Terrestrial locomotion in sea snakes: the effects of sex and species on cliff-climbing ability in sea kraits (Serpentes, Elapidae, *Laticauda*)

X. BONNET[1]*, I. INEICH[2] and R. SHINE[3]

[1]*CEBC–CNRS, 79360, Villiers en Bois, France*
[2]*Muséum national d'Histoire naturelle, Département de Systématique et Evolution, USM 602 Taxonomie et Collections—Reptiles & Amphibiens, Case Postale No30, F-75231 Paris Cedex 05, France*
[3]*Biological Sciences A08, University of Sydney, New South Wales 2006, Australia*

Ecomorphological theory predicts a match between an organism's environment and its locomotor abilities, such that animals function most effectively under the conditions they experience in nature. However, amphibious species must simultaneously optimize performance in two different habitats posing incompatible demands on locomotor morphology and physiology. This situation may generate a mismatch between environment and locomotor function, with performance optimized only for the more important habitat type; alternatively, selection may fine-tune locomotor abilities for both types of challenges. Two species of sea kraits in New Caledonia offer an opportunity to examine this question: *Laticauda laticaudata* is more highly aquatic than *L. colubrina*, and males are more terrestrial than females within each taxon. We examined an aspect of locomotor performance that is critical to coming ashore on steep-walled rocky islets: the ability to climb steep cliffs. We also measured the muscular strength of these animals, a character that is likely critical to climbing performance. *Laticauda colubrina* was heavier-bodied and stronger (even relative to its body mass) than the more aquatic *L. laticaudata*; and within each species, males were heavier-bodied and stronger than females. The same patterns were evident in cliff-climbing ability. Thus, the ability of different species and sexes of sea kraits to climb steep cliffs correlates with their body shape even though these primarily aquatic animals use terrestrial habitats only rarely. © 2005 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2005, **85**, 433–441.

ADDITIONAL KEYWORDS: adaptation – body shape – escape tactic – muscular strength – sex dimorphism.

INTRODUCTION

Most animals need to move about during their day-to-day activities and therefore more effective and/or efficient locomotion presumably enhances individual fitness (Losos, Irschick & Schoener, 1994; Barbosa & Moreno, 1999; Irschick, 2003). For example, high speed and stamina enhance the ability to escape predators, and consequently are likely to enhance lifetime reproductive success (Domenici & Blake, 1991; Srygley & Kingsolver, 2000); thus, performance ability is often used as an intermediate step between morphology and fitness (Arnold, 2003). Accordingly, we expect,

and see, a broad match between the locomotory challenges posed by an organism's environment, and its ability to move around in that type of environment (Losos, Walton & Bennett, 1993, 1994; Bauwens *et al*., 1995; Melville & Swain, 2000; Vanhooydonck, Van Damme & Aerts, 2000; Irschick & Garland, 2001; Irschick, 2002). However, the issue becomes complex when an organism exploits more than one type of environment, especially when the different habitats pose different, incompatible selective pressures on locomotory ability (Gillis, 1998; Biewener & Corning, 2001; Ashley-Ross & Bechtel, 2004). In such cases, at least two outcomes are plausible. First, selection may produce a phenotype that is able to move around effectively in both habitats, somehow avoiding the

*Corresponding author. E-mail: bonnet@cebc.cnrs.fr

tradeoffs that would seem implicit in the two locomotory challenges. Second, the organism may remain well adapted to one (primary) habitat, substantially sacrificing locomotor performance in the other (minor) habitat type. Whether or not such constraints have shaped organismal phenotypes has been a major debate in evolutionary biology (Gould, 1980; Lauder, 2000).

The two alternatives posed above are amenable to direct empirical testing. If organisms can simultaneously optimize locomotor performance in two dissimilar habitats, we expect to see a match between the extent to which an organism uses the 'minor' habitat type and its performance in that habitat: animals that rely more upon the 'minor' habitat should be better able to deal with the locomotory challenges that it poses. In contrast, the second alternative suggests that locomotor performance within the 'minor' habitat should be unrelated to small differences in usage; that is, we should not detect specific adaptations for locomotor performance in the 'minor' habitat. To test this proposition, we need a study system with multiple entities (species, sexes) differing in their use of the minor habitat type; and the physical challenges posed by the minor habitat type should differ dramatically from those posed by the primary habitat. For example, in many taxa, male mating success increases with mobility. Hence, we may expect that males would be able to cope with the 'minor' habitat locomotor challenge more efficiently than would conspecific females.

