

# Aquatic and terrestrial locomotor speeds of amphibious sea-snakes (Serpentes, Laticaudidae)

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(Accepted 19 June 2002)

## Abstract

Amphibious animals may be subject to strong but conflicting selective pressures to enhance locomotor performance both on land and in the water. Biomechanical models suggest that in snakes, adaptations to swimming (e.g. reduction of ventral plates, flattening of tail) will reduce their ability to move on land. The locomotor speeds of six taxa of amphibious (laticaudid) sea-snakes, plus one entirely marine (hydrophiid) species were measured. Because the relative dependence on aquatic vs terrestrial habitats varies with a laticaudid's species, sex and body size, a previous study predicted that these factors should generate significant variation in locomotor speeds within laticaudids. Measurements of swimming and crawling speeds supported this prediction. Some species were faster than others and, within each species, males were faster than conspecific females. The degree of locomotor superiority of males was greater for terrestrial (>40%) than for aquatic (20%) locomotion. Smaller snakes were faster than larger animals in relative speed (body lengths/s) but slower in absolute terms (m/s). The hydrophiid *Emydocephalus annulatus* was slow in water as well as on land, perhaps because it eats immobile prey and thus, does not depend on speed for foraging. The diversity of locomotor abilities within laticaudid sea-snakes provides a remarkable opportunity to identify factors that influence evolutionary trade-offs between conflicting evolutionary optima.

**Key words:** crawling, *Laticauda*, sea krait, swimming, trade-off

## INTRODUCTION

It is impossible to simultaneously optimize performance in two tasks that require mutually incompatible morphologies or physiologies. Under such circumstances, natural selection is expected to result in some intermediate phenotype that provides reasonable performance at both tasks but optimal performance in neither (Gans, 1974; Gould & Lewontin, 1979). Because such trade-offs may be widespread, information on phenotypic traits under such conflicting selective forces may provide general insights into the nature of adaptive compromises. Conflicting optima can occur for many kinds of traits, but the easiest to study are those in which performance can be easily quantified and optima identified. Locomotor speed is convenient in this sense, because it is readily measured and presumably, faster is generally better. The speed that an animal moves may determine its ability to evade predators and/or capture prey, and hence we expect that locomotor abilities will be under strong selection in many species (Arnold & Bennett, 1988).

However, the evolution of rapid locomotion may be constrained by the organism's need to move effectively in a

variety of situations that require different (and potentially, contradictory) morphological adaptations. For example, adaptations that enhance a lizard's ability to run across a flat surface may be incompatible with adaptations that enhance its climbing ability (Losos, 1990; Losos, Walton & Bennett, 1993; but see Vanhooydonck, Van Damme & Aerts, 2000). Similarly, muscle structures that optimize swimming in snakes may differ from those that optimize terrestrial movement (Jayne, 1982). Thus, the most clearcut examples of trade-offs in locomotor performance involve species that move in highly contrasting ways, such as running vs flying or swimming. If these different locomotor tasks require conflicting morphological adaptations, then studies of relative locomotor ability in the two habitats may enable quantification of the trade-offs involved. That is, to what degree do adaptations to one locomotor mode constrain performance in another, and how do factors such as an organism's species, sex and body size influence its relative proficiency in the two tasks?

Snakes provide excellent model systems with which to investigate this topic. Although terrestrial crawling and aquatic swimming are superficially similar activities, their biomechanical basis differs profoundly. In terrestrial lateral undulatory locomotion, the propulsive forces are generated by the lateral surfaces of the body as they

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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): snakes that show the most extreme adaptations for aquatic locomotion (flattened paddle-like tails, reduction of ventral scutes, etc.) are typically slow when moving on land (Heatwole, 1999). The most interesting cases involve amphibious animals that are presumably under selection for effective locomotion both on land and in the water. Proteroglyphous (front-fanged) snakes provide several examples of such 'intermediate' stages in the evolutionary progression from purely terrestrial to purely aquatic locomotion, with the most diverse and speciose lineage being the sea kraits (Laticaudidae). These snakes forage in the ocean (two in a freshwater lake) but return to land to digest their prey, to slough their skins, to court, to mate and to lay their eggs (Heatwole & Guinea, 1993). Some laticaudid species spend considerable time on land and may move far inland (e.g. *L. colubrina*) whereas others are rarely found far from the water's edge (e.g. *L. crockeri*; Cogger *et al.*, 1987). Even within a single population, the sex and body size of the snake influence the proportion of time it spends in the water (Shetty & Shine, 2002c).

