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Swimming speed variation in amphibious seasnakes (Laticaudinae): A search for underlying mechanisms

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ABSTRACT

An understanding of the proximate (morphological, physiological and behavioural) mechanisms that affect locomotor speed can clarify reasons for intraspecific and interspecific variation in this ecologically relevant performance measure. To explore such mechanisms, we selected a study system involving animals with highly simplified external morphology (snakes) moving through a homogeneous medium (water). In laboratory trials, swimming speeds in two species of amphibious sea kraits (61 *Laticauda laticaudata* and 35 *L. saintgironsi*) varied from 0.14 to 1.39 body lengths per second. Miniature accelerometers attached externally to these snakes recorded the frequency and lateral acceleration of bodily undulations that the snakes used to propel themselves through the water. Frequency of undulation was constant along the length of the body, but amplitude of lateral acceleration increased in posterior sections. The frequency and amplitude of lateral acceleration of undulations were highly correlated with swimming speeds, suggesting (a) that intraspecific and interspecific variation in swimming speeds reflects underlying variation in undulatory mechanics; and (b) that data from miniature accelerometers implanted in the body cavity could provide accurate estimates of swimming speeds of free-ranging snakes.

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1. Introduction

To understand the ways in which natural selection works on the functional traits of organisms, we need information not only on phenotypic variation among individuals in performance traits (e.g., locomotor speed), but also on the fitness consequences of that variation, and on the underlying proximate mechanisms that enable one organism to perform better than another (Arnold, 1983; Garland and Losos, 1994). Only by integrating information across these multiple levels of organisation can we fully understand the adaptive significance of organismal traits linked to performance (Arnold, 1983; Garland and Losos, 1994; Irschick and Garland, 2001). The challenge is considerable, in that many kinds of animals are difficult to observe in the course of their day-to-day lives, so that even measuring the speed with which they travel through the environment poses significant problems. Documenting fitness consequences of performance variation also is difficult (although mark-recapture approaches have the potential to do so—e.g., Warner and Andrews, 2002; Miles, 2004; Le Galliard et al., 2004; Husak, 2006). Understanding the proximate mechanisms that determine performance levels also is challenging, especially in free-ranging animals (Garland and Losos, 1994; Le Galliard et al., 2003).

In the current study, we examine a system that facilitates empirical documentation of the proximate mechanisms underlying a major performance trait. Like most researchers in this field, we selected locomotor speed as the performance trait to study because it is easy to measure, highly repeatable, and plausibly linked to individual fitness (e.g., through ability to escape predators or capture prey, Domenici and Blake, 1991). To further reduce logistical problems, we selected study organisms with highly simplified external morphology (snakes), so that the mechanisms generating propulsion (body undulations) can be quantified more easily than would be the case with animals using a combination of other body parts (e.g., limbs, fins, or tails) for locomotion (Jayne, 1985; Gillis, 1996; Munk, 2008). Lastly, we restricted our attention to swimming, thereby removing complexities arising from substrate heterogeneity that can massively influence movement rates (Gans, 1962; Hertel, 1966). For a seasnake swimming through clean still water, locomotor speed should be determined primarily by the frequency and amplitude of undulations that push against the water column and propel the snake through the water (Jayne, 1985; Gillis, 1996; Munk, 2008; Pattishall and Cundall, 2008).

Previous studies on the biomechanics of snake locomotion have relied on detailed video-based analysis of snake postures (Jayne, 1985; Graham et al., 1987; Munk, 2008; Pattishall and Cundall, 2008). An alternative methodology that has been applied with great success to studies of locomotion in other kinds of animals involves miniature animal-borne data-loggers to gather physiological and behavioural

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information (an approach known as bio-logging, see Ropert-Coudert and Wilson, 2005). Logistical, cultural, and economic constraints have limited the types of organisms to which this new technology has been applied (i.e., species of economic values or large bodied species; Bonnet et al., 2002; Clark and May, 2002; Ropert-Coudert et al., 2006, 2009). As a result, most bio-logging studies have focused on birds, mammals and sea turtles, ignoring smaller animals (Ropert-Coudert et al., 2006; Brischoux et al., 2008; Ropert-Coudert et al., 2009). Recent technological improvements in bio-loggers are changing this situation, with a new generation of data-loggers small enough for deployment on smaller species (Angelier et al., 2007; Brischoux et al., 2007c; Lagarde et al., 2008; Brischoux et al., 2009). One type of miniaturized animal-borne data-logger is the accelerometer, which has revolutionized our understanding of animal movements (e.g. Yoda et al., 2001; Ropert-Coudert et al., 2004; Kato et al., 2006). These devices measure the acceleration (in one, two or three dimensions) of the body of a freely-moving animal. That information allows researchers to access biomechanical parameters of animal movements in the wild (e.g., to quantify limb movements; Ropert-Coudert et al., 2004; Watanuki et al., 2006; Sato et al., 2007). In turn, such information can clarify costs of transport (Mori et al., 2010) and facilitate fine-scale analyses of an animal's movements and/or energy expenditure (Wilson et al., 2008).

