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THE MATING SYSTEM OF YELLOW-LIPPED SEA KRAITS (*LATICAUDA COLUBRINA*: LATICAUDIDAE)

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ABSTRACT: We studied sea kraits (*Laticauda colubrina*) on a small Fijian island during the mating season (September–December) in two successive years. These snakes forage at sea but return to islands to mate (and to lay their eggs, slough their skins, and digest their prey). On land, many females are accompanied by one or more courting males. The males align their bodies with that of the female and occasionally twitch spasmodically. These groups may remain together for days, with overt courtship by males much less frequent and intense than in most previously-studied snake species. Experimental trials in outdoor arenas showed that larger females attracted more intense courtship than did smaller animals. Females containing recently-ingested prey items were no more or less attractive to males than were unfed females. The intensity of courtship did not vary significantly among different times of day, nor was it consistently correlated with ambient temperature or with group size (operational sex ratio). Male sea kraits did not interact with each other in any overt way during courtship, and larger body size did not enhance male reproductive success. In several respects, the courtship of *L. colubrina* differs from that reported for other snake species.

Key words: Courtship; Fiji; Mating; Reproduction; Reptile; Sea-snake; Snake

THE social behavior of reptiles has attracted increasing scientific research over recent years, but detailed analyses have been firmly focussed on only a few “model systems”. Thus, although there are now extensive descriptive and experimental data

on the mating tactics of American garter snakes (Mason and Crews, 1986; Noble, 1937; Whittier et al., 1985) and European adders (Andren, 1986; Madsen et al., 1993), other lineages of snakes have attracted much less attention. This is especially true for field studies, because most snake taxa make relatively difficult subjects for quantitative research on reproductive behavior under field conditions (Seigel, 1993). However, we will need to study a diversity of taxa if we are to comprehend fully the diversity of mating systems exhibited by snakes. As a first step in this direction, we describe several aspects of the mating system of a snake species that is morphologically, phylogenetically, and geographically far removed from the taxa that have been the subject of previous studies in this field.

Laticaudid sea snakes are widely distributed through tropical oceans and are abundant in several areas. They have thus been the focus of several studies on reproductive biology. For example, the reproductive biology of *L. semifasciata* and *L. laticaudata* has been examined in the Philippines (Bacolod, 1983), and that of *L. semifasciata* in Japan and Taiwan (Toriba and Nakamoto, 1987; Tu et al., 1990). The species that we studied, *L. colubrina*, has attracted previous research in New Caledonia (Saint Girons, 1964), the Solomon Islands (Ackman et al., 1991; Cogger et al., 1987), Borneo (Stuebing, 1988), and Fiji (Guinea, 1986; Pernetta, 1977), as well as in the Philippines (Gorman et al., 1981). Nonetheless, these analyses have been concerned primarily with reproductive output rather than with courtship or mating behavior. That is, previous work has focussed on the numbers and sizes of eggs produced by females, and the seasonal timing of reproduction. Although many authors have mentioned courting aggregations of laticaudids on tropical islands (e.g., Greer, 1997; Stuebing, 1988; Voris and Voris, 1995), there have been no quantitative analyses of this phenomenon. The present paper provides the first information of this kind.

Our work focused on the following basic questions. (1) How does the general court-

ship behavior of sea kraits compare with that of previously-studied snake species? (2) 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; and/or from particular environmental conditions stimulating more intense courtship? (3) What attributes (e.g., size) of individual snakes influence whether they are found in courting groups or singly, and whether or not they mate?

METHODS

Species

Yellow-lipped sea kraits are large, black-and-white banded, amphibious snakes. They are proteroglyphous (front-fanged) species, and they may be most closely related to the terrestrial elapids of Asia and Australia (Keogh et al., 1998; McDowell, 1987). Although they forage in the ocean, both sexes spend substantial time on land. Courtship and mating may occur in the water as well as on land (Greer, 1997). The snakes also return to land to slough their skins and to digest their prey; radiotelemetric monitoring suggests that individuals of both sexes move between the land and the sea approximately once every 10 days (Shetty, 2000). Females attain much larger sizes than do males; in our study area, females of *L. colubrina* grow to 150 cm snout-vent length (SVL) and 1800 g, whereas males do not exceed 100 cm and 600 g (Shetty and Shine, 2002; Shine and Shetty, 2001).