In the only previous study of locomotor ability in sea kraits, Shine & Shetty (2001a,b) quantified speeds of crawling and swimming in a Fijian population of the widespread taxon *Laticauda colubrina*. These authors reported that the snakes not only swam much faster than they crawled, but also that their locomotor speeds were affected by body size and sex. For example, small snakes were slower than larger conspecifics in absolute speed (m/s), but faster in terms of relative speed (body lengths/s). Males were faster than females, especially on land. During fieldwork with other laticaudid species, locomotor speeds of snakes were measured both on land and in the water. Our aim was to assess the generality of patterns detected for Fijian *L. colubrina* by Shine & Shetty (2001b), such as the male superiority in locomotor speeds. We also wished to test the prediction of significant interspecific diversity in aquatic vs terrestrial locomotor abilities within this lineage of snakes. Additionally, we took advantage of an opportunity to record swimming and crawling speeds of a 'true' (entirely aquatic) sea-snake, the hydrophiid *Emydocephalus annulatus*, for comparison with the amphibious laticaudids.

## MATERIALS AND METHODS

### Study species

Laticaudid sea-snakes are abundant on many island groups within the Pacific Ocean (Cogger, 1975; Heatwole, 1999). Radio-telemetric monitoring of Fijian *L. colubrina* showed that these animals spend approximately equal time

on the land and in the ocean, moving between the 2 habitats on a weekly or fortnightly basis (Shetty & Shine, 2002c). Presumably reflecting their strong philopatry (Shetty & Shine, 2002b), populations frequently display significant morphological divergence between different island groups. For example, the *L. 'colubrina'* from New Caledonia are morphologically distinct from other populations of this species. Current revisions will certainly increase the number of species recognized within the Laticaudidae (H. G. Cogger, pers. comm.). Thus, for the purposes of this paper, isolated populations of the 2 wide-ranging laticaudid 'species' (*L. laticaudata* and *L. colubrina*) are treated as separate taxa. The 'species' studied were:

- (1) *L. colubrina*, a large heavy-bodied snake with a wide geographic distribution. Fijian and Vanuatu specimens are banded in black and white, whereas New Caledonian animals have a brown to orange coloration between the black bands;
- (2) *L. frontalis*, a dwarf taxon endemic to Vanuatu and the Loyalty Islands, and superficially similar to *L. colubrina* except for its much smaller body size;
- (3) *L. laticaudata*, a geographically widespread slender-bodied taxon with brilliant blue between the black bands;
- (4) the turtle-headed sea-snake *Emydocephalus annulatus*, a shallow-water hydrophiid species that spends its life in the ocean, never emerging onto land.

### Methods

Snakes were collected by hand, usually while the animals were active on land or in shallow water. The Vanuatu snakes were collected in November 2000 on the island of Efate, within 20 km of the village of Paoningisu (Nagar Resort: 17°35'S, 168°29'E). The New Caledonian laticaudid specimens were collected in January 2002 from small islands (Porc-Epic and Signal) in the Noumea Lagoon (22°16'S, 166°26'E). The *Emydocephalus* was collected in the Baie des Citrons off Noumea, and were measured and tested within 2 h of capture to reduce stress. Most laticaudids were also tested within 1 day of capture, but some were maintained in damp cloth bags for a few days before testing. Table 1 lists the sample sizes and mean body sizes of our samples, and also includes the Fijian sample of *L. colubrina* upon which Shine & Shetty's (2001b) work was based. Raw data from that study were used to compare the Fijian snakes with those from other areas.