Amphibious sea snakes (genus *Laticauda*) in the Pacific Ocean are well-suited to such a study. These snakes move about extensively to forage in the ocean for eels, but return to land to court, mate, slough their skins, digest their prey, and lay their eggs (Saint Girons, 1964; Pernetta, 1977). While on land, the snakes are relatively sedentary (Shetty & Prasad, 1996; Shetty & Shine, 2002). Radiotelemetric studies suggest that the snakes probably return to land about once a week, often selecting gently sloping rather than steep cliffs to do so (Shetty & Shine, 2002). However, some of the islands (or at least major areas along the island's edge) that these snakes use for hauling-out are steep-sided, such that snakes must navigate vertical cliffs to reach flat land above. The ability to climb steep cliffs offers a dramatically different locomotory challenge than that posed by swimming, and we might expect strong trade-offs between the features that facilitate each of these disparate activities (Clobert *et al.*, 2000; Shine & Shetty, 2001; Vanhooydonck *et al.*, 2001; but see Van Damme, Aerts & Vanhooydonck, 1997; Vanhooydonck & Van Damme, 2001). Importantly, there is substantial interspecific and intraspecific diversity among sea kraits in the degree of dependence on terrestrial habitats (and hence, on

the importance of cliff-climbing ability). For example, *L. colubrina* frequently travels long distances overland, with males moving significantly further from the beach than do females, perhaps in order to maximize the number of contacts with females (Shetty & Shine, 2002). The same sex difference is evident in *L. laticaudata*, but this species is rarely found >2 m from the water's edge (pers. observ.). Previous research has quantified locomotor speeds of sea kraits swimming in water and travelling across flat terrestrial surfaces (Shine & Shetty, 2001; Shine *et al.*, 2003), but cliff-climbing in these snakes (although often seen in the field: Greer, 1997; pers. observ.) has not attracted any previous study.

The main goal of this paper was to examine the extent to which differences between the four snake categories (two species, two sexes) in ability to traverse the 'minor' habitat (cliffs), was related to differences in their usage of that habitat. We predicted that the most terrestrial species, and the most terrestrial sex (males) within each species, will exhibit the best climbing abilities.

MATERIAL AND METHODS

STUDY SITE, STUDY SPECIES AND COLLECTION METHODS

In November and December 2003 we visited three islets (Îlot Signal, Îlot Brosse, and Îlot Bayonnaise) in the lagoon of New Caledonia. Two species of sea-kraits (locally named 'tricots rayés'; Ineich & Laboute, 2002) are common on each of these islets: *Laticauda colubrina* (common tricot rayé) and *L. laticaudata* (blue tricot rayé). During their transitions between the sea and the land, these snakes sometimes have to climb steep cliffs. Although such activities represent a very small proportion of the total time spent moving by these snakes on a weekly or monthly basis, they nonetheless comprise a significant locomotor challenge. We collected the snakes by hand and kept them in calico bags for 1–10 h before measuring. We recorded each snake's sex (by tail shape in adults and/or eversion of hemipenes in juveniles), snout vent length (SVL, the snake was stretched along a flexible ruler tape attached to a large plank), tail length (± 1 cm) and body mass (BM, ±1 g). We gently palpated the abdomen of each snake to detect prey (moray eels and conger eels) or enlarged ovarian follicles (or eggs). All the snakes were released <24 h after capture.

### MEASURES OF MUSCULAR STRENGTH

The relatively simple morphology of snakes facilitates assessment of their muscular mass and strength in the field. First, dissections have shown that variation