Study Area

Mabualau (17° 97.119' S, 178° 75.6' E) lies 6 km off the south-east coast of Viti Levu, about 25 km from Suva. It is a small (4 ha) elliptical, limestone islet with a maximum height of 5 m above sea level, and it is surrounded by shallow reef flats. Mabualau (also known as "Bird Island") is uninhabited by humans apart from occasional fishing parties, and there is little anthropogenic modification of the native vegetation. In each of two successive years (1998 and 1999), we camped on Mabualau



FIG. 1.—A natural courting group of yellow-lipped sea kraits on Mabualau. The female is longer than the males that are courting her, and much thicker because her body is distended by a recently-ingested eel.

for 3-mo periods from September to December–January. This time of the year is slightly warmer (mean daily air temperature in Suva = 26.5 C in December, versus 24.5 C in June: Fiji Meteorological Service) and wetter (mean monthly precipitation = 263 mm in December versus 164 mm in June: Fiji Meteorological Service) than most other months. It coincides with the main mating period for *L. colubrina* in this area (Guinea, 1986, 1994).

Observations were made on natural courting groups throughout the study (Fig. 1). In order to conduct observations on the reproductive behavior of *L. colubrina* in more detail, in the second year of the study we set up a series of 10 open-topped 1 × 1 × 1 m polypropylene arenas on Mabualau. These arenas were held open and upright by a wooden framework. Each arena was shaded and was large enough to hold up to 12 snakes. We collected courting groups from the wild, paint-marked the animals to enable individual identification, and transferred them to the arenas with minimal disturbance. Courting always

recommenced <2 h after the snakes had been moved. All groups in arenas were monitored once per 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, with body spasms/twitching; 4 = copulating.

Before any of the snakes were released, we measured their body sizes (SVL and mass). We also placed 10 groups of randomly picked males and females (found solitary in the field) in arenas to compare the behavior of these animals to those that were in courting groups when collected.

RESULTS

Description of Courtship by Yellow-lipped Sea Kraits

The reproductive behavior of *Laticauda colubrina* can most easily be described in terms of the three “typical” phases of snake courtship defined by Gillingham (1987). The first phase, the “tactile-chase”,

involves male snakes approaching, chasing, and contacting females. Guinea (1986) observed that at 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 the female. In support of this proposition, we often found tracks of female sea kraits on the sand accompanied by tracks of several males.

The second and third phases of Gillingham's (1987) scheme involve mounting, body alignment and courting ("tactile-alignment"), and the actual copulation ("intromission and coitus"), respectively. Upon locating a female sea krait, the males attempted to mount her. If the female was still moving, the males struggled to keep up with her. The female typically showed no overt response to the males' activities. If a female lay motionless, the courting males aligned their bodies with her own and begin rhythmic contractions with their bodies draped over the female's body (Fig. 1). These rhythmic contractions by males do not fit the typical pattern of male courtship described in Gillingham's (1987) review. Courting groups of *L. colubrina* on Mabualau often remained 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 our hourly observations ($n = 1891$) of snakes in arenas, we recorded no overt activity or alignment by any of the snakes. The male snakes were aligned with the female's body on 23.5% of the observation times. Actual courtship behavior, such as a male twitching his body, was seen only in the remaining 3.5% of observations. Our data from the arena trials indicate that the average duration of continuous intense courtship exhibited by males was 2.6 h (SD = 1.8, $n = 30$). Guinea (1986) reported that the body spasms increased to about 23/min during the most intense courtship, and that copulation in *L. colubrina* lasted for only about 10 min. In contrast, 11 copulations that we observed averaged 2 h in duration (range 1–4 h).