Each snake's snout-vent length (SVL), tail length and mass were recorded, and its sex determined by tail shape and/or manual eversion of hemipenes. Locomotor speeds were measured in wooden raceways 2.5 m long, 28 cm wide, and with wooden walls 30 cm high. The top of the raceway was open, allowing us to film snakes as they moved along the track. For the terrestrial trials, the bottom of the raceway was removed and the sides were set down on firmly compacted, level damp sand on a beach near the

**Table 1.** Sample sizes and body sizes of sea-snakes for which locomotor speeds were measured. NC, New Caledonia

Species	Location	Sex	N	Snout-vent length (cm)		Mass (g)	
				Mean (SE)	Range	Mean (SE)	Range
<i>Laticauda colubrina</i>	Fiji	Female	46	90.7 (4.7)	35–131	443.7 (53.6)	10–1360
<i>L. colubrina</i>	Fiji	Male	38	71.5 (2.3)	37–92	161.1 (13.1)	17–310
<i>L. colubrina</i>	Vanuatu	Female	22	81.7 (6.5)	44–136	253.5 (57.7)	26–906
<i>L. colubrina</i>	Vanuatu	Male	20	65.0 (3.4)	40–89.3	111.0 (15.4)	26–227
<i>L. colubrina</i>	NC	Female	14	90.4 (2.2)	78–107	299.3 (28.9)	150–500
<i>L. colubrina</i>	NC	Male	15	70.8 (1.7)	54–80	149.6 (8.3)	80–190
<i>L. frontalis</i>	Vanuatu	Female	10	64.0 (3.5)	41–78	108.5 (13.0)	30–176
<i>L. frontalis</i>	Vanuatu	Male	11	57.3 (2.0)	40–65	84.2 (5.6)	46–119
<i>L. laticaudata</i>	NC	Female	13	76.5 (6.6)	48–115	169.7 (40.5)	30–430
<i>L. laticaudata</i>	NC	Male	16	80.7 (3.9)	44–96	164.5 (20.5)	38–330
<i>L. laticaudata</i>	Vanuatu	Male	13	73.9 (4.2)	41–88	130.9 (16.8)	25–216
<i>Emydocephalus annulatus</i>	NC	Female	6	53.4 (4.7)	38–66	177.5 (38.8)	55–280
<i>E. annulatus</i>	NC	Male	10	52.3 (1.3)	46–60	124.6 (10.6)	81–196

water's edge. For aquatic trials the raceway was submerged to 20 cm depth in water. Body temperatures of snakes and water temperatures were taken immediately before and after trials; all were within the range 26–29 °C, and did not change during the trial. Each snake was released at 1 end of the raceway and encouraged to move down it by light taps on the tail. Each snake was run twice, and then rested for at least 60 min before being tested in the other habitat. Half the snakes were run on land first and then water, and the other half in water first and then on land. Preliminary analysis showed that the order of testing did not affect locomotor speeds, so this factor was deleted from the analyses.

Throughout each trial, snakes were filmed 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, the mean speed for each snake and its' fastest speed over any 50-cm segment of the raceway was determined. Our analyses did not include speeds over the first or last segments of the raceway, to avoid situations where the snakes were clearly accelerating or decelerating. Our analyses are based on 2 measures of speed: both absolute (m/s) and relative (body lengths (SVLs)/s). Van Damme & Van Doren (1999) suggested that the latter variable offers a more robust measure of locomotor performance than absolute speed, and may be a better indicator of the snake's ability to evade predation. However, too little is known of the ecological significance of locomotor speeds in laticaudids to judge the relative significance of the 2 types of measures, and thus both were included.

The simplest way to evaluate relative locomotor speeds of 1 sex compared to the other, or in water vs on land, is to compute a ratio of the 2 speeds. This approach was used; but the calculation method was slightly modified to ensure symmetry above and below a ratio of 1.0 (Gibbons & Lovich, 1990). This technique involves calculating the