in the mass of muscles used for locomotion explains a large proportion of the total variation in body condition among individuals (Bonnet *et al*., 1998); hence, snake mass scaled by size can provide a simple index of locomotor muscle mass. Second, the maximal contractile strength of a snake is highly correlated with the mass of its locomotor muscles (Lourdais *et al*., 2004). Body condition scores were calculated as residual values from the least squares linear regression ln-BM vs. ln-SVL. In order to measure maximal contraction strength, the snake was held at both extremities by the manipulator (always the same person) with a spring balance (maximum 10 kg, precision 100 g) attached both to a solid substrate and to the manipulator's wrist. When the snake's body was stretched out, the animal always reacted by contracting its body in order to escape the grip. The maximal contraction (usually the first among five tests) of each of 368 snakes was recorded. Similar methods of measuring strength have been validated on several snake species (Schwaner & Sarre, 1990; Lourdais *et al*., 2004). For analysis, we deleted data ($N = 86$) for all snakes containing prey items, or containing enlarged follicles (because both of these circumstances modify the snake's mass, and thus affect the mass/strength relationship). All tests were performed at nearly similar air (and thus, body) temperatures (22–27 °C), with snakes kept in calico bags (stored in the shade) prior to testing.

CLIMBING TESTS

We estimated the ability of the snakes to cross a typical reef-cliff, from the point where the animals leave the sea to the point where they reach the flat surface of the island. We limited our tests to the ascent only. These tests were performed on 168 snakes on Îlot Bayonnaise'. Along the perimeter of this island, sandy beaches alternate with relatively flat beach rocks and steep coral cliffs (usually vertical, and extending >2 m above sea level). As on other islands in New Caledonia, Vanuatu and Fiji we often saw snakes climbing these cliffs to reach the land or to return from the land to the sea (pers. observ.). Most cliffs were strongly eroded at their base, and thus overhung the ocean. We tested climbing abilities on a cliff whose base was 80 cm underwater at high tide and out of water at low tide. To climb over the cliff, a snake coming from the ocean must first climb up the overhanging part and then traverse the upper vertical area (Fig. 1). Although the eroded coral provides numerous irregularities, the overhanging section of the cliff provides a significant locomotor challenge; a snake that loses its grip will fall immediately towards the rocks or water below.

Each snake was tested only once. We randomly allocated snakes to two groups, that were placed either on
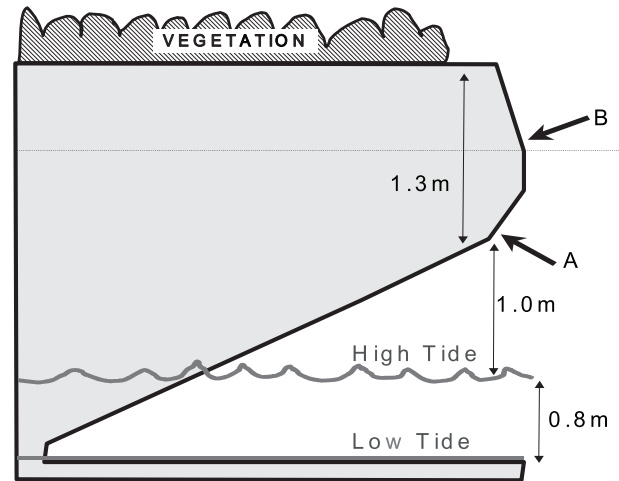
Figure 1. A schematic lateral view of the cliff used to test the climbing ability of sea-snakes. The dotted zone represents the old-eroded coral cliff. The hatched zone represents vegetation (*Pandanus* roots, bushes and grasses). Arrows A and B show the places where the snakes were placed to test their ability to climb in the over-hanging and vertical part of the cliff, respectively.

the over-hanging (A, Fig. 1), or vertical (B, Fig. 1) part of the cliff. Some snakes dropped off the cliff into the water below. For others that attempted to climb, we recorded the snake's position (and hence, its displacement) after 5 s and after 2 min. We also measured the length of time for which the snake retained its hold onto the cliff, and the total distance it travelled. The tests were performed during the day and the night, and during high and low tide. We classified a fall from the cliff as potentially risky to the snake at low tide and at night (because the snake cannot see the substrate under these conditions), and safe during the day at high tide. To avoid injuries, falling snakes were caught by hand in mid-air. The temperature of the substrate varied between 24.1 °C and 26.5 °C (mean = 25.7 ± 0.8 °C). Body temperatures of 38 snakes were correlated with, and similar to substrate temperatures ($r = 0.84$, $P < 0.0001$).

ANALYSES

We natural log-transformed the data for all analyses involving body size and body mass. As some cells in the contingency tables had a sample size below 5, we applied Yate's correction to calculate χ^2.

