*	*0.9*	*Present Study, 1998*
Toberua Island, Fiji	*215*	*84.8*	*0.3*	*107*	*114.6*	*0.9*	*Present Study, 1998*
Mabualau Island, Fiji	17	88.3	78 - 99	12	129.3	119 - 135	Pernetta, 1977
Makaluva Island, Fiji	11	89.5	80 - 106	10	122.5	93 - 139	Pernetta, 1977
S.E. Viti Levu, Fiji	6	90.5	5.8	10	130.3	3.8	Guinea, 1986
South Reef Is., Andamans, India	31	84.6	58 - 104.9	24	139.5	114 - 161.5	Shetty and Sivasundar, 1998
South Reef Is., Andamans, India	58	90.7	74.5 - 114	41	143.4	100.5 - 169.5	Bhaskar, 1996
Taiwan	7	87.0	69 - 104	16	115.6	65.9 - 165.2	Mao and Chen, 1980
Taiwan	-	-	-	6	80.7	10.9	Huang, 1996
Petit Taenia Islet, New Caledonia	3	82.0	4.0	4	104.1	5.1	Saint Girons, 1964

In my study, I was able to test for geographic variation (on a local scale) by comparing a large number of individuals (over 100 adult snakes of each sex) from two adjacent islands. The two samples were taken simultaneously, so that seasonal or weather-induced variation in sampling biases would not confound the comparison. Remarkably, I found a significant difference in mean body sizes of adult male sea kraits between Mabualau and Toberua Islands (Table 2.1). These two islands are only 5.3 km apart, with no obvious barriers to sea-snake movement between them (as is evidenced by the fact that Toberua snakes released on Mabualau rapidly found their way home: see Chapter 6). The causes for geographic variation on this local scale may be quite different from those responsible for variation on a regional scale (Table 2.4).

Geographic variation in body size occurs in many snake species (Fitch, 1981; Sweet, 1985; Hasegawa and Moriguchi, 1989; Schwaner and Sarre, 1990; Shine and Fitzgerald, 1995). Such variations can be attributed to at least three different processes. First, geographic differences in mortality schedules can generate populations that differ in mean ages. If body size is related to age, such a difference can generate differences in mean body size. Second, the two areas may differ in resource levels that influence growth rates. Thus, snakes from adjacent areas can differ in mean body size because they grow more quickly in one area than another. Thirdly, the populations may differ genetically, in traits that influence mean adult body size. Such differences might be driven either by adaptation or by non-selective forces such as founder effects or genetic drift (Futuyma, 1979).

In practice, few snake species have been studied in enough detail for us to test among these alternative possible explanations. In the only experimental study on this topic, Madsen and Shine (1993) showed that strong geographic variation in mean adult body sizes and in the degree of sexual size dimorphism in European grass snakes (*Natrix natrix*) was a phenotypically plastic response of growth rates to differing prey resources. Although this is an area that needs further experimental investigation, the inter-island difference in mean adult body sizes of male sea kraits in the present study offer an interesting case. This is because most of the previously-proposed explanations (above) do not seem appropriate to this system. Sea kraits captured on Toberua and Mabualau inhabit and forage around the same reef system. Hence, it is unlikely that food supply varies dramatically between these two adjacent islands, or that the populations on these two islands are sufficiently isolated genetically to have evolved different allelic frequencies at loci affecting body size. Selective pressures on traits such as diet and life-history attributes are also likely to be similar.

Why, then, were male sea kraits larger on Toberua than on Mabualau? There are two plausible explanations. The most likely is that higher levels of human disturbances on Toberua Island have somehow shifted the age distribution of the snakes. Younger (smaller) males may have either died or emigrated from Toberua. Another possibility is that recruitment has been reduced on Toberua, resulting in fewer young males entering the population. In keeping with this interpretation, the difference between the two islands in mean adult body sizes of male snakes is mostly due to the scarcity of males on Toberua just above the minimum size at maturation (Fig. 2.1). The only other plausible explanation for the virtual absence of these small (recentlymatured?) males on Toberua would be sampling bias. That is, the Toberua staff who collected snakes on my behalf may have neglected to collect this size class. I have no reason to suspect that this was the case, nor any way to evaluate the possibility.

Sexual Dimorphism

Previous studies have shown that *L. colubrina* are sexually dimorphic in mean adult body size (Saint Girons, 1964; Pernetta, 1977; Guinea, 1986). My data confirm these reports, and also extend them. Male and female sea kraits differ in several aspects of body shape and colouration, as well as in absolute body size. Males have smaller heads, more bands and longer tails, and weigh more, than do females of the same SVL. These sex differences (except mass), are apparent even among juvenile snakes, as originally suggested by Pernetta (1977). Such sex differences are likely to reflect multiple selective pressures and are considered below.

The degree of sexual size dimorphism in a population reflects the end result of competing selective pressures acting independently in the two sexes (Andersson, 1994). Sex differences in body size are widespread in snakes, and generally take the form of females growing larger than conspecific males (Shine, 1978, 1993, 1994). However, the degree of sexual dimorphism in *L. colubrina* is greater than that in most other snakes. Using the system of Gibbons and Lovich (1990), the mean degree of sexual size dimorphism in the sea kraits from my study area (combining data for Toberua and Mabualau) is 0.394. That is, adult females were on average 39.4% longer than adult males. This value is exceeded by only 10 of the 375 snake species reviewed by Shine (1994). Because mass increases rapidly with increasing SVL, the degree of sexual dimorphism would be much greater if calculated in terms of mass rather than body length.

Why do female sea kraits grow so much larger than males? The answer is likely to be complex, involving three processes:

(i) fecundity selection on body size in females (Seigel and Ford, 1987). Larger female sea kraits produce larger clutches (Gorman et al., 1981; Guinea, 1986). Thus, genes for larger female size may increase in frequency through this process.

(ii) sexual selection on body size in males may favour small size, or at the very least, provide no advantage to larger body size. In snake species that display overt male-male combat, larger males tend to win the battles and thus, obtain more opportunities for mating (Schuett and Gillingham, 1989; Madsen et al., 1993; Schuett, 1997). The same may be true, to a lesser degree, even in many snake species where males scramble physically for mating opportunities but do not show ritualised combat (Madsen and Shine, 1993a; Shine et al., 2000a). However, my observations of many mating groups of *L. colubrina* provided no evidence of any vigorous physical interactions among competing males. Crucially, male sea kraits that copulated were no larger than those that did not (Chapter 4). Thus, male sea kraits may not be under any sexual selection for larger body size. Indeed, smaller body size might benefit a male by enabling him to resist a long period of fasting associated with reproductive activity, as seen in many other snake species (Shine, 1980;

Mushinsky, 1987; Olsson et al., 1997). In my study, male sea kraits rarely contained prey items during the mating season (see above).

(iii) natural selection may have reinforced the size dimorphism originally generated by fecundity selection. Body size can affect many aspects of an organism's biology, including its locomotor performance (Chapter 5). In sea kraits, as in at least two other distantly-related aquatic snake species, males and females diverge in both dietary habits and probably, foraging habitats as well (Mushinsky et al., 1982; Houston and Shine, 1993). The tendency for females to eat very large eels, and for males to specialise on small eels (e.g. Fig. 2.11) may have provided advantages to each sex in developing adaptations to foraging in different places for different kinds of prey. Natural selection of this type could thus amplify existing sex differences in aspects such as body size and relative head size.

My data document a strong difference between male and female sea kraits in head size relative to body length. As in the case of body-size dimorphism, such divergence is relatively common in snakes but is rarely so extreme as it is in *Laticauda colubrina*. A review of head-size divergence between the sexes suggested that *L. colubrina* were among the most extreme such cases (Shine, 1991b), and my data reinforce this conclusion. Pernetta (1977) noted the head-size dimorphism in Fijian sea kraits, and attributed it to ecological divergence between sexes. My data support this idea. It is difficult to see any other plausible functional basis for the observed divergence in head-size. It is so extreme that it is unlikely to have evolved by non-adaptive processes such as neutral allelic substitutions. There is nothing in the mating system of this species that suggests any role for relative head size in sexual selection (Chapter 2). Head size in sea kraits almost certainly plays a role in prey-handling and ingestion, as indicated by the relationship between prey size and snake size (Fig. 2.11). It would be physically impossible for a male sea krait to ingest some of the large eels consumed by females. Thus, in this gape-limited predator, selection to ingest larger prey items has presumably played a role in selecting for larger relative head size in females. Smaller heads might enable male sea kraits to reach further into crevices to obtain eels (e.g. Radcliffe and Chiszar, 1980).

Dietary specialisation is widespread in snakes and is associated with the evolution of many modifications of the head for ingesting different types of prey (Savitsky, 1983; Cundall, 1987; Scanlon and Shine, 1988). However, intraspecific (sex-based) dietary divergence has attracted much less study than has interspecific divergence in this respect. In many ways, the two sexes of sea kraits are different ecological entities. Females tend to eat Conger eels, while males and juveniles consume more Moray eels. This taxonomic distinction is accompanied by a habitat divergence: most Congers are found in deep water rather than around reefs, whereas many Morays are shallow-water species with smaller maximum sizes (Randall et al., 1990).

One of the most interesting aspects of my results is the demonstration that the sexes diverge in prey sizes relative to predator size even if head size (rather than SVL) is used as the measure of predator body size (above). That is, the divergence in prey sizes cannot simply be attributed to gape-limitation combined with sex differences in relative head size. If this latter hypothesis was correct, then the sexes should follow identical relationships between prey size and head size. They do not. In combination with my other data, this result fits well with the notion that male and female sea kraits have evolved morphological adaptations that suit them to foraging in different areas (shallow *versus* deep water) on different sizes and kinds of eels. Thus, the divergence in head sizes is a consequence rather than a cause of the sex difference in foraging biology.

My study not only confirms that the sexes of yellow-lipped sea kraits diverge in ecological (dietary) as well as morphological (relative head size) traits, but also shows that the sexes begin to diverge in this aspect even before reaching maturity. Thus, even if the initial selective pressure that generated morphological divergence between the sexes was related to reproductive biology (fecundity selection), the final result has been to force ecological and morphological divergence further back in the life-history, into the juvenile stage.

Sea kraits also show sex-based divergence in other traits. The adaptive significance of these divergences (if indeed there is any such significance) remain obscure. Males in most snake species have longer tails than females (Burt, 1928; Clark, 1967; Shine et al., 1999) and this pattern is seen also in *L. colubrina*. Males with longer tails may have an advantage in manipulating the female tail or in "tail wrestling" (King, 1989; Shine et al., 1999; Shine et al., 2000a). Males in my study did use their tails to manipulate (hold on to) the female tail while attempting to copulate. Thus, a longer tail might enable a male to court or to position himself more effectively to achieve copulation.

Sexual selection may operate in diverse ways on relative tail length. For example, mate-searching males appear to move around (on land but possibly also in the water) much more than do females (Chapter 3). Perhaps a longer tail serves as a more (or less?) efficient means of propulsion, especially in aquatic locomotion. If relative tail length correlates with hemipenis length in sea kraits as it does in at least one other snake species (Shine et al., 1999), then possible advantages of having longer hemipenes become relevant to the evolution of longer tails in males. For example, my observations on 11 copulations revealed that the females often moved the posterior part of their bodies during coitus. In at least four cases, considerable fluid (semen?) spilled from the joined cloacas during these movements. A longer hemipenis might reduce the amount of leakage, or enable a male to maintain copulation for a longer period.

Other sexually dimorphic traits such as body shape (mass relative to length) and colouration are equally difficult to explain. The heavy build of adult females might be related to fecundity selection, or to their need to store larger amounts of energy to fuel the reproductive process (e.g. Bonnet et al., 1998). The presence of more bands on the tail of males than of females clearly reflects the longer tail of the male, but the difference in trunk bands (males > females) is more puzzling. Male and female snakes often differ in the number of vertebrae in the body (and thus, in the number of ventral scales: e.g. Lindell et al., 1993; Lindell, 1994; Shine, 2000). *Laticauda* shows this kind of dimorphism (Gans and Taub, 1965; Guinea, 1986). The sex divergence in the number of bands might simply reflect the greater number of "segments" (vertebrae) within the bodies of females than males.

CHAPTER 3. TERRESTRIAL BEHAVIOUR

INTRODUCTION

Information on the behaviour of animals, including such simple aspects as daily patterns in what they do and where they do it, can be a valuable first step towards more detailed investigations of ecological issues. Unfortunately, there is surprisingly little quantitative information of this kind for many types of organisms. In the case of snakes, researchers frequently draw attention to the logistical obstacles associated with quantitative studies of topics such as habitat use and diurnal patterns of activity (e.g. Turner, 1977). Many snake species are relatively uncommon, and individual snakes are generally inactive and hidden for much of the time. When approached by humans, many species flee, and some venomous taxa pose a significant threat to human safety. Thus, we have detailed information on activity patterns for relatively few snake species - and such data are not available for many sea snakes.

Sea kraits are not only abundant on Mabualau Island, but are also very accessible to study. They are brightly-banded and thus readily detectable, and spend much of their time out in the open where they are easy to observe. Thus, they are much more suitable subjects for behavioural surveys than are most other snake species (Gibbons and Semlitsch, 1987). I took advantage of this opportunity to conduct standardised observations on behaviours of these snakes under natural conditions. However, my work was restricted to the terrestrial life of these amphibious creatures, because of the logistical (and safety) problems associated with attempting to study them in the ocean. Hence, both of my field trips were planned to coincide with the mating season of the sea kraits. Thus, it is likely that behavioural patterns during this period are linked to reproductive behaviour. Because I conducted detailed studies on the latter topic, I will deal with it separately in the following chapter. However, I also included some information on courting activity (as measured in my surveys) during the current chapter.

Early studies on the terrestrial behaviour of sea kraits identified some environmental factors influencing activity patterns (Herre, 1942; Saint Girons, 1964) and speculated about others (e.g. Pernetta, 1977). More recently, researchers have gone a step further in quantifying activity in relation to environmental factors and time of day (e.g. Guinea, 1986; Shetty and Prasad, 1996). However, as with morphological investigations on this species (Chapter 2), these studies have revealed regional differences in the behavioural patterns of *L. colubrina*. Such differences are difficult to interpret: some of them may reflect methodological variation among studies, some may reflect short-term (e.g. seasonal) variation in behaviour patterns of the snakes, and some may reflect geographic variation in other important factors (such as the abundance of predators) that influence snake activity. This situation is frustrating, because the wide geographic distribution of *L. colubrina*, and the corresponding diversity of biotic and abiotic factors that it encounters, mean that studies of this species have considerable potential to clarify the determinants of activity patterns in sea snakes. The first step towards understanding this topic is to make quantitative measurements of activity patterns in a single population, to provide a baseline against which others may be compared. Hence, my aims in this study were to identify factors influencing the behaviour of sea kraits on Mabualau. I hope that in future, similar studies in other regions will enable researchers to distinguish between general behavioural patterns of *L. colubrina* and local factors that generate deviations from these general patterns.

METHODS

I employed two techniques - surveys and radiotelemetry - to collect behavioural data and monitor snake activity. These methods are described below.

Habitat and Activity Survey (1998)

In order to quantify activity patterns of sea kraits, I conducted a survey during the first field season of my study (i.e. between October 1998 and January 1999). The survey involved walking two 200 m transects along the length of Mabualau Island, one located inland and one along the boundary of the island, at various times of the day and night. The "inland" transect ran approximately parallel to the cliffs that form the edge of the island. The "edge" transect ran about 20 m from those cliffs along the shoreline. Both transects were sampled in rapid succession in order to eliminate any temporal effects of environmental conditions. Although the surveys were distributed evenly across four time periods: morning (0400 – 1200 h), afternoon (1200 – 1800 h), early night (1800 – 2200 h) and late night (2200 – 0400 h), the time periods were unequal in duration for logistical reasons. Snakes sighted within 10 m either side of the transect, during both day and night, were included. On average, each 200 m transect took 15 minutes to walk. The undulating terrain and the short duration required to walk to transect meant that snakes in one transect were not encountered in the other.

For every snake or group of snakes encountered, I recorded the following information:

(i) Location of transect - inland or along the edge of the island

(ii) Sex and age class - adult male, adult female or juvenile

(iii) Time of day - morning, afternoon, early-night or late-night (see above)

(iv) Group size - whether or not the snake was in a courting group. If so, I also recorded the size and composition of the group

(v) Activity of the snake when sighted – whether the snake was moving, resting or courting (only males exhibited courting behaviour)

(vi) Microhabitat used by the snake, when sighted – in rock, in open, or in mud/log (snakes with their bodies either under the ground or under logs were grouped in this category).

(vii) Whether or not the snake was sloughing, as indicated by opaque eyes and white appearance of the body scales

Movement Survey (1999)

In the second field season (i.e. between September and December 1999), another survey was conducted to quantify the movement patterns of snakes with respect to tide. Six sites along the edge of Mabualau Island were chosen, and at each of these sites I selected two areas differing in slope (steep *versus* gentle). The number, age class (adult or juvenile) and sex of snakes entering and leaving the island at these sites were monitored over a total of 25 nights. Every survey was conducted at 2000 hrs, but at different tide levels. Tide levels were classified into three broad categories with respect to high tide:

(i) ± 0 to 2 hours

(ii) ± 2 to 4 hours and

(iii) ± 4 or more hours

Equal numbers of samples were collected in each of these categories. For each survey and at each site, the following details were recorded for every snake sighted within a 5 m radius from a fixed point at the centre of the observation area:

(i) sex of snake

(ii) direction of movement - landward, seaward or parallel to edge of island

Depending on the level of the tide, it took between 30 and 45 minutes to complete each survey, although time spent at each site did not exceed 5 minutes.

Radiotelemetry

The use of radiotelemetry has revolutionised 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). I used this technique to study the terrestrial behaviour of sea kraits.

Telemetry equipment

I used 3.4 g (21 x 13 x 7 mm case size; 150 mm whip-antenna) temperature - sensitive radio transmitters with a battery life of 35 weeks at 30⁰C. These units were made by Holohil Systems, Canada (model # PD-2T). Before the transmitters could be calibrated and surgically implanted in the snakes, they were fully sealed to stop corrosion of the transmitter within the snake's body, and to prevent any abrasion of the snake's body tissue by the transmitter, once implanted. The whip-antenna of the transmitter was encased in rubber tubing (1.02 mm internal diameter SILASTIC® laboratory tubing) and then the entire transmitter was sealed with two layers of an inert, quick-drying, heavy duty flexible rubber coating (clear PLASTIDIP®). The transmitters were then allowed to cure for at least 72 hours before being calibrated.

Calibration

Because my transmitters incorporated thermistors, their pulse rates were directly proportional to temperature. The calibration procedure involved measuring the average time interval between two successive signals at six different temperatures (20, 23, 27, 30, 35 and 40°C). I did this by placing all transmitters in a water bath, maintained at the above temperatures using a precision thermometer. Once these data were obtained, I calculated regression equations to predict the body temperature of the snake containing that transmitter, given the time interval between two signals.

Surgery

The surgery required to implant the transmitters was conducted by Dr. Peter Harlow and Prof. Richard Shine (Plate 4). All necessary precautions were taken to minimise stress and enable speedy recovery of the snakes. Surgical equipment and transmitters were sterilised in 75% ethanol for at least 30 minutes. The site of incision and its surrounds were cleaned thoroughly using an iodine-based surgical scrub (Povidine-Iodine Detergent). Brietal Sodium (Methohexitone Sodium) was injected subcutaneously to anaesthetise the snake. The dose rate used was 5 mg of Brietal/kg of snake, which provided effective anaesthesia for approximately 30 minutes.

An incision (~30 mm long) was made in the abdominal region (around the ninth band from the tip of the tail) on the left-hand side of the snake, opposite the lungs. The transmitter plus antenna was then inserted into the abdominal cavity and the incision closed using a synthetic absorbable suture ("Coated Vicryl" 4.0 violet braided Polyglactin 910 suture with a tapered 17 mm alloy needle; Ethicon™, Johnson and Johnson Medical Pty Ltd., USA). The sutured incision was then treated with an antibiotic powder (Cicatrin™, Welcome Australia Ltd., Cabarita, NSW). Finally, I

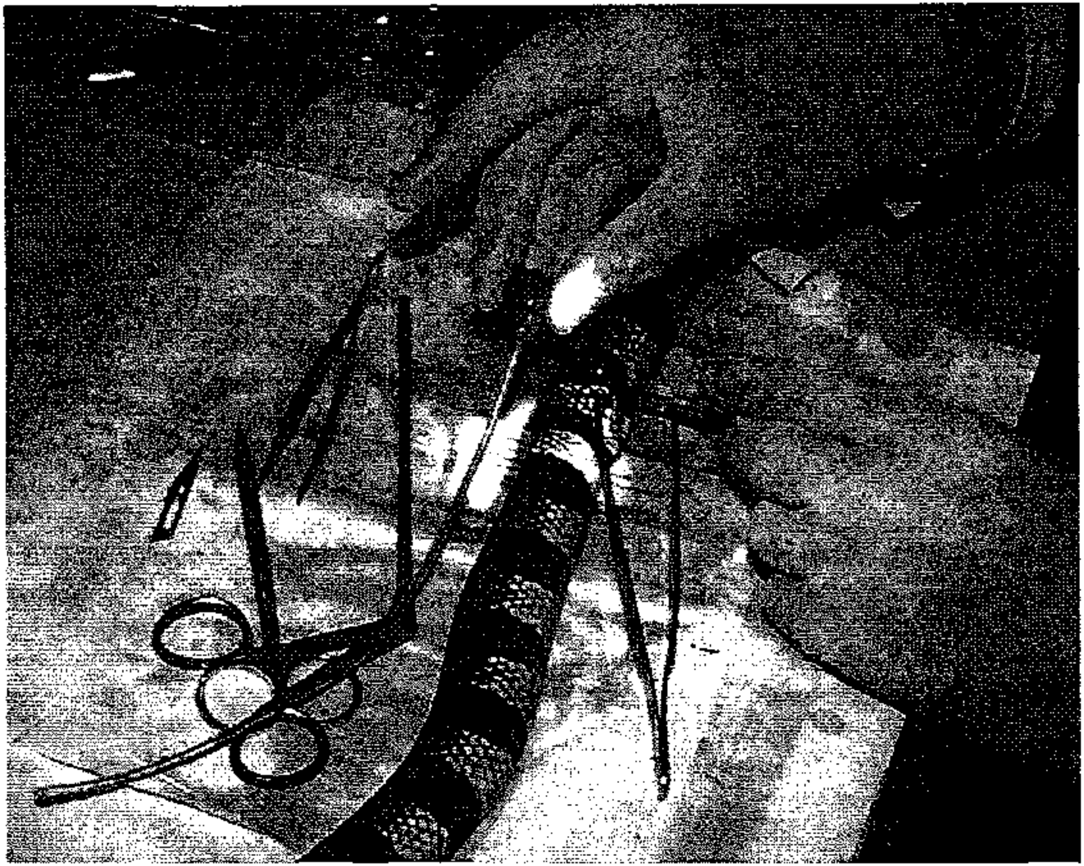


Plate 4. A transmitter (in right hand) being surgically implanted into a male sea krait.

applied a moisture vapour permeable spray dressing (OpSite™, Smith and Nephew Medical Ltd., Hull, England) to completely seal the wound from infection.

It took about 48 hours for the snakes to recover from the effects of the anaesthetic. However, the snakes were kept in captivity for a further 24 to 48 hours, under observation, before being released. Of the 16 individuals implanted with transmitters (8 of each sex), 15 (7 males and 8 females) provided useful information.

In the second year of the study I selected four large female snakes and surgically inserted not only transmitters, but also miniature, waterproof, thermal data-loggers (StowAway Tidbit Data Loggers, Onset Computer Corporation, Massachusetts). These data loggers were 30 mm wide x 41 mm tall x 17 mm thick, and weighed 22.7 g. These data loggers were coated with PLASTIDIP prior to surgery as with the transmitters (see above). I only recaptured one of these females at the end of the study, but her data-logger provided information on temperatures during time spent at sea as well as on land.

Tracking

The frequency of transmitters used ranged between 150.231 and 150.947 MHz. A hand-held H-frame antenna attached to a Telonics Scanner-Receiver and a Digital Processor were used to track the radio signals. Snakes in terrestrial locations provided strong radio-signals, but initial trials showed that the signal disappeared completely when the snakes entered salt-water. I took advantage of this fact to quantify the duration of time that telemetered snakes spent on land *versus* in the ocean. Upon release after surgery, the snakes were monitored (present/absent) at least once a day. Actual locations of the snakes, if present on the island were determined and plotted on a map once every week. The tracking procedure involved scanning all 16 frequencies from elevated sites on Mabualau Island, chosen such that the receiver would pick up a signal from wherever the snake was located on the island. Because the signal could not be detected when the snake was underwater (see above), I interpreted a lack of signal as evidence that the snake was at sea.

In addition to a presence-absence check, I also recorded the millisecond reading between two consecutive signals at different times of the day and night. I could then determine body temperature of the snakes by using the regression equations obtained from the calibration procedure.

Measurement of operative temperature regimes

During the first year of the study, while I was monitoring body temperatures of radio-tracked sea kraits, I set out six Hobo XT Temperature Data Loggers (Onset Computer Corporation, Massachusetts) in representative habitats on Mabualau. I used these data-loggers to measure operative temperatures every 30 minutes throughout the three-month duration of my stay on Mabualau. The tip of each probe was placed inside a hollow copper model 150 mm in length and 10 mm in diameter. I placed two data loggers in each of three types of site: places with full exposure to the sun's rays (to record maximum temperatures available to snakes), places 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).

During the second year of the study, when I placed miniature data-loggers inside the snakes, I also measured operative temperatures as above. The only difference was that the copper models that I used measured 450 mm in length and 40 mm in diameter.

Observations in arenas

Two of the reasons that sea kraits come ashore are to digest their prey and to slough their skins (Guinea, 1986; 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, I captured snakes and kept them in outdoor arenas until they had either digested their prey, or shed their skins.

Digestion time

Snakes that had recently fed were easily recognisable by their distended stomachs. Such animals were always located near the edge of the island; their locomotor capacities are severely reduced by the presence of a prey item (Chapter 5). It was during my regular walks around Mabualau that I looked for such snakes, collected them and assigned them to a series of experimental enclosures (see Chapter 4 for details on these enclosures). I noted the date of capture, and every day thereafter I gently squeezed the stomach of the snake to check if the prey item was still detectable. As soon as palpation revealed no evidence of the prey item, the snake was released and the date noted. The difference between the date of capture and release gave an indication of the approximate time taken to digest the prey.

Time to complete sloughing

When sea kraits slough their skins, the first sign of such an event is that the outer skin becomes white as it lifts away from the underlying epidermis. Snakes about to slough are thus very recognisable. As I walked around the island I looked for such snakes. Given that these animals rarely move far between initiating the cycle and finally sloughing (pers. obs.), most of the animals that I collected had probably initiated the cycle only shortly before they were collected. As above, these snakes were collected and placed in the enclosures, and released after they had shed their skins. The date of collection and release were noted and the difference gave me an approximate time taken for the sloughing cycle.

RESULTS

Diel Activity Patterns (1998 Surveys)

I will first present data from both transects combined to show overall patterns, and then analyse data from each transect separately to investigate spatial variation in these patterns.

Numbers, sex ratio and age class of snakes encountered

Combined data: The relative numbers of adult males, adult females and juveniles encountered varied significantly among the four time periods ($\chi^2 = 37.15$, 6 df, $P < 0.0001$). The significant result reflects the fact that 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.

Data split by location of transect: When the data were split by location, the relative numbers of adult male, adult female and juvenile sea kraits encountered differed significantly across the four time periods, but only on the transect along the edge of the island ($\chi^2 = 30.34$, 6 df, $P < 0.0001$). Changes in the sex and age-class composition of the sample were not statistically significant for the island transect ($\chi^2 = 6.9$, 6 df, $P = 0.30$). This significant divergence from the null hypothesis (that equal numbers of adult male, adult female and juveniles should have been seen) for the "edge" transect is due to the same biases noted above. That is, juveniles were more often seen in the afternoons than at other times, adult males were seen during late-night, and females were most often seen in the mornings (Fig. 3.1).