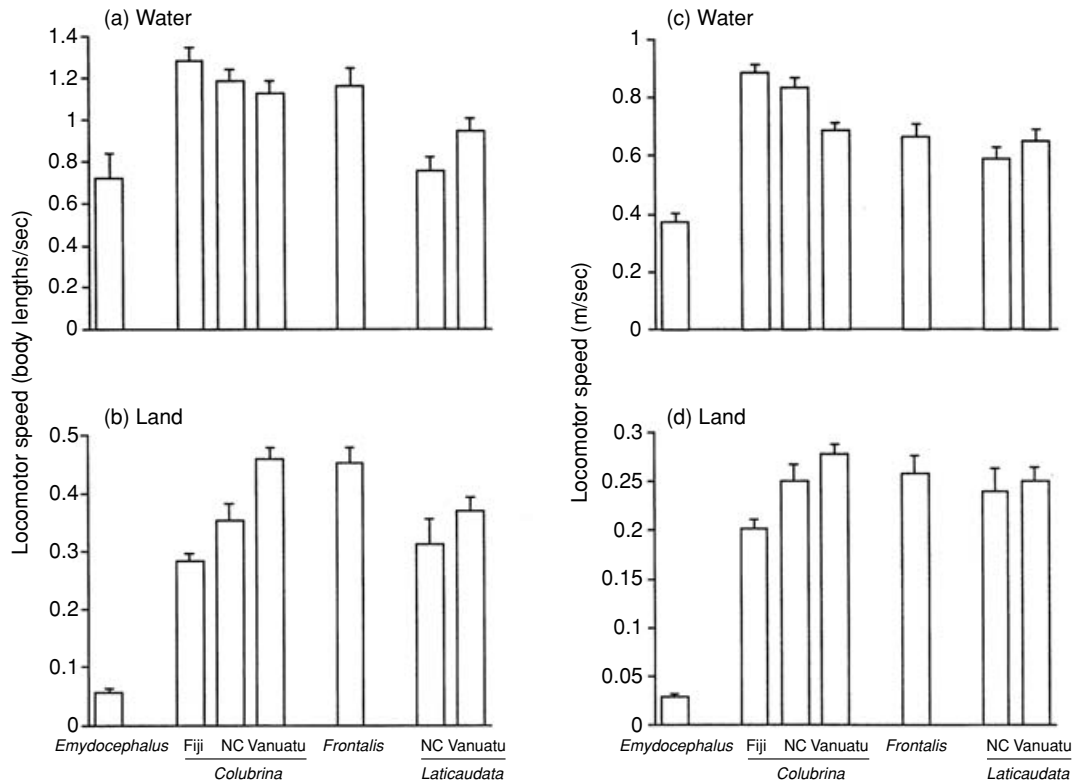
ratio of the larger to the smaller number, with the result arbitrarily scored as negative or positive depending on the direction of the difference (positive if males were faster than females, or if snakes swam faster than they crawled).

## RESULTS

Data were obtained for 134 laticaudids (75 males, 59 females) and 16 hydrophiids (10 males, six females). Together with data on 84 Fijian *L. colubrina* from Shine & Shetty's (2001b) study, these provide the most extensive data yet available on the locomotor speeds of amphibious snakes. Considerable diversity was evident in locomotor speeds, with individual snakes crawling at mean speeds of 0.02–0.63 body lengths/s (0.02–0.46 m/s), and swimming at 0.35–2.04 body lengths/s (0.23–1.41 m/s). Below, the effect of species, sex and body size on locomotor speeds in water and on land are documented.

### Differences among species

Because of significant sex differences in locomotor ability (see below), our comparisons among species were based only on males (the sex for which we had largest sample sizes). A one-factor repeated-measures ANOVA with species as the factor, habitat (land/water) as the repeated measure and average relative speed (body lengths/s) as the dependent variable, revealed a highly significant interaction term ( $F_{6,111} = 11.30, P < 0.0001$ ). That is, species differed in the way in which habitat type affected speeds relative to body length. Excluding the hydrophiid (*Emydocephalus*) from this analysis did not alter the result (interaction  $F_{5,102} = 12.77, P < 0.0001$ ). Because this interaction renders main effects uninterpretable, separate one-factor ANOVAs on speed in either land or water were made separately. Interspecific differences were highly significant both for aquatic speeds ( $F_{6,111} = 11.09, P < 0.0001$  see Fig. 1a) and for terrestrial speeds ( $F_{6,111} = 27.91, P < 0.0001$  see Fig. 1b). *Post hoc*