RESULTS

MORPHOLOGY

In our sample, averaged *L. laticauda* size was larger than *L. colubrina*; two factor ANOVA with species and

sex as the factors ($F_{1,364} = 59.62$, $P < 0.0001$; Fig. 2A). In both species, females were larger than males (same design ANOVA $F_{1,364} = 14.79$, $P < 0.0001$; Fig. 2A). *Laticauda colubrina* individuals were more heavily built than *L. laticaudata* individuals (two factor ANCOVA with ln-BM as the dependent variable, species and sex as the factors, and ln-SVL as a covariate; $F_{1,276} = 60.48$, $P < 0.0001$); males were also heavier-bodied relative to SVL than were conspecific females ($F_{1,276} = 21.40$, $P < 0.0001$; Fig. 2B, C).
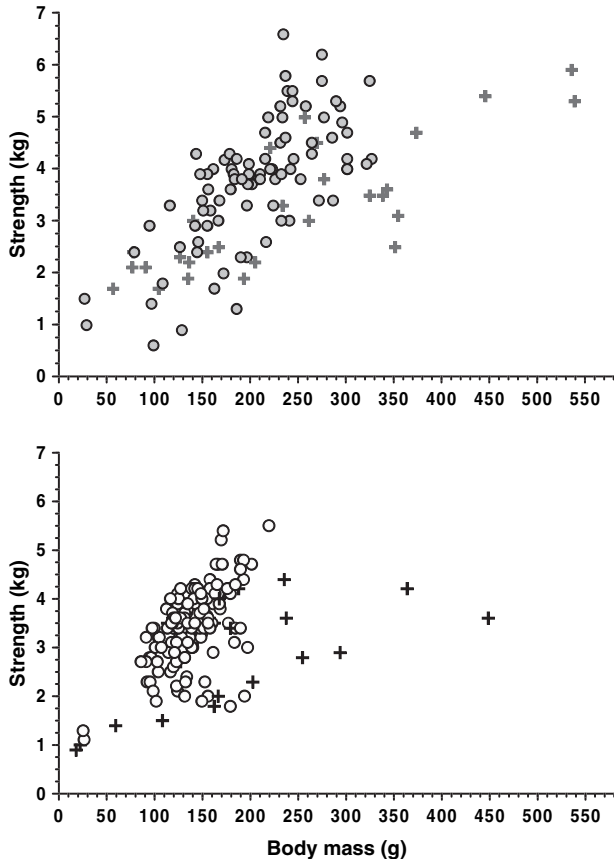
CONTRACTION STRENGTH