Courting groups from Mabualau Island were comprised of one female plus 1–9 males. Of the 57 groups found during our study, 51% were male and female pairs; 16% were made up of two males and a female; and groups with 3–9 males plus a female made up the remaining 33%. Even in these large groups, we saw no evidence of male-male interaction.

What Factors Influence Courtship Intensity?

Plausibly, three different factors might interact to determine the intensity of courtship observed in any arena trial. Courtship might be more intense when (a) the arena contained females that were particularly attractive, (b) the arena 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, we examined data on the trials where we included more than one female per arena. The advantage of this data set is that we can compare the intensity of courtship directed to each female. If one female attracts significantly more male attention than the other, then we 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 our study included only one female, we used the data from the randomly-selected groups (which comprised two females and at least two males) for this analysis. To test the hypothesis, we 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 predicted a positive correlation between these differential scores. That is, if male 1 directed more courtship to female 1 than to female 2, we expected male 2 to show the same pattern. As expected, some females were significantly more attractive to males than were other females; 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. However, 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 such variation, we compared the courtship intensity directed to each of the two females within the same arena during the same trial. If factors such as weather and male traits generate variation in courtship intensity, we expected to see that in trials where one female was strongly courted, we would 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 ($r = 0.73$, $n = 113$ trials, $P < 0.0001$). 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, we 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 arenas: 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 ($F_{1,66} = 10.59$, $P < 0.002$). Courtship intensity among natural courting groups averaged 1.06 (SE = 0.07, $n = 58$ groups) on our scale of 0–4 (see above), whereas that of randomly selected individuals averaged 0.47 (SE = 0.15, $n = 10$ groups). Hence, it seems 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 (means of 120.7 cm versus 108.8 cm SVL; $F_{1,70} = 19.53$, $P < 0.0001$). The courted females were similar in body condition to the solitary females (ANCOVA with SVL as covariate, \ln mass as dependent variable: $F_{1,68} = 0.02$, $P = 0.91$). Mean body sizes of solitary males and courting males were similar, with the randomly-collected males averaging slightly larger than the courting-group animals (means of 84.0 versus 82.2 cm SVL; $F_{1,142} = 3.10$, $P = 0.08$). The randomly-collected males were slightly more heavy-bodied (on average) than the males found in courting groups (heterogeneity of slopes test with SVL as covariate and \ln mass as the dependent variable: $F_{1,140} = 4.41$, $P = 0.04$). Because of the significant differences between natural versus randomly-selected groups in traits such as female body size and male courtship intensity, all of our subsequent analyses (below) excluded data from the random groups. To avoid pseudoreplication, we 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.

*What Environmental Factors Stimulate
Sea Krait Courtship?*

(a) *Temperature.*—We tested for thermal effects on courtship intensity at two different temporal scales.

Across 2-h time periods within a day: There was little change in the courtship intensity of males due to time of day. Di-

viding the day into 12, 2-h periods, a one-factor ANOVA with time period as the factor detected no significant temporal variation in the intensity of courtship ($F_{11,352} = 1.56$, $P = 0.11$; Fig. 2).

Across 2-wk periods: To test if there was a change in courtship intensity through our study (i.e., seasonal effects), we divided the study period into 2-wk time periods. There were significant changes in the average courtship intensity of males through these two-week periods. A one-factor ANOVA with the 2-wk period as the factor revealed that courtship was more intense in early November than at other times during our study ($F_{3,516} = 19.51$, $P < 0.0001$).

(b) *Lunar cycles*.—Courtship intensity showed temporal variation relative to lunar periodicity, but no clear pattern (Spearman Rank Correlation between mean daily courtship intensity versus number of days from full moon: $r = 0.40$, $n = 15$, $P = 0.14$).

What Biological Factors Stimulate Sea Krait Courtship?