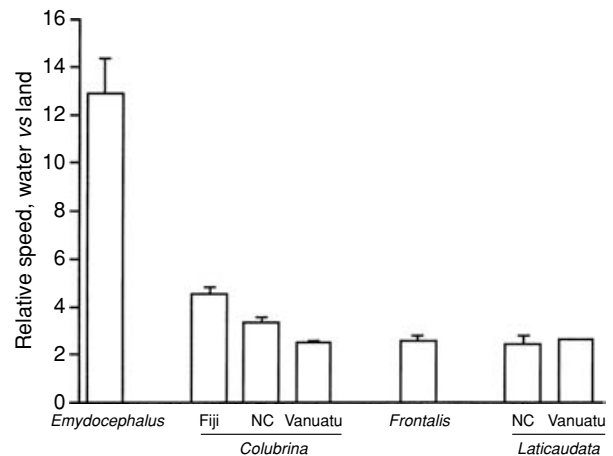


**Fig. 1.** Locomotor speeds of five taxa of laticaudid sea-snakes and one hydrophiid sea-snake species. (a) and (b), Speed in relative terms (body lengths/s); (c) and (d), absolute speeds (m/s); (a) mean speeds (body lengths/s) for snakes travelling along a raceway through water; (b) mean speeds (body lengths/s) of snakes crawling on firm sand; (c) mean speeds (m/s) for snakes travelling along a raceway through water; (d) mean speeds (m/s) of snakes crawling on firm sand. NC, New Caledonia; error bars, 1 SE.

(Fishers' PLSD) tests showed that many species differed significantly from each other, even in closely related taxa. For example, *L. colubrina* from Vanuatu crawled significantly faster than *L. colubrina* from New Caledonia, which in turn were significantly faster than *L. colubrina* from Fiji ( $P < 0.05$  in each comparison). However, swim speeds of these three taxa did not differ significantly (*post hoc* all  $P > 0.05$ ).

Absolute speeds (m/s) showed very similar patterns to the relative speeds analysed above. The repeated-measures ANOVA showed that species differed in the way in which habitat type affected speeds (interaction  $F_{6,111} = 20.59$ ,  $P < 0.0001$ ; excluding *Emydocephalus*,  $F_{5,102} = 20.71$ ,  $P < 0.0001$ ). Separate ANOVAs confirmed highly significant interspecific differences in absolute locomotor speeds both on land ( $F_{6,111} = 22.80$ ,  $P < 0.0001$ ) and in water ( $F_{6,111} = 23.53$ ,  $P < 0.0001$ ). Figures 1c, d show these data.

To clarify the effects of habitat type on locomotor speeds among taxa, we calculated relative speeds in the water vs on land (i.e. mean swimming speed divided by mean crawling speed) for each animal. This measure is identical whether based on absolute or relative speeds. A one-factor ANOVA on this ratio confirmed that the ratio of terrestrial to aquatic speeds differed among species ( $F_{6,111} = 21.80$ ,  $P < 0.0001$  see Fig. 2). *Post hoc* tests showed that most pairwise comparisons were significant, including all those among different populations of



**Fig. 2.** Speeds in water divided by those on land, for five taxa of laticaudid sea-snakes and one hydrophiid sea-snake species. NC, New Caledonia; error bars, 1 SE.

*colubrina* ( $P < 0.05$ ). In summary, males of different laticaudid taxa differ in their locomotor speeds on land and (to a lesser degree) in the water, with the result that relative locomotor ability in the land vs the water also differs significantly among species. As expected, the hydrophiid tested was poor at terrestrial locomotion (Fig. 1b), but also, was not particularly fast when swimming (Fig. 1a).