On average, the snakes were able to pull 22 times their own body mass (mean 22.2 ± 7.3, range 6.1–55.6; Fig. 2D). Heavier snakes were stronger ($F_{1,277} = 202.6$, $P < 0.0001$, Fig. 3); consequently, we incorporated body mass as a covariate in our subsequent analyses. A snake's species and sex affected its strength (ANCOVA with species and sex as the factors: $F_{1,277} = 4.4$, $P = 0.037$, and $F_{1,277} = 61.0$, $P < 0.0001$,
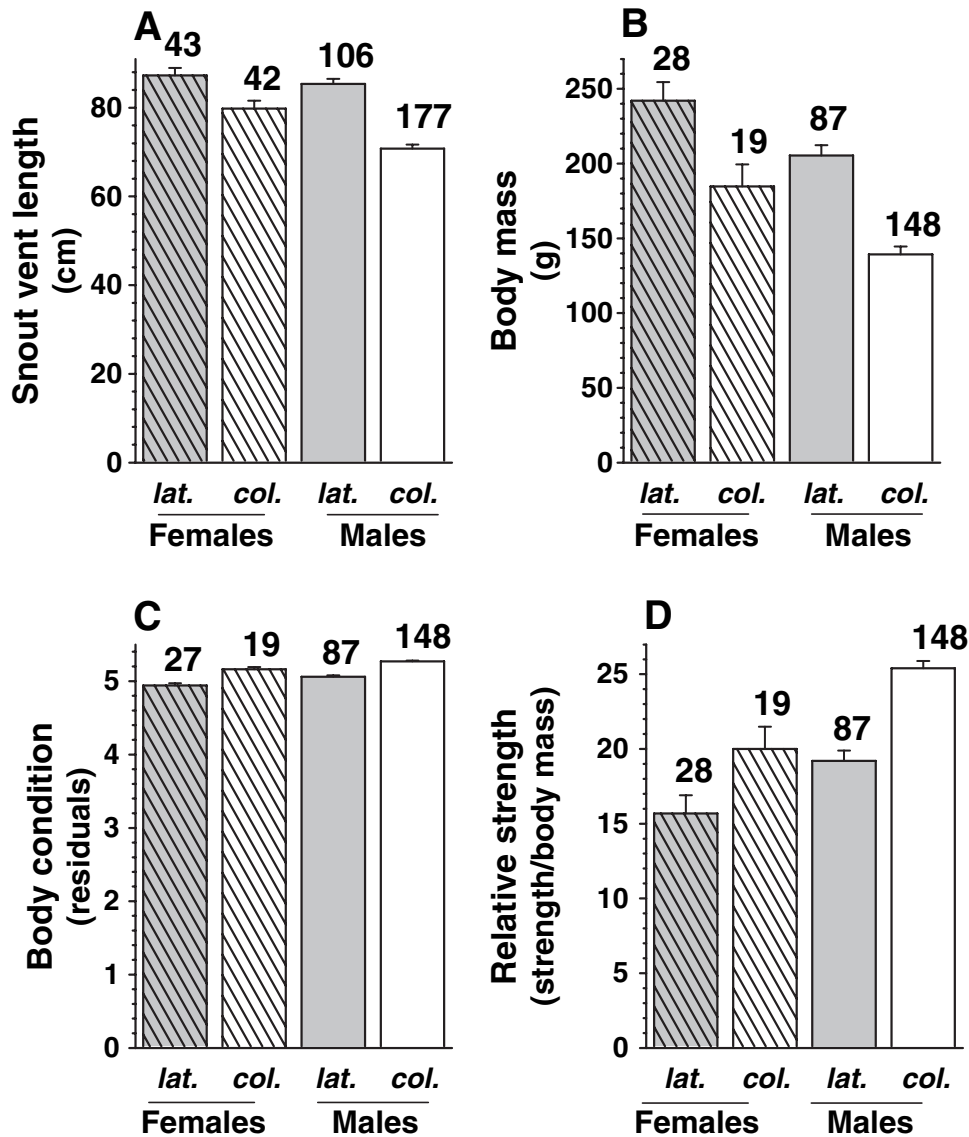
Figure 2. Comparisons between females (hatched bars) and males (open bars), of two species of sea-kraits: *Laticauda laticaudata* (grey bars) and *L. colubrina* (white bars). A, Mean snout vent length (SVL) ($\pm$ SE); B, Mean body mass (BM) ($\pm$ SE); C, Mean body condition ($\pm$ SE), calculated as residual values from the linear least squares regression between ln-BM and ln-SVL. D, Muscular strength relative to body mass ($\pm$ SE). Snakes with palpable prey in the stomach or enlarged follicles (or eggs) were removed from analyses that included body mass (B, C, D). Numbers above bars indicate sample size.

Figure 3. The relationship between body mass and maximal contraction strength in sea kraits. Each symbol represents an individual. Upper graph: female *Laticauda laticaudata* (grey crosses), male *L. laticaudata* (grey circles); lower graph: female *L. colubrina* (black crosses), male *L. colubrina* (open circles). The range of body masses encompasses the smallest and the largest snakes in the population. Data on snakes with a prey in the stomach or with enlarged follicles (or eggs) were removed from this analysis.

respectively, Figs 2D, 3), with no significant interaction between the two factors ($F_{1,277} = 0.47$, $P = 0.50$). Relative to its body mass, *L. colubrina* was stronger than *L. laticaudata*, and in both species, males were stronger than females of the same body mass (Fig. 4A).