Very few juvenile snakes were seen inland (4 compared to 44 seen on the edge of the island). It is also interesting to note that although almost equal numbers of snakes were seen along the two transects (475 snakes seen on the "edge" *versus* 470 snakes seen "inland"), the sex ratios differed ($\chi^2 = 74.2$, 1 df, $P = 0.0001$). The ratio of males to females inland was 0.87:1 ($\chi^2 =$

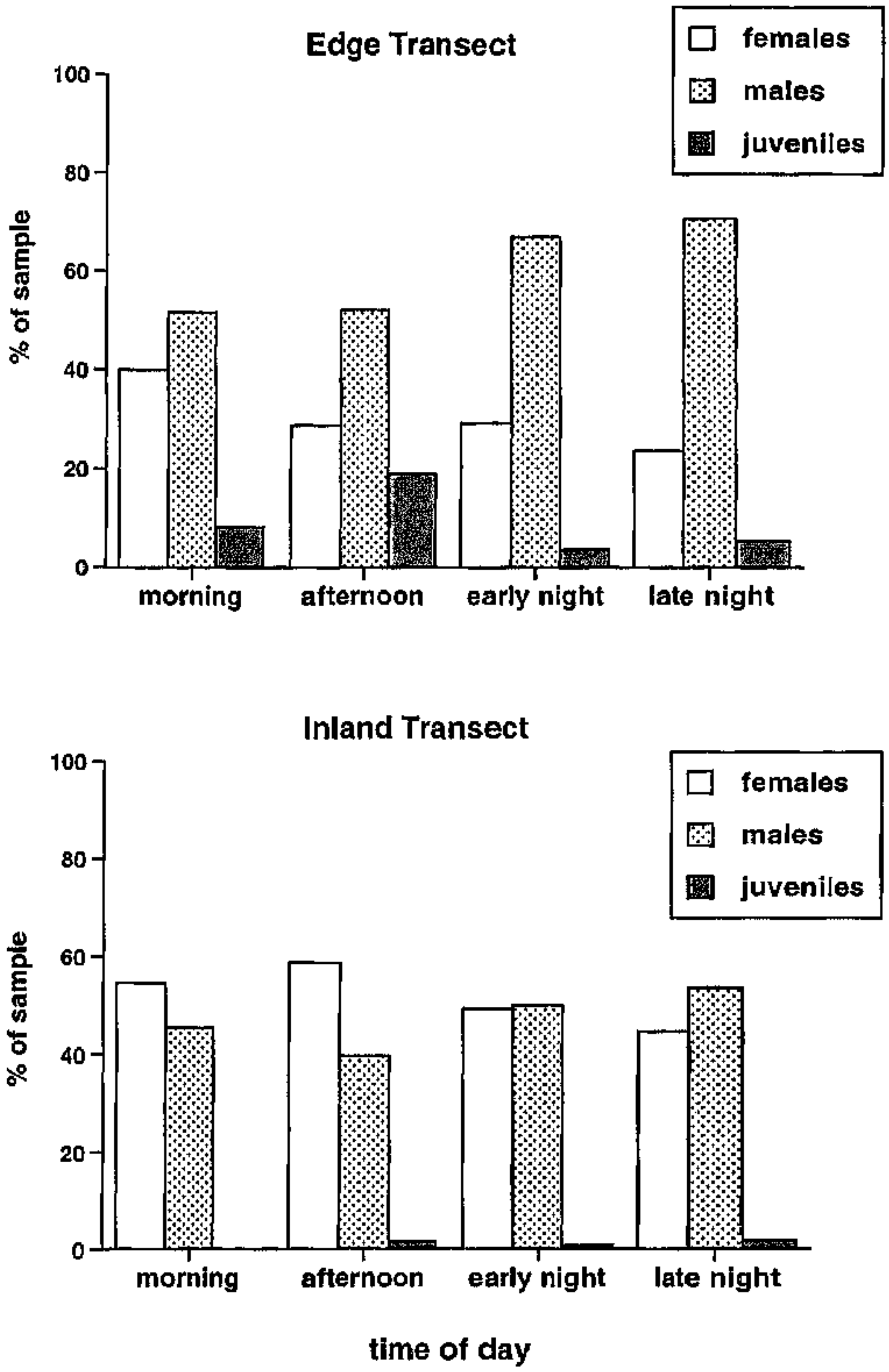


Figure 3.1 Occurrence of sea kraits along two transects, at different times of the day and night. One transect ran along the edge of the island, whereas the other was about 20 m inland.

2.2, 1 df, P = 0.14) while that on the edge of the island was 1:1.97 ($\chi^2 = 46.1$, 1 df, P = 0.0001).

Activity

Of the three types of activity recorded, only males exhibited "courting". Hence, the data were analysed for each sex separately.

Adult Females

Combined data: The relative numbers of snakes involved in the two activity categories (moving or resting) varied significantly with time of day (dividing the day into 4 periods: $\chi^2 = 10.93$, 3 df, P = 0.012; Fig. 3.2a) and with lunar periodicity (number of days from full moon: $\chi^2 = 28.6$, 11 df, P = 0.003; Fig. 3.4).

Data split by location of transect: The temporal shift in activity of females on the edge of the island was not significant ($\chi^2 = 5.37$, 3 df, P = 0.15), whereas female activity along the inland transect differed significantly with time of day ($\chi^2 = 8.59$, 3 df, P = 0.035). Again, however, the general patterns were similar in the two areas. In both cases, females were more often recorded as moving in the late-night period and resting in the morning (Fig. 3.2a).

Adult Males

Combined data: As for females, the relative numbers of adult male snakes involved in the three activity categories (moving, resting or courting)

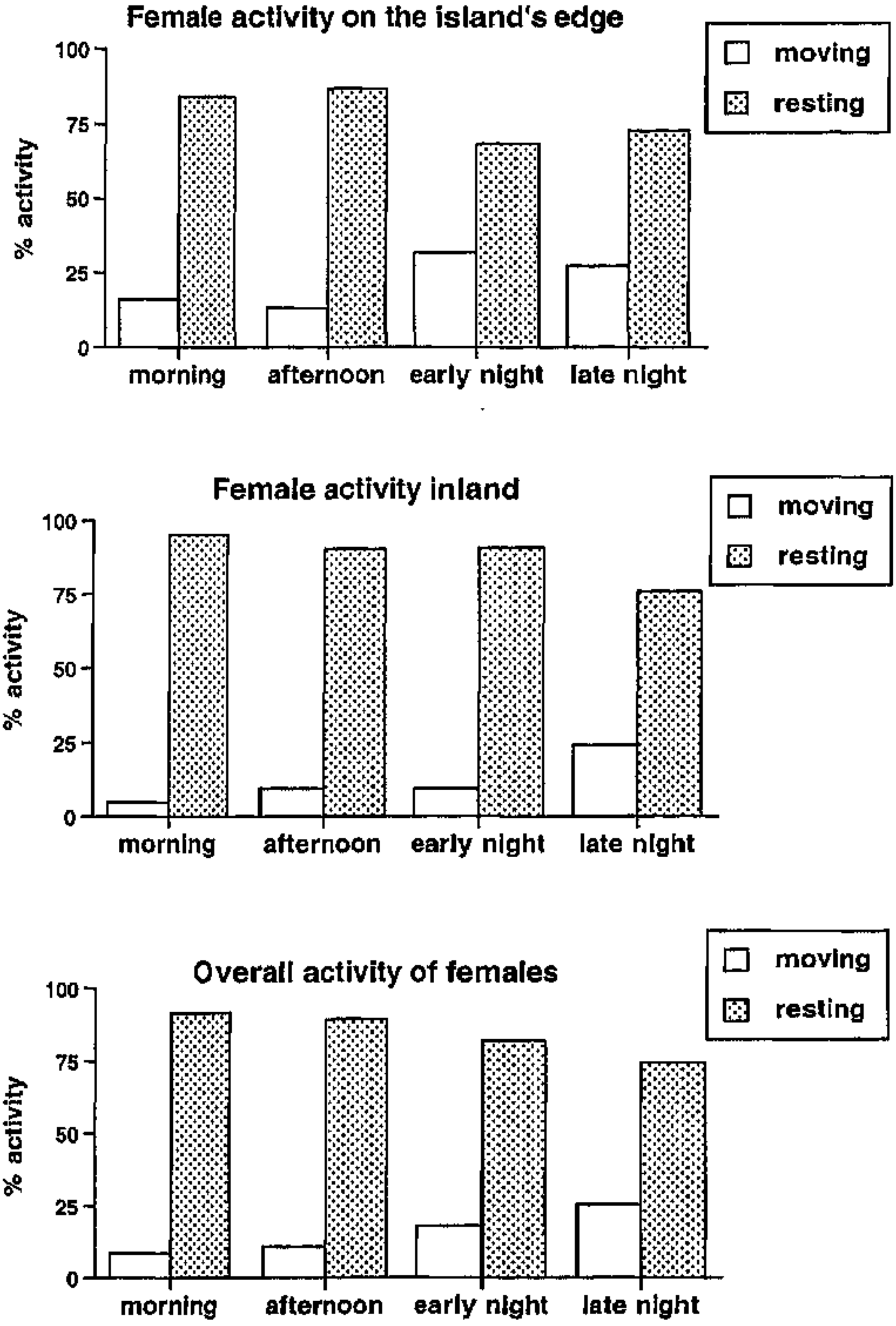


Figure 3.2a Activities of female sea kraits at different times of day along two transects. Also shown is the combined result from both transects, depicting overall activity.

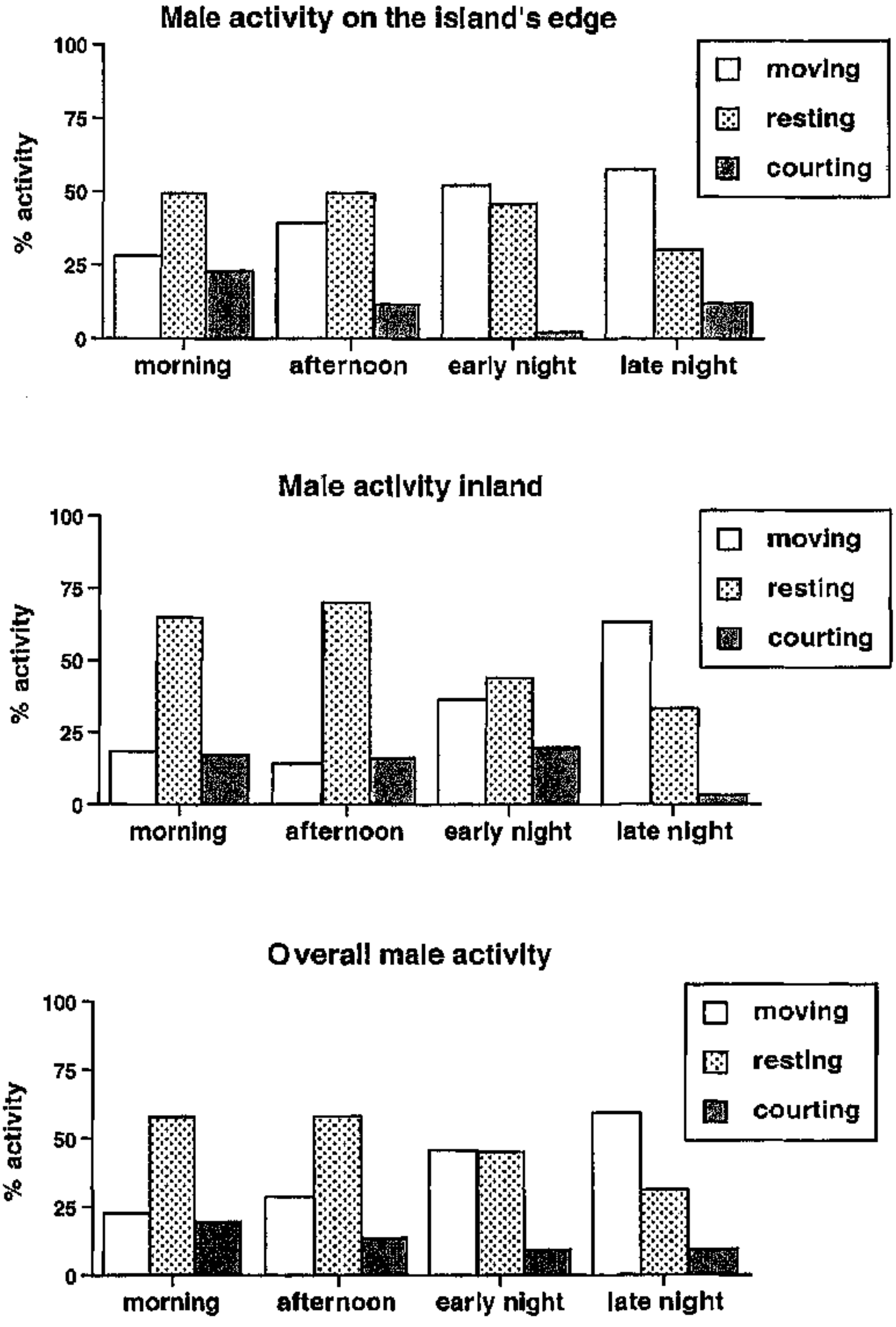


Figure 3.2b Activities of male sea kraits at different times of day along two transects. Also shown is the combined result from both transects, depicting overall activity.

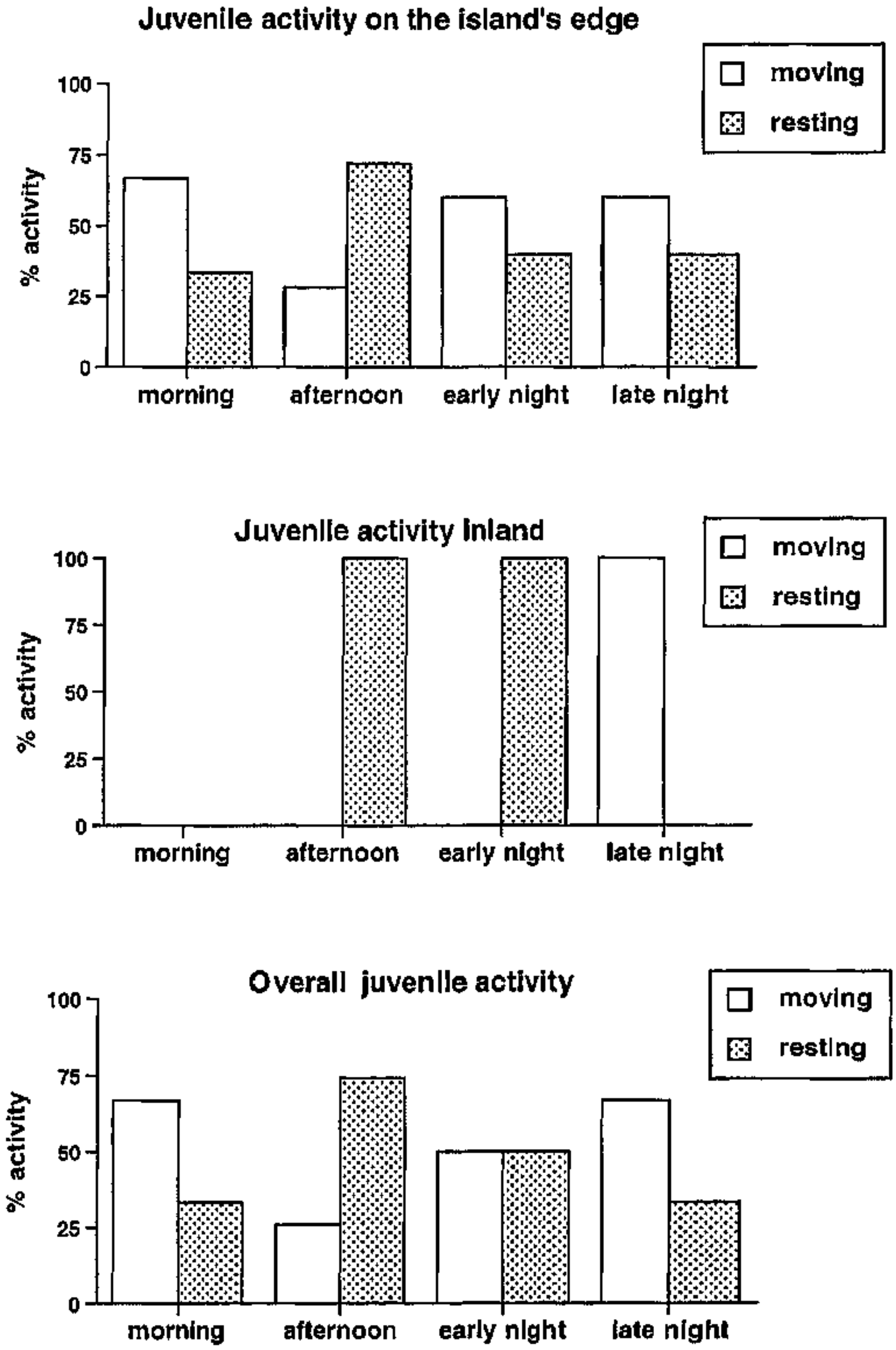


Figure 3.2c Activities of juvenile sea kraits at different times of day along two transects. Also shown is the combined result from both transects, depicting overall activity.

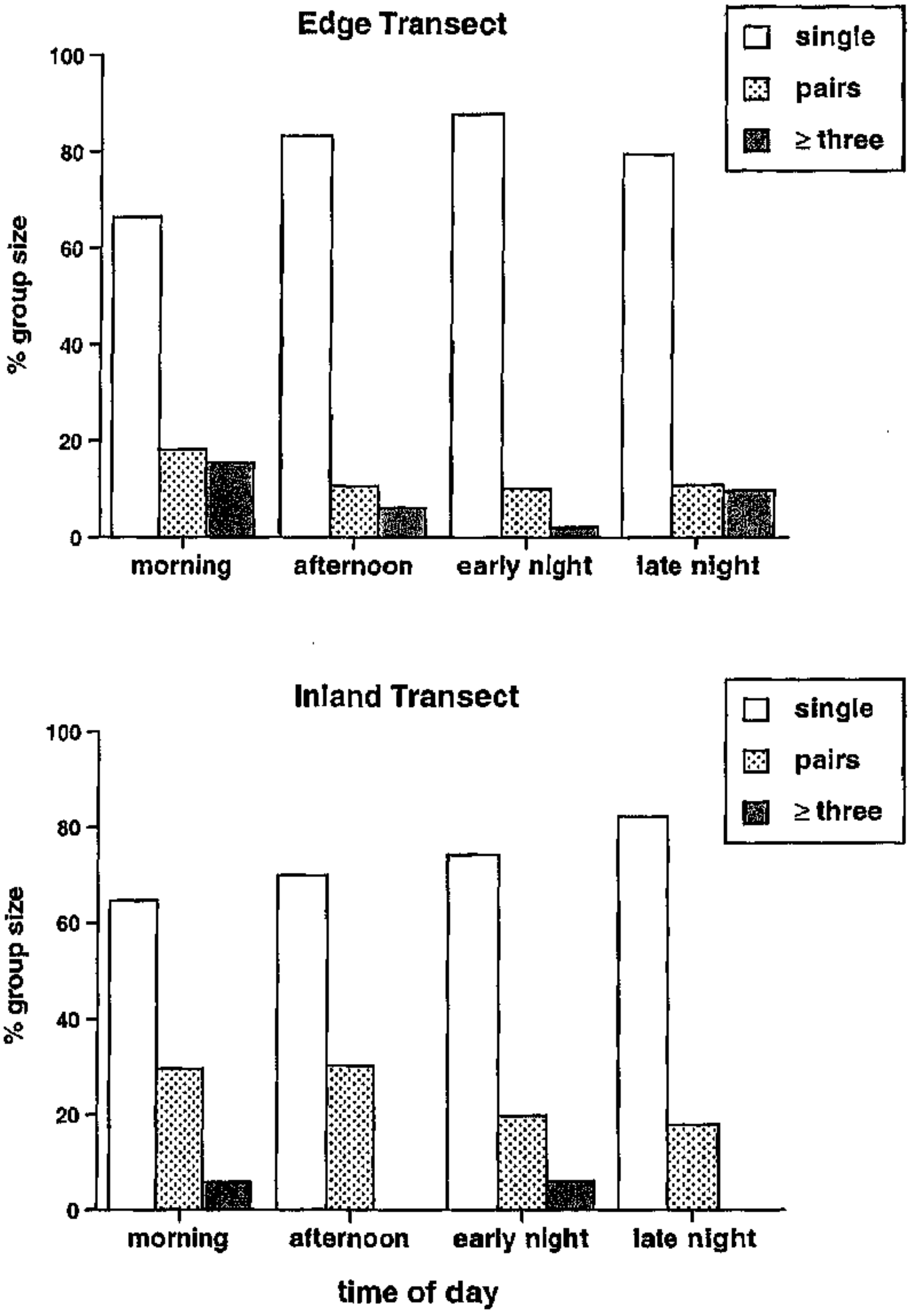


Figure 3.2d Occurrence of aggregations of sea kraits along two transects, at different times of the day and night.

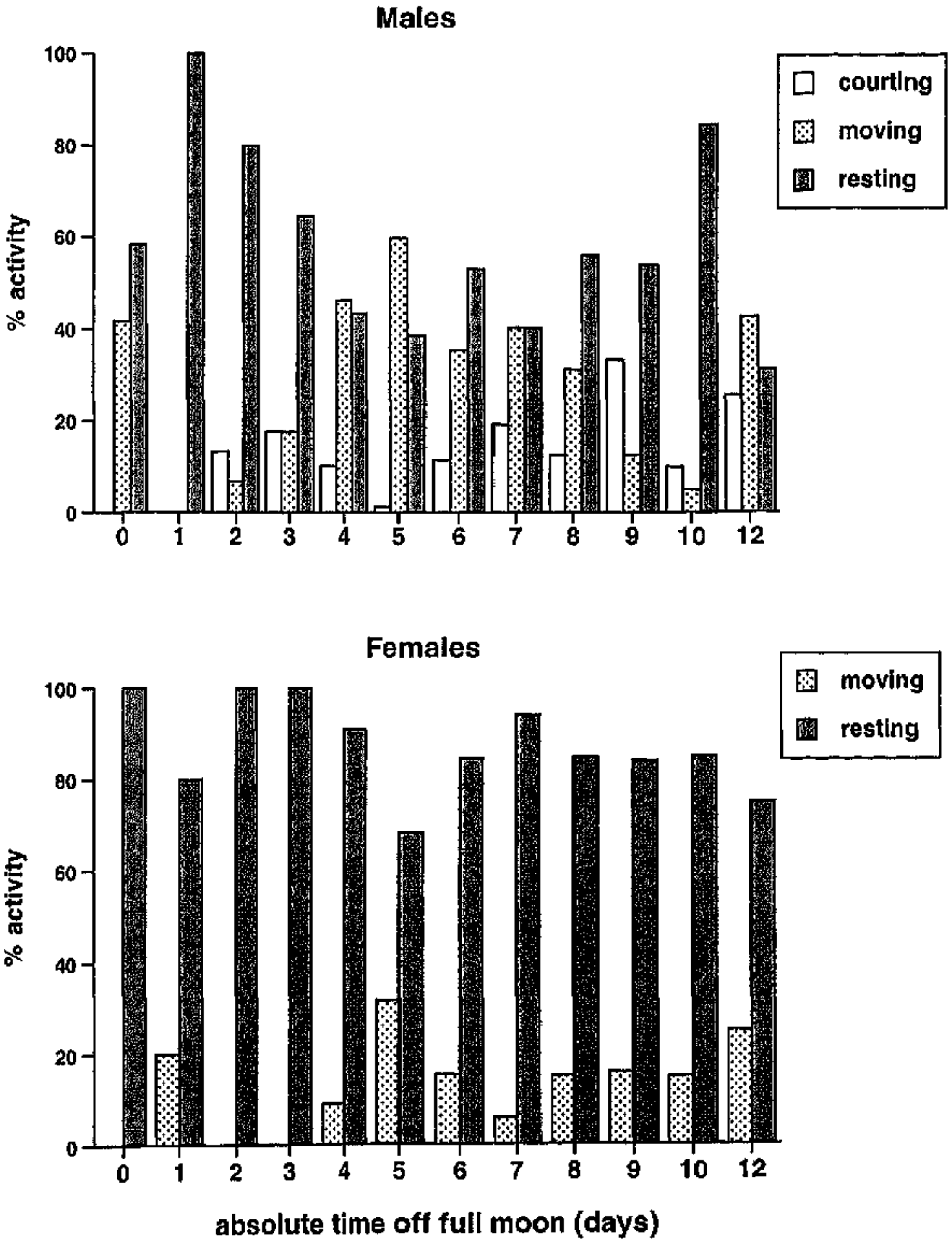


Figure 3.4 Variation in activity patterns of free-ranging male and female sea kraits as a function of lunar periodicity.

varied significantly with time of day ($\chi^2 = 42.03$, 6 df, $P < 0.0001$) and lunar periodicity ($\chi^2 = 76.10$, 22 df, $P < 0.0001$; Fig. 3.4).

Data split by location of transect: Patterns of activity were similar along the two transects, and in each case they differed significantly with time of day (edge of the island: $\chi^2 = 25.38$, 6 df, $P = 0.0003$; inland: $\chi^2 = 31.02$, 6 df, $P < 0.0001$; Fig. 3.2b). Adult male sea kraits were generally recorded moving late at night, courting in the morning, and resting in the afternoon.

The table below summarises the time of day when a particular activity was encountered most often (based on post hoc cell contributions from contingency analysis)

Male Activity	Time of Day and Night		
	Locations combined	Edge of island	Inland
Courting	Morning	Morning	Early night
Moving	Late night	Late night	Late night
Resting	Morning/Afternoon	Afternoon	Afternoon/Morning

Juveniles

No significant differences were detected in juvenile activity patterns with time of day, or with lunar periodicity, along either transect (Fig. 3.2c and Fig. 3.4). This result may reflect the low power of the tests, due to the relatively small number of animals sighted and their patchy distribution.

Courting groups

Combined data: Overall, snakes were seen in courting groups (i.e. at least one male and one female) more often in the mornings, whereas most snakes seen at night were solitary. This temporal shift was statistically significant ($\chi^2 = 21.72$, 3 df, $P < 0.0001$). A similar result was seen for group sizes. Groups of two or more snakes were encountered more often in the morning than at other times ($\chi^2 = 27.51$, 6 df, $P < 0.0001$).

Data split by location of transect: 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, $P = 0.06$). Nevertheless, both areas exhibited the same pattern as in the combined data set – groups of courting snakes were more common in the mornings and solitary snakes were more common early at night (Fig. 3.2d)

Microhabitat use

Adult Females

Combined data: Microhabitat use by females differed significantly throughout the day ($\chi^2 = 25.04$, 6 df, $P = 0.0003$; Fig. 3.3a).

Data split by location of transect: Significant differences in microhabitat use were also seen at each location when they were analysed separately (edge of island: $\chi^2 = 19.11$, 6 df, $P = 0.004$; inland: $\chi^2 = 17.05$, 6 df, $P = 0.009$; Fig. 3.3a). Adult female sea kraits were generally recorded on rocky

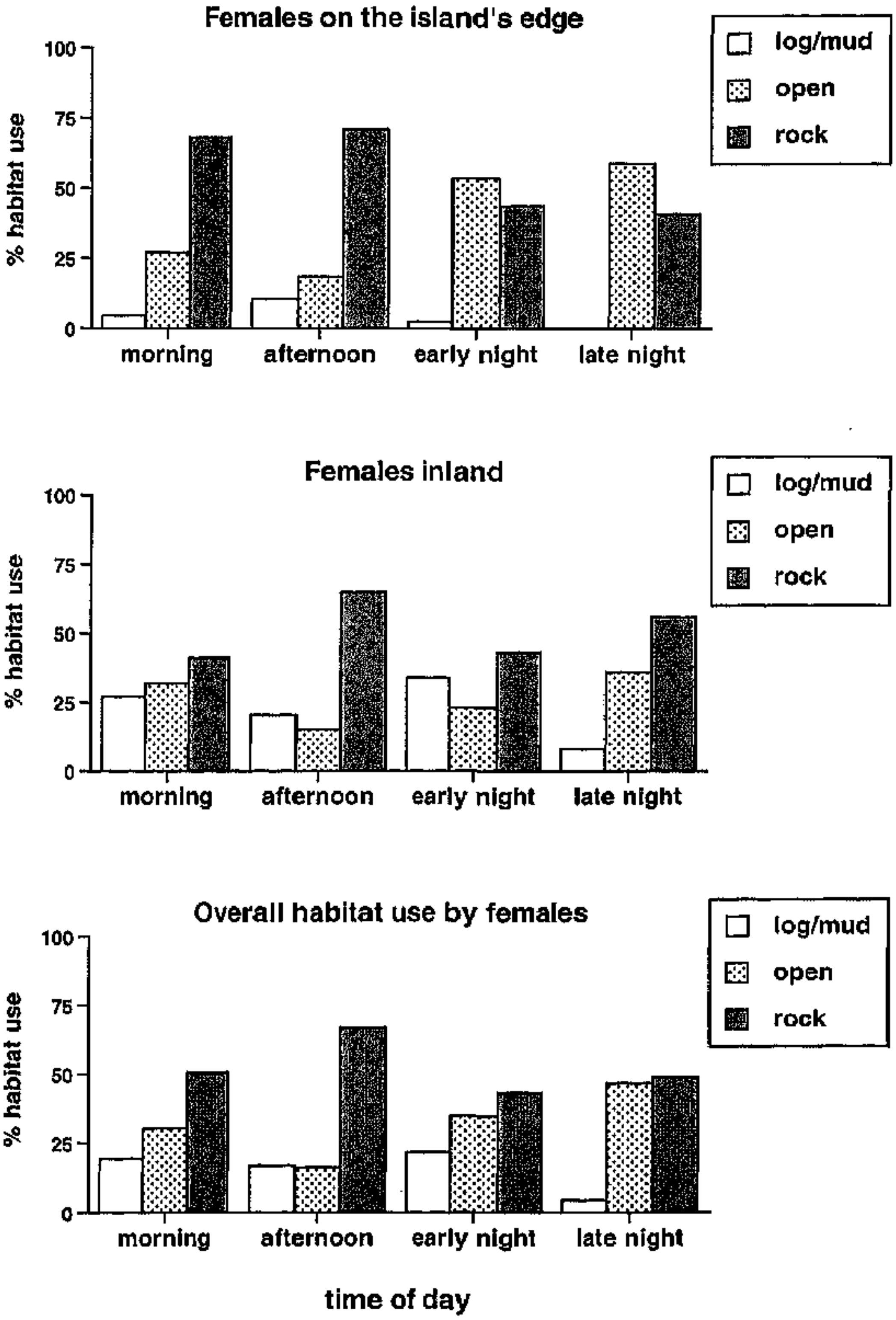


Figure 3.3a Habitat use by female sea kraits in transects along the edge of the island and inland. Also shown is the overall habitat use by females.