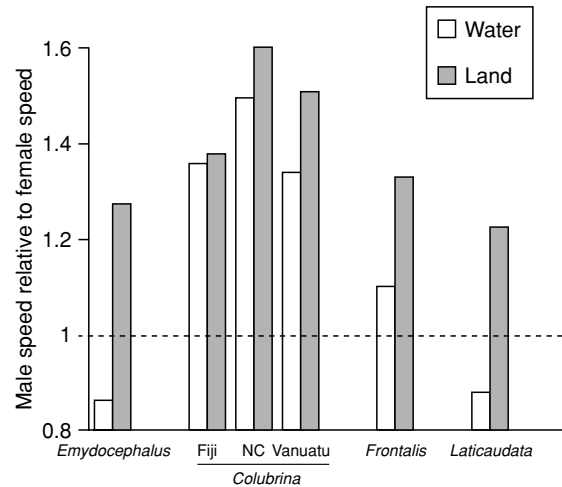
### Differences between sexes

A two-factor repeated-measures ANOVA with species and sex as the factors, habitat (land/water) as the repeated measure and average relative speed (body lengths/s) as the dependent variable, revealed a highly significant interaction term between species, sex and habitat ( $F_{5,204} = 3.50$ ,  $P < 0.005$ ; omitting Vanuatu *L. laticaudata* for which no females were available). That is, the way in which sex affected relative locomotor ability on land vs water differed among species. To clarify this effect, separate two-factor ANOVAs on speeds in land and water were conducted separately. Again, however, the analyses revealed significant interactions between sex and species both for terrestrial ( $F_{5,204} = 2.76$ ,  $P < 0.02$ ) and aquatic ( $F_{5,204} = 3.81$ ,  $P < 0.003$ ) locomotion. That is, sex affected locomotor speed relative to SVL differently in different species, both on land and in the water. A similar analysis on absolute speeds (m/s) also showed a significant three-way interaction term ( $F_{5,204} = 2.73$ ,  $P < 0.03$ ). Separate two-factor ANOVAs on absolute speed had non-significant interactions between sex and species (for terrestrial speeds,  $F_{5,204} = 1.59$ ,  $P = 0.17$ ; aquatic speeds,  $F_{5,204} = 2.25$ ,  $P = 0.05$ ), facilitating interpretation of the main effects. Species differed significantly in absolute speeds (terrestrial,  $F_{1,204} = 31.73$ ,  $P < 0.0001$ ; aquatic,  $F_{1,204} = 21.67$ ,  $P < 0.0001$ ). More interestingly, absolute speeds were higher for males than females in terrestrial locomotion ( $F_{1,204} = 28.65$ ,  $P < 0.0001$ ) but not in swimming ( $F_{1,204} = 1.86$ ,  $P = 0.17$ ).

The ratio of speed in water divided by that on land was thus examined. The interaction term in this two-factor ANOVA was non-significant ( $F_{5,204} = 1.98$ ,  $P = 0.08$ ), facilitating interpretation of the main effects. Both were significant. A snake's speed in water vs that on the land was affected not only by its species ( $F_{5,204} = 28.79$ ,  $P < 0.0001$ ) but also by its sex (males were faster than females;  $F_{1,204} = 11.22$ ,  $P < 0.0001$ ). Figure 3 provides a graphical analysis of these data in terms of the ratio of male to female speeds, and shows that the margin by which male snakes exceeded speeds of conspecific females averaged 17% in water, vs 44% on land (Fig. 3; for laticaudids only, 24 vs 48%). In summary, male laticaudids were quicker than females, and this sex difference was more pronounced on land than in the water.

### Effects of body size

A snake's body size affected its locomotor speed in all species tested. For simplicity, these data were analysed with a two-factor ANCOVA (species group (*colubrina* or *laticaudata*) and sex as factors, SVL as covariate) and mean speeds as dependent variables. Species-group was used rather than species in this analysis because of the broad similarity in body shape within each of these two clades. For relative speeds (i.e. body lengths/s), larger snakes were slower both on land ( $F_{1,208} = 83.76$ ,  $P < 0.0001$ ) and in the water ( $F_{1,208} = 196.05$ ,



**Fig. 3.** Sex differences in locomotor speed for five taxa of laticaudid sea-snakes and one hydrophiid sea-snake species. The ratio of male to female speeds for each species is given separately for swimming and crawling. Dotted horizontal line, males and females equally fast; above dotted line, males faster than females. For ratios  $< 1.0$ , the method of Gibbons & Lovich (1990) was used to achieve symmetry (i.e. equal decrements in the independent variable generated equal shifts in the ratio). NC, New Caledonia. See text for further explanation.

$P < 0.0001$ ). However, larger snakes were faster not slower than smaller conspecifics when absolute speeds (m/s) were used as the dependent variables (land,  $F_{1,208} = 8.04$ ,  $P < 0.005$ ; water,  $F_{1,208} = 12.70$ ,  $P < 0.0005$ ). A snake's body size did not influence its relative ability to move about on land vs in the water (two-factor ANCOVA with species and sex as factors, and water/land speed ratio as the dependent variable: effect of SVL,  $F_{1,208} = 0.30$ ,  $P = 0.59$ ). These patterns were consistent among individual species as well as in the overall dataset.