CLIMBING ABILITY

Over-hanging cliff
During the first five seconds of the test, the proportion of snakes that fell vs. climbed did not differ significantly between the two species (Yates $\chi^2 = 0.93$, d.f. = 1, $P = 0.33$; $N = 49$ *laticaudata* and $N = 68$ *colubrina*, Fig. 4C). However, after two minutes, almost all the *L. laticaudata* had fallen whilst many *L. colubrina*

continued to cling to the cliff (Yates $\chi^2 = 8.55$, d.f. = 1, p = 0.003; Fig. 4C). Using only snakes that climbed for more than 5 s, *L. colubrina* traversed greater distances on the over-hanging cliff (means of 100 cm vs. 68 cm; Mann–Whitney U-test = 225.5, $P = 0.05$; $N = 35$ *colubrina* and $N = 19$ *laticaudata*). Snakes were more likely to fall from the cliff under conditions that we classified as relatively safe (in daylight and/or high tide) than under riskier circumstances (night and/or low tide: Fig. 4B). An interspecific difference in the proportion of falling snakes was evident when falling was risky (Yates $\chi^2 = 7.31$, d.f. = 1, $P = 0.007$), but not when diving into the water offered a safe option (Yates $\chi^2 = 0.73$, d.f. = 1, $P = 0.39$). In other words, *L. colubrina* attempted to escape by climbing when falling was risky, but readily leapt into the water when it was safe to do so; in contrast, *L. laticaudata* never (except one male) managed to escape by climbing (Fig. 4C). Females from both species exhibited lower climbing performances than males for all of the traits measured, but sample sizes were too small for robust statistical analysis of this apparent pattern.

Vertical cliff
Almost all snakes were able to climb this section of the cliff, with no significant difference between the species after either 5 s or 2 min of testing (Fig. 4D, Yates $\chi^2 = 0.64$, d.f. = 1, $P = 0.42$, and Yates $\chi^2 = 2.06$, d.f. = 1, $P = 0.15$, respectively; $N = 25$ *laticaudata* and $N = 26$ *colubrina*). The 'risky vs. safe' dive parameter did not influence snake behaviour (all results non-significant); >78% of the snakes stayed on the cliff, and 70% of them reached the top within two minutes. However, *L. colubrina* reached the top of the cliff more often than did *L. laticaudata* (61% vs. 39%; Yates $\chi^2 = 3.74$, d.f. = 1, $P = 0.05$).