Seasnakes provide excellent models in this respect because of their structurally simple morphology (as previously discussed). Additionally, studies on seasnakes have the potential for broad comparisons, because snakes of several lineages have adapted to aquatic habitats (Heatwole, 1999). Thus, this system can clarify the locomotor challenges faced by organisms in the course of a major evolutionary transition in habitat types (Aubret and Shine, 2008). Finally, implanted data-loggers may offer a way to document significant aspects of snake behaviour when the animals are at sea, and thus are unobservable by most methods of study.

Our aims in the present study were to measure swimming speeds of two species of seasnakes, and explore the degree to which interspecific and intraspecific variation in locomotor speeds was the result of corresponding variation in biomechanical aspects (frequency and amplitude of lateral acceleration of body undulations) that we could record with miniature accelerometers attached to the snakes' body. Our rationale was that robust empirical associations between accelerometer data and snake speeds would clarify the reasons for among-individual variation in locomotor performance, and also would enable us to evaluate the feasibility of using miniature (internally-placed) accelerometers to predict speeds of free-swimming snakes in the field.

2. Materials and methods

2.1. Study species

Sea kraits (laticaudine seasnakes, family Elapidae) are amphibious medium-sized snakes (<1.40 m) common through coral-reef habitats over most of the Indo-Pacific (Heatwole, 1999). Two sympatric species occur in the lagoon of New Caledonia: *Laticauda laticaudata* and *L. saintgironsi*. Both species forage at sea, mostly for anguilliform fish (eels) but return on land to digest, slough their skins, mate and lay their eggs (Brischoux and Bonnet, 2009). Although easily observable when on land, sea kraits evade direct observation during their foraging trips at sea (which can last for at least 15 days: Brischoux et al., 2007b,c; Brischoux and Bonnet, 2009). To quantify interspecific differences in body shape, we measured total lengths (TL, ±0.5 cm), and body heights and widths at intervals along the snake's length (10% of TL starting 5% after the snout, ±0.1 mm) of 12 adult individuals of each species (6 males and 6 females).

Snakes were captured by hand on a small coral island (Signal islet, 22°17′45 S, 166°17′34 E, see Brischoux and Bonnet, 2009 for details) close (<15 km) to the city of Nouméa. Snakes were then sexed, measured for body length (SVL [Snout-Vent Length] ± 0.5 cm) and

total length (TL ± 0.5 cm), and weighed (± 0.5 g, Brischoux and Bonnet, 2009). The animals were transported to Nouméa in cloth bags, where they were housed with *ad libitum* freshwater. We conducted three capture sessions on Signal islet (each <3 days), followed by three swimming speed measurement sessions in Nouméa (each <4 days), after which each individual was released at its location of capture (<7 days after initial capture). A total of 96 snakes were used in the experiments: 61 *L. laticaudata* and 35 *L. saintgironsi*.

2.2. Experimental procedures

2.2.1. Experimental pool

All experimental procedures were conducted at the "Aquarium des Lagons" research facility (Nouméa, New Caledonia). The experimental pool consisted of a concrete tub (5 m-long, 40 cm wide, 50 cm deep) filled with constantly renewed seawater. This open-circuit system provided water conditions similar to those experienced by free-ranging sea kraits (mean temperature 25.8 °C).

Once fitted with the data-logger (see sections 2.2.3 and 3.2 for details on the logger position), each individual was released at one end of the experimental pool. Most individuals immediately began swimming toward the opposite end of the pool. We did not manually stimulate the snake. We recorded times to travel the 4 m-long raceway, for 10 consecutive swimming trials per individual (mean number of trials per snakes 9.61 ± 1.11, range 3–10 because a few snakes refused to keep swimming). Swimming speed was measured using a stop-watch synchronized with the accelerometer. Swimming speed was calculated relative to body length ($SVL \cdot s^{-1}$) to provide a more meaningful measure of locomotor performance than absolute speed (Van Damme and Van Doren, 1999; see also Shine et al., 2003a, b). We conducted a total of 144 experimental bouts on the 96 snakes (i.e., some snakes were tested more than once; see below, effect of logger position).