### Effects of body shape

To test whether a snake's tail length and mass (relative to its SVL) influence its locomotor speed, these two factors were introduced as additional covariates (together with SVL) in a two-factor ANCOVA as above. To quantify shape variation, residual scores from the general linear regression of either tail length against SVL, or  $\ln$  mass against SVL were used to generate descriptors that were uncorrelated with SVL. No interaction terms in these ANCOVA analyses were significant for absolute or relative speeds either on land or in water. Thus, we can delete these non-significant interactions and examine main effects and covariates only. SVL remained a significant covariate in all analyses, reinforcing the conclusions above. Males were also significantly faster than females for terrestrial but not aquatic speeds (both absolute and relative), again mirroring the above results. Relative body mass (i.e. mass relative to SVL) significantly influenced the speed of terrestrial locomotion, both in absolute terms

( $F_{1,203} = 7.35$ ,  $P < 0.005$ ) and relative to body length ( $F_{1,203} = 4.33$ ,  $P < 0.04$ ). However, neither sex nor relative body mass significantly affected aquatic speeds (all  $P > 0.05$ ). Tail length relative to SVL did not exert a significant influence in any of the ANCOVAs. The two species groups differed in swimming speeds (*colubrina* were faster than *laticaudata*, in terms of absolute speeds ( $F_{1,207} = 12.60$ ,  $P < 0.005$ ) as well as relative to SVL ( $F_{1,207} = 16.94$ ,  $P < 0.0001$ ) but crawling speeds were similar between snakes from the two lineages (all  $P > 0.05$ ).

These analyses indicate that heavier-bodied snakes were slower on land but not in the water, and that relative tail length did not influence speeds significantly. Equally, the continued significant effects of sex and species-group suggest that the differences in terrestrial speed between males and females, and the differences in swimming speeds between *colubrina* and *laticaudata*, are not simply the result of sex-based or species-based divergence in either mass or tail length relative to SVL.

## DISCUSSION

Our data show that locomotor speeds of amphibious sea-snakes vary among species, differ between the sexes within species, and shift with body size. A snake's species and sex also affect its relative speed in terrestrial vs aquatic locomotion. Below, each of these effects are examined with the aim of evaluating conclusions and predictions from an earlier study (Shine & Shetty, 2001b).

### Differences among species

Highly significant interspecific differences were found in mean speeds both on land and in water, and in relative speeds in one medium vs the other. Among laticaudids, males of the different taxa averaged  $< 0.8$  to  $> 1.2$  body lengths/s in water, a 50% variation among taxa. Speeds on land were much slower (species means  $< 0.3$  to  $> 0.45$  lengths/s) but with a similar level of interspecific variation. The relatively heavy-bodied *L. colubrina* was faster than the elongate *L. laticaudata* in water (Fig. 1a) but not on land (Fig. 1b). This result runs counter to the simple prediction that locomotor speeds of laticaudids will mirror their relative usage of aquatic vs terrestrial habitats (Shine & Shetty, 2001b). *Laticauda colubrina* is more frequently reported in terrestrial locations, including those far from the water, than is the more strictly aquatic *L. laticaudata* (Greer, 1997). The biomechanical bases for the interspecific variation in locomotor performance remain unknown. The laticaudid taxa in our sample display considerable variation in morphological traits that might influence locomotor performance (Shine & Shetty, 2001a). However, analyses that held the two most obvious such traits constant (body mass relative to SVL; tail length relative to SVL) did not eliminate the interspecific or sex-based differences in speeds. Examining the morphology

of these animals in much greater detail may offer a useful model system in which to identify the morphological determinants of variance in locomotor speeds.