CLIMBING SPEED

Our analyses of speed are based on 94 cases, after deleting data on snakes that fell almost immediately or that remained immobile after entering a crevice. We retained data from snakes that climbed for >5 s before falling. On average, these 94 snakes climbed for 44 ± 39 s. Many females (especially large individuals) fell almost immediately or stayed immobile, precluding statistical analyses of climbing speed. Examining data for males only, we found a strong interspecific difference in mean climbing speed ($F_{1,83} = 8.71$, $P = 0.004$). Male *L. colubrina* climbed more than twice as quickly as male *L. laticaudata* on the vertical cliff (two-factor ANOVA with species and cliff-type as factors: effect of cliff, $F_{1,81} = 73.86$, $P < 0.0001$; effect of species, $F_{1,81} = 33.05$, $P < 0.0001$; interaction, $F_{1,81} = 14.14$, $P = 0.0003$; Fig. 4E). Restricting the analysis to *L. colubrina*, males were faster climbers than
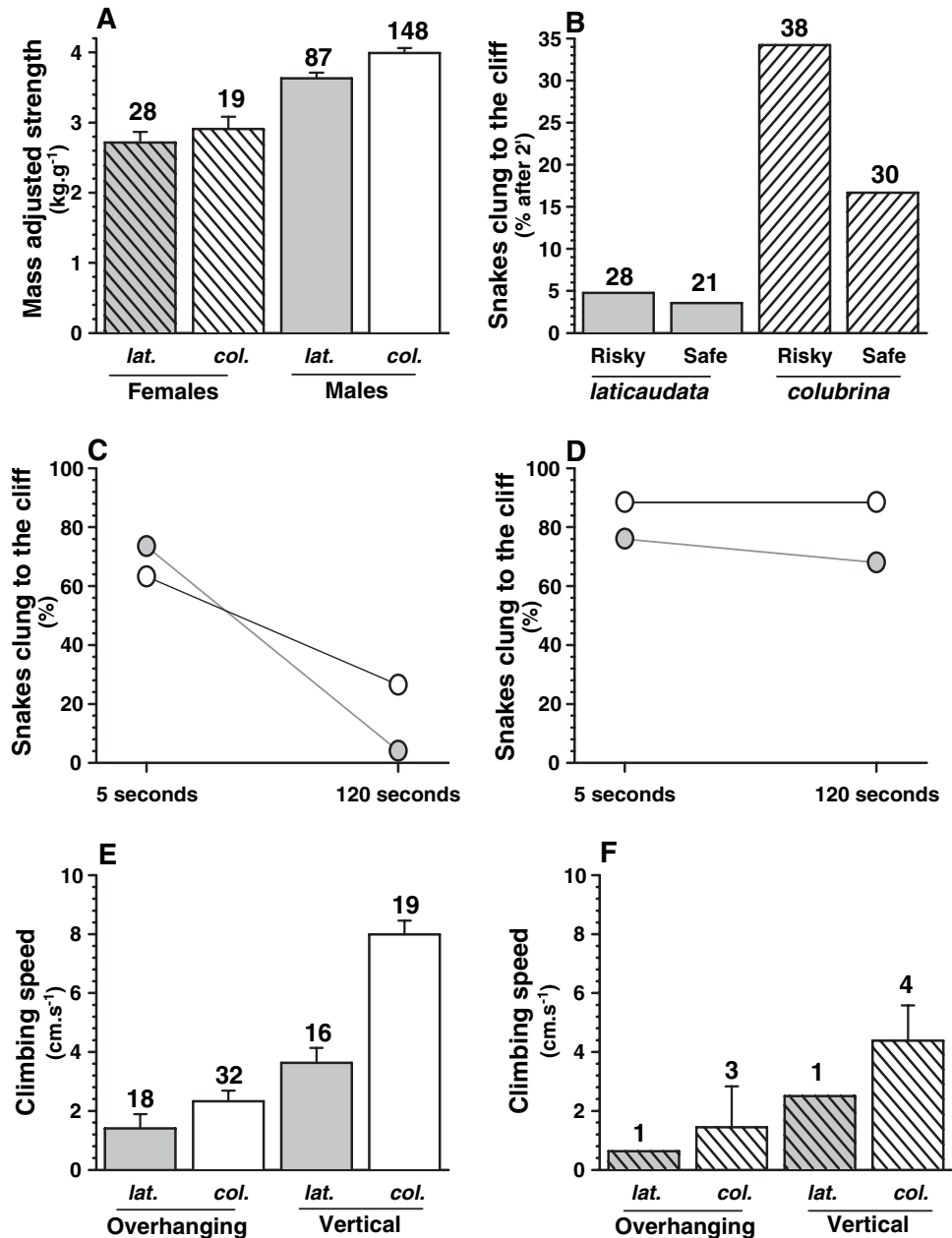
Figure 4. Strength and climbing performances of sea kraits. A, Comparison of the mass-adjusted strength (snake's body mass as a covariate) between species and sexes: 'lat.' means *Laticauda laticaudata*, 'col.' means *L. colubrina*. B, Influence of the falling risk (see text) on climbing success (number of snakes that clung vs. fell from the cliff) in *L. colubrina* and *L. laticaudata* after 2 min. C, Comparison of the climbing success after 5 s and 120 s on the over-hanging part of the cliff (arrow A, Fig. 1) for *L. laticaudata* (grey circles) and *L. colubrina* (open circles). D, As for (C), but the test was performed on the vertical part of the cliff (arrow B, Fig. 1). E, Comparison of the climbing speed of male *L. laticaudata* and *L. colubrina* in the two parts of the cliffs. F, Comparison of the climbing speed of female *L. laticaudata* and *L. colubrina* on the two parts of the cliffs. Numbers above bars indicate sample sizes.

females (two-factor ANOVA with sex and cliff-type as factors: effect of cliff, $F_{1,54} = 19.27$, $P < 0.0001$; effect of sex, $F_{1,54} = 5.24$, P = 0.026, Fig. 4E, F). The same trends were seen in *L. laticaudata*, but were not testable due to the small number of females (Fig. 4F).

DISCUSSION

In the Introduction to this paper, we outlined competing predictions from alternative hypotheses about the degree to which amphibious animals are adapted for

effective locomotion both in their secondary and their primary habitats. Our results support the idea that natural selection may have optimized locomotor abilities in both situations, because the patterns we detected in climbing ability (*L. colubrina* more adept than *L. laticaudata*; males more adept than females within each species) mirror interspecific and intraspecific patterns in relative usage of the terrestrial habitat. That is, species/sex classes that use terrestrial habitats more frequently, are better able to negotiate steep cliffs. Under the alternative hypothesis – that sea snakes are adapted for aquatic locomotion only – we would neither have expected such remarkable climbing ability, such major divergences in climbing abilities, nor any correlation between climbing ability and terrestrial habitat use.