(a) *Group size*.—Group size was incorporated in the analyses in terms of operational sex ratio (OSR), 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 (Spearman Rank Correlation: $r = -0.13$, $n = 58$ groups, $P = 0.31$). 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, or the mean body sizes of the males within the group. Larger females attracted more courtship (Spearman Rank Correlation: $r = 0.34$, $n = 58$ groups, $P = 0.006$; see Fig. 3). However, heavier-bodied females (residual scores from the linear regression of \ln mass to SVL) were not courted more intensely (Spearman: $r = 0.04$, $n = 58$ groups, $P = 0.75$), and groups of larger

males did not court more or less vigorously (mean male SVL versus intensity of courtship—Spearman: $r = -0.11$, $n = 58$ groups, $P = 0.70$). The body size of a female was not correlated with the mean body size of the males found courting her (Spearman: $r = -0.20$, $n = 58$ groups, $P = 0.53$).

(c) *Feeding status of females*.—Female snakes with large prey items in their stomachs were often seen in the wild being courted intensely by males. However, 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 in the arenas ($F_{1,52} = 0.59$, $P = 0.45$). The same result was obtained in an ANCOVA, after removing the effect of female body size (see above).

What Traits Determine Male Reproductive Success?

In the arena trials, males that achieved copulation were not significantly larger or smaller than males that failed to obtain a mating ($F_{1,113} = 0.56$, $P = 0.45$ for males; Fig. 4). The same was true for male body condition (residual score from the linear regression of \ln mass versus SVL: $F_{1,139} = 1.81$, $P = 0.18$). Similarly, a female's body size did not affect whether or not she mated (Fig. 4; $F_{1,53} = 0.54$, $P = 0.47$). We did not detect any tendency to size-assortative mating (SVLs of females that copulated versus SVLs of the males they mated with—Spearman: $r = -0.01$, $n = 11$, $P = 0.44$).

DISCUSSION

Our data are broadly consistent with previous descriptions of reproductive behavior in yellow-lipped sea kraits (e.g., Guinea, 1986; Stuebing, 1988) but provide more detail than prior studies. Most published descriptions of courtship behavior in snakes have been based on terrestrial colubrids and viperids from the Northern Hemisphere (Andren, 1986; Carpenter, 1986; Carpenter and Ferguson, 1977; Klauber, 1956). Broad similarities in the form of courtship have encouraged the development of general schemes to summa-