2.2.2. Data-logger

We used a four-channel accelerometer (M190L-D2GT, cylindrical 60 × 15 mm, 20 g; Little Leonardo, Japan) to simultaneously monitor depth (every second), temperature (every second) and acceleration (32 Hz) along two axes. The logger weighed, on average, 10% of snake mass (range 3–19%), about half the mass of prey items taken by these snake species (mean relative prey mass 18%, range 3–95%, Brischoux et al., 2007a). The logger was externally attached to the snake's back using small pieces of adhesive tape (Tesa tape). The snake's scales were cleaned and dried before attachment and the tape encompassed the entire circumference of the circular body. The tape width (<2 cm) was designed to avoid impeding the normal lateral flexion of the snakes' vertebral column. The attachment of the logger was manually checked before each trial to ensure a close fit between the logger and the snake's body. The orientation of the logger was precisely set in order to measure acceleration along two axes: surging acceleration was measured along the longitudinal body axis of the snake, and swaying acceleration was measured laterally to record the undulatory movements of a swimming snake (Fig. 1a and b).

To investigate the frequency and amplitude of lateral (sway) acceleration (henceforth "sway amplitude" for simplicity) of undulations (Fig. 1b), a spectrogram of the sway acceleration was calculated by continuous wavelet transformation with the Morlet wavelet function using Ethographer (Sakamoto et al., 2009) on Igor Pro (version 6.04, Wavemetrics, USA). For each trial, a mean value was calculated for both the sway amplitude and the frequency of undulation, providing for each value of relative swimming speed a corresponding value of sway amplitude and frequency of snake movements.

2.2.3. Effect of logger position on swimming speeds and undulations

As well as recording overall patterns of association between speeds and undulation parameters, we conducted initial trials to check the reliability of the data obtained from the logger.
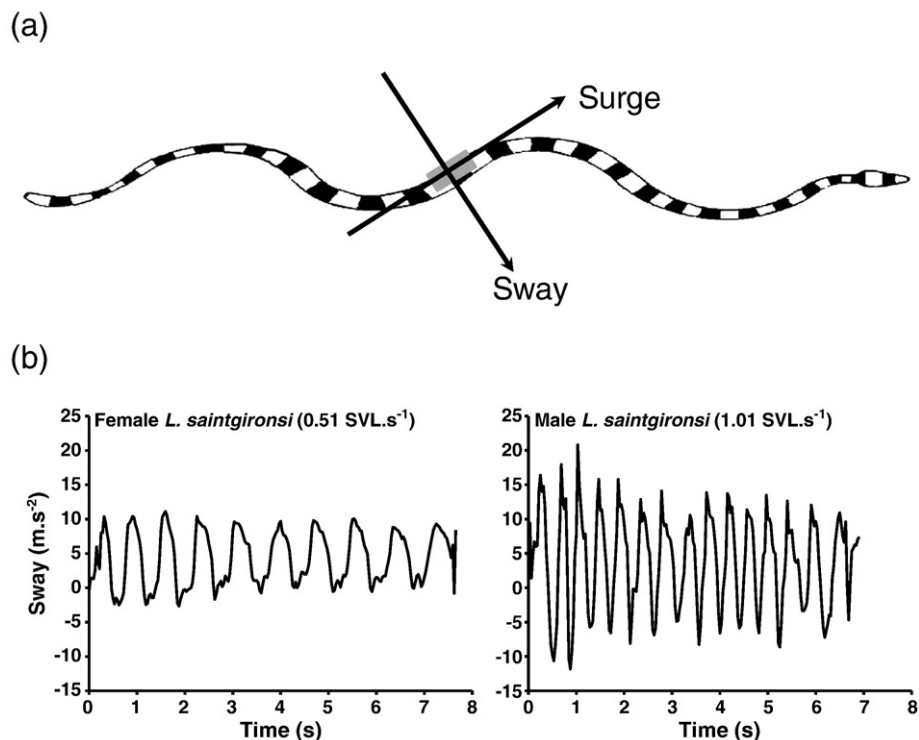
Fig. 1. (a): View from above of a snake fitted with the logger in mid-body position (grey box). Acceleration was measured along two axes: surging (surge) along the longitudinal body axis of the snakes, and swaying (sway) laterally to record the typical undulatory movements of a swimming snake. (b): examples of recordings of sway acceleration for two swimming speeds (both expressed as body lengths per second). Left: a female *L. saintgironsi* (0.51 SVL·s^{-1}); right: a male *L. saintgironsi* (1.01 SVL·s^{-1}). Note the difference in both the sway amplitude and frequency of the undulations.