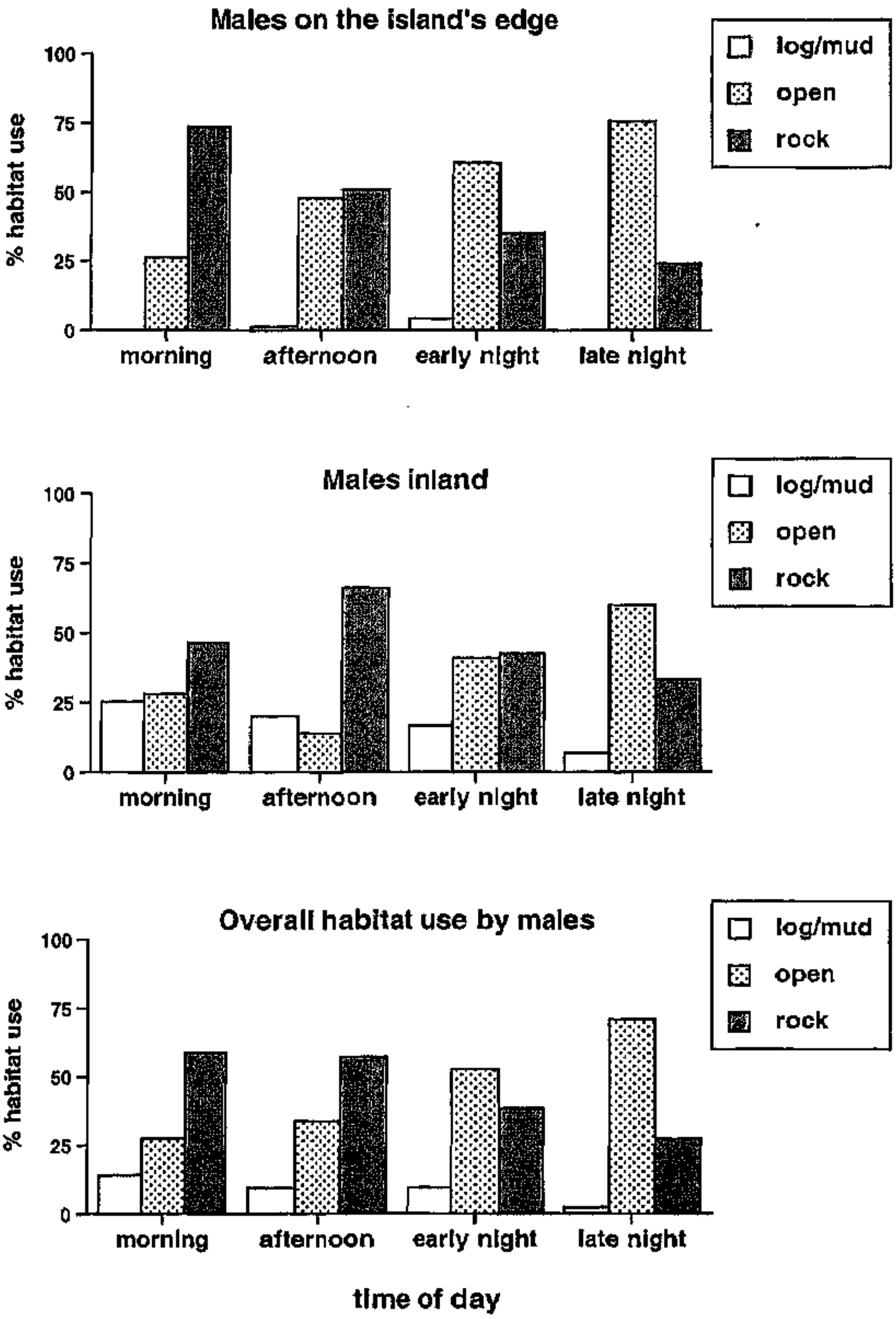


Figure 3.3b Habitat use by male sea kraits in transects along the edge of the island and inland. Also shown is the overall habitat use by males.

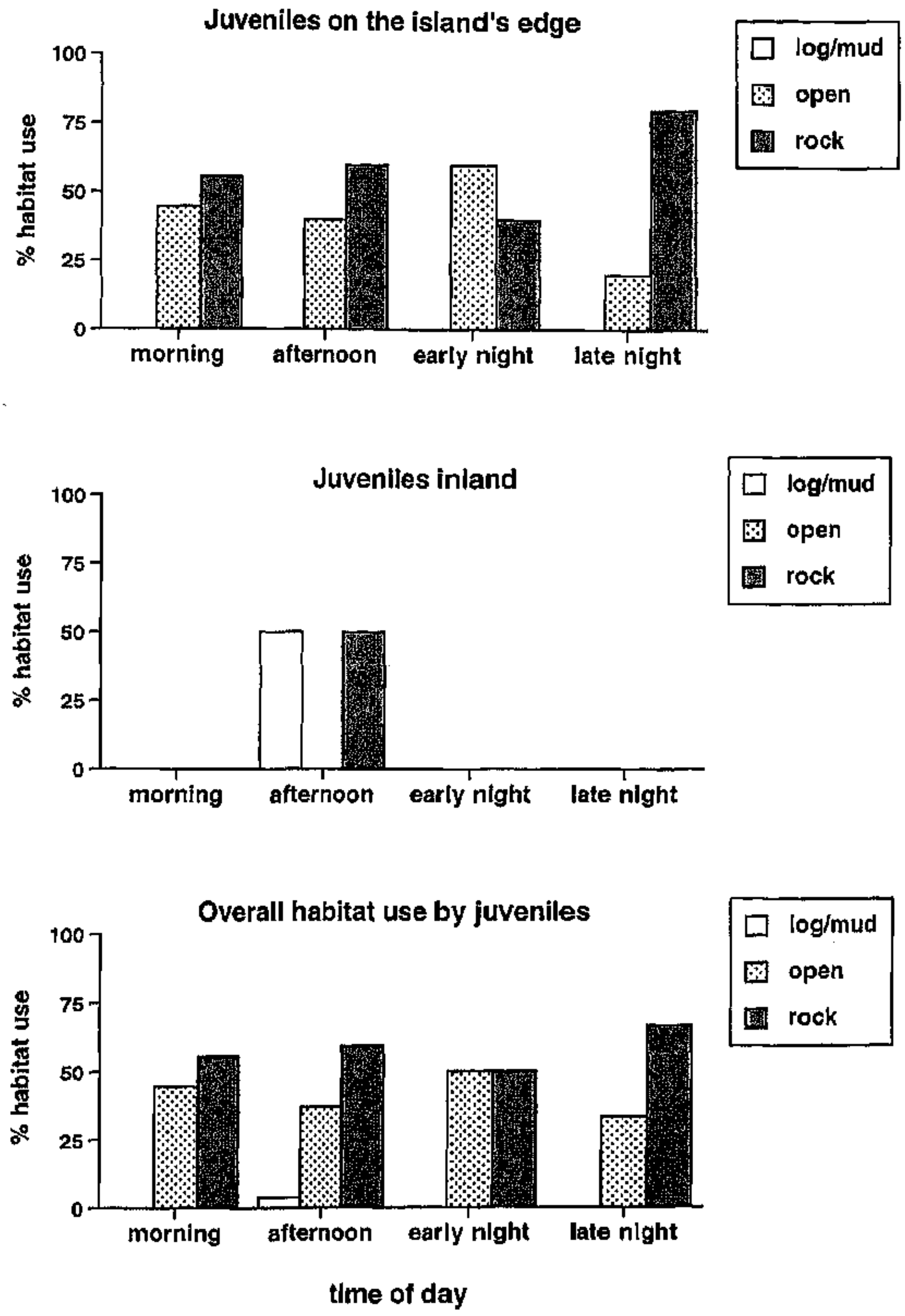


Figure 3.3c Habitat use by juvenile sea kraits in transects along the edge of the island and inland. Also shown is the overall habitat use by juveniles

habitats in the afternoon, inside mud/log during the early-night, and in the open areas late at night.

The table below (based on post hoc cell contributions from contingency analysis) shows the time of day when each kind of microhabitat was used most often by female snakes (also see Fig. 3.3a).

Microhabitat	Time of Day and Night		
	Locations combined	Edge of island	Inland
Mud/Log	Early night	Afternoon	Early night
Open	Late night	Late/Early night	Morning
Rock	Afternoon	Afternoon	Afternoon

Adult Males

As for females, adult male snakes were recorded in different habitats at different times of day. This temporal heterogeneity was statistically significant both in the overall sample ($\chi^2 = 54.4$, 6 df, $P < 0.0001$) and also when each area was considered separately (edge of the island: $\chi^2 = 40.30$, 6 df, $P < 0.000$; inland: $\chi^2 = 23.10$, 6 df, $P = 0.0008$; Fig. 3.3b).

The table below (based on post hoc cell contributions from contingency analysis) shows the time of day when adult male snakes were encountered most often using particular microhabitats (also see Fig. 3.3b)

Microhabitat	Time of Day and Night		
	Locations Combined	Edge of island	Inland
Mud/log	Morning	Afternoon	Morning
Open	Late night	Late night	Late night
Rock	Morning/Afternoon	Morning	Afternoon

Juveniles

No significant differences were detected in juvenile habitat use with time of day, along either of the transects (Fig. 3.3c). Again, this probably is a result of the restricted distribution of juveniles.

Sloughing individuals

From my surveys, I found 69 individuals (7.3% of the total sample) that had gone into a moult. Of these snakes, 71% were females, 24.5% were males and the remaining 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, $P < 0.0001$).

Movement Patterns (1999 Surveys)

Due to differences in activity patterns of male and female sea kraits (see results above), the data on movement were analysed separately for each sex, taking into account the effects of site, slope and tide on the landward and seaward movement patterns of snakes.

Adult Females

In adult females, only one factor (slope) had significant main effects on the number of snakes recorded as moving in either direction (landward: $F_{1,292} = 26.70$, $P < 0.0001$; seaward: $F_{1,292} = 5.80$, $P = 0.02$). Females clearly selected gentle slopes to move between habitats. Movement patterns of females were not influenced by tidal conditions, nor did they differ significantly among sites (unlike male patterns: see below).

Adult Males

General movement

During the mating season, male sea kraits frequently pursue females, courting them vigorously whenever the female stops moving (Saint Girons, 1964; Guinea, 1986). Thus, movement patterns of males are clearly influenced by the movement of females, as well as by other factors such as weather and local topography. For this reason, I 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 if numbers of females were high ($F_{1,292} = 20.20$, $P < 0.0001$). 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.

Landward movement

There were 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, I 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 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. 3.5).

Seaward movement

There were no 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

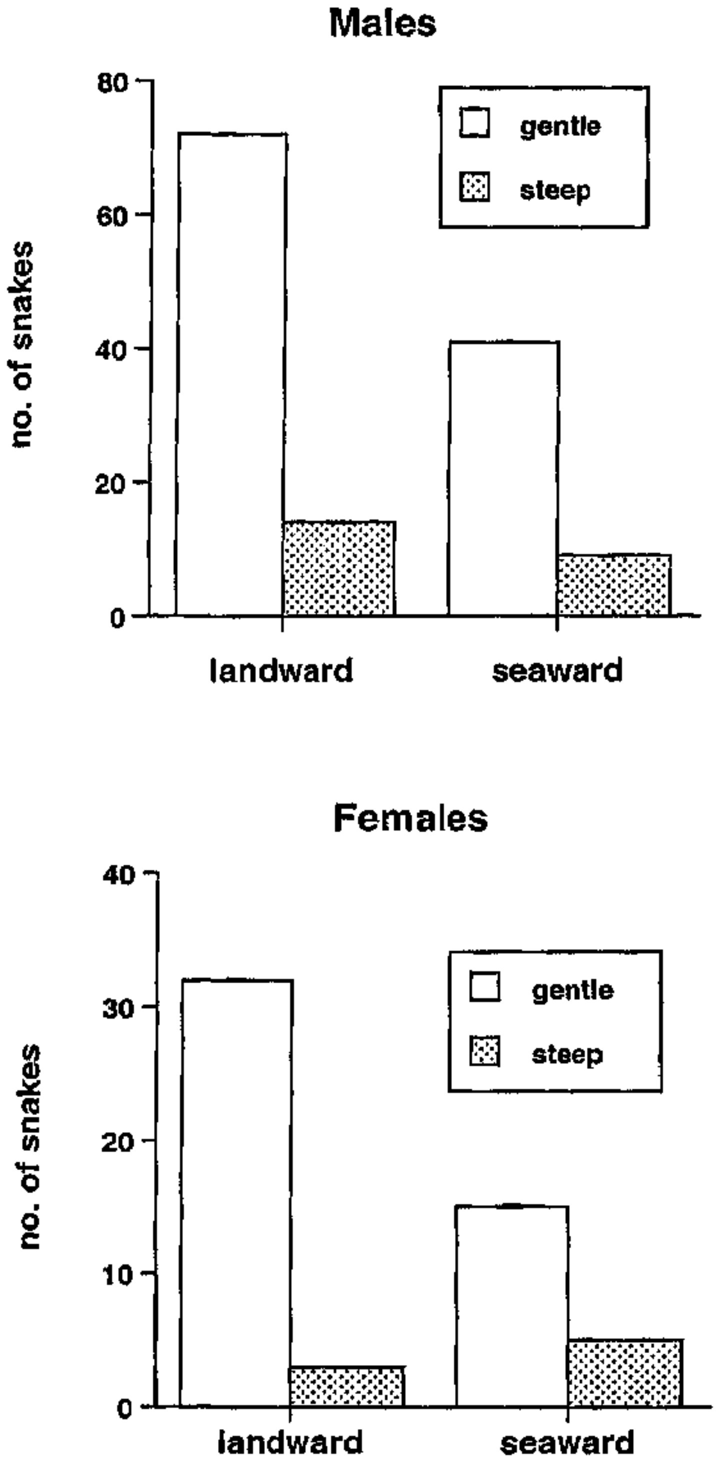


Figure 3.5 The number of sea kraits of each sex encountered at gentle or steep slopes on Mabualau Island, moving towards the land or sea.

than steep slopes, and more preferred to leave the island from some sites than from others (Fig. 3.5).

Radiotelemetry

There are no published studies of radiotelemetric monitoring on any laticaudid species, including *Laticauda colubrina*. Hence, my objectives here were simply to clarify some very basic aspects of the biology of sea kraits. In spite of its limitations for use underwater (indeed, because of those limitations), I was able to use this technique to collect information on the balance between aquatic and terrestrial activity in sea kraits.

Time spent on land *versus* at sea

Daily monitoring for presence/absence of the telemetered snakes began as soon as the snakes were released. Thereafter, the snakes spent an average of 22.8 days on the island before moving into the sea. This delay may indicate the approximate time taken for the snake to recover from surgery.

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, I was able to determine the amount of time that each of these animals spent on land and in the sea. All of the radio-tracked snakes spent approximately equal amounts of time in each of these habitats, moving between them on a fairly regular basis. 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; Fig. 3.6). Note that for these analyses, I excluded the time spent on land immediately after release of the snakes, as this was the recovery time.

Movement between land and sea

Although general patterns of habitat use were similar for males and females (above), the number of times that radio-tracked snakes shifted from one habitat to another over the course of my study did differ (though not significantly) between the sexes (t = -1.85, 13 df, P = 0.09; Fig. 3.7). On average, males moved between land and sea 5.3 times over an average of 67.5 days, whereas females moved an average of 3.9 times between the two habitats over the same period (Fig. 3.8).

Body temperatures and operative temperatures

The Hobo temperature data loggers provided an indication of the range of operative temperatures available to snakes on Mabualau during the period that I radio-tracked selected animals. I sorted and averaged these data and calculated hourly average temperatures. Figure 3.9 shows these data, as well as the mean hourly body temperatures of the radio-tracked snakes. Not surprisingly, copper models in full sunlight attained high temperatures (> 35°C), whereas models in full shade remained cooler (< 28°C) and relatively stable (Fig. 3.9). Thermal maxima inside full-sun models were not attained until the afternoon. Water temperatures were generally higher than those in full shade on land, and exhibited only modest diurnal fluctuations.

Mean body temperatures of telemetered snakes in terrestrial habitats were intermediate between those of the water and shaded habitats on land (Fig. 3.9). The temperatures of male snakes were consistently higher than those of females, with mean body temperatures averaging 28.4° C in males and 27.7°C in females. These values were significantly different (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. 3.9).

During the second field season (between October and November 1999), we implanted Tidbit Data Loggers (Onset Computer Corporation, Massachusetts) along with radio transmitters in four female snakes. I only obtained useful data from one of these animals; two snakes died and one was not recaptured. This record provided data on the temperature regimes exhibited by this snake in water as well as on land. I also placed Tidbit Data Loggers in three locations to monitor ambient thermal conditions.

The models that I used in 1999 provided data similar to that obtained from the copper models in 1998. Models in full sun attained very high temperatures (> 38°C) on most days, although intermittent rainy periods and overcast days (e.g. 10th to 20th October) severely depressed these maximum values. Nonetheless, body temperatures > 25°C were typically available to the snakes throughout most of the day. Operative temperatures of the model in full sun increased relatively slowly during the morning, but were high throughout the afternoon. Minimum temperatures were generally more constant, typically averaging around 25°C (Figs. 3.10 and 3.11).

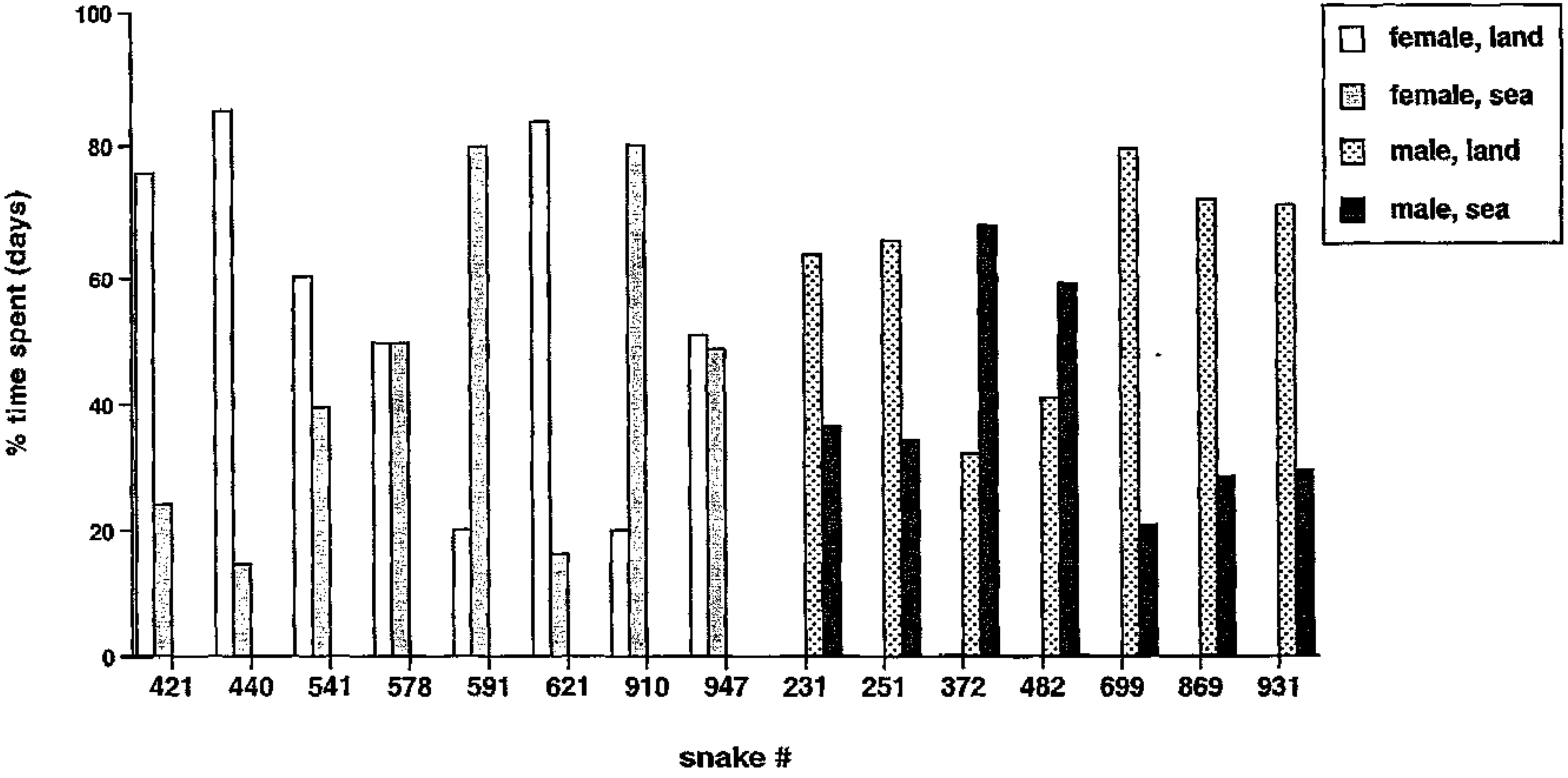


Figure 3.6 Mean time (%) spent by telemetered female and male sea kraits on land and at sea.

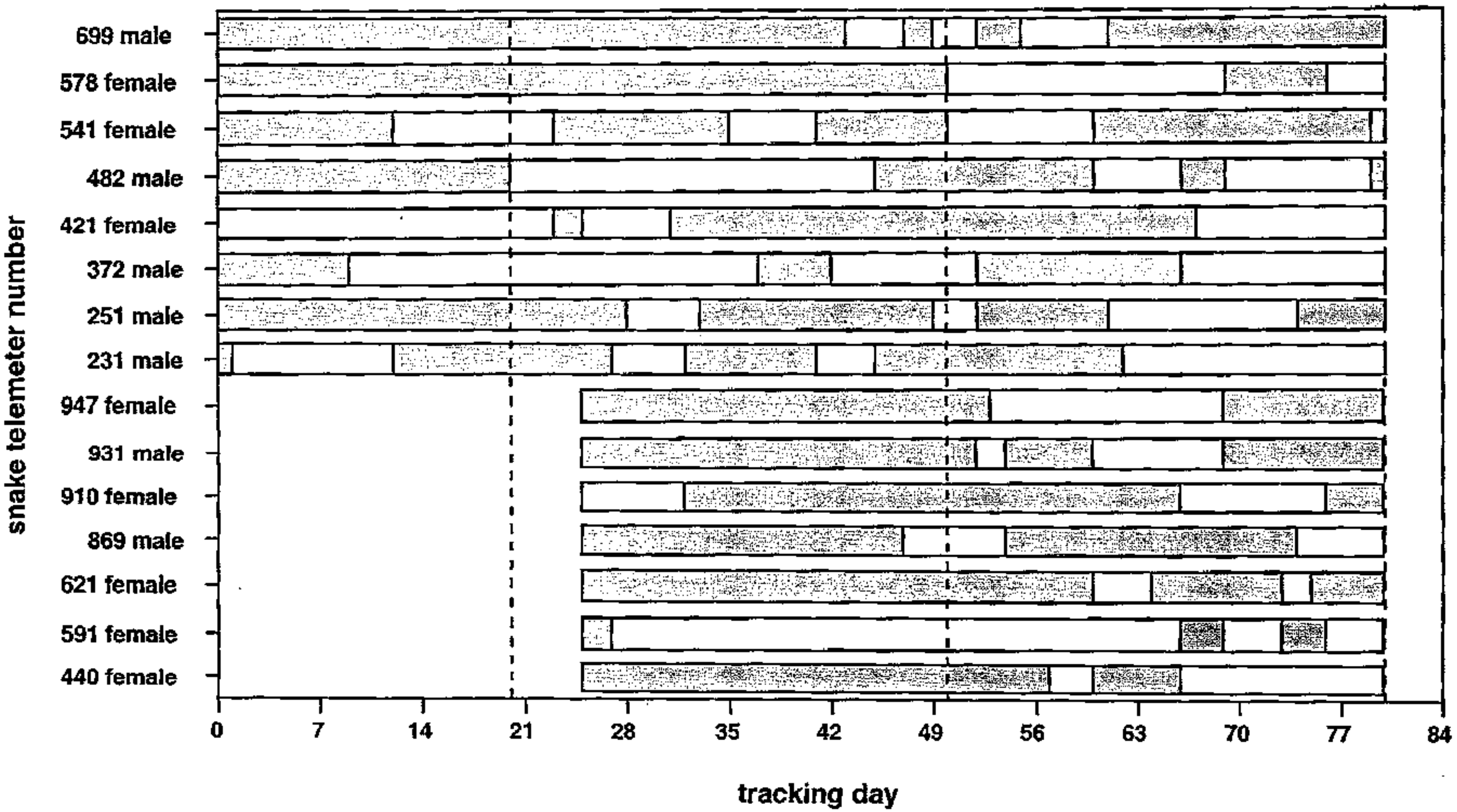


Figure 3.7 The number of days spent on land (dark blocks) and sea (light blocks) by telemetered sea kraits. The dotted vertical lines indicate full moon days. Note that snake # 947 through to snake # 440 were implanted with transmitters 25 days after the first batch of snakes.

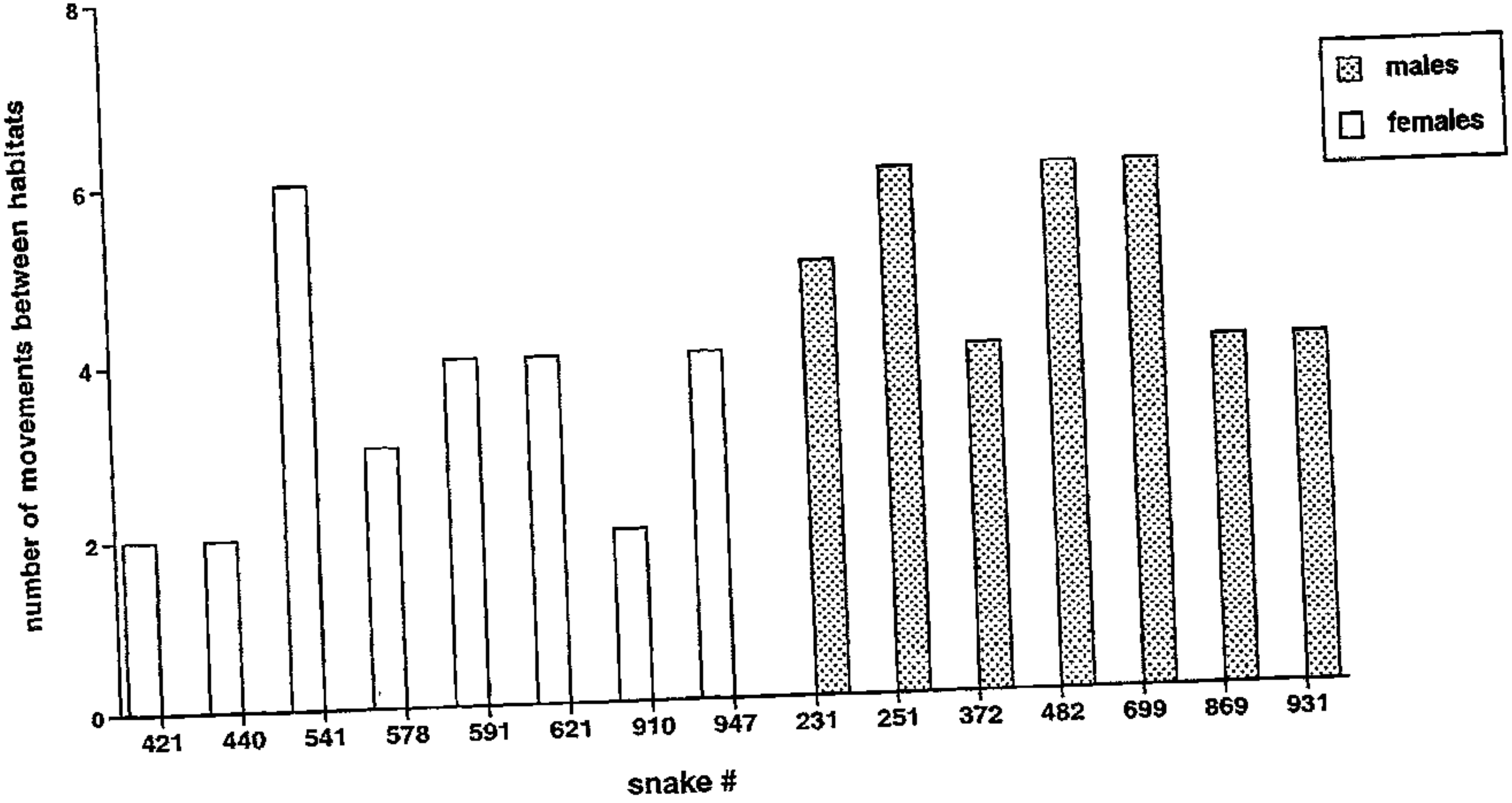


Figure 3.8 Total number of movements between land and sea by snakes of each sex during the study period.