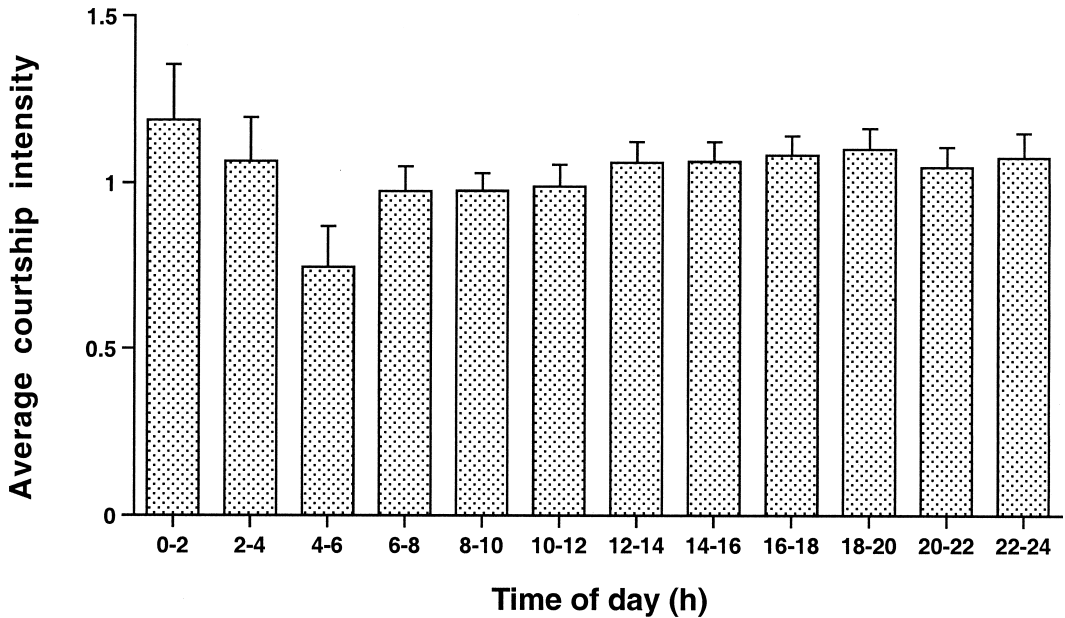


FIG. 2.—Variation in the intensity of courtship by male sea kraits as a function of the time of day. The histograms show mean values ± 1 SE for courtship intensity of males in 33 groups in arena trials, calculated separately for each 2-h period of the diel cycle. Courtship intensity was scored on a four-point scale, and was treated as a continuous variable for analysis.

rise the major phenomena involved (Gillingham, 1987). However, it is important to recognize (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

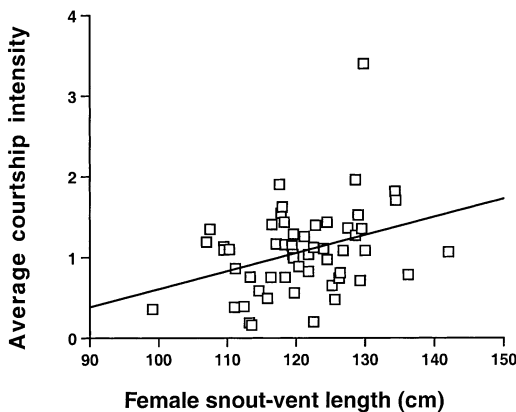


FIG. 3.—The intensity of courtship by male sea kraits as a function of the body length of the female being courted. These data were obtained from 56 groups of snakes found courting in the field and transferred to outdoor arenas. See text for statistical analysis of these data.

in terms of geographic distribution, phylogenetic relationships, and habitat types. The limited data available on other kinds of snakes suggest that courtship behavior 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.

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

One clear theme in snake courtship is a reliance on pheromonal communication

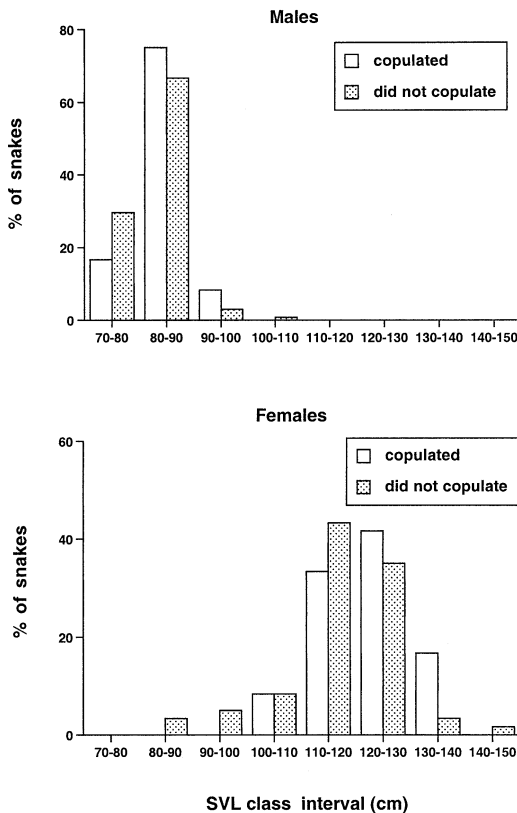


FIG. 4.—Frequency distributions of body sizes (snout-vent lengths) of sea kraits that copulated in our arena trials, compared to those that did not. Sample sizes = 12 mated males, 12 mated females, 41 unmated males, 101 unmated females.