Biomechanical studies on swimming snakes indicate that the frequency of undulations remains constant along the snake's length, but that the amplitude of undulations increases posteriorly (Jayne, 1985; Graham et al., 1987; Munk, 2008). To check that the logger data exhibit this pattern, the logger was attached at three different positions: anteriorly (ANT, 15% TL), at mid-body (MID, 50% TL) and posteriorly (POST, 85% TL) on a sub-sample of individuals (N = 12 *L. laticaudata* and N = 12 *L. saintgironsi*). Each of these individuals swam three series of 10 consecutive trials (3 experimental bouts with a different logger position each time, 1 day between bouts). The order of the logger position was randomised to avoid any effects of testing sequence.

2.3. Statistics

Because individual snakes contributed more than once in the analyses we used generalized linear mixed-effects models (GLMM, Schall, 1991) fitted by restricted maximum likelihood (REML, Patterson and Thompson, 1971). We nested each trial within the individual, which was set as a random factor, in order to avoid problems of pseudoreplication and individuals with varying statistical weights. Most of the following analyses follow this statistical design, unless otherwise stated (see Results). Preliminary analyses showed that swimming speed was constant over time through the 10 successive trials, except for *L. saintgironsi* which displayed a lower swimming speed for the first trial only (repeated-measures ANOVA, post-hoc tests reveal the first trial to differ significantly from the others at p = 0.03 for *L. saintgironsi*, all other p > 0.05). Thus, for consistency, we excluded the first swimming trial for all snakes (including *L. laticaudata*) in the following analyses. We tested the data for deviations from normality before using parametric statistics (ANOVAs, repeated-measures ANOVAs), although the F-test is robust to violations of the normality and homoscedasticity assumptions (Lindndman, 1974). The snakes' body condition index (BCI) was calculated as the residuals of the regression between SVL and body mass (log-

transformed for linearity, Bonnet and Naulleau, 1994). All analyses were performed using JMP 6.03 (SAS Institute, USA), and means are presented ± S.D.

3. Results

3.1. Snake morphology

The two species differed significantly in body shape. *L. saintgironsi* is more heavy-bodied, and thus exceeded *L. laticaudata* in relative body height (repeated-measures ANOVA with height at each position along the body as the repeated measure, $F_{9,198} = 2.78$, p < 0.001, Fig. 2a) and relative body width (repeated-measures ANOVA as above, $F_{9,198} = 6.57$, p < 0.001, Fig. 2b).

3.2. Effect of logger position on swimming speeds and undulations

The logger position affected swimming speed in *L. saintgironsi* ($F_{1,302} = 3.55$, p = 0.04, post-hoc test has ANT significantly different from MID, Fig. 3), but not in *L. laticaudata* ($F_{1,321} = 1.05$, p = 0.36, Fig. 3). For both species, snakes tended to swim slowly when the logger was attached anteriorly (Fig. 3), where its cross-sectional area is almost equal to the diameter of the snake (relative cross-sectional area of the logger for *L. laticaudata*, ANT 0.93 ± 0.06, MID 0.69 ± 0.04 and POST 0.73 ± 0.05; and for *L. saintgironsi*, ANT 0.93 ± 0.08, MID 0.64 ± 0.05 and POST 0.69 ± 0.05).