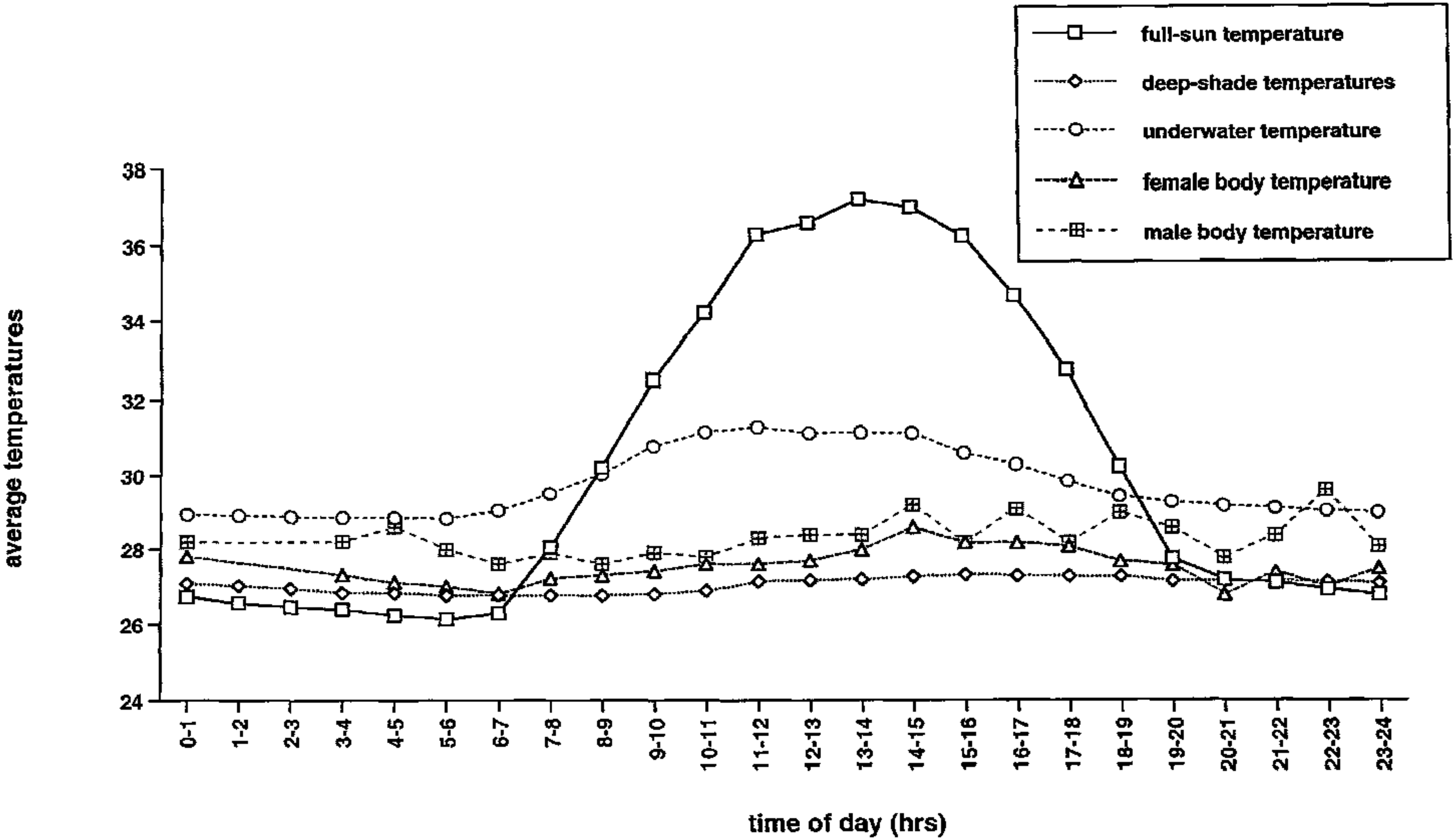


Figure 3.9 Diurnal variation of average body temperatures of telemetered male and female sea kraits, and average habitat temperatures, on Mabualau Island.

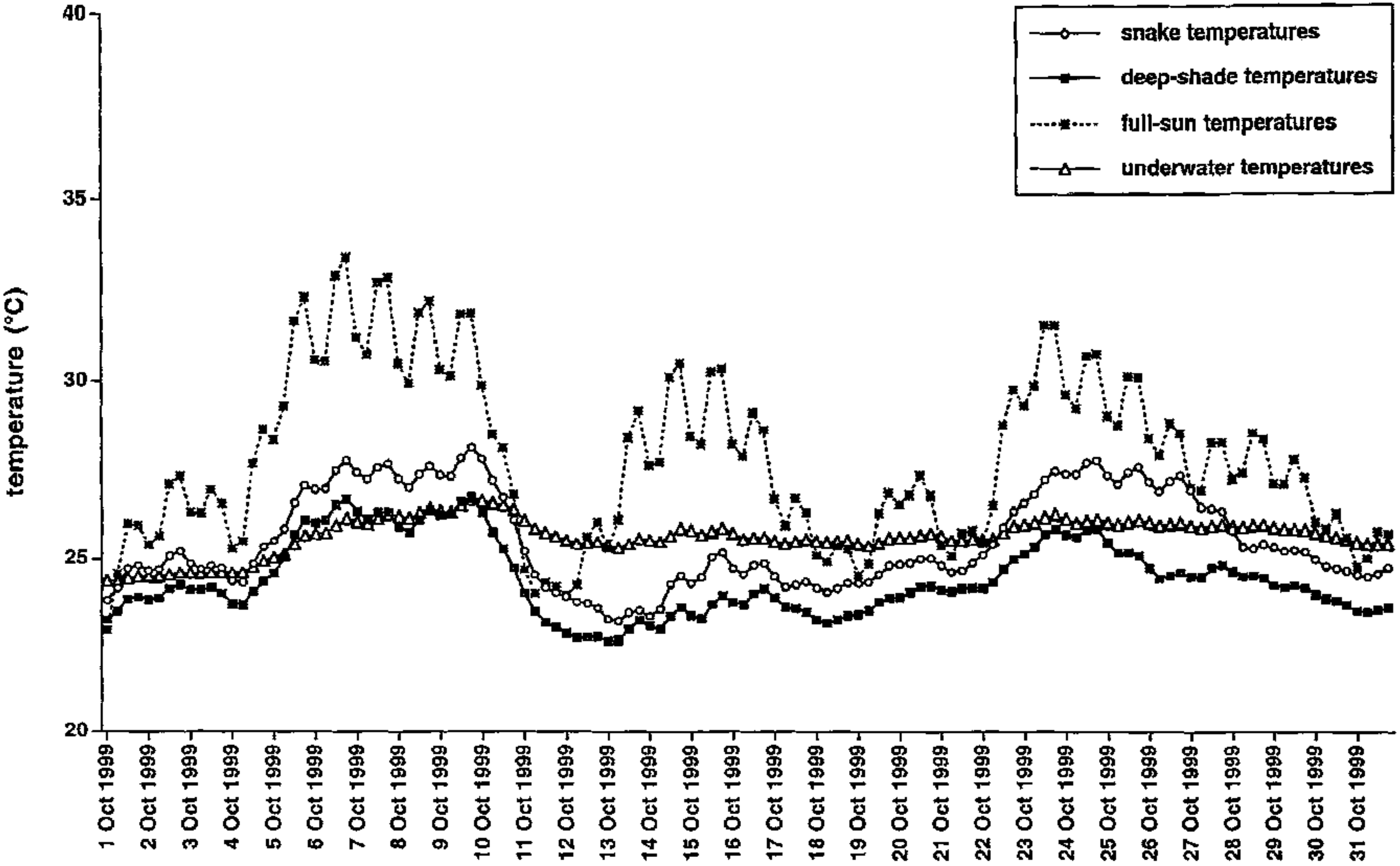


Figure 3.10 Six-hourly average body temperatures of one female sea krait for the month of October 1999. The graph also shows corresponding operative temperatures as measured by thermal data loggers. These data loggers were placed underwater, in full shade on land, and in full sun exposure on land.

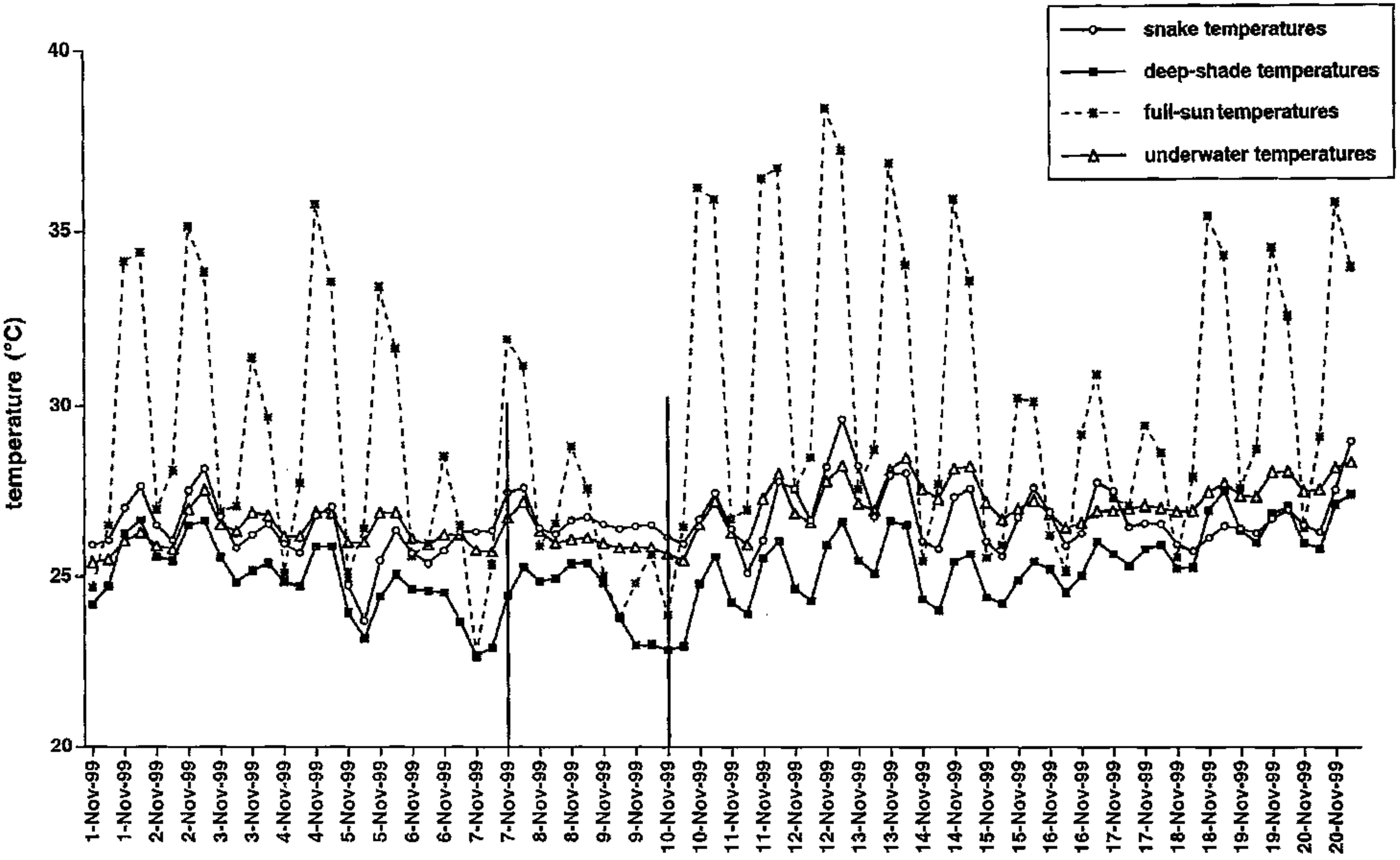


Figure 3.11 Six-hourly average body temperatures of one female sea krait for the month of November 1999. The graph also shows corresponding operative temperatures as measured by thermal data loggers. These data loggers were placed underwater, in full shade on land, and in full sun exposure on land . Note that body temperature of this snake between 7th and 10th November 1999 corresponds with her absence from the island.

Figures 3.10 and 3.11 show the thermal regime exhibited by the female snake implanted with a miniature data logger in 1999. She left the island only once during the monitoring period, for three days (Fig. 3.11). During her three days in the ocean, the radio-tracked female maintained high and constant body temperatures. Her average temperature was 26.6°C (± 0.5°C), compared to means of 25.9°C and 27.2°C over the three-day periods on land preceding and following her time in the ocean. The variance in body temperature of this animal was significantly lower during her aquatic phase than during either the preceding or following terrestrial phases (SDs = 0.5, 0.9 and 1.1 respectively). We can test the significance of these differences using an equality of variances F test, comparing thermal variances before, during and after the aquatic phase. This test confirms that the variance in body temperatures of the female snake was significantly lower while she was in the ocean than when she was on land (before *versus* during: $F_{1,15} = 3.20$, $P = 0.03$; during *versus* after: $F_{1,15} = 5.60$, $P = 0.001$).

Sloughing and digestion times

The table below summarises the results for this aspect of the study.

Activity	Time to complete activity (days)								
	Adult males			Adult females			Overall		
	Mean	N	Range	Mean	N	Range	Mean	N	Range
Digestion	8.7	3	6-10	7.7	23	3-11	7.8	26	3-11
Sloughing	12.6	7	5-24	11.2	12	7-13	11.7	19	5-24

Males and females did not differ significantly in the duration of these activities (digestion: t = 0.8, 24 df, P = 0.40; sloughing: t = 0.7, 17 df, P = 0.50). The average time taken by sea kraits to digest their prey was 7.8 days and the average time to shed their skin was 11.7 days.

DISCUSSION

Although the large terrestrial congregations and tolerant disposition of *L. colubrina* make them particularly well-suited to behavioural studies, few conclusive results on topics such as activity and behavioural patterns have emerged. For example, some studies have linked activity of sea kraits with time of day (Herre, 1942), whereas others have emphasised the influence of tide on their movement patterns (Saint Girons, 1964). Guinea's (1986) observations are the most extensive yet available, encompassing different times of the year. Guinea identified environmental cues such as tidal cycle, rainfall and sunset as key factors in the stimulation of sea krait activity. My own research combines information from surveys and radiotelemetric studies, and provides a clearer picture of behavioural patterns in sea kraits and the factors that may influence them.

In their review of activity patterns in snakes, Gibbons and Semlitsch (1987) concluded that many studies had detected significantly non-random patterns of activity, but the actual causes for such patterns remained elusive in almost all cases. For example, adult males and females differ in habitat selection and times of activity in some snake taxa, but species differences make it difficult to discern any general patterns. Clearly, we will need more detailed studies, on a geographically and taxonomically wider range of snake species, before any such generalities can be formulated. The review by Gibbons and Semlitsch (1987) also highlighted the need for more research to be carried out on components of the population that have attracted little attention (especially juveniles), and emphasised the need for tests of causal explanations, rather than mere quantification. Nonetheless, careful quantification must be the first step in this process.

My research has attempted to address the above questions. As predicted, I found significant differences between the behavioural patterns of adult males and females, and also between adults and juveniles. From my results, the following can be inferred about the diel activity of sea kraits.

Adult snakes of both sexes are most often seen at night and they are most likely to be moving during this time. Most of the snakes encountered were adult males. However, females were also seen at night, moving towards either habitat (i.e. towards land or sea). Females with prey items were also seen during this time although they were resting rather than moving. It is likely that such females were exhausted as even the ones seen moving were not seen actively swimming. Rather, they allowed themselves to be washed ashore by the waves. Some females that had recently consumed prey were observed lying motionless around the high-tide line. If the tide was moving out, such females were often stranded on the open reef, lying motionless for hours about 50 to 100 m away from the edge of the island. Such an exposed location may place the female at risk from predation or overheating during daylight hours, so it is not surprising to see that such movements from the ocean to the land generally occurred at night.

Along the edge of the island, females heading in either direction (towards land or sea) were actively pursued by males. Females that had just come ashore slowly made their way inland to look for resting sites, being pursued by males at the same time. Females that were grossly distended by recently-ingested prey items were literally covered by males, probably because the females were too exhausted to move. In one instance, nine males simultaneously courted a female that had just come ashore.

The movement of adult female snakes between land and the sea continued through the night until early morning. Females were mostly encountered in the mornings when they were found resting. Females may have been raising their body temperatures by basking at this time, before ambient temperatures rose to their afternoon peak (Fig. 3.9). Males that had succeeded in following females to their resting sites began courting the females during this time. By afternoon, the sightings of courting males decreased. Again, thermal factors may drive this reduction in activity. Most males seen during the middle of the day, either in groups or singly, were motionless.

Greer (1997) cogently summarised our ignorance of the day-to-day lives of sea kraits by posing a simple question: are these animals basically marine organisms that occasionally come to land, or terrestrial snakes that occasionally go to sea? The answer, clearly, is somewhere in between these two extremes. Landing et al., (1991) estimated that sea kraits spend only about 30% of their time on land, based on the proportion of marked animals that they could locate in any given census. However, some terrestrial snakes may be difficult to locate by visual searching: this was certainly the case for telemetered animals on Mabualau. My telemetric monitoring shows that adult sea kraits divided their time relatively evenly between the two habitats. I found no significant difference in the average time spent on land *versus* at sea, nor did the two sexes differ in this respect. However, males did tend to move between the two habitats more frequently than the females (Fig. 3.8).

The average times taken to digest prey and to slough (from the enclosure trials) fit well not only with the telemetric data on the duration of the terrestrial phase but also with observations of captive *L. colubrina* in the Monterey Bay Aquarium (California). This study revealed that the snakes (sexes unknown) took nine to 13 days to shed their skin, once the moulting process began (Franklin, 1997). The same study also estimated that on average, the snakes sloughed once every two months.

Past researchers have suggested that tides influence the movement patterns of sea kraits (Pernetta, 1977; Guinea, 1986). However, my study suggests that such effects are relatively minor. Tidal conditions did not affect migration of females between land and sea. The general activity of females on land was influenced by lunar periodicity, with more terrestrial activity around the new moon phase.

In adult male sea kraits, both activity on land and landward movements were influenced by tidal conditions. Additionally, there were certain locations on the island where movement of males was more frequent.

In general, movements between land and sea took place at those sites on the island where the cliffs gently sloped. These snakes are very capable of climbing steep, out-facing cliffs (note that males are faster than females on land: Chapter 5), but clearly prefer not to do so. Observations of sea kraits arriving at the shore show that they experience difficulty in moving from the water to the rocks if there is heavy wave action. Under these conditions, snakes are often bounced against the rocks for some time before managing to make the transition to land. Selecting gently-sloping areas greatly facilitates rapid and risk-free movements. The spatial variation in movement patterns presumably reflects the fact that some sites provide easier ingress and egress than others, or that fringing reefs concentrate inward-bound snakes in particular areas.

Juvenile sea kraits are subject to different selective pressures than adults, due to ontogenetic shifts in factors such as diets and vulnerability to predators (Mushinsky, 1987). Most juvenile snakes I encountered were either moving between land and sea, or resting in rock crevices, along the edge of the island. This observation accords well with Guinea's (1986) statement that the activity of juvenile sea kraits was concentrated along the fringes of the island. This similarity in the activity times of juvenile and adult snakes (i.e. active during the mornings or at night) is not surprising as snakes of all body sizes need to avoid dangerously high temperatures during the day.

However, the marked differences in habitat use by adults and juveniles is intriguing (Guinea, 1986) who also speculated that this restriction in habitat use by juveniles was an anti-predator behaviour as juveniles are prone to a wider range of terrestrial predators (e.g. crabs). My study supports and substantiates this speculation that juveniles tend to use shelters on the edge of the island as they are closer to the shoreline.

The fact that I found prey items in 47% of all juveniles that I collected for the study (31% of which had multiple prey items) suggests that juveniles spend most of their time either foraging or resting, and are encountered in terrestrial habitats while transiting between land and sea. Further, juveniles are faced with two major requirements when on land - thermoregulation and moving between habitats. And it is during this time that they are most vulnerable to predators. Although they are faster on land than adults (Chapter 5), their locomotor abilities are restricted by the fact that juveniles have lesser stamina than adults. Also, snakes emerging from resting sites are bound to be cooler, and those emerging from the sea are likely to have prey items in their stomach.

The rocks along the edge of the island are not only closer to the water mark, but also warmer (as they are exposed to direct sunlight). By staying close to the water's edge, they reduce the distance needed to be covered while making the transition between land and sea. Juvenile snakes can therefore increase body temperatures both prior to their movement into the water and upon returning to land to digest food and simultaneously minimise their exposure time to predators. However, more data on snake temperatures relative to microhabitat temperatures are needed to confirm this.

The surveys allowed me to collect information on variation in microhabitat usage through time of day. Not surprisingly, both males and females were found in open habitats mostly in the night or early mornings, evidently avoiding high temperatures. In the afternoon, when temperatures reached the daily maximum, individuals of both sexes were found inhabiting rocky habitats. Presumably, this is because of the relatively constant temperatures found under rocks (deep shade temperatures: Fig. 3.9).

Adult female sea kraits preferred to use logs or crab burrows in the evenings, while males used these sites in the mornings or afternoons. No information on temperatures in these specific microhabitats is available. It seems likely that patterns in movement and habitat selection by sea kraits are strongly influenced by the need to avoid dangerously high temperatures in the afternoon. However, testing this hypothesis will require additional research on the thermal regimes in microhabitats used by these snakes, as well as on the snakes' thermal preferenda and tolerances.

CHAPTER 4. REPRODUCTIVE BEHAVIOUR

INTRODUCTION

In previous chapters I have described the general activity and movement patterns of sea kraits in my study area in the Fijian islands. I will now focus on a specific aspect of the terrestrial lives of these animals - their reproductive behaviour. In contrast with many other aspects of the biology of laticaudids, their reproductive habits have received a significant amount of scientific attention. Work on this topic has been conducted in several scattered locations within the wide geographic range of these animals. For example, the reproductive biology of *L. semifasciata* and *L. laticaudata* from The Philippines was studied by Bacolod (1983), and that of *L. semifasciata* reproduction in Japan and Taiwan was studied by Toriba and Nakamoto (1987) and Tu et al., (1990) respectively. The species that I studied, *L. colubrina,* has attracted previous research in New Caledonia (Saint Girons, 1964), the Solomon Islands (Cogger et al., 1987; Ackman et al., 1991), and Fiji (Pernetta, 1977; Guinea, 1986), as well as in The Philippines (Gorman et al., 1981).

Although reproduction has thus attracted more scientific attention than most other aspects of laticaudid biology, previous analyses have been concerned primarily with reproductive output. That is, work has focussed on the numbers and sizes of eggs produced by females, and the seasonal timing of reproduction. Reproductive behaviour has attracted far less study. Many authors, in both the scientific and popular press, have described courting aggregations of laticaudids on tropical islands, but to the best of my knowledge, nobody has ever published any quantitative analyses of this phenomenon. The present chapter provides the first information of this kind.

The lack of detailed study on mating systems within *Laticauda* might seem somewhat surprising, given that these animals are abundant and tolerate human presence. However, the same lack of attention has been the case with other snake species that are similarly well-suited to studies of this kind. Only in recent years have there been detailed field-based analyses of reproductive behaviour in the red-sided garter snake, *Thamnophis sirtalis parietalis*, a species long known to form massive mating aggregations. I used a study conducted by Shine et al., (2000a,b,c,d) on the reproductive behaviour of *T. s. parietalis* as a model for my own studies on the mating system of *L. colubrina*. As was the case for the garter snake study, I took advantage of the tolerant disposition of my study animals to set up courting groups in field enclosures. This method enabled me to quantify characteristics such as courtship intensity under controlled conditions, where I could maintain particular combinations of animals together rather than working with field groups that inevitably changed in size and composition over the course of my observations.

Being the first study of its kind on sea kraits, my work focused on answering some basic questions, such as:

(i) how does the general courtship behaviour of sea kraits compare with that of previously-studied snake species?

(ii) what factors determine the intensity of courtship within a group of sea kraits? That is, does this variation result from some females being more attractive than others; from some males being more vigorous courters than others; or from some particular environmental conditions stimulating more intense courtship?

(iii) what are the attributes (size, etc.) of individual snakes in courting groups compared to other snakes found singly?

(iv) what attributes of male and female snakes affect the intensity of courtship?

(v) what characteristics of the individual (male or female) determine mating success?

METHODS

Observations were made on natural courting groups throughout the study. In order to conduct observations on the reproductive behaviour of *L. colubrina* in more detail, I set up a series of ten 1 m^3 polypropylene enclosures (old wool sacks) on Mabualau Island (Plate 5). These enclosures were held open and upright by a wooden framework. Each enclosure was large enough to hold up to a dozen snakes and high enough to prevent them from escaping. All enclosures were located under shade over the limited flat area available on the island.

Because these snakes are extremely passive it was possible to bring courting groups from the wild (Plate 6) into the enclosures without significant

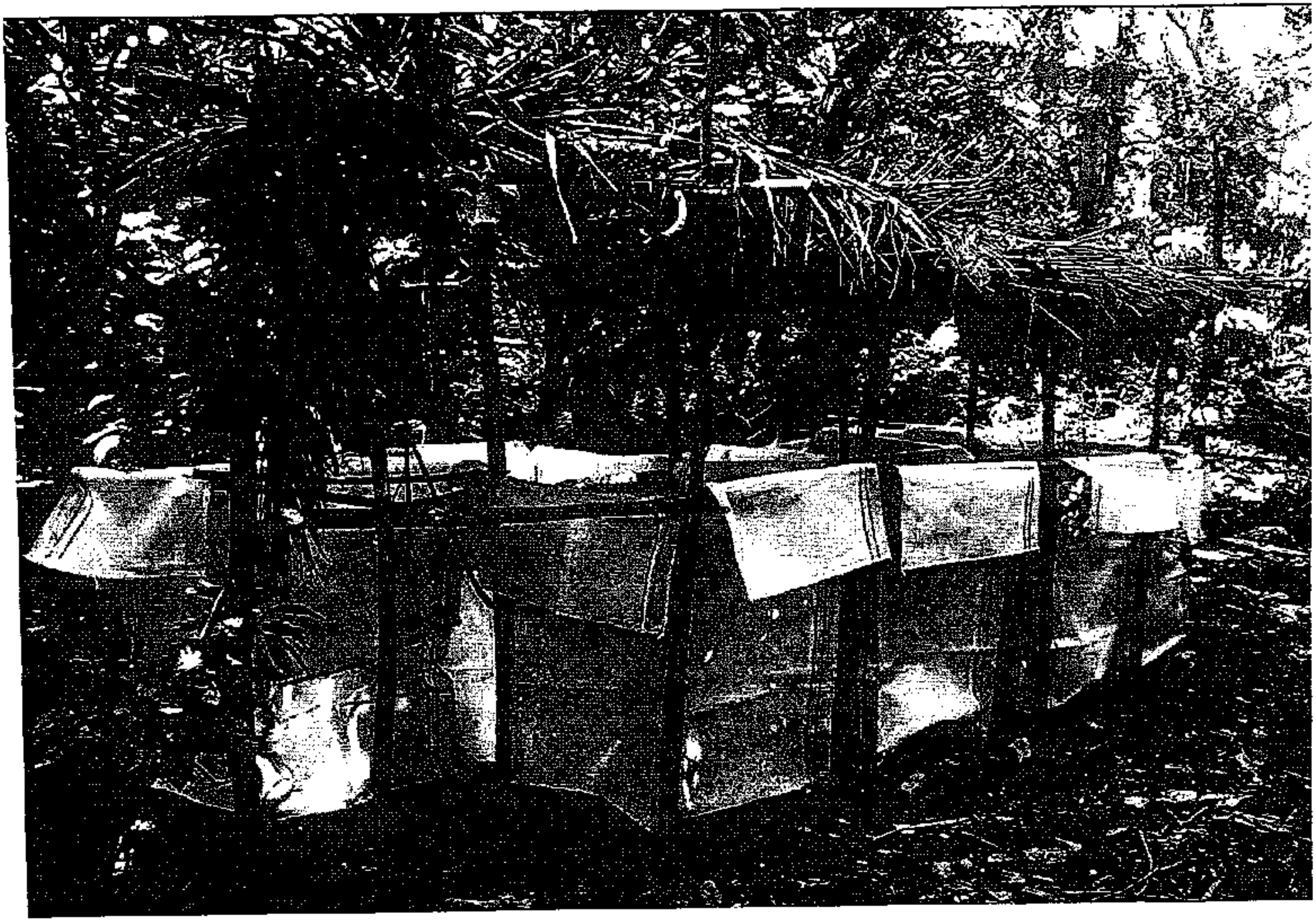


Plate 5. Outdoor arenas in which courting sea kraits were observed.