### Differences between sexes

Male laticaudids were significantly faster than conspecific females in all of the taxa studied, especially in trials conducted on land (Fig. 2). This sex difference in relative locomotor abilities was noted for Fijian *L. colubrina* by Shine & Shetty (2001b), and our more extensive dataset suggests that it is a general feature of laticaudid biology. The morphological features and ecological pressures that have generated this difference remain unknown. Terrestrial movements may be more important for (mate-searching) males than for females in most or all laticaudid species, as suggested by Shine & Shetty (2001b). Alternatively, faster locomotion by males than females may be widespread even in terrestrial snakes (e.g. *Thamnophis*. Kelley, Arnold & Gladstone, 1997, but see Jayne & Bennett, 1989). Intriguingly, our results for laticaudids mirror those of Scribner & Weatherhead (1995) for North American natricine snakes: males were faster than females, and this sex difference was greater for terrestrial than for aquatic locomotion. These sex differences in locomotor speed may reflect a trend for greater relative muscle mass in male snakes than in conspecific females (Bonnet *et al.*, 1998).

### Effects of body size and shape

As in Fijian *L. colubrina* (Shine & Shetty, 2001b), larger snakes were found to be faster in absolute terms, but not relative to body size. However, our results for relative tail length differed from those of Shine & Shetty (2001b), in that no significant effects of relative tail length on locomotor abilities were found. A more thickset body shape (greater mass relative to SVL) impaired locomotor speeds on land but not in the water, as predicted from biomechanical models that include the differing effects of gravity in water vs on land. Unfortunately, interpretation of such patterns in terms of selective forces is impossible without more information. For example, is absolute or relative speed more significant for organismal fitness? Plausibly, both may be targets of (opposing) selection. Our ignorance of such selective forces precludes understanding how variation in locomotor speeds might translate into variation in fitness. Laticaudids may be under selection to escape predators both on land (sea eagles: Stuebing, 1988; Shetty & Prasad, 1996) and in the sea (tiger sharks: Heatwole, 1999; P. Laboute, pers. comm.), but there is likely to be strong geographic variation in such pressures. For example, sea eagles do not occur in New Caledonia, but ospreys sometimes consume sea kraits there (F. Bernaleau, pers. comm.). The role of locomotor speeds in foraging remains equally unclear. The snakes probably capture their prey (mainly moray and conger eels: Cogger *et al.*, 1987; Shetty & Shine, 2002a)

in crevices (Radcliffe & Chiszar, 1980) and thus, speed may not be crucial for foraging success. The same factors may explain the slow speeds recorded for *Emydocephalus* (Fig. 1). Although intuition suggests that a fully aquatic snake species should have enhanced swim speeds (because it is no longer constrained by conflicting requirements for terrestrial locomotion), this species feeds entirely on immobile prey (fish eggs: Heatwole, 1999) and hence, may derive little benefit from rapid swimming.

In summary, the major result from this study has been to document significant variation in locomotor speeds of amphibious snakes, and to identify three factors that generate much of this variation: species, sex and body size. The magnitude of locomotor variation induced by each of these three factors is similar, and so large (c. 50% differences in mean speeds among species, between sexes, and across the size range within populations) that it seems unlikely to be trivial in terms of effects on fitness. Unfortunately, it is difficult to link this variation to selective forces, or to discern the biomechanical factors responsible. Previous studies on the action of natural selection on locomotor speeds in snakes (Jayne & Bennett, 1990) and on the biomechanics of locomotion (e.g. Arnold & Bennett, 1988; Kelley *et al.*, 1997) have dealt primarily or entirely with terrestrial rather than aquatic species. Our study reveals a high level of variation in locomotor traits of laticaudid sea-snakes, but detailed ecological and morphological research is needed before either the proximate (mechanistic) or the ultimate (evolutionary) mechanisms underlying that diversity can be understood.

### Acknowledgements

Our fieldwork in Vanuatu was expedited by the people of Paoningisu village (especially, Chief Henry Cyrell), and our work in New Caledonia was made possible by assistance from Pierre Laboute and P. Borsa (IRD), Claire Gorain, Sylvain Perron, Fabrice Bernaleau and Jocelyn Dubois (Noumea Aquarium). We thank John Llewelyn for scoring videos, R. Cambag and V. Watch for general assistance, and the Australian Research Council for funding. Long-term research opportunities and manuscript preparation were aided by Contract DE-AC09-76SROO-819 between the U.S. Department of Energy and the University of Georgia's Savannah River Ecology Laboratory and with Financial Assistance Award Number DE-FC09-96SR18546 from U.S. Department of Energy to the University of Georgia Research Foundation.

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