Logger position affected sway amplitude but not frequency of undulations in both species (with swimming speed as a covariate: for *L. laticaudata*, effect of logger position on undulation frequency, $F_{1,321} = 0.09$, p = 0.91 and sway amplitude, $F_{1,321} = 10.16$, p < 0.001; and for *L. saintgironsi*, effect of logger position on frequency, $F_{1,302} = 0.27$, p = 0.76 and on sway amplitude, $F_{1,302} = 33.90$, p < 0.001; Fig. 3). That is, for a given speed, the frequency of body undulations was constant along the snake's body length, but the sway amplitude of undulations increased from anterior to posterior (Fig. 3).
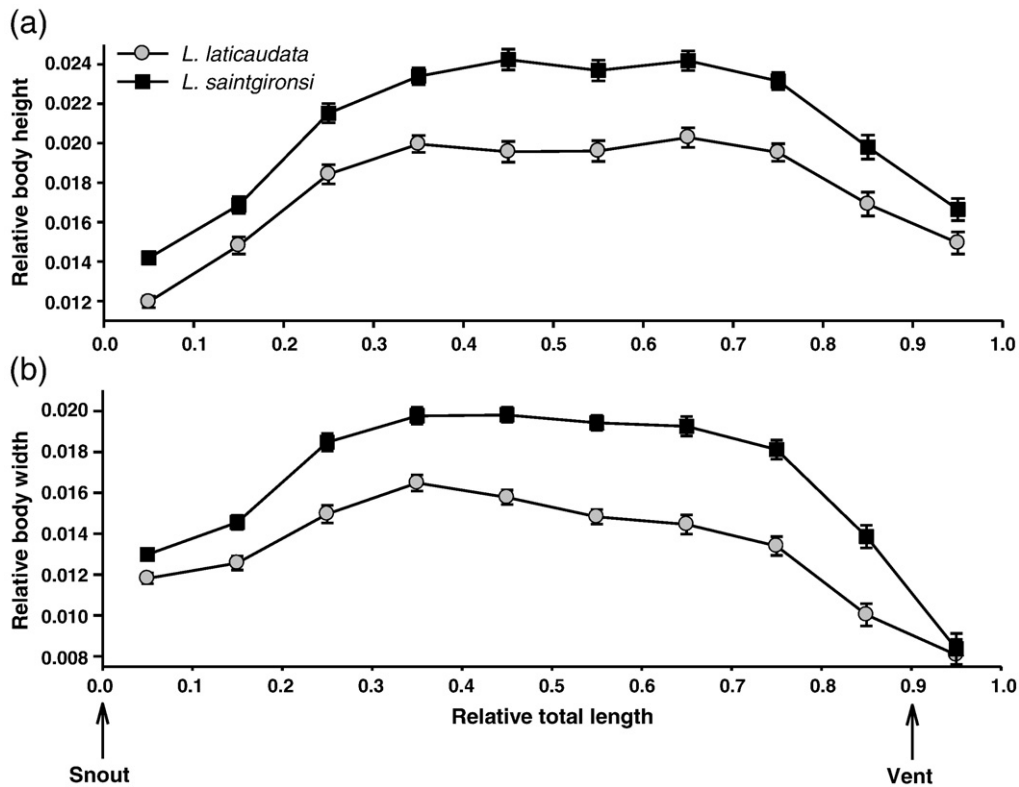
Fig. 2. Body shape (relative body height (a) and body width (b)) measured regularly along the length of two species of laticaudine sea snakes. The two species differed significantly for both morphological measurements. Means are presented ± SD. Note that the difference is strongly marked from mid-body posteriorly (~45% TL), the area where lateral flattening occurs in actively swimming sea kraits.

Because logger position affected swimming speed, we standardised logger position (in MID position) and all following analyses were based on data gathered with the logger in MID position only.

3.3. Effect of snake species, sex and body size on swimming speed and undulations

The species and sex of a snake affected its swimming speed, and the frequency and the sway amplitude of its undulations (Table 1, Fig. 4). *L. saintgironsi* was quicker than *L. laticaudata* and displayed more frequent and extreme undulations (Fig. 4). Within both species, males were faster than females and displayed more frequent and more extreme undulations (Fig. 4, see also Fig. 1b).

Mean body sizes differed between species (Student's t-test t = 4.51, df = 94, p < 0.0001; mean SVL = 91.4 ± 1.5 for *L. laticaudata* and 81.6 ± 1.8 for *L. saintgironsi*) and between sexes within each species (for *L. laticaudata*, t = −4.37, df = 58, p < 0.0001, mean SVL = 99.8 ± 2.0 for females and 87.4 ± 1.4 for males, for *L. saintgironsi*, t = −8.25, df = 34, p < 0.0001, mean SVL = 94.8 ± 1.9 for females and 72.2 ± 1.6 for males). Swimming speed relative to SVL decreased in larger snakes (Spearman rank correlation SVL vs relative speed, $r_s = -0.48$, p < 0.05), so we repeated the above analyses on speeds and undulations after correcting for SVL by including this factor as a covariate. Relative to body length (SVL), *L. saintgironsi* was faster and exhibited more rapid and wider undulations than did *L. laticaudata*, but males and females within each species did not differ significantly either in mean speeds or in undulation parameters (Table 1).