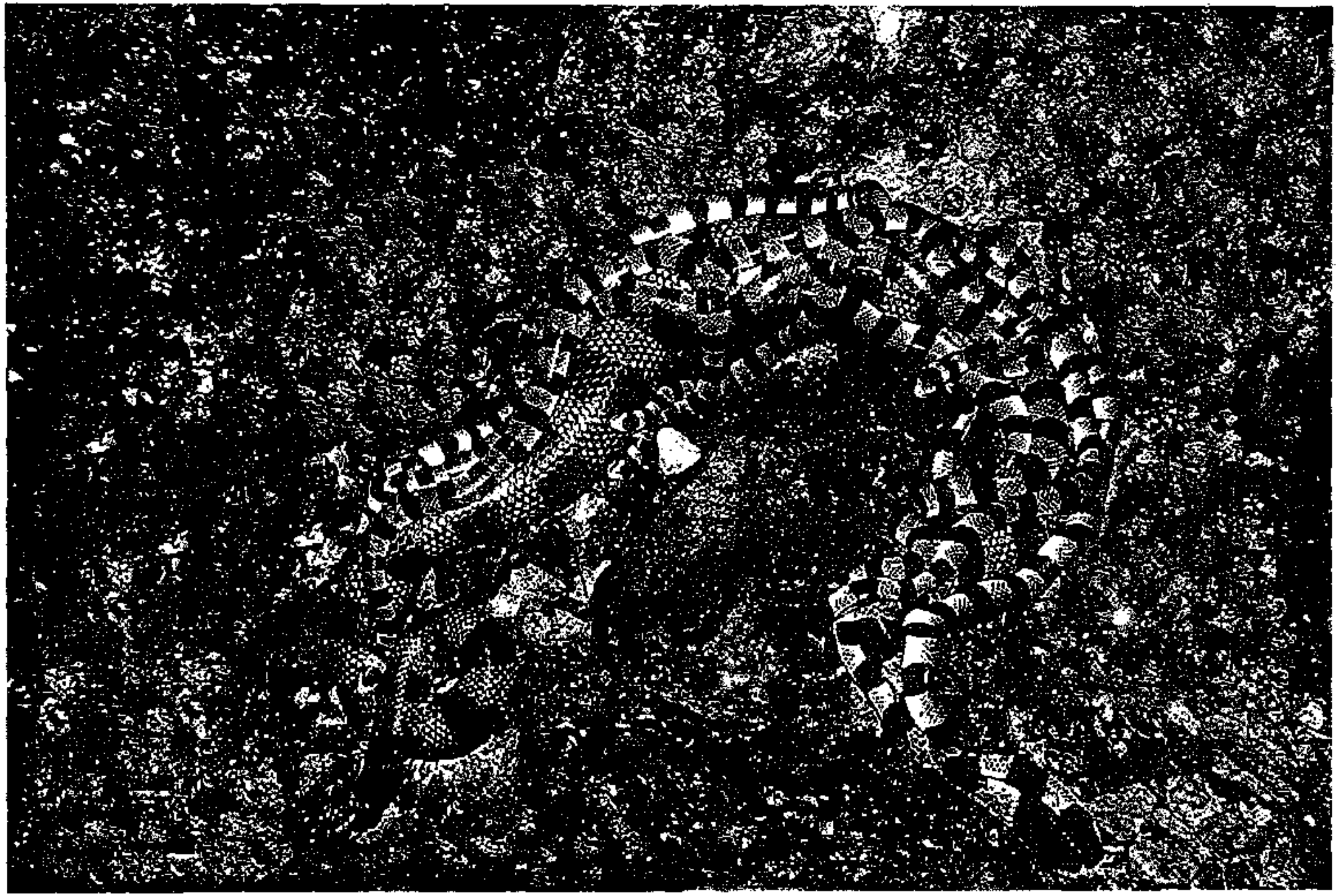


Plate 6. Courting groups in sea kraits range from one to nine males per female. This group has five males courting a female.

disturbance (see above). The snakes were then paint-marked to enable individual identification. After that, it took from 30 minutes to two hours for the snakes to settle down sufficiently to recommence courting. Preliminary observations revealed that the snakes were not distracted but chemical cues left in the enclosures by previous courting groups.

Courting groups from Mabualau Island were comprised of only one female and between one to nine males. Of the 57 groups used in my study, 51% were male and female pairs; 16% were made up of two males and a female; and groups with 3 to 9 males plus a female made up 33%.

All groups in enclosures were monitored every hour and the activity of each male was scored using the following index:

- 0 = not courting; no contact with female
- 1 = brief contact with female
- 2 = male body aligned with the female
- 3 = male actively courting female; (active courtship = intense twitching of a male's body when aligned over the female)
- 4 = copulating

Before any of the snakes were released, I measured the body size (SVL and mass), tail length, head length and head width of all snakes in each courting group.

Ten groups of randomly picked males and females were also placed in enclosures to compare the behaviour of these animals to those that were in courting groups when collected.

RESULTS

Description of courtship by yellow-lipped sea kraits

Although anecdotal notes about courting sea kraits are available from several authors, the most detailed observations to date on mating and courtship behaviour come from work by Guinea (1986) on Fijian sea kraits. Below, I will briefly summarise the reproductive behaviour of *Laticauda colubrina,* in terms of the three "typical" phases of snake courtship (Gillingham, 1987), based on my own observations and those of Guinea (1986).

The first phase, the "tactile-chase", involves the approach, chase and contact with females by male snakes. Guinea (1986) observed that around high tide, male sea kraits would swim around the reefs surrounding the island and upon detecting the point of exit by a female (presumably via chemical cues) would leave the water in pursuit of a female. This observation concurs with my own observations of sea kraits in the Andaman Islands and at Toberua Island (female tracks on the sand were accompanied by tracks of several males).

The second and third phases involve mounting, body alignment and courting ("tactile-alignment"), and the actual copulation ("intromission and coitus"), respectively. Upon locating a female sea krait, the males attempt to mount her. If the female is still moving, the males struggle to keep up with her. The female shows no overt response to the males' activities, except in some cases, when she returns to the sea. A receptive female lies motionless and allows the courting males to align their bodies with her own. Once aligned, the males begin rhythmic contractions with their bodies draped over the female's body. These rhythmic contractions by males do not fit the typical descriptions of male courtship in Gillingham's (1987) review. In many snake species, courting males are active constantly, and push their chins firmly against the female's body as they move forward and align with her. Males are in almost constant motion, and courtship lasts for a relatively brief period prior to coitus (e.g. Gillingham, 1987; Madsen et al., 1993). In strong contrast, courting groups of L. *colubrina* on Mabualau often remain in place for days rather than hours.

Most of the time, there was little movement to be seen in "courting" groups either in the field, or within the arenas during observation periods. Indeed, in 73% of these observations I recorded no overt activity by the snakes. The male snakes were aligned with the female's body for 21% of these observations. Actual courtship behaviour, such as a male twitching his body, was seen in only 2% of observations. My data from the arena trials indicate that the average duration of continuous intense courtship exhibited by males was 2.6 hours (SD = 1.8, n = 30). Guinea (1986) reported that the body spasms increased to about 23 per minute during the most intense courtship and copulation in *L. colubrina* lasted for only about 10 minutes, but, the 11 copulations that I observed averaged two hours in duration (range = 1 to 4 hours).

Courtship by male sea kraits not only progresses more slowly than in many other snake species, but it also does not include any overt interaction between rival males. Their non-aggressive nature during courtship is in accord with their remarkably tolerant approach to humans. Guinea (1986) pointed out the lack of reaction from courting male sea kraits to interference by a human observer. Upon release, the males simply resume whatever activity they were performing prior to handling.

What factors influence courtship intensity?

Plausibly, three different factors might interact to determine the intensity of courtship observed in any enclosure trial. Courtship might be more intense when: (a) the enclosure contained females that were particularly attractive; (b) the enclosure contained males that were particularly vigorous courters; and/or (c) environmental conditions at the time stimulated courtship activity.

To test which of these factors was likely to be important, I examined data on the trials where I included more than one female per arena. The advantage of this design is that I can compare the intensity of courtship directed to each female. If one female attracts significantly more male attention than the other, then I can conclude that females do indeed vary in attractiveness - and that this variation generates variance in overall courtship intensity. Because all natural courting groups in my study included only one female, I used the data from the randomly-selected groups (which comprised two females and at least two males) for this analysis. To test the hypothesis, I calculated the differential in courtship intensity directed to each of the females by each of the males. If males "agree" on which female is the more attractive, then we predict a positive correlation between these differential scores. That is, if male #1 directs much more courtship to female #1 than to female #2, we expect male #2 to show the same pattern. As expected, some females were significantly more attractive to males than others: the differential scores for the two males within each arena were significantly positively correlated ($r = 0.89$, $n = 14$, $P < 0.0001$).

This result suggests that at least part of the variation in courtship intensity among trials was due to differences in attractiveness among females. But, was this the only factor? Other variables (such as environmental conditions or levels of male arousal) might also generate variation in courtship intensity, independent of shifts in female attractiveness. To test for variation in courtship intensity independent of female attractiveness, we can compare the courtship intensity directed to each of the two females within the same enclosure during the same trial. If factors such as weather and male traits generate variation in courtship intensity, we expect to see that in trials where one female was strongly courted, we will also see intense courtship to the second female. As predicted by this hypothesis, average courtship intensities directed towards the two females in a group were significantly correlated ($r = 0.73$, $n = 113$, $P < 0.0001$). Thus, variation in courtship intensity among trials was a function of at least two effects. First, some females were more attractive than others. Second, some males and/or some environmental conditions resulted in more vigorous courtship. Below, I explore possible candidates for factors generating this variation.

What makes a female sea krait attractive to males?

Can we use the characteristics of female sea kraits that were courted by males in the field to provide an indication of which female traits stimulate courtship by males? This comparison relies upon the assumption that solitary females in the field are those that were less attractive to males. Alternatively, these solitary animals might simply not have been located by males, or have managed to escape from their attentions. To test the validity of this assumption, we can compare the intensity of courtship between the two types of groups in enclosures: that is, naturally occurring *versus* randomly-selected groups. If solitary females are indeed less attractive than courted females, then we should see a lower intensity of courtship in trials using the randomly-selected females.

As predicted, the intensity of courtship by males was significantly higher in naturally occurring courting groups than in the "randomly-selected" groups ($F_{1,1889} = 105.82$, $P < 0.0001$; Fig. 4.1). Courtship intensity among natural courting groups averaged 1.04 (SE = 0.02, n = 1622) on my scale of 0 to 4 (see above), whereas that of randomly selected individuals averaged 0.50 (SE = 0.04, n = 269). Hence, it is clear that males actively select among available females and court only a proportion of the adult female population at any one time.

What characteristics make one female sea krait more attractive than another? Females in naturally occurring groups were significantly larger than the randomly-selected females ($F_{1,70} = 19.53$, $P < 0.0001$; Fig. 4.2). The courted females were also in slightly, but not significantly, better body

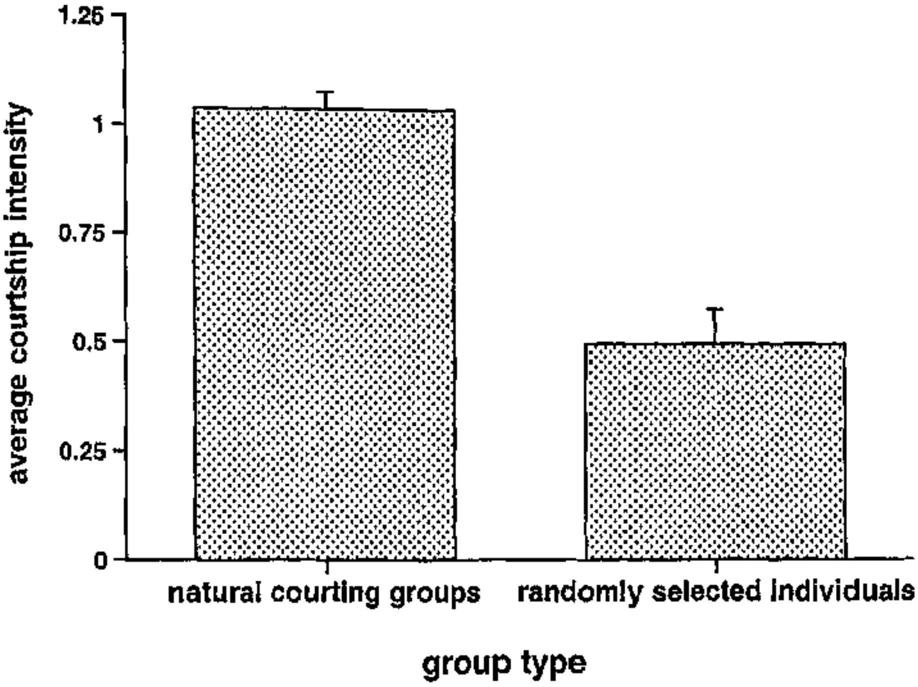


Figure 4.1 Mean courtship intensity of male sea kraits in natural and random groups (± 2 SE).

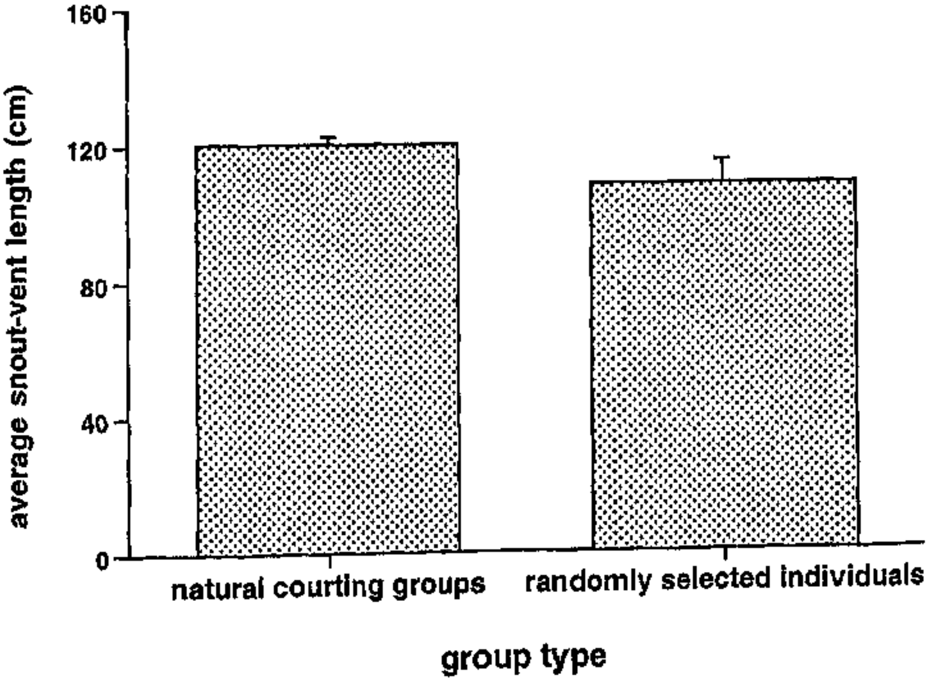


Figure 4.2 Average female body length in natural and random groups (± 2 SE).

condition than the solitary females (ANCOVA with SVL as covariate, *ln* mass as dependent variable: $F_{1,68} = 0.02$, $P = 0.91$).

We can ask the same question about males also. Were solitary males somehow different to the males in courting groups? However, my analysis does not support this idea. Mean body sizes of solitary males and courting males were similar ($F_{1,142} = 3.10$, $P = 0.08$). Indeed, the randomly-collected males averaged slightly larger than the natural courting group animals (means of 82.2 versus 84.0 cm SVL). The randomly-collected males were slightly more heavy-bodied (on average) than the males found in courting groups (heterogeneity of slopes $F_{1,140} = 4.41$, $P = 0.04$). Because of the significant differences between natural *versus* randomly-selected groups in traits such as female body size and male courtship intensity, all of my subsequent analyses (below) excluded data from the random groups.

What environmental factors stimulate sea krait courtship?

Environmental factors such as temperature and lunar cycles might plausibly affect courtship intensity, and so were used in the following analyses. For these analyses, I used the average courtship intensity of one randomly selected male from all naturally occurring groups. Thus, each group is represented by only one animal, to avoid pseudoreplication.

(a) Temperature

I tested for thermal effects on courtship intensity at two different temporal scales:

Across two-hour time periods within a day: There was little change in the courtship intensity of males due to temperature or time of day. Dividing the day into 12 two-hour periods, a one-factor ANCOVA with time period as the factor and temperature as the covariate detected no significant temporal or temperature-associated variation in the intensity of courtship ($F_{1,1608}$ = 0.47, P = 0.52 for temperature; $F_{11,1609}$ = 0.83, P = 0.61 for time period; Fig. 4.3).

Across two-week periods: To test if there was a change in courtship intensity through my study (i.e. seasonal effects), I divided the study period into two-week time periods. Interestingly, there were significant changes in the average courtship intensity of males through these two-week periods. A one-factor ANCOVA with the two-week period as the factor and temperature as the covariate revealed a significant interaction between the two-week period and temperature ($F_{3,1614}$ = 3.01, P = 0.03; Fig. 4.4). That is, the way in which ambient temperature influenced courtship intensity differed among the two-week periods. To investigate this relationship further I carried out a regression analysis between courtship intensity and temperature for each two-week period separately. This regression revealed a significant relationship between ambient temperature and courtship intensity during the first two weeks of November ($F_{1,720}$ = 11.18, P = 0.0009), but not during any other two-week time period.

(b) Lunar cycles

Courtship intensity showed significant temporal variation relative to lunar periodicity (one-factor ANOVA with absolute time from nearest full moon as

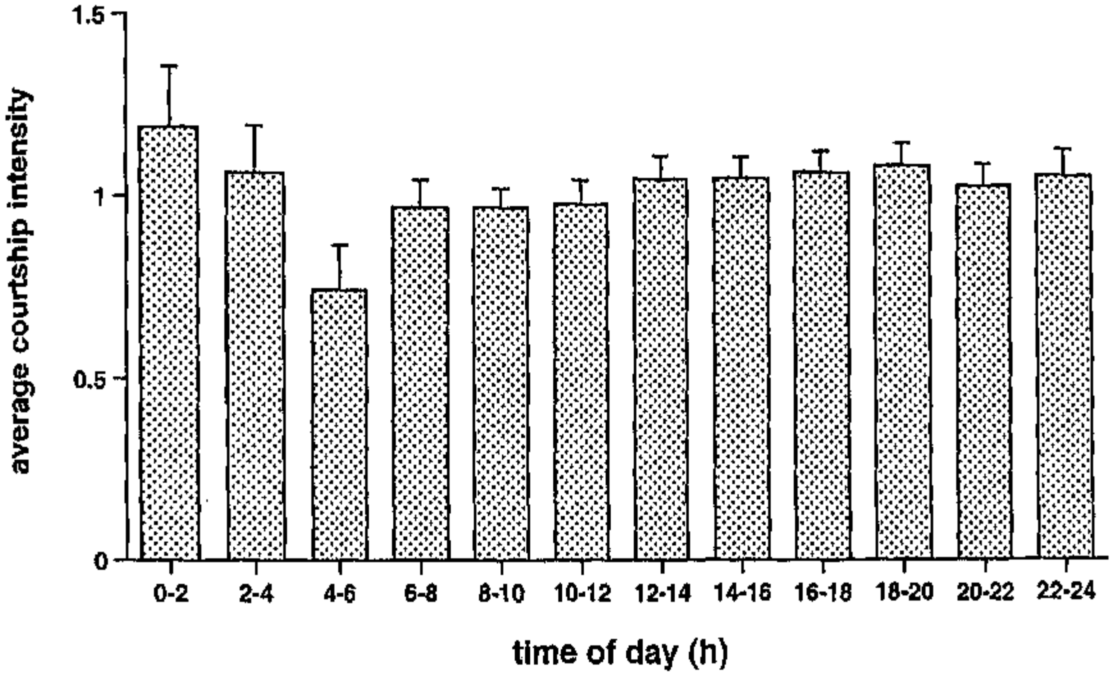


Figure 4.3 Variation in courtship intensity of male sea kraits through the day (± SE).

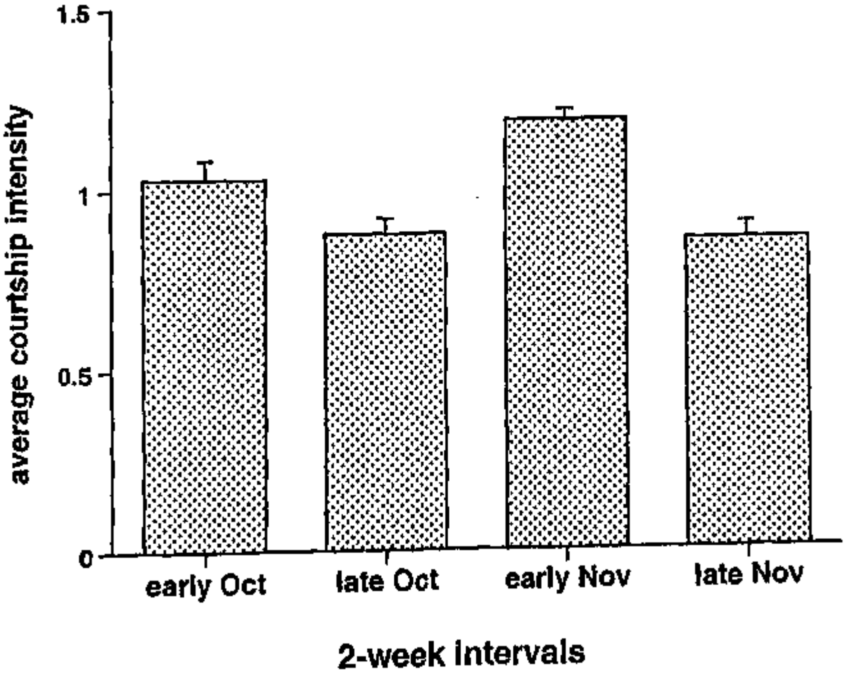


Figure 4.4 Variation in courtship intensity of male sea kraits through the study period (± SE).

the factor, $F_{14, 1607} = 9.32$, $P < 0.0001$). Visual inspection of these data however shows no clear pattern (Fig. 4.5).

What biological factors stimulate sea krait courtship?

For this set of analyses, I calculated mean values of courtship intensity for all males within a single trial. Thus, the trial rather than the male was the unit of replication.

(a) Group size

Group size was incorporated in the analyses in terms of Operational Sex Ratio (OSR) which is the ratio of fertilisable females to sexually active males (Emlen and Oring, 1977). There was no significant correlation between the OSR and average intensity of courtship per trial ($r = 0.12$, $Z = 0.9$, $P = 0.40$). That is, large groups did not consistently display more or less intense courtship than did smaller groups.

(b) Body sizes of females and courting males

The average intensity of courtship per trial was significantly correlated with the body size of the female in that trial, but not with the female's body condition, the mean body sizes of the males within the group, or the number of males per group. Larger females attracted more courtship ($r = 0.34$, $n = 55$, $P = 0.01$; see Fig. 4.6). However, groups of larger males did not court more or less vigorously (mean male SVL *versus* intensity of courtship: $r = 0.10$, $n = 58$, $P = 0.50$).

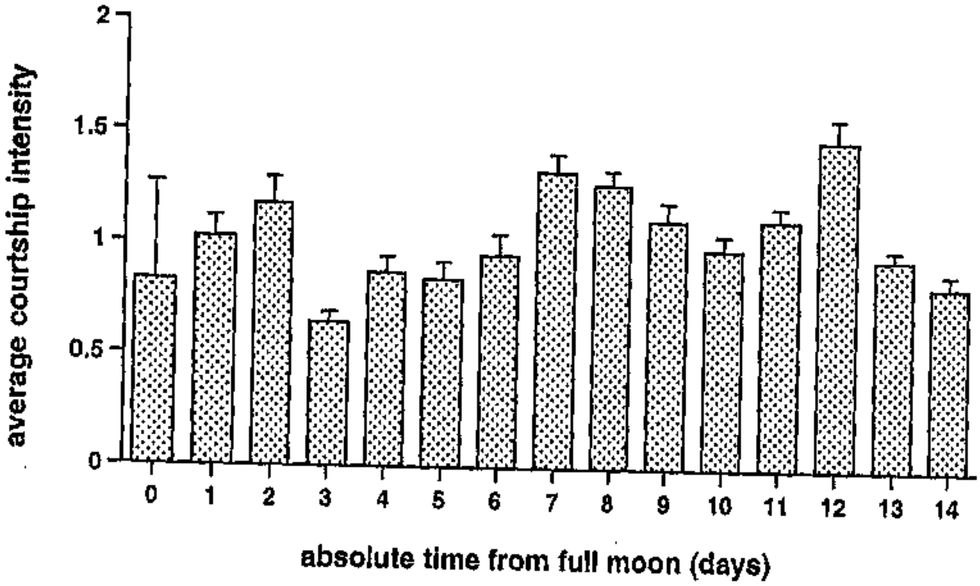


Figure 4.5 Change in courtship intensity of male sea kraits as a function of the lunar cycle (± SE).

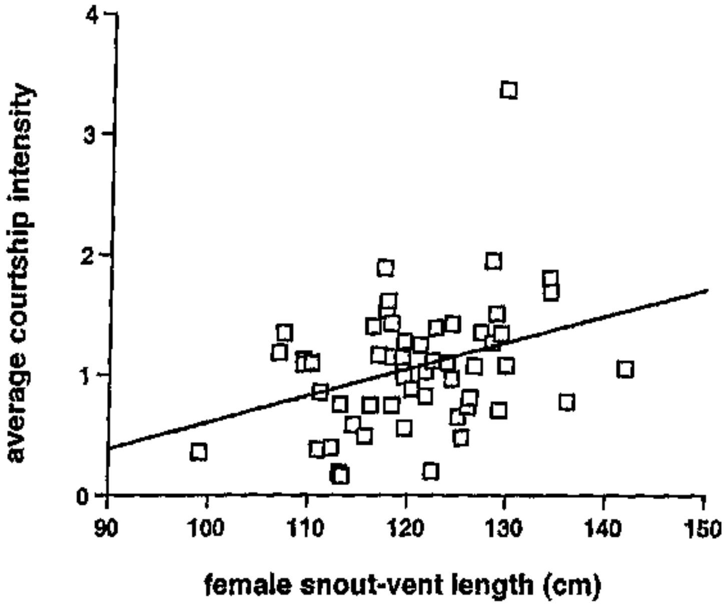


Figure 4.6 Average courtship intensity of males towards females of different sizes.

In garter snakes, the intensity of courtship depends not only on the body sizes of males and females, but also on the body sizes of males relative to females (Shine et al., unpubl.). That is, larger males tend to court larger females. I looked for the same effect in sea kraits, but found no evidence of it. The body size of a female was not correlated with the sizes of the males found courting her ($r = 0.006$, $n = 58$, $P = 0.96$). I also examined data on the intensity of courtship in arena trials. I divided males into two size classes based on their body lengths (SVLs < or > 85 cm) and females into three classes (< 115, 115-125, and > 125 cm SVL). I then used male size class and female size class as categorical variables in a two-factor ANOVA with courtship intensity as the dependent variable. As expected from the analyses above, larger females attracted more intense courtship ($F_{2,52} = 3.64$, $P = 0.03$). However, male body size did not affect courtship intensity ($F_{1,52} = 0.0002$, $P = 0.99$). More importantly, there was no significant interaction between body sizes of males and females in this respect ($F_{2,52} = 1.76$, $P = 0.18$).