Although sea kraits spend only a small proportion of their time climbing cliffs, it is nonetheless a biologically relevant locomotor challenge for these animals. Throughout the extensive geographical range of laticaudid snakes, many of the small islands they use are partly or totally surrounded by steep cliffs similar to the one upon which we tested their climbing ability (pers. observ.). Although snakes prefer to utilize gently sloping rather than steeper points of exit and entry to the land when both types of passage are available, local topography often forces the snakes to use steep cliffs as points of access (Shetty & Shine, 2002; pers. observ.). Hence, it is often vitally important for the snakes to be able to cross steep cliffs. Presumably reflecting this importance, these 'sea snakes' proved to be remarkably adept at traversing both vertical and over-hanging cliffs. This situation provides a striking contrast with the other major group of sea snakes (i.e. the 'true' sea snakes *Aipysurus*, *Emydocephalus*, *Hydrophis*) which are barely able to move on land, even on a flat surface (Heatwole, 1999; Shine *et al*., 2003).

Our data reveal a strong sexual dimorphism in body composition: males were more muscular, stronger and better able to climb than were conspecific females of the same body mass. This dimorphism in body plan and locomotor performance is likely to be very common in the animal kingdom (Bonnet *et al*., 1998), but has been documented only rarely (Schulte-Hostedde, Millar & Hickling, 2001). As male reproductive success likely increases with the number of females that a male can locate (Madsen *et al*., 1993), the ability to cross steep cliffs repeatedly may be more important to reproductive success in male sea kraits than in females.

Although the data thus match our predictions, it remains possible that these patterns result from some other causal process. One possibility is to reverse cause-and-effect: that is, patterns of terrestrial activity may be driven by the snake's ability to move effectively in such a habitat, rather than vice versa. For example, male *L. colubrina* may be the most terrestrially active group simply because they are best at terrestrial locomotion. It is difficult to dismiss such an alternative, but we note that the patterns of relative terrestriality accord well with those expected from the snake's general biology (e.g. importance of mate-searching for males). This concordance suggests that habitat use drives locomotor adaptation rather than vice versa.

The most directly comparable study to our own involved measurements of aquatic and terrestrial locomotion in the same species, including specimens from New Caledonia (Shine *et al*., 2003). This study found (as we did) that males were faster than conspecific females, especially on land. However, although these authors predicted that the more terrestrial *L. colubrina* would be faster than *L. laticaudata*, they found no significant difference between the two species. Interestingly, the more challenging physical task of climbing a steep cliff produced a very different result, with the heavier-bodied *L. colubrina* much more adept than the slender *L. laticaudata* in the present study. This result thus supports the prediction of Shine *et al*. (2003), although their own data set did not.

Our study was not designed to reveal the mechanistic basis of climbing ability in sea kraits (Gans, 1975; Jayne, 1986; Cundall, 1987; Losos, Creer & Schulte, 2002), but the correlations between body condition (mass relative to length), muscular strength and climbing ability suggest that strength is a critical aspect. Thus, male sea kraits are heavier-bodied and stronger than same-sized females, and presumably the extra mass in males consists at least partly of muscle tissue, as it does in other species of snakes (Bonnet *et al*., 1998). However, strength varied between the groups even at the same body mass; thus, for example, male *L. colubrina* were stronger than expected even given their heavier build, perhaps reflecting a greater proportional muscle mass in males (Bonnet *et al*., 1998). Given the physical strength required to cling to the overhanging cliff in our trials, it is not surprising that the relatively stronger species, and relatively stronger sex within each species, proved to be more effective climbers. However, the precise physiological basis for that performance superiority remains unclear. The detailed biophysical basis of terrestrial (and aquatic) locomotion of amphibious sea snakes warrants further study, especially given the wide diversity in degree of reliance on terrestrial habitats exhibited within this group (Cogger, 1992; Greer, 1997).

ACKNOWLEDGEMENTS

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