3.4. Can we predict swimming speed from undulation sway amplitude and frequency?

A model that incorporated snake species, sex, body size, tail size and condition into a single analysis suggested that the frequency and the

sway amplitude of body undulations were the main determinants of speed (Table 2). However, the relationship linking undulation parameters and speed differed between the species: for any given combination of undulation speed and sway amplitude, *L. saintgironsi* was faster than *L. laticaudata* (with undulation parameters added as covariates, species effect $F_{1,1121} = 93.47$, p < 0.0001, mean speed = 0.49 ± 0.004 and 0.58 ± 0.005 for *L. laticaudata* and *L. saintgironsi* respectively, Fig. 5). Multiple linear regressions generated the following equations to calculate swimming speeds based on undulation characteristics (Fig. 5): for *L. laticaudata*, Swimming Speed (SVL.s^{-1}) = 0.0866 + 0.0234 Sway amplitude (m.s^{-2}) + 0.2079 Frequency (Hz), r² = 0.70, $F_{2,747} = 884.11$, p < 0.0001; and for *L. saintgironsi*, Swimming Speed (SVL.s^{-1}) = 0.1474 + 0.0285*Sway amplitude (m.s^{-2}) + 0.2084 Frequency (Hz), r² = 0.65, $F_{2,466} = 378.56$, p < 0.0001. To further test the reliability with which we can predict swimming speeds from undulation parameters, we re-calculated these equations on a sub-set of swimming speeds and undulation parameters (half of the trials per individuals, odd numbers), and then applied those equations to predict swimming speeds in the remaining part of the data set (half of the trials per individual, even numbers). There was no significant difference between measured and predicted swimming speeds (paired t-test, t = 0.43, df = 1218, p = 0.66; for *L. laticaudata*, 0.43 ± 0.13 SVL·s^{-1} versus 0.45 ± 0.13 SVL·s^{-1} for measured and predicted speeds respectively, and for *L. saintgironsi*, 0.68 ± 0.19 SVL·s^{-1} and 0.65 ± 0.17 SVL·s^{-1} for measured and predicted speeds respectively).

4. Discussion

Our deployment of animal-borne accelerometers to analyse snake movement has provided encouraging results. Although external attachment of the data-logger affected snake hydrodynamics and thus speeds (as also occurs in some endothermic species, Wilson et al., 1986; Ropert-Coudert et al., 2000, 2007; see Fig. 3), the broad patterns
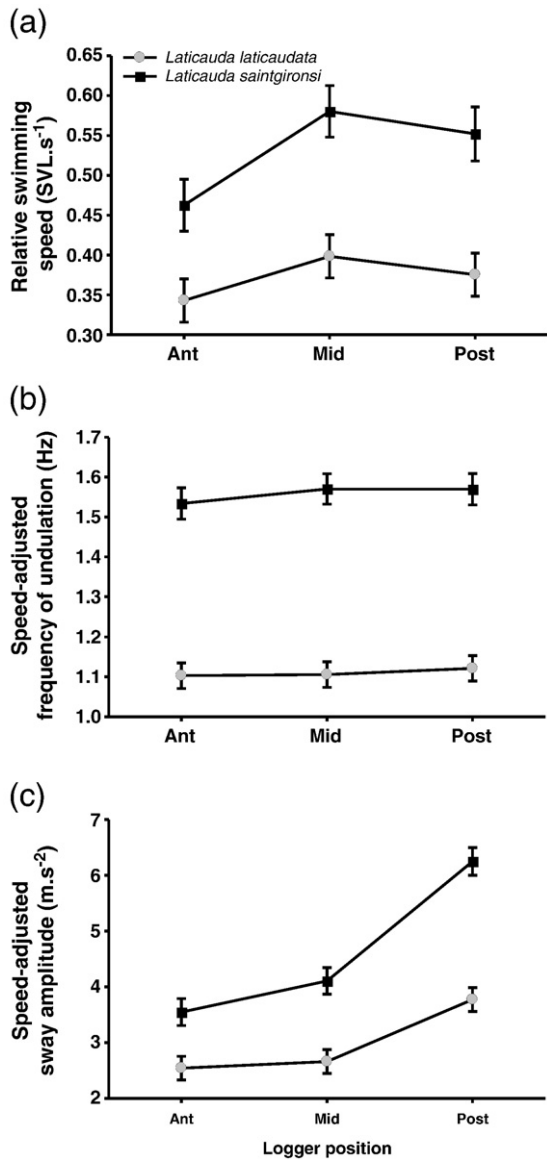