(c) Feeding status of females

Female snakes with noticeably distended stomachs (an indication of having consumed prey recently) were often seen in the wild being courted intensely by males. I wanted to test if there was a difference in the intensity of courtship between these (fed) females *versus* females that had not fed recently. Some of the females in enclosure trials had eaten recently whereas others had not. A one-factor ANOVA with feeding status of females as the factor revealed no significant difference in the average courtship intensity directed to fed *versus* unfed females ($F_{1,52} = 0.59$, $P = 0.45$; Fig. 4.7). The same

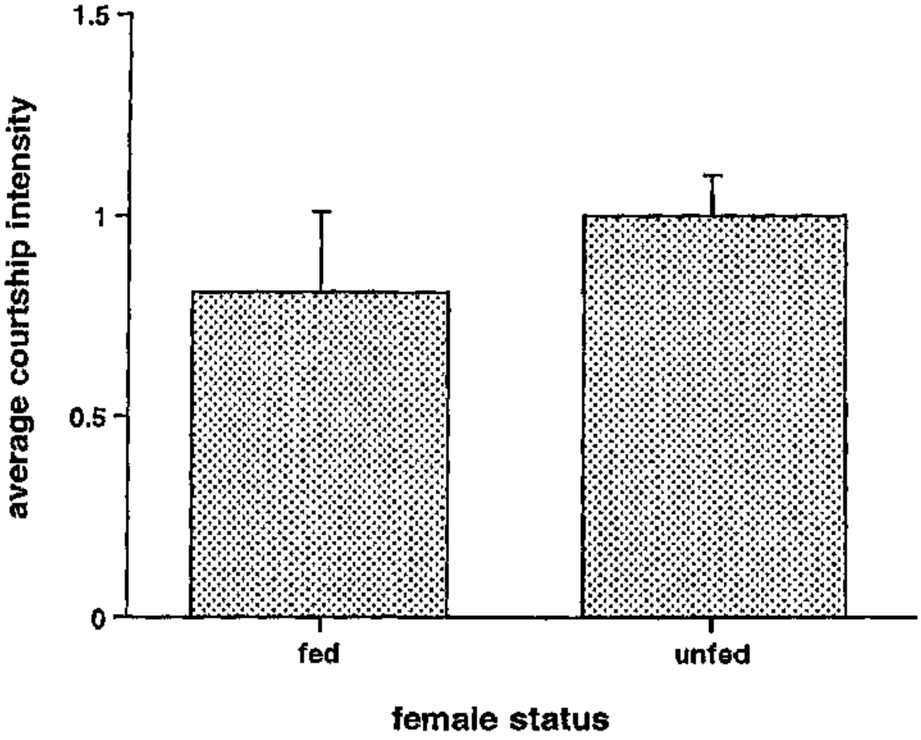


Figure 4.7 Comparison of courtship intensity towards female sea kraits that had recently eaten and those that had not fed (± SE).

result was obtained in an ANCOVA, after removing the effect of female body size (see above).

What traits determine male mating success?

In the enclosure trials, males that achieved copulation were not significantly larger or smaller than males which failed to obtain a mating ($F_{1,113} = 0.56$, $P = 0.45$ for males; Fig. 4.8). The same was true for male body condition (mass relative to SVL: $F_{1,139} = 1.81$, $P = 0.18$). These results do not reveal any clear link between a male's phenotype and his mating success.

My data also suggest that a female's body size did not affect whether or not she mated (Fig. 4.8; $F_{1,53} = 0.54$, $P = 0.47$). I did not detect any tendency to size-assortative mating (SVLs of females that copulated *versus* SVLs of the males they mated with: $r = -0.01$, $n = 11$, $P = 0.44$).

DISCUSSION

My data support and extend previous reports on reproductive behaviour in yellow-lipped sea kraits. My observations are broadly consistent with previous descriptions of this behaviour, but enable me to examine the topic in more detail than has been possible in prior studies.

Courtship behaviour has been described in detail in several snake species, primarily terrestrial colubrids and viperids from the Northern Hemisphere (Klauber, 1956; Carpenter and Ferguson, 1977; Andren, 1986;

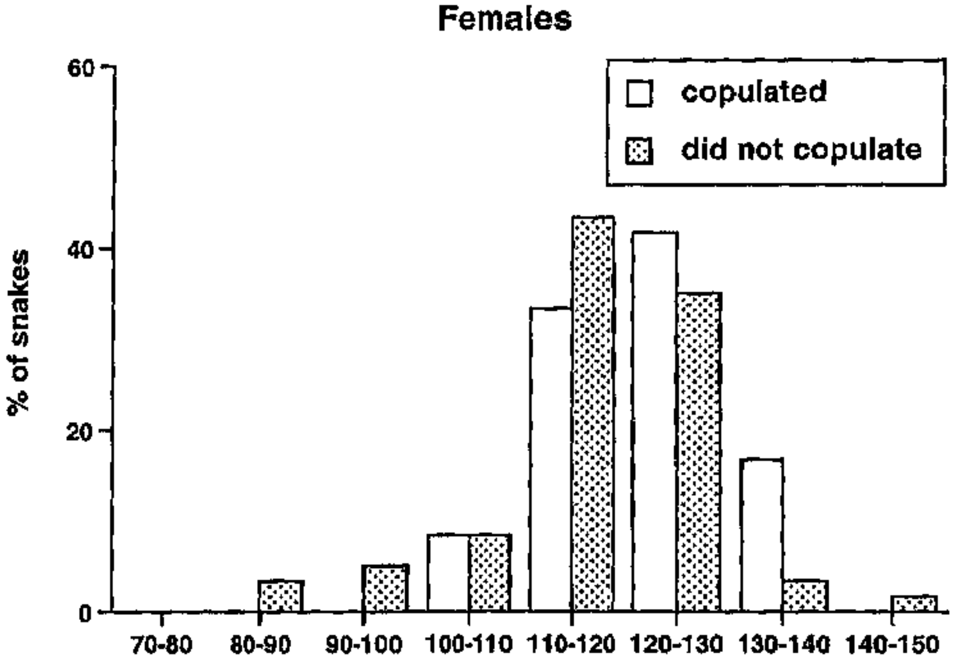


Figure 4.8 Size distributions of male and female sea kraits that copulated and those that did not.

Carpenter, 1986). Broad similarities in the form of courtship have encouraged the development of general schemes to summarise the major phenomena involved (Gillingham, 1987). However, it is important to recognise (as did Gillingham) that only a small proportion of all snake species have been studied in this respect, and that these comprise a highly non-random assemblage in terms of geographic distribution, phylogenetic relationships and habitat types. The limited data available on other kinds of snakes suggest that courtship behaviour may be substantially more diverse than is apparent from published literature. For example, tropical aquatic proteroglyphous species are virtually unstudied, and anecdotal reports (e.g. Guinea, 1996 for the hydrophiid *Emydocephalus annulatus*) indicate that courtship may take quite different forms than it does in the more intensively-studied North American and European terrestrial snake fauna.

My studies, in combination with those of previous workers, indicate that courtship in *Laticauda colubrina* differs in important ways from that in the so-called "typical" snake scenario outlined by Gillingham (1987). Below, I briefly review some of the general features of sea krait courtship, emphasising firstly the attributes they share with other snakes, and then the attributes that differ.

One clear theme in snake courtship is a reliance on pheromonal communication (e.g. Kubie et al., 1978; Gartska et al., 1982; Ford and Low, 1984; Mason and Crews, 1985; Mason, 1992). The marine environment may pose special difficulties in this respect - certainly, it is hard to imagine scent trails being followed as easily as they can be in terrestrial systems. Nonetheless, it is likely that male sea kraits do indeed rely upon pheromonal cues during courtship. Observations of frequent tongue-flicking by males pursuing females strongly suggest a role for external chemical cues in sex recognition. Experimental investigation of this aspect of sea krait biology, along the same lines as pursued successfully in other snake lineages (e.g. Mason, 1992; Weldon et al., 1992) would be of great interest.

Another aspect of sea krait reproductive behaviour that resembles the situation seen in other snake taxa is the general demeanour of the two sexes. Males pursue females rather than vice versa. Some males devote very substantial time and energy to these activities, despite the low frequency of overt courtship in arena trials. For example, I watched two males in pursuit of a female, following her around for more than two hours (Plate 7).

Males essentially ignore the presence of their rivals (but see below) and focus instead on aligning their body with that of the female, in a position such that they can insert a hemipenis if the female elevates her tail to open the cloaca. A tendency for females to grow much larger than conspecific males, and for males of such species to engage in "scramble" competition rather than ritualised combat, is widespread in snakes (Shine, 1994).

Nonetheless, the behaviours exhibited by male sea kraits during courtship differ in significant ways from those reported in other snakes. Most notably, courting males are frequently inactive (simply lying draped over the female), and the only sign of activity is a spasmodic twitching of the male's body. These spasms are similar to the twitching of brooding pythons to regulate egg temperatures, but more intense. At the peak of courtship these spasms become more frequent and intense - so much so that the male's

Plate 7. The first phase in the courtship of sea kraits, the "tactile-chase", involves male snakes approaching, following and contacting females.

body almost lifts part of the (much larger) female's body off the ground. Another interesting aspect to this behaviour is that, although a female is often accompanied by more than one male (true for 47% of the groups observed in my own study; Plate 6), it is rare to see two males simultaneously engaged in this spasmodic twitching. Instead, they appear to take turns in this respect. On only one occasion did I see two males actively courting the same female simultaneously. In the other cases when one male was actively courting the female, the other males in the continued to maintain contact or remain aligned with the female's body.

As noted above, females rarely showed any overt response to courtship by males. However, any movement by the female (especially tail-waving) generally induced a vigorous response from males. When the females waved their tails about, males persistently tried to maintain tail alignment.

The above observations suggest that males may use a variety of strategies during courtship. Some males attempt to stimulate females while others are opportunistic and wait. When ready to copulate (either in response to male stimulation or other unknown reasons), females signal the males by waving their tails. This "tail-waving" by the female may involve cloacal gaping, and is probably necessary for intromission (Gillingham, 1979; Schuett, 1986). Males that detect this signal and rapidly align their cloaca with that of the female succeed in copulating. Clearly, more detailed observations are needed to test these speculations. Since these processes are extremely slow (courting males were only active for 6% of the times they were observed), such a test would require continuous and intensive observations over considerable lengths of time. Time-lapse videophotography might well facilitate such a study.

The only clear determinant of a female sea krait's attractiveness to males (as indicated by the intensity of courtship directed to her) was her body size. Snout-vent length was the best predictor in this sense, rather than mass relative to length. In at least one other snake species (the garter snake *Thamnophis sirtalis*), males prefer not only larger females, but also more heavy-bodied females (Hawley and Aleksiuk, 1975; Hawley and Aleksiuk, 1976; Luiselli, 1996). In sea kraits, males that selected females based on relative body mass would be likely to spend their time courting females that had recently ingested eels. The distension of the body caused by a large prey item is much greater than the normal range of variation in condition seen among unfed females (pers. obs.). Thus, body size rather than body shape may provide the best indication of the probability that a female will mate. In many snake species, the frequency of reproduction increases with maternal body size (Seigel and Ford, 1987), but we do not know if this is the case with *L. colubrina*.

Environmental factors such as temperature, time of day and month may also influence the intensity of courtship. Previous studies by Guinea (1986) had shown that courtship is seasonal within Fijian populations of *L. colubrina*. In keeping with these reports, courtship and copulation occurred more frequently in November than earlier during my fieldwork. Both courtship and copulation occurred over a relatively broad temperature range (23 - 29°C) and peaked between 25 and 26°C (Fig. 4.9). Although the frequency of courtship was high during the afternoon and night, most

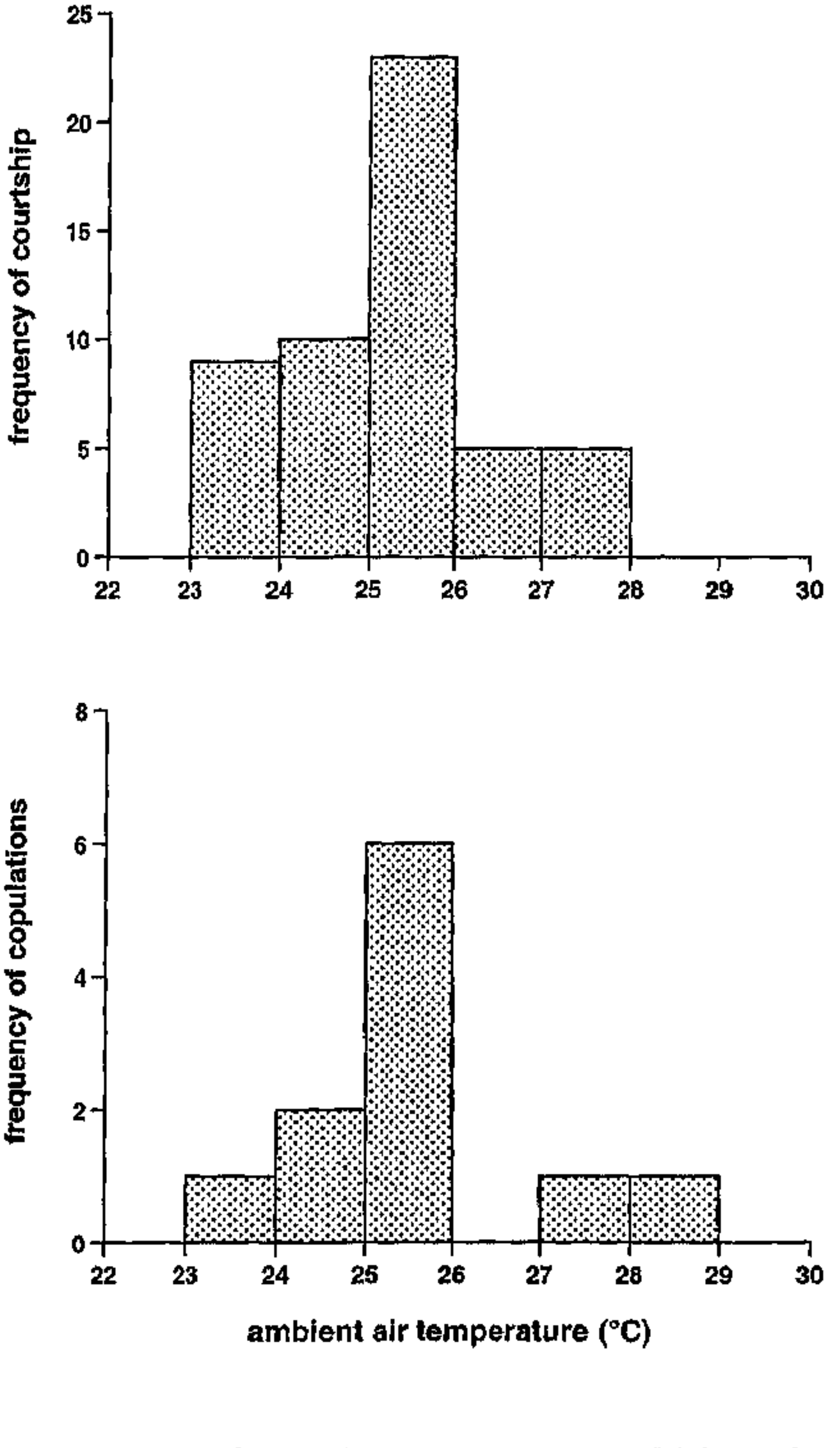


Figure 4.9 Ambient air temperatures at which sea kraits on Mabualau Island courted and copulated.

copulations occurred at night (Fig. 4.10). The field surveys undertaken during 1998 (Chapter 3) revealed a different pattern to that seen in the enclosure trials. From my surveys, courtship was recorded more frequently in the morning. However, in the arenas, courtship occurred more often in the afternoon and at night. This comparison is confounded by year, as the observations were conducted during different field seasons (even though the environmental conditions were broadly similar during these two years). The most likely reason for the difference in daily timing of courtship is that snakes were more visible in the field during the morning, before they had moved under shade. Thus, courting behaviour may have been more obvious then, even if it was less frequent than during the afternoon. The enclosure studies overcome this bias in observability, and demonstrate the advantages of conducting observations under controlled conditions.

When the study period was divided into two-week time periods, the frequency of courtship was highest during the first two weeks of October and November, but the number of copulations was highest during November. These differences may be weather-dependent. Visual comparison between these graphs and the temperature graphs (see Figs. 3.10 and 3.11 in Chapter 3) shows that the maximum temperatures were higher in November than in October. Also, the dates when copulations occurred in the arenas (for e.g. 8th, 15th and 25th October 1999; Fig. 3.10 in Chapter 3) were followed by a marked decrease in maximum temperatures (rainy days).

Lastly, my study provided information on the phenotypic traits of male sea kraits that obtained copulations compared to those that did not. No consistent differences were found between these two groups of snakes: the

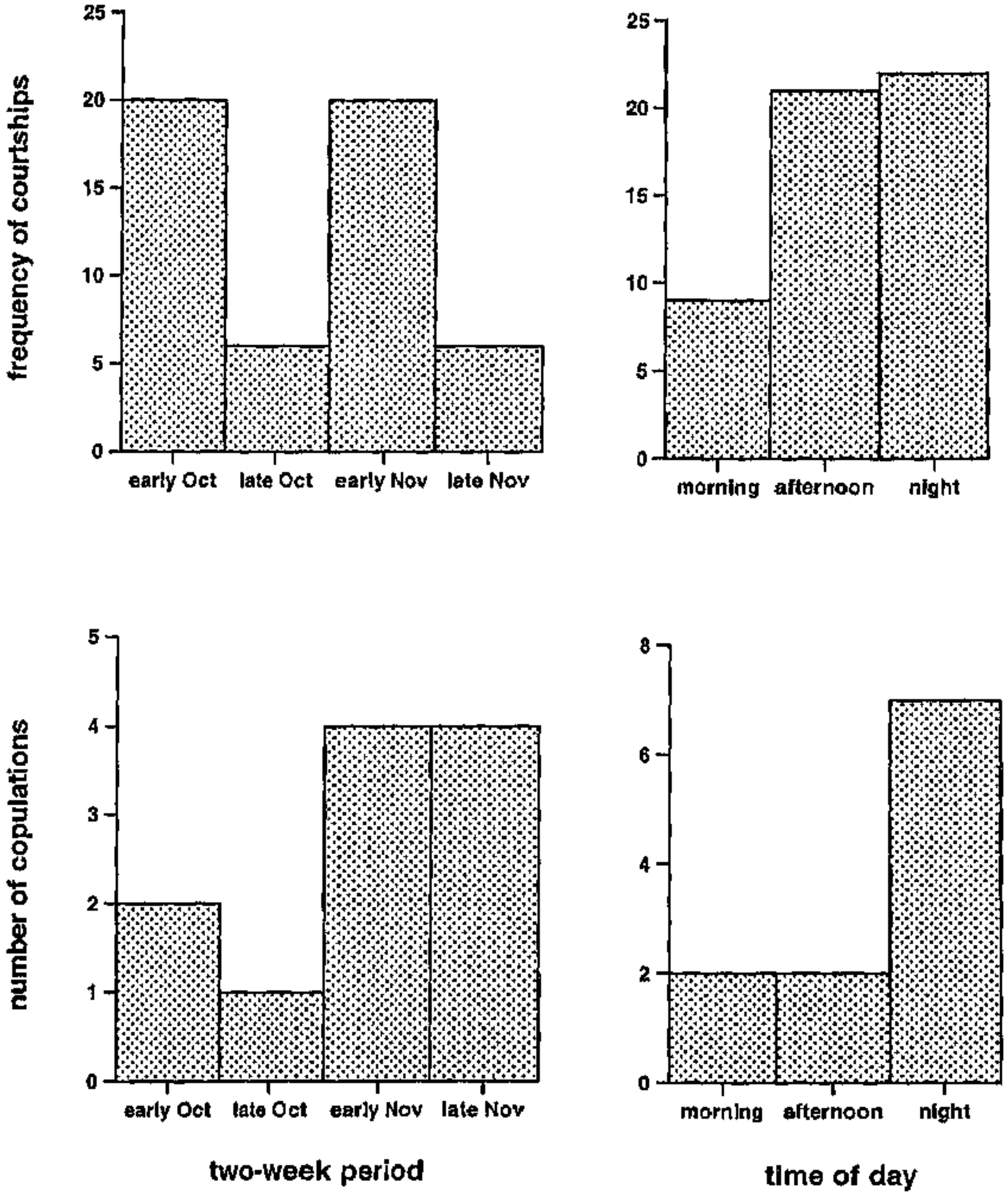


Figure 4.10 The frequency of courtship and the number of copulations in sea kraits, across time of day and across two-week periods through the study.

males that mated were no longer or fatter than those that did not succeed in doing so. Previous studies on snakes have examined the question of body-size advantages in different types of mating systems. In snake species that display ritualised male-male combat, several studies suggest that larger males typically win the battles and thus, obtain more matings (Duvall et al., 1992; Madsen et al., 1993; Duvall et al., 1993). In contrast, male body size may have less relevance to mating success in species where males do not physically battle with each other for mating opportunities. Although the latter proposition seems plausible, and successfully predicts general patterns of sexual size dimorphism compared to mating systems within snakes (Shine, 1978, 1994), empirical data are scarce. An experimental study using outdoor arenas similar to my own, concluded that male body size did not influence mating success in garter snakes (Joy and Crews, 1988). However, a more recent and comprehensive study on exactly the same population came to the opposite conclusion (Shine et al., 2000a). Experimental studies on European grass snakes, *Natrix natrix* (another species with "scramble" competition rather than male-male combat) similarly reveal subtle but significant mating advantages to larger males (Madsen and Shine, 1993a; Luiselli, 1996).

My data are thus somewhat unusual in displaying no effect of male body size on mating success. My sample size is relatively low for mated males, but the general observations of courtship behaviour fit well with the lack of a size advantage. Unlike courting garter snakes or grass snakes, male sea kraits do not engage in vigorous tail-wrestling matches, nor push strongly against the bodies of rival males as they attempt to maintain their position on the female. Thus, the greater strength of larger males does not seem likely to play any role in determining mating success. A similar lack of body-size effect on male success has been reported in another aquatic snake species, *Acrochordus arafurae*, which likewise does not appear to display physical struggles among rival males within mating aggregations (Shine, 1986).

CHAPTER 5. LOCOMOTOR ABILITIES

INTRODUCTION

Most phylogenetic lineages of organisms are conservative in terms of habitat use, but some groups display major shifts in this trait. Some of the most spectacular examples of such phylogenetic shifts involve the invasion of aquatic (especially, marine) habitats by terrestrial taxa. Because of the very different physical properties of air *versus* water, selective pressures for effective locomotion can generate massive morphological divergences. Thus, for example, whales, seals and dolphins superficially resemble fish rather than terrestrial mammals in their general body form. Such changes almost inevitably compromise locomotor performance in the ancestral environment: whales cannot move about on land, and penguins cannot fly. Multiple invasions of oceanic habitats by terrestrial organisms thus provide an excellent opportunity to investigate the process of adaptation in general, and the nature and magnitude of tradeoffs involved in adaptive shifts between alternative modes of locomotion.

Among reptiles, phylogenetic shifts between aquatic and terrestrial habits have occurred independently within the turtles, crocodilians and squamates (Porter, 1972). One group of particular interest in this respect are the snakes, because this lineage (unlike their sister taxon, the lizards) has displayed exceptional lability in evolving to exploit aquatic *versus* terrestrial environments. Independent invasions from the land to the oceans have occurred within the ancestors of present-day acrochordids, homalopsines, natricines, hydrophiids, and laticaudids (Greene, 1997; Heatwole, 1999). Two of these lineages (the "sea snakes", a polyphyletic group comprising laticaudids and hydrophiids) display highly convergent morphological adaptations for aquatic locomotion, most notably the evolution of a flattened paddle-like tail (Heatwole, 1999).

Terrestrial locomotor ability has clearly been compromised by such shifts, to the extent that some laticaudids and all hydrophiids are virtually unable to crawl about on dry land (Dunson and Minton, 1978; Greer, 1997). Biomechanical analyses of snake locomotion suggest a reason for this effect. Despite their superficial similarity, swimming and crawling in snakes differ in many ways (Cundall, 1987). In terrestrial lateral undulatory locomotion, the propulsive forces are generated by the lateral surfaces of the body as they push against irregularities in the substrate. In contrast, a swimming snake moves forward by accelerating portions of the surrounding water; the reaction to this effect produces progression (Gans, 1975). Thus, morphological adaptations for effective swimming are likely to reduce terrestrial locomotor ability, and vice versa (Jayne, 1985; Cundall, 1987).

Laticaudid sea snakes offer a unique opportunity to clarify the ways in which locomotor abilities shift during the invasion of a novel habitat. In most other lineages, the transition to marine life has been complete, such that there is no longer any effective selection on terrestrial locomotion. Thus, all we can compare are the endpoints of adaptation to either medium. Ideally, the tradeoff between aquatic and terrestrial locomotion would be revealed more clearly with an organism that retained the need to move about both on land and in the water. Laticaudid snakes fall into this category. Although they possess many of the marine adaptations of "true" sea snakes (hydrophiids), such as valvular nostrils, salt glands and paddle-like tails, the laticaudid "sea kraits" are still tied to land for many of their activities. They are oviparous, and hence the females need to crawl on land to find oviposition sites. Also, they return to land to slough their skins, digest their food, and mate (Saint Girons, 1964; Pernetta, 1977; Guinea, 1986; Heatwole, 1999). Telemetric studies suggest that adults of one species (*L. colubrina*) spend about half their time in the ocean, and the other half on land (Chapter 3).

Not only do laticaudids represent an intermediate stage in the balance between aquatic *versus* terrestrial life, but sub-groups within the population may also differ in the degree to which they depend on either type of habitat. For example, juvenile *L. colubrina* are largely restricted to the water and to areas of land immediately adjacent to water (Guinea, 1986; Chapter 3.). Adults of both sexes spend similar amounts of time on land, but mate-searching males move about much more actively on land than do females, and hence may be under much stronger selection for effective terrestrial locomotion. Although we have no data on movements in the ocean, adult female *Laticauda* eat large (deep-water) eels whereas males and juveniles eat small (shallow-water) eels (Pernetta, 1977). Thus, females may be under more intense selection for effective aquatic locomotion.

Although several authors have commented on the locomotor abilities of laticaudids (e.g. Guinea, 1986; Greer, 1997), there appears to have been no previous quantitative study on this topic. Thus, I conducted this component of the study collaboratively with my supervisor, Professor Richard Shine. We gathered data on speeds of sea kraits in water and on land to address the following questions:

(1) How has locomotor ability shifted with the invasion of the oceans? That is, how quickly do sea kraits swim and crawl compared to the ancestral forms that first adopted marine habits? To address this question, we measured locomotor speeds of three species of terrestrial elapids, for comparison with *Laticauda*.

(2) Do locomotor speeds of sea kraits depend upon sex or body size and if so, do these effects differ between land and water? To address this question, we measured locomotor speeds in sea kraits of both sexes, over a wide range of body sizes.

(3) Does feeding compromise locomotor speed? Studies on terrestrial garter snakes have revealed that a full stomach decreases locomotor speeds (Garland, 1983; Ford and Shuttlesworth, 1986). Differential sensitivity of aquatic *versus* terrestrial locomotion in this respect might explain why sea kraits return to land after feeding (e.g. Saint Girons, 1964). To address this question, we compared speeds of snakes that did or did not contain freshly-ingested prey items.

METHODS

We measured locomotor speeds of snakes using a wooden raceway 2.5 m long and 27 cm wide, with side-walls cm 25 high. The top of the raceway was open, allowing us to film snakes from above as they moved along the track. The rough wooden floor of the raceway was covered in gravel (glued to the wood) and sand, providing traction for snakes during the terrestrial trials. For trials of swimming speed, we simply submerged the entire raceway to a depth of 20 cm in the ocean (for sea snakes), or used a concrete pool filled with freshwater (for terrestrial snakes).

A snake was placed at one end of the raceway and encouraged to move along it by vigorously tapping its tail. Each snake was "run" two or three times in quick succession, then allowed to rest for at least 60 minutes prior to its next trial. Half of the snakes were first tested in aquatic trials, whereas the others were first tested with terrestrial trials. Body temperatures of a sample of snakes (n = 40) were taken immediately before and after trials, to determine whether or not snakes changed appreciably in temperature during the trial. A quick-registering electronic thermometer, inserted 1 cm into the cloaca, was used for this purpose, and also to measure water and air temperatures during the trials. At the end of the snake's second trial, we measured its snout-vent length (SVL) and mass, determined its sex (by manual eversion of hemipenes) and palpated the animal for evidence of recent feeding (prey in the gut).

Throughout each trial, we filmed snakes from directly above the raceway using a Sony TRV46E (Hi8) video camera. Lines marked at 50 cm intervals along the floor and sides of the raceway enabled us to determine the time taken for the snake to move across each 50 cm segment. The video was transferred to U-matic tape for analysis in a Sony U-matic Editing Control Unit (RMU50CE). From these tapes, we determined the mean speed for each snake, and its fastest speed over any 50 cm segment of the raceway. Our analysis deals with these numbers directly, as well as with the same data transformed into body lengths travelled (SVLs) per second rather than metres per second. This latter variable may offer a more robust measure of locomotor performance than the raw data, and be a better indicator of the snakes' ability to evade predation (Van Damme and Van Doren, 1999).