(e.g., Ford and Low, 1984; Gartska et al., 1982; Kubie et al., 1978; Mason, 1992; Mason and Crews, 1985). 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, at least during terrestrial courtship. Frequent tongue-flicking by males pursuing females 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

behavior 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, we watched two males pursue a moving female for more than 2 h. Males essentially ignored the presence of their rivals and focussed instead on aligning their bodies with that of the female, in a position such that they could insert a hemipenis if the female elevated her tail to open the cloaca. Similar behaviors have been reported in a phylogenetically diverse array of snake species in which courting males form aggregations around receptive females (e.g., Duvall et al., 1993; Shine, 1986; Slip and Shine, 1988).

Nonetheless, the behaviors exhibited by male sea kraits during courtship differ in significant ways from those reported in other snakes. 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. Courtship lasts for a relatively brief period prior to coitus (e.g., Gillingham, 1987; Madsen and Shine, 1993). In contrast, courting male sea kraits 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 look similar to the twitching of brooding pythons to regulate egg temperatures, but more intense. At the peak of courtship, these spasms are more frequent and may lift part of the female's body off the ground. Although a female is often accompanied by more than one male (true for half of the groups in our own study), it is rare to see two males simultaneously engaged in this spasmodic twitching. Instead, they appeared to take turns in this respect. On only one occasion did we see two males actively courting the same female simultaneously. In the other cases, when one male was actively courting the female, the other males simply continued to maintain contact with the female's body.

Although females rarely showed any

overt response to courtship by males, 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. These 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, females may signal the males by waving their tails (Gillingham, 1987; Schuett and Gillingham, 1989). Males rapidly align their cloaca with that of the female and attempt to copulate. Clearly, more detailed observations are needed to test these speculations. Because these processes are extremely slow, such a test would require intensive observations over considerable lengths of time. Time-lapse video photography might facilitate such a study.

The only clear determinant of a female sea krait's attractiveness to males was her body size. This result was evidenced not only by the body sizes of females that were courted in the field (larger than non-courted females) but also, within the size range of "attractive females", by the intensity of courtship directed to females of different body sizes within arenas. Snout-vent length was the best predictor in this sense, rather than mass relative to length. Larger females typically produce more or larger offspring in *L. colubrina* as in many other snake species (e.g., Bacolod, 1983; Guinea, 1986). Thus, the fitness accruing from a mating is likely to be higher for a male mating with a large rather than small female. 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 Aleksuk, 1975, 1976). 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 (personal observations; see Fig. 1). Thus, body size rather than body shape may pro-

vide 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 was most frequent during the first 2 wk of October and November, and copulations were most frequent during November. Both courtship and copulation occurred over a relatively broad temperature range (23–29 C).

Lastly, our study provided information on the phenotypic traits of male sea kraits that obtained copulations compared to those that did not. The males that mated in our arena trials were no longer or more heavy-bodied 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, larger males typically win the battles and, thus, obtain more matings (Duvall et al., 1992, 1993; Madsen et al., 1993; Schuett, 1997). 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 our own, concluded that male body size did not influence mating success in garter snakes, *Thamnophis sirtalis* (Joy and Crews, 1988). However, a more recent study on the same population came to the opposite conclusion (Shine et al., 2000). Experimental studies on European grass snakes, *Natrix natrix* (another species with "scramble" competition rather than male–male combat), similarly reveal subtle but significant mating advan-

tages to larger males (Luiselli, 1996; Madson and Shine, 1993).

Our data are thus somewhat unusual in displaying no effect of male body size on mating success. Although the sample size of matings is low, our general observations of courtship behavior 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, the filesnake *Acrochordus arafurcae*, which likewise does not display physical struggles among rival males within mating aggregations (Shine, 1986). The clear message from our study is that we require more detailed information, on a wider range of taxa, before we can make valid general statements about the mating systems of snakes.

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