We conducted two sets of trials, as follows:

(1) We measured locomotor speeds of recently-captured *Laticauda colubrina* on Mabualau Island. The snakes had all been captured within two days of the trials, and were kept in shaded open-topped enclosures (1 x 1 x 1 m) during the intervening period. The locomotor trials were conducted over a three-day period (30th August to 1st September 1999), with air temperatures ranging from 25.3 to 28.6°C and water temperatures from 26.4 to 27.0°C. Resampling of body temperatures before and after trials showed that all snakes exhibited temperatures within the range 26.8 to 29.0°C, and that body temperatures of snakes did not change by > 1°C during any given trial. All snakes were released at the conclusion of the trials.

(2) Three species of terrestrial elapids from mainland Australia were run on an identically-sized raceway using the same methods. These comprised five eastern tiger snakes (*Notechis scutatus*), three black snakes (*Pseudechis porphyriacus*), and three swamp snakes (*Hemiaspis signata*). All three species are most abundant in swamps, marshes and riparian habitats, and frequently enter the water to forage and to escape from predators (Shine, 1977, 1987a,b). The specimens used were captive snakes held at a local Reptile Park. The tiger snakes came from western Victoria, whereas the black snakes and swamp snakes were from the Gosford area (coastal NSW). Air temperature during the trials (all conducted on 23rd February 2000) ranged from 25.4 to

28.0°C, and water temperature was 22°C. Body temperatures of snakes ranged from 25.6 to 29.3°C, and did not shift by > 2°C during a trial.

RESULTS

Throughout our analyses, locomotor speeds over both the distances that we assessed (mean speed over 1 m, and fastest [burst] speed over 50 cm) showed very similar patterns. We first compare our results for terrestrial elapids with those for *Laticauda colubrina* overall, and then analyse the data on sea kraits in more detail to examine effects of sex, body size and recent feeding on locomotor speeds.

Locomotor performance of terrestrial elapids relative to *Laticauda colubrina*

The 11 individuals of the three species of terrestrial elapids were similar to the 84 sea kraits in average body sizes (mean SVLs = 89.5 *versus* 82.0 cm, respectively: $F_{1,93} = 0.69$, $P = 0.41$). Because of this similarity in size, comparisons between the two groups of snakes are affected only slightly by whether we calculate speeds in absolute speeds (m/sec) *versus* relative terms (body lengths/sec). For simplicity, we use the latter measure in the analyses below. Both the sea kraits and the terrestrial elapids moved faster in water than on land (see next section for analyses of sea kraits). For the elapids, we used each individual as a separate data point rather than nesting them within species (so n = 11). A repeated-measures ANOVA on elapids showed that (like sea kraits) they were faster in water than on land (for average speed: $F_{1,9} = 16.98$, $P = 0.003$; for fastest speed: $F_{1,9} = 14.41$, $P = 0.004$).

However, this difference was less than in the sea kraits (approx. 50%, *versus* 450% in *Laticauda;* see Fig. 5.1). To compare these two groups of snakes statistically, we used one-factor repeated-measures ANOVA with the factor being snake type (terrestrial/aquatic) and the repeated measure being trial substrate (land/water). This test yielded a significant interaction term (for average speed: $F_{1,92} = 26.67$, $P = 0.0001$; for fastest speed: $F_{1,92} = 39.16$, $P = 0.0001$). That is, sea kraits were slower on land than were terrestrial elapids, but faster in the water.

Locomotor performance of *Laticauda colubrina*

We obtained data on the locomotor performance of *L. colubrina* of both sexes, and spanning a wide range of body sizes (35 to 131 cm SVL). As noted above, sea kraits swam more rapidly than they crawled. This result held true for both sexes, but males and females differed in their relative speeds on land *versus* in the water (Fig. 5.2). To analyse these data, we used a one-factor repeated-measures ANOVA with sex as the factor, substrate (land/water) as the repeated measure, and locomotor speed as the dependent variable. This analysis revealed a significant interaction between sex and substrate type both for mean speed ($F_{1,82} = 12.36$, $P = 0.0007$) and for fastest speed ($F_{1,82} = 8.45$, $P = 0.005$). When we analysed the data for each substrate separately, male sea kraits exceeded females in the average speeds at which they swam ($F_{1,82} = 12.59$, $P = 0.001$) and crawled ($F_{1,82} = 7.48$, $P = 0.008$). In terms of maximum speeds, males also moved faster than females both in water ($F_{1,82} = 8.57$, $P = 0.004$) and on land ($F_{1,82} = 7.13$, $P = 0.009$).

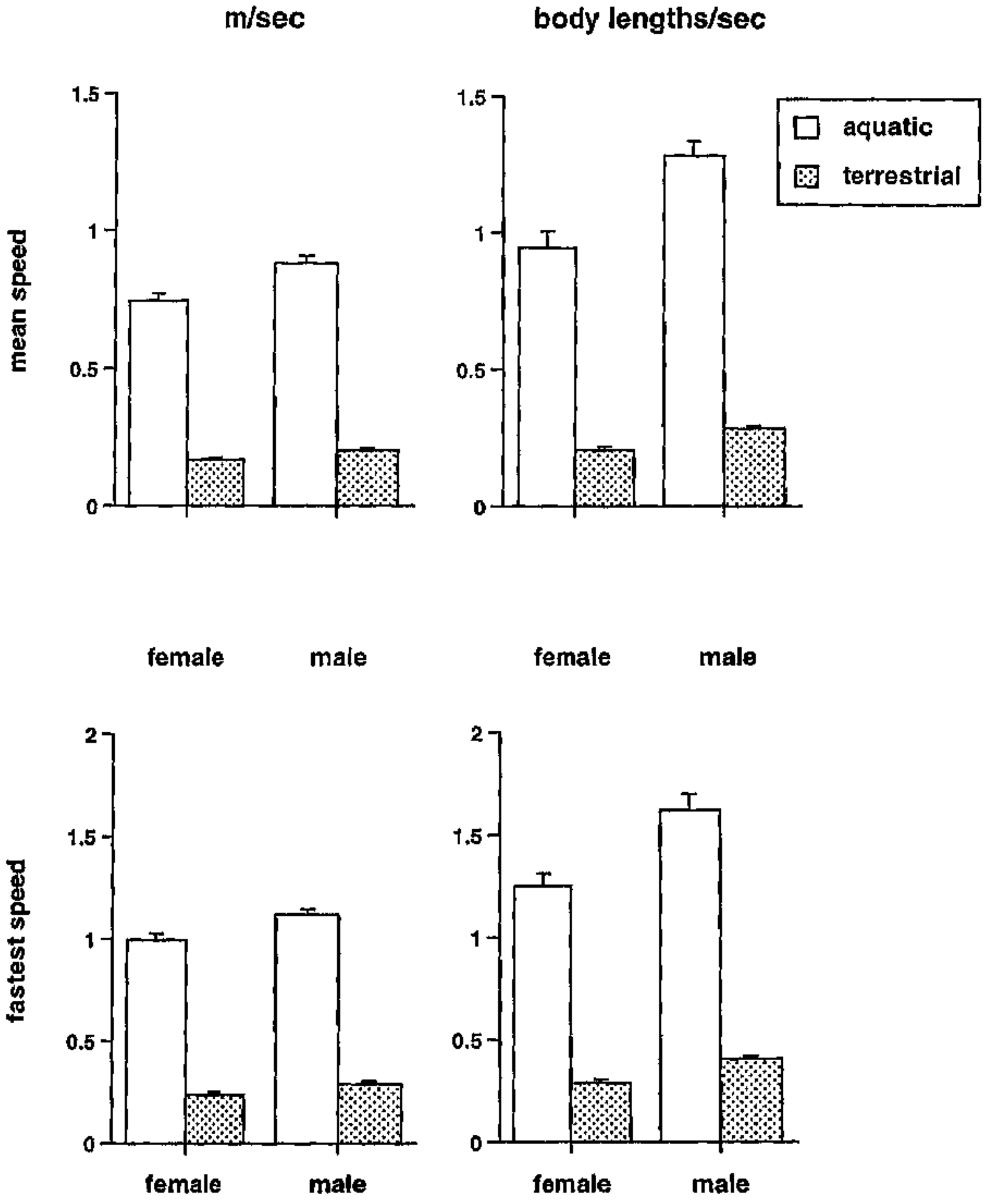


Figure 5.1 Mean locomotor speeds of sea kraits, *Laticauda colubrina*, on land and in the water (± SE). Data are shown separately for male and female snakes, and are calculated on the basis of
(a) absolute speed (m/sec, in left-hand graphs) and
(b) relative speed (body lengths/sec, in right-hand graphs).

The same patterns were observed when we analysed locomotor speeds in relative terms (body lengths/sec) rather than in absolute terms (metres/sec). Mean speeds differed between the sexes even more than in the previous analysis based on absolute speed (Fig. 5.2). This difference in results reflects the fact that females attain substantially larger sizes than males within this population (mean SVLs in our sample = 91 cm for females, 72 cm for males). A significant interaction term showed that the disparity between rates of aquatic *versus* terrestrial locomotion differed between male and female snakes for mean speed ($F_{1,82} = 9.07$, $P = 0.003$) but not for fastest speed ($F_{1,82} = 3.51$, $P = 0.06$: see Fig. 5.2).

These results suggest that body size affects locomotor speeds in sea kraits, but not necessarily in the same way in water *versus* on land, or in males *versus* females. To clarify these effects, we used a one-factor ANCOVA with sex as the factor, SVL as the covariate and locomotor speed as the dependent variable. This analysis (and all others reported in this paragraph) were based only on data from snakes < 96 cm SVL, to ensure overlap between the sexes (Sokal and Rohlf, 1981). Larger snakes swam faster in absolute terms (m/sec), with a significant difference between the sexes in this respect (slopes homogeneous $F_{1,56} = 0.41$, $P = 0.52$; effect of SVL $F_{1,57} = 6.18$, $P = 0.016$; effect of sex $F_{1,57} = 7.74$, $P = 0.007$). The same was true for speeds on land (slopes homogeneous $F_{1,56} = 2.06$, $P = 0.16$; effect of SVL $F_{1,57} = 29.10$, $P = 0.0001$; effect of sex $F_{1,57} = 6.80$, $P = 0.012$). A more interesting analysis, however, involves speed in relative rather than absolute terms. Relative to their own body lengths (SVL), smaller snakes swam and crawled faster than did larger conspecifics (Fig. 5.3). The sexes followed different trajectories in this respect (for swimming, slopes homogeneous: $F_{1,56} = 0.96$, P

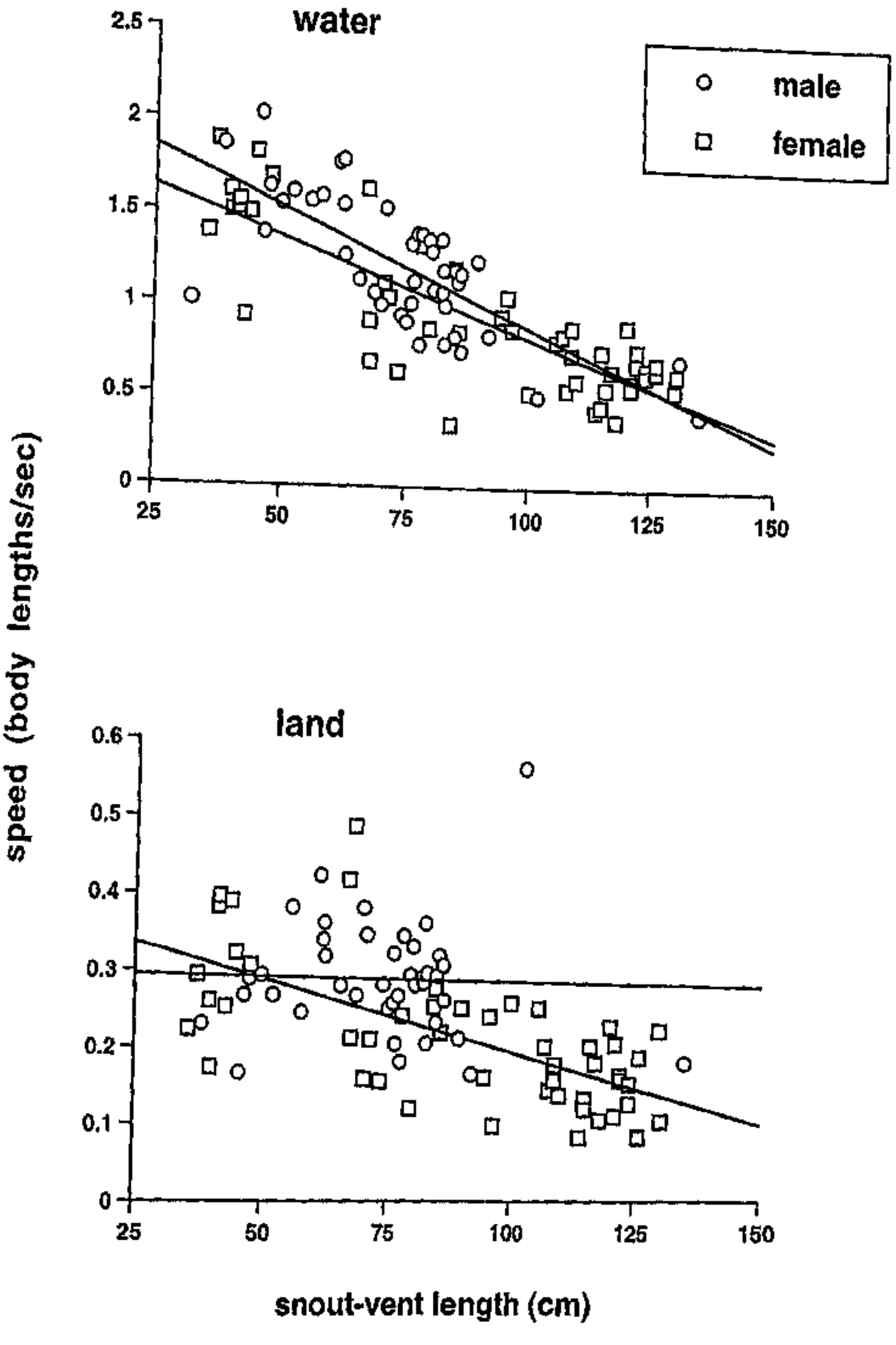


Figure 5.2 The effect of sex and body size on locomotor speeds of yellow-lipped sea kraits, *Laticauda colubrina*, on land and in the water. Speeds are calculated in relative terms (number of body lengths/second).

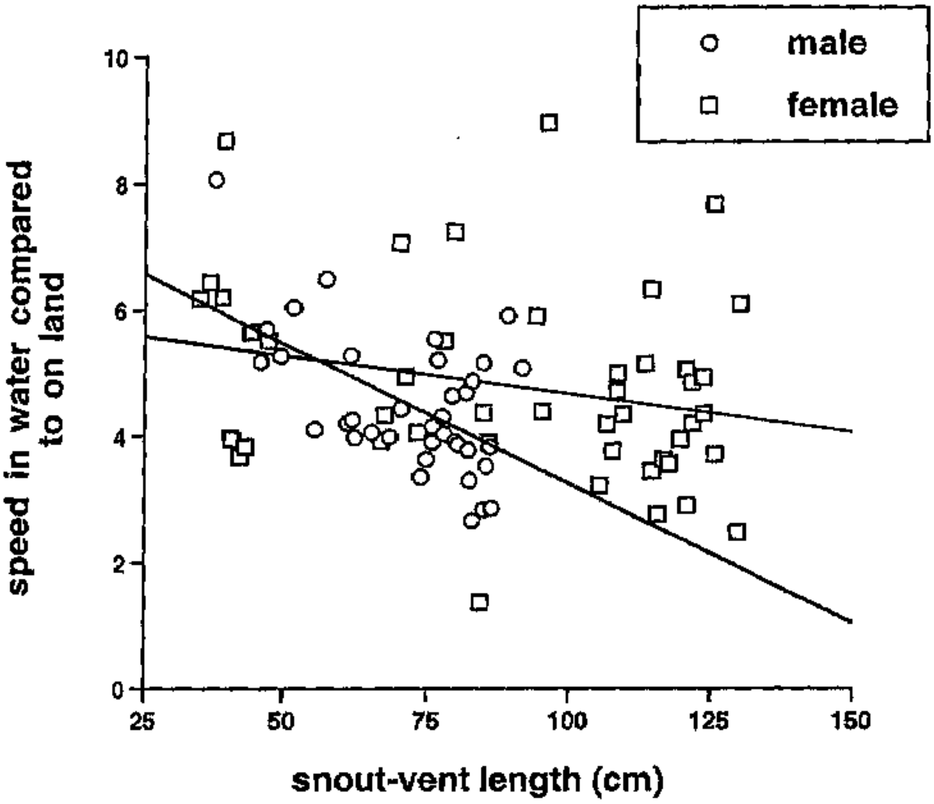


Figure 5.3 The effect of sex and body size on relative locomotor speeds of yellow-lipped sea kraits, *Laticauda colubrina*, on land *versus* in the water. Relative speeds were calculated for each snake by dividing its mean speed in water by its mean speed on land.

= 0.33; effect of SVL: $F_{1,57} = 61.29$, $P = 0.0001$; effect of sex: $F_{1,57} = 6.64$, $P = 0.013$; for crawling, slopes homogeneous: $F_{1,56} = 2.05$, $P = 0.16$; effect of SVL: $F_{1,57} = 5.10$, $P = 0.028$; effect of sex: $F_{1,57} = 3.78$, $P = 0.057$). That is, small snakes travelled faster (in terms of body lengths/sec) and male sea kraits moved faster than females of the same body length.

To compare the relative speeds at which the snakes travel across land *versus* through water, we can calculate a simple ratio score (mean speed on water divided by mean speed on land) for each snake. Analysis using one-factor ANCOVA (with sex as the factor and SVL as the covariate) shows that the ratio declined with increasing body size ($F_{1,56} = 14.60$, $P = 0.003$), and that this decrease was more rapid in males than in females (interaction: $F_{1,56} = 4.57$, $P = 0.037$). That is, snakes of all body sizes were quicker in water than on land, but the magnitude of this difference was greater for small snakes than for large ones, and decreased with body size more rapidly in males than in females (Fig. 5.4). Paradoxically, the combination of these two patterns results in an approximate equality between the two sexes in mean values for speed on land *versus* water. Because the ratio decreased with size less rapidly in females, but females span a wider body-size range, the end result was a similarity in average values between the sexes. Male sea kraits swam an average of 4.7 times faster than they crawled, whereas females swam an average of 4.8 times faster.

Plausibly, a snake's locomotor speed might be affected not only by its sex and body size, but also by its feeding status. Sea kraits eat prey (eels) that are large relative to the snake (Pernetta, 1977; Heatwole, 1999). Thus, a full stomach might impair locomotor performance. Our data allow us to test

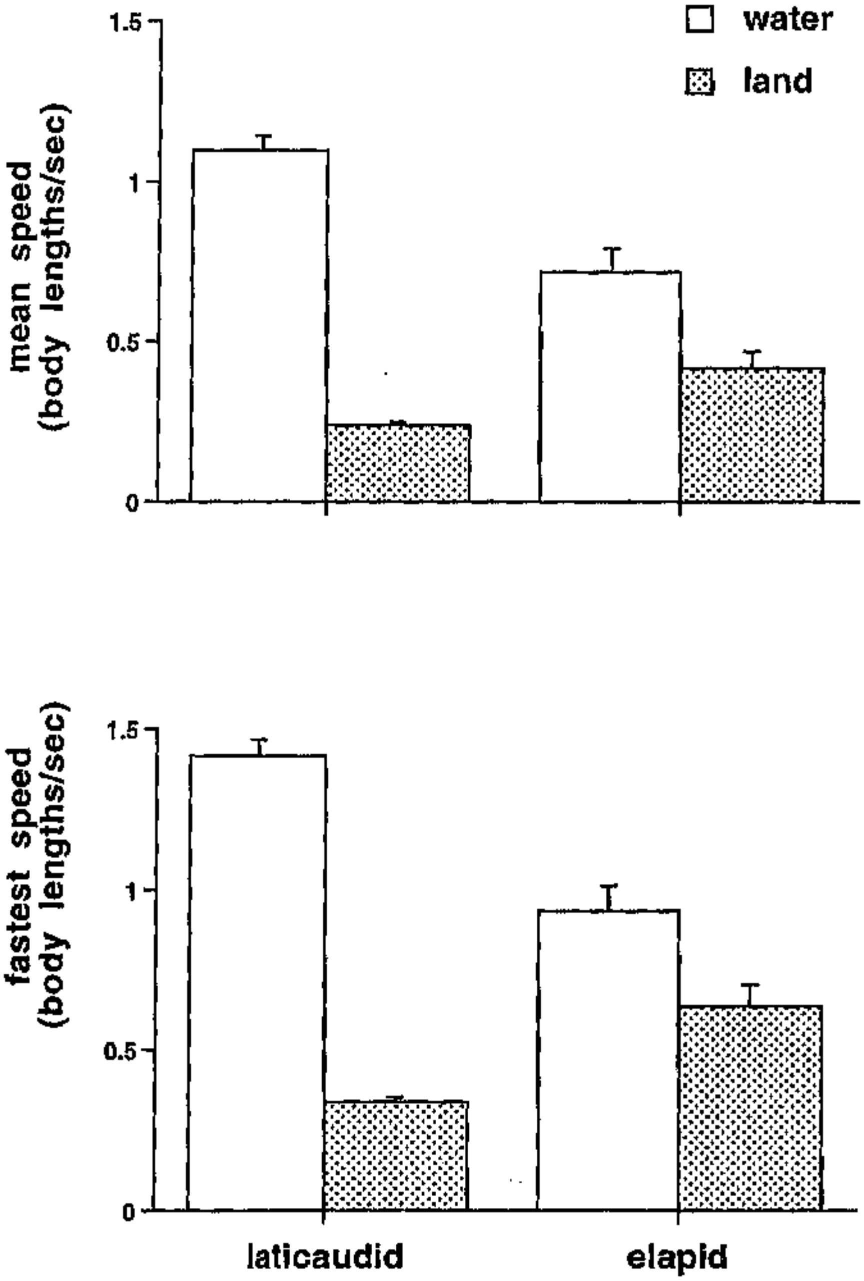


Figure 5.4 Locomotor speeds of 11 individuals belonging to three species of terrestrial Australian elapid snakes (*Hemiaspis signata, Notechis scutatus, Pseudechis porphyriacus*) compared to those of 84 Fijian sea kraits (*Laticauda colubrina*), on land *versus* in the water (± SE).

for such an effect, because 15 of the snakes contained prey that were detectable by palpation. As predicted, these animals were slower than unfed animals. A two-factor repeated-measures ANCOVA with sex and feeding status as factors, substrate type as the repeated measure and SVL as the covariate, detected a significant effect of feeding on locomotor speeds. The average fastest speed was 18% lower in recently-fed snakes than in unfed animals, and the average mean speed was 22% lower. The ANCOVAs showed no interaction effects, but significant main effects of feeding on average speed ($F_{1,80} = 5.33$, $P = 0.024$) and burst speed ($F_{1,80} = 5.65$, $P = 0.02$). That is, feeding impaired locomotion to about the same degree in males and females, and to a similar degree on land as in the water.

Lastly, we directly compared speeds of individual *Laticauda* to see if a snake that was faster in the water was also faster (or slower) on land. That is, do we see a tradeoff at the level of the individual, whereby (for example) morphological features that enhance swimming ability concurrently reduce crawling speeds? Analysis refutes this prediction, because it reveals positive rather than negative correlations between speeds in the two media. This result held true for both sexes, and the same trend was seen for average as well as maximum speeds (calculated in terms of body lengths/sec; females, average speed: $n = 46$, $r = 0.74$, $P = 0.0001$, fastest speed: $n = 46$, $r = 0.69$, $P = 0.0001$; males, average speed: $n = 37$, $r = 0.46$, $P = 0.004$, fastest speed: $n = 37$, $r = 0.16$, $P = 0.35$). That is, individuals within each sex that were faster swimmers, were also faster on land.

DISCUSSION

Our data reveal substantial variation in locomotor speeds as a function of substrate type (water *versus* land), species (terrestrial *versus* aquatic), sex, body size, and feeding status. These factors also interact in complex ways to determine locomotor performance. Thus, for example, a sea krait's sex and body size affect its speed differently on land *versus* in the water. The following discussion is oriented around two issues: (1) phylogenetic shifts in locomotor speed in the evolutionary history of sea kraits; and (2) sources of variation in locomotor performance within a sea krait population.

Comparisons between terrestrial snakes and sea kraits

We measured speeds in a small sample of terrestrial Australian elapids, to compare to our larger data set on laticaudid locomotion. Can we use these data to infer the situation in the terrestrial ancestors of *L. colubrina*? Clearly, the three terrestrial species that we tested are not direct ancestors of sea kraits, nor are they particularly close to the sea kraits phylogenetically. Sea kraits probably arose from terrestrial elapids somewhere close to the time when Asian species first entered Australia (Keogh et al., 1998). Thus, laticaudids might be basal to the Australian elapid radiation, or an early offshoot from it. Regardless, most elapids are relatively conservative in general body form and in several aspects of their feeding ecology. Notably, most elapid species are slender-bodied snakes that move about and actively search for prey items (Shine, 1991a, b; Greene, 1997). Also, many elapid species forage in crevices (Shine, 1991b). *Laticauda* has retained these features, despite departing dramatically from most other elapids (except hydrophiine species) in habitat type and the evolution of "sea snake" morphology. Thus, the three terrestrial elapids that we studied may provide a reasonable basis for comparison. They are similar in general body form to *Laticauda,* and forage actively in riparian habitats. All three species have been reported to forage underwater for tadpoles and fishes, but probably take most of their prey from terrestrial habitats (Shine, 1991b).

If we take the terrestrial elapids as our reference point, we infer that the ancestral laticaudid was probably somewhat faster in the water than on land, even before it evolved features such as the paddle-like tail. A similar superiority in swimming speed over crawling speed may characterise many other terrestrial (especially riparian) snake species (Weatherhead and Robertson, 1992). The evolutionary change to oceanic life has involved a substantial increase in aquatic locomotor ability in laticaudids: our sea kraits swam about 60% faster than did similar-sized terrestrial elapid species. However, the sea kraits have paid a substantial penalty in terms of terrestrial locomotor ability: they averaged about 80% slower on land than did their terrestrial counterparts.

It is difficult to judge the significance of locomotor speed in these two situations, in terms of selective pressures. Because the snakes capture eels within burrows (West, 1990), speed underwater may not be important for foraging. Similarly, speed on land may confer only a limited advantage. Terrestrial predators are rare in many areas where *Laticauda* is found (including on Mabualau), although crabs may take hatchling snakes (Guinea, 1986) and in some parts of their range, eagles may take adult snakes (Heatwole, 1999). Although previous work on garter snakes has revealed directional selection for higher locomotor speeds (Jayne and Bennett, 1990b), we do not know the relative intensity of selection on this trait (or more importantly, on aquatic *versus* terrestrial locomotor capacity) for sea kraits.

Although our data are preliminary, they suggest that proteroglyphous snakes (elapids and their allies) might provide an excellent model system with which to investigate the ways in which adaptations to aquatic life modify organismal performance in both the "new" and "old" habitats. The potential for comparative analysis is high because:

(i) the six living species of laticaudids differ considerably in the degree to which they use terrestrial habitats. For example, the freshwater *L. crockeri* is rarely if ever seen on land (Cogger et al., 1987). Anecdotal reports suggest that this diversity is associated with interspecific differences in the ability to move about on land (Greer, 1997; H. G. Cogger, pers. comm.).

(ii) other lineages of terrestrial elapids also contain species (e.g. *Boulengerina annulata, Micrurus lemniscatus, M. surinamensis, Bungarus multicinctus*: Campbell and Lamar, 1989; Roze, 1996; Greene, 1997) that have evolved to feed on fishes and hence, occupy aquatic niches. Additionally, some hydrophiid sea snakes such as "mud snakes" of the genus *Ephalophis* crawl over mudbanks at low tide to forage (S. Sweet, pers. comm.) and hence retain an ability to move about on land. Hydrophiids thus offer another lineage in which to quantify tradeoffs between terrestrial and aquatic locomotion.

Ideally, we need not only information on locomotor speeds, but also a more fully-resolved phylogeny of elapid relationships. Cladistic analysis of amino acid sequences of short-chain neurotoxins suggests that *L. colubrina* may be the most "primitive" laticaudid (Slowinski, 1989; but see Greer, 1997). This suggestion fits well with the observation that this species is more agile on land than are other laticaudids (Greer, 1997). Thus, phylogenetic shifts in locomotor performance within this genus may provide an unusually clear-cut example of a progressive evolution of swimming ability, and a concurrent decline in the ability to move around on land.

Comparisons within the sea krait population

Our data suggest that a sea krait's locomotor speed is a function not only of the medium in which it travels, but also depends on a snake's sex, body size and feeding status - and on interactions among these factors.

Body size

Allometric effects on locomotor speed are widespread, in snakes as in many other kinds of organisms. It may generally be true that larger individuals are faster in absolute terms, but not relative to body size (Heckrotte, 1967; Jayne, 1985; Jayne and Bennett, 1990a). In the case of *Laticauda colubrina*, a snake's body size is related to its ecology, and specifically to the relative amounts of time that it spends moving around on land *versus* in the water. For example, juvenile sea kraits are rarely active on land (Chapter 3). At first sight, this result seems paradoxical: the size class best-suited to terrestrial locomotion is the one which spends least of its time engaged in terrestrial locomotion. However, the two observations are easily reconciled. If juveniles are disproportionately at risk on land (due to their greater vulnerability to terrestrial predators), then we might expect them not only to avoid land, but also be capable of rapid terrestrial locomotion. Alternatively, there may be simple biomechanical reasons why smaller body size enhances speed more on land than in the water. Our data do not allow us to tease apart this issue; comparative data on other species would be of great interest in this respect.

Sex

To our knowledge, the only previous reports of sex differences in locomotor speeds in snakes involve the effects of pregnancy on maternal mobility (Seigel et al., 1987; Jayne and Bennett, 1990a) and the effects of time since emergence from hibernation (Shine et al., 2000a). Neither of these were a factor in our study. Why do male and female *Laticauda* differ in locomotor performance? Part of the answer lies in the extreme female-larger sexual size dimorphism within *L. colubrina*: larger snakes are slower (relative to body length), so females are slower because they are larger. However, this bias provides only a partial answer, because females are slower than males even if the body-size difference is factored out of the analysis (Fig. 5.3).

Sex differences in locomotor abilities within our sea kraits may be attributable to either (or both) morphology and/or ecology. In terms of morphology, males are much more slender-bodied and small-headed than females, and have massively larger tails relative to snout-vent length (Camilleri and Shine, 1990; Chapter 2). These attributes would plausibly enhance male speeds relative to female speeds. In terms of ecology, male *L. colubrina* spend much of their time actively moving about on land, whereas females are much less active when on land. This sex difference clearly reflects the mate-searching behaviour of males (Saint Girons, 1964; Chapter

3). Hence, males may be under more intense selection for terrestrial locomotor performance than are females. These two arguments (morphological and ecological) are not mutually incompatible. Males may have evolved to be small and slender because these traits enhanced their mate-searching ability on land.

Feeding

A full stomach reduced locomotor speeds in our snakes, both on land and in the water. The same effect has previously been reported for one genus of terrestrial snakes (Garland, 1983; Ford and Shuttlesworth, 1986) although our study provides the first example of this phenomenon with regard to aquatic locomotion. Sea kraits were slowed-down by feeding to approximately the same degree on land as in the water, so that this effect cannot explain the tendency for recently-fed snakes to return to land until they have digested their prey (Saint Girons, 1964; Chapter 3). Neither can thermal cues, because body temperatures are relatively similar when snakes are on land as when they are in the water (Chapter 3). A reason for the strong trend in sea kraits to return to land after feeding must, hence, be looked for in other aspects of the species' ecology. Plausibly, a recently-fed snake may be more vulnerable to predators in the water (e.g. sharks often eat sea snakes: Heatwole, 1999), whereas there are few or no predators of large snakes in the terrestrial environment (Guinea, 1986). We can also speculate that the bulky eels consumed by the snakes may compress the lungs and thus reduce the lung capacity. This might result in the snakes having to surface more often to breathe and thereby increase their energy expenditure.

Because of the differing biomechanical requirements of terrestrial *versus* aquatic locomotion (Cundall, 1987), we might expect to see a strong tradeoff between performance in these two tasks. In practice, we saw this tradeoff only in our interspecific comparison (between sea kraits and terrestrial elapids). No such tradeoff was evident in the comparison between the sexes: males were faster than females both in water and on land. At the individual level (within each sex), we similarly saw no clear tradeoff. Indeed, snakes that were faster in the water were also generally faster on land. This result does not, however, imply the absence of a tradeoff. Variation among individuals in traits such as general body condition, vigour, or response to handling, would tend to generate positive rather than negative correlations between performance in each medium. Such variation may well obscure underlying tradeoffs, even in circumstances where other information clearly reveals that such tradeoffs occur (van Noordwijk and de Jong, 1986; Doughty and Shine, 1997).

CHAPTER 6. CONSERVATION ASPECTS

INTRODUCTION

In some parts of their geographic range, sea kraits have been the targets of commercial harvesting. The skins from sea kraits have considerable value for high-quality leather goods, and the animals are remarkably easy to collect in large numbers. This ease of collection reflects their abundance, their concentration on small islands (Lading et al., 1991), and their tolerance of humans (reluctance to try and escape or retaliate when approached). In The Philippines, sea snake populations have been severely depleted as a result of unmanaged local hunting: one large population of sea kraits may indeed have gone extinct (Bacolod, 1983, 1984, 1990). Fortunately, sea snakes are not harvested commercially in Fiji (pers. obs.; Michael Guinea, pers. comm.). I therefore had the opportunity to study relatively undisturbed populations of sea kraits in the Fiji Islands.

Although Fijian populations of sea kraits are not under immediate threat of commercial exploitation, such a situation can change rapidly. Hence, there is an urgent need to document aspects of sea krait biology relevant to their ability to tolerate harvesting. This information might also be relevant to commercially-exploited populations of sea kraits in other geographic areas. For example, it might help to frame management plans, establish sustainable quotas for offtake, and so forth (e.g. Fitzgerald et al., 1991; Heatwole, 1997). Even if Fijian sea kraits are not the direct targets of commercial activities, there can be little doubt that continuing anthropogenic modification of their habitats (e.g. modification of coastal areas and offshore islands for tourist developments) will impact to some degree on population viability. Ecological data on native fauna can help us make informed decisions on these kinds of issues as well.

Although my study was framed primarily to provide basic ecological and behavioural information on these poorly-known animals, several aspects of the work provided information that may be relevant to conservation and management. For example, the radiotelemetry has clarified the time scale over which the snakes move between aquatic and terrestrial habitats (Chapter 3). The dietary data tell us about the fish resources that are required to sustain sea krait populations, and also suggest that any precipitous decline in laticaudid abundance might well have broader effects via changes in the abundance of eels. In this chapter I will focus on other aspects of the ecology of *Laticauda colubrina* that have particular relevance to conservation issues.

First, my mark recapture study enabled me to document growth trajectories of these animals, and hence establish the ages at maturation in male and female sea kraits. Mathematical models of harvesting have identified generation time (age to maturity) as a crucial variable in determining the ability of a population to withstand any given level of offtake (Caughley, 1977; Caughley and Sinclair, 1994). I also took advantage of this data set to explore factors that might affect growth rates, and hence age at maturation.

Second, my data provided a basis for comparison of the sea krait populations on two adjacent islands (Mabualau and Toberua). Although separated by only 5.3 km, these islands offer a strong contrast in many respects. For example, Mabualau is essentially uninhabited by humans apart from occasional fishing parties, and there is little evidence of substantial modification of the native vegetation. In contrast, Toberua is a resort island with several buildings, a permanent human presence, and large-scale habitat modification (including the clearing of native vegetation and the planting of exotic trees). The lack of replication makes it impossible to attribute causation to any differences observed between sea krait populations on Mabualau *versus* Toberua, but any such differences may suggest hypotheses for future study. Additionally, the degree of interchange of individuals between these two islands is of great interest. Are sea krait populations discrete units, such that each island has its own animals? Or do the snakes move about over broader areas, hauling up onto different islands after each foraging trip? The answers to these questions will determine, for example, the spatial scale at which events on one island (such as habitat modification, commercial harvesting, introduction of terrestrial predators) will impact populations of snakes using nearby areas.

Although conceptually separate, the information on growth rates, population sizes and island fidelity all resulted primarily from the same aspect of my methods: that is, the mark-recapture study. By individually marking snakes during the first year of my study, and then recapturing them in the subsequent field season, I was able to obtain estimates of all of these variables. Thanks to the regular collection of snakes by the staff at Toberua Island Resort, I was able to look at the consequences of relocating snakes from Toberua to Mabualau. The mark-recapture study also enabled me to identify movements by marked snakes between islands, and hence clarify the homing abilities and island fidelity exhibited by these snakes.

METHODS

Island fidelity and inter-island movement

During the first field season, after measuring and marking individual snakes, I released all snakes on Mabualau Island irrespective of their origin. In subsequent collections (from both Mabualau and Toberua Islands), any previously marked snakes were identified. I kept records of such snakes along with details of date and origin of initial capture and recapture. Once again, I released these recaptured individuals on Mabualau Island, irrespective of their origin.

This procedure enabled me to determine if snakes originally collected and marked from Mabualau Island frequented Toberua Island and vice versa. I also hoped to determine if snakes that were displaced from Toberua Island remained on Mabualau or returned.

Population densities

A capture-mark-recapture method was used to determine the population densities on both Mabualau and Toberua Islands. During the first field season (between October 1998 and January 1999) snakes from both islands were captured and marked. Chapter 2 provides a detailed description of the capture and marking techniques. During the second field season (between September and December 1999), I attempted to recapture the previously marked snakes. I did this by routinely examining all snakes that were encountered during my fieldwork, and retaining and measuring the recaptured animals. I used a modified version of the Lincoln-Petersen method to estimate the population of sea kraits from each island.

To calculate abundance from the recapture data, I used the following equation:

$$N_c = \frac{(n_1 + 1)(n_2 + 1)}{(m_2 + 1)} - 1$$

The approximate unbiased variance is given by

$$\mathrm{var}\, N_c = \frac{(n_1 + 1)(n_2 + 1)(n_1 - m2)(n_2 - m2)}{(m_2 + 1)^2 (m_2 + 2)}$$

Where,

n_1 = all animals caught in the first field season.

n_2 = all animals captured in the second field season

m_2 = number of animals in n_2 that are marked.

An approximate 95% confidence interval, assuming normality for N_c is given by:

$$N_c \pm 1.96 \times (\mathrm{var}\, N_c)^{0.5}$$

A detailed discussion of the methods and assumptions of this method can be found in Pollock et al., (1990).

Growth rates

During the second field season, I collected morphometric measurements of marked snakes that were recaptured as above (see Chapter 2). The difference between a snake's size at first and second captures gave me an indication of how much the snake had grown in the intervening year. Since I marked only a small number of juveniles (139) in my first field season, I anticipated a low recapture rate for this size class during the second field season. In order to obtain a better estimate of growth rates in juveniles, I intensively marked juveniles during the first three weeks of the second field season. I then attempted to recapture as many of these animals as possible during the last three weeks of this second field season. The average time between captures in this case was 60 days. To minimise error in the measurement of traits such as body length and head size, all measurements were taken by the same person (myself) in a standardised fashion.

RESULTS

Population structure

Remarkably, the two adjacent islands exhibited very different age/size class structures. On Mabualau, 55% of the population was comprised of adult males, 25% adult females, and 20% juveniles. At Toberua, adult males made up 65% of the population, adult females 33% and juveniles only 2% of the population. That is, juveniles were a substantial proportion of the population on Mabualau, but were rarely encountered on Toberua.

Sex ratios showed less geographic variation. The ratio of numbers of adult females to adult males (~1:2) was similar on both islands – 68.9% males on Mabualau Island (against a null of 50% male: $\chi^2 = 49.5$, 1 df, P = 0.0001) and 66.8% males on Toberua ($\chi^2 = 31.7$, 1 df, P = 0.0001). The sex ratio for juveniles on Mabualau was close to 1:1 ($\chi^2 = 0.2$, 1 df, P = 0.70).

Island fidelity and inter-island movements

My mark-recapture study revealed extreme philopatry in sea kraits, and rapid homing of snakes displaced from Toberua to Mabualau. Table 6.1 summarises data on the numbers of marked snakes captured and recaptured on either island. It is clear that snakes originally captured on Mabualau were never recaptured on Toberua; and that Toberua snakes were never recaptured on Mabualau. My data indicate that the snakes were extremely philopatric despite the short distance between the two islands. This result is further emphasised by multiple recaptures of 23 individuals from Toberua Island. The average time between recaptures was 30.7 days (SD = 19.2), with the recapture intervals ranging between 2 and 76 days. Thus, these snakes returned home not only accurately, but also rapidly.

Philopatry was also evident on a longer temporal scale. When I returned for my second field season, I found large numbers of marked snakes. Without exception, these animals were on their "own" island: that is, the place where they had originally been captured. Table 6.1 shows that

Table 6.1. Numbers of sea kraits recaptured on two Fijian Islands, as a function of their initial site of capture. Table shows numbers of males and females in parentheses, after total number of snakes.

Island where recaptured	Year recaptured	Year marked	Initial island of capture	
			Mabualau	Toberua
Mabualau	1998	1998	36 (7/29)	0
Toberua	1998	1998	0	102 (81/21)
Mabualau	1999	1998	278 (48/232)	0
Toberua	1999	1998	0	114 (90/24)

sample sizes for these recaptured snakes were large, that both sexes of sea kraits were involved, and that the fidelity of snakes to their "home" island was absolute.

Population densities

Because the mark-recapture results indicate that the two islands have essentially separate populations of sea kraits, I will deal with the populations of each island separately. On Mabualau Island, the total number of snakes marked initially in 1998 (n_1) was 541. The total number of snakes caught on the second trip in 1999 (n_2) was 1198. Of these, the number of individuals that were marked (m_2) was 278. Substituting these values in the equation above, I estimate the population of sea kraits on Mabualau Island to be 2328 ± 87, during the period 1998 - 1999.

On Toberua Island, I initially marked (n_1) 322 snakes, and the total number of snakes caught on the second trip (n_2) was 320. Of these, 114 individuals were marked (m_2). Substituting these values in the equation above, I estimate the population of sea kraits on Toberua Island to be 900 ± 105, during 1998 - 1999.

Growth rates

I was only able to recapture 25 juveniles from the mark-recapture studies conducted on both field trips. Thus data for adults and juveniles were combined in the growth rate analyses. The average time interval between the recaptures was 284.8 days (SD = 50.5). During this time snakes of both sexes had significantly increased in body and head sizes (Table 6.2). Growth

Table 6.2. A summary of the paired t-test showing the mean difference in the morphological traits of male and female sea kraits from both Mabualau and Toberua Islands combined, the degrees of freedom and statistical significance values. The average time interval between measurements was 284 (SD 50.5).

	MALES			FEMALES		
	mean diff.	**df**	**P - value**	**mean diff.**	**df**	**P - value**
snout-vent length (cm)	2.3	293	< 0.0001	5.2	63	< 0.0001
tail length (cm)	0.4	293	< 0.0001	0.5	63	< 0.0001
mass (g)	9.0	293	< 0.0001	97.2	63	0.0006
head length (mm)	0.8	293	< 0.0001	2.4	63	< 0.0001
head width (mm)	0.2	293	0.0004	0.6	63	0.03

rate was calculated by dividing the growth increment (final minus initial snout-vent length) by the duration of time between initial capture and recapture. This provided a value for the increase in body size in terms of cm/day. I then multiplied this value by 30 to give me the growth in cm/month. The average growth rates for females, males and juveniles were 0.4 cm/month (SD = 0.3), 0.2 cm/month (SD = 0.2) and 1.9 cm/month (SD = 0.9) respectively (Fig. 6.1). These growth rates differed significantly (ANOVA for data in Fig. 6.1: $F_{2,325} = 310.3$, $P < 0.0001$; all post hoc comparisons have $P < 0.0001$ also).

Based on the rates of growth of marked snakes in my study, I estimate that the "typical" growth trajectory for Fijian sea krait might be as follows. The snakes hatch from their eggs at a snout-vent length of approximately 30 cm (Guinea, 1981). They grow rapidly during the first year of life. For example, one male snake grew from 40.8 to 58.5 cm SVL in 12 months, and another grew from 49.7 to 70.5 cm SVL. A female grew from 48.7 to 70.4 cm SVL over the same period. All three of these animals were presumably hatched out at the end of the previous breeding season (i.e. from Guinea 1981, eggs laid in early December, usually hatch in late March). They would thus have been approximately six months old when they were first marked, having grown from 30 to about 40 to 50 cm within the first six months of life. Based on their growth rates over the next 12 months (above), I infer that these snakes probably attain an average SVL of about 60 to 70 cm at 18 months of age. Growth then slows appreciably, especially in males. The mean annual growth increment for a 65 cm male snake was only 11 cm SVL (i.e. a male sea krait marked at 65 cm, grew to an average of 76 cm SVL over the next 12 months: see Fig. 6.2). In contrast, females continued to grow

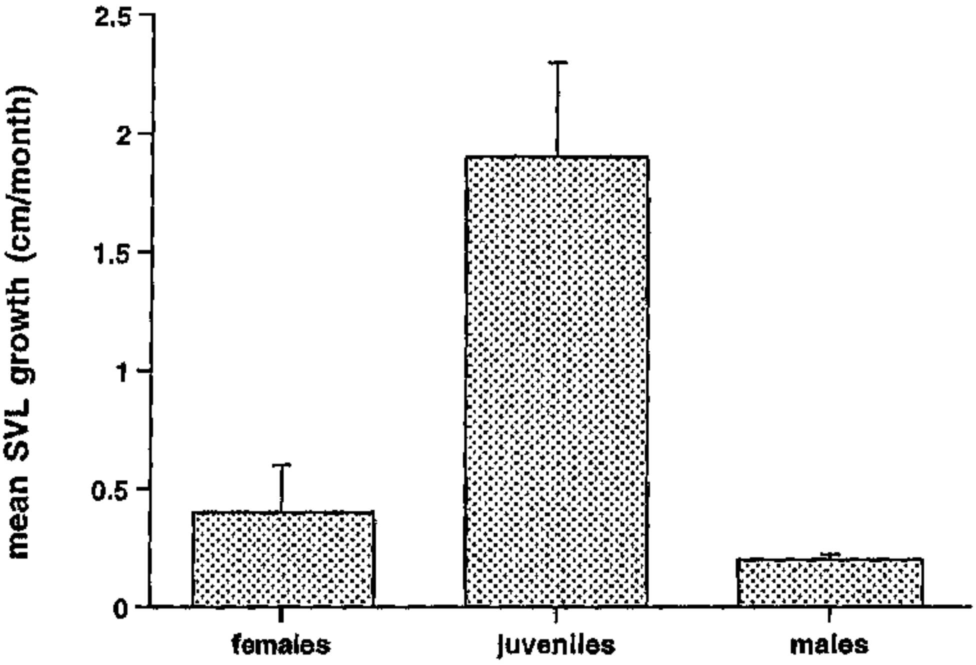


Figure 6.1 The mean growth rates of adult male, adult female and juvenile sea kraits from Mabualau and Toberua Islands combined (± 2 SE).

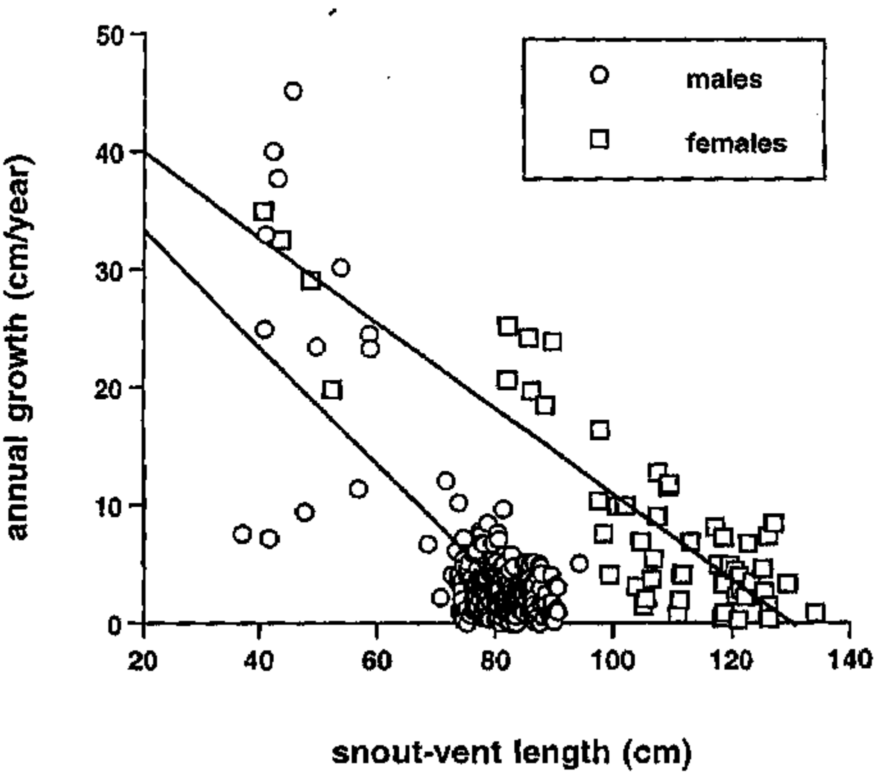


Figure 6.2 Mean annual growth increments (SVL, in cm) of male and female sea kraits during my study. The growth increment is plotted against the snakes' mean SVL over the period between recaptures.

rapidly at this size: the mean annual growth increment for a female sea krait measuring 65 cm SVL was 24 cm (i.e. she grew to an average of 89 cm over this period: see Fig. 6.2).

Figure 6.2 shows annual growth rates of sea kraits as a function of body size (mean SVL over the period between recaptures). A one-factor heterogeneity of slopes test confirms that growth rate decreased with size, and that at any given body size, females grew faster than males (interaction between sex and body size: $F_{1,351} = 40.77$, $P < 0.0001$). We can use this relationship to estimate ages at maturity in both sexes. Based on dissections by Guinea (1986), male *L. colubrina* in Fiji mature at about 70 cm SVL, whereas females do not mature until they are approximately 90 cm SVL. Thus, a male sea krait would reach sexual maturity at about 18 months of age. Mating activity is seasonal, so that if a male was not mature at 18 months of age, his next opportunity to mate would come in the subsequent breeding season (by which time he would be 30 months old). Even if females grow faster than males during early juvenile life, it is unlikely that they could grow fast enough to reach maturity at 18 months of age. However, their rapid growth over the next 12 months (above) means that many (probably most) females would be above the minimum size at maturity by the following breeding season, when they were 30 months old.

We can also compare growth rates among islands, because individual snakes can unambiguously be assigned as either Toberua or Mabualau animals (see above). I did this by incorporating location as an additional factor in the heterogeneity of slopes test reported earlier in this section. The analysis revealed a significant three-way interaction term between sex, location and mean body size ($F_{1,354} = 7.23$, $P = 0.008$). I thus conducted tests on data for each sex separately, with location as the factor and mean body size as the covariate. These tests revealed no difference in growth rates between female snakes from the two islands (slopes: $F_{1,58} = 0.27$, $P = 0.61$; intercepts: $F_{1,59} = 0.003$, $P = 0.96$). In male sea kraits, however, growth rates were higher for Mabualau snakes than for their conspecifics from Toberua (slopes: $F_{1,296} = 9.62$, $P = 0.002$).

Finally, it is possible that stress caused to the animals while measuring and marking them, might impact on their growth. If this occurred, my estimates from recaptured snakes might underestimate the growth rates of unmarked (= unstressed) animals. In order to examine this possibility, I compared the body condition of the marked snakes that were recaptured in the second season with that of randomly picked unmarked snakes in the same season. A one-factor ANCOVA with *ln* mass as the dependent variable, *ln* snout-vent length as the covariate, marked *versus* unmarked as the factor, was conducted for each sex. I found significant main effects of both the factor and the covariate, in both females (covariate: $F_{1,404} = 782.38$, $P < 0.0001$; factor: $F_{1,404} = 25.51$, $P < 0.0001$) and males (covariate: $F_{1,1046} = 1454.65$, $P < 0.0001$; factor: $F_{1,1046} = 25.15$, $P < 0.0001$). The results show that the body condition of unmarked females was slightly better than the recaptured females. However, the reverse was true for males.

DISCUSSION

The most striking result from these data is the degree to which sea krait populations on two adjacent islands constitute separate biological entities.

Not only do snakes remain philopatric to their own island if undisturbed, they also return rapidly to their own island if displaced. In consequence, the snake populations on these two islands can potentially diverge in biological characteristics without having such differences diluted by migration. Indeed, this has occurred. The two populations differ in several respects including mean body sizes of adult males (Chapter 2), population structure and growth rates (above).

Although local geographic variation in such traits is probably widespread in snakes as in many other kinds of animals (Schwaner and Sarre, 1988; Madsen and Shine, 1993b), the populations involved are generally isolated by large distances or by some obvious barrier to migration. This is not the case with my Fijian study system. Mabualau and Toberua are only 5.3 km apart, and the intervening area consists primarily of a shallow reef crest that is an important foraging area for the sea kraits (pers. obs.). The rapid return of displaced snakes confirms that there is no effective physical barrier to migration. Thus, the extreme site fidelity of yellow-lipped sea kraits must be due to some intrinsic behavioural mechanism, rather than an externally-imposed pressure.

Further research on this topic would be of great interest. For example, do juvenile sea kraits (which are more highly aquatic than adults: see Chapter 3) display the same philopatry? If so, there may be a possibility for regional genetic differentiation due to limited dispersal. Molecular genetic techniques might be a feasible approach to answering this question. It would also be of interest to quantify the extent and location of foraging areas used by both adult and juvenile sea kraits. Given that adult animals typically remain at sea for several days on foraging trips (Chapter 3), they might potentially move far from the island. This idea fits well with the ability of displaced snakes to home rapidly, because this ability indicates that such snakes have a strong sense of location. However, if snakes do indeed travel large distances in the ocean, why do they bother to return to exactly the same island that they left?

The fidelity of sea kraits to their "home" island is interesting not only in its own right, but because of its implications for conservation planning. Clearly, we need to treat each local population as a separate entity. Local disturbance is likely to severely impact on the snakes living in the immediate area, but is unlikely to have geographically widespread consequences. This is not necessarily either "good news" or "bad news" from an overall conservation perspective, but is a crucial piece of information in allowing us to predict the spatial scale at which local peturbations may influence sea krait populations. For example, it means that the impact of anthropogenic activities can most usefully be examined on a smaller spatial scale than would have been suggested by intuition.

The underlying causes for inter-island differences in biological traits of sea kraits are difficult to identify. As noted above, Toberua and Mabualau differ in many respects that might influence the day-to-day lives of sea kraits, but we have no way to evaluate such influences. The scarcity of juvenile snakes on Toberua might plausibly reflect the much lower availability of suitable habitat for this size class. On Mabualau, juvenile snakes are generally found very close to the water, often in honeycombed rocks that allow the snakes to move directly from shelter sites to the water (and vice versa), at almost any tide, without terrestrial exposure. Such sites are rare on Toberua, partly because of anthropogenic modifications associated with the construction of a tourist resort on this island many years ago.

If sea kraits do indeed continue to use the same island throughout their lives, we might expect that a reduction in habitat for juveniles (as occurred on Toberua) would not only reduce the numbers of hatchlings, but also eventually shift the age structure among adults. This process offers a plausible reason for the prevalence of very large (old) male snakes on Toberua (Chapter 2). Certainly, my growth data falsify the most likely alternative explanation - faster growth for Toberua snakes, leading to a larger average body size. In fact, the reverse situation occurs: the Toberua male snakes are larger on average despite growing more slowly than their Mabualau counterparts.

The marking procedure did not drastically affect the growth rates of snakes in my study. Even if it did, the effect was negligible as the calculated ages at maturation for Fijian sea kraits in my study fit well with previous estimates where there was no marking involved. Saint Girons (1964) and Guinea (1986) have both inferred growth trajectories based on monthly variation in the frequency distributions of body sizes of field-collected snakes. Saint Girons' (1964) data came from a New Caledonian population of *L. colubrina*, whereas Guinea's (1986) analysis was based on specimens from a variety of localities in Fiji. Guinea (1986) also measured (but did not mark) juveniles in the same site at two different times six months apart. He inferred that the increase in mean body size of animals at this site (from 39.1 cm SVL in July to 62.8 cm SVL the following January) represented average growth rates. My data are based on recaptures of individually marked snakes, and thus are more reliable than the extrapolations of earlier workers. Nonetheless, my results are in good agreement. Both Saint Girons (1964) and Guinea (1986) suggested that *L. colubrina* mature at about 18 months of age (males) to 30 months of age (females).

There are few data on other sea snakes with which to compare these estimates. The hydrophiid *Aipysurus laevis* shows delayed maturation relative to my laticaudids (3 years for males, 4 to 5 years for females: Heatwole, 1999). However, there is considerable variation in such traits (and probably even within the genus *Laticauda*, because the degree of sexual size dimorphism at maturity varies considerably among species: Bacolod, 1983). Another hydrophiid, *Enhydrina schistosa*, matures at the same ages as *Laticauda colubrina* (1.5 years in males, 2.5 years in females: Voris and Jane, 1979). Many terrestrial proteroglyphs also mature at about the same ages as the laticaudids (Shine, 1978), as do similar-sized snakes of several other lineages (Parker and Plummer, 1987). Males tend to mature at smaller body sizes and hence, younger ages, than do conspecific females in many snake species (e.g. Shine, 1994). This pattern (also seen in *L. colubrina*) may reflect the greater costs of reproduction for females than for males, and the advantages to females of accumulating substantial energy reserves before embarking on reproductive activity (e.g. Andersson, 1994; Madsen and Shine, 1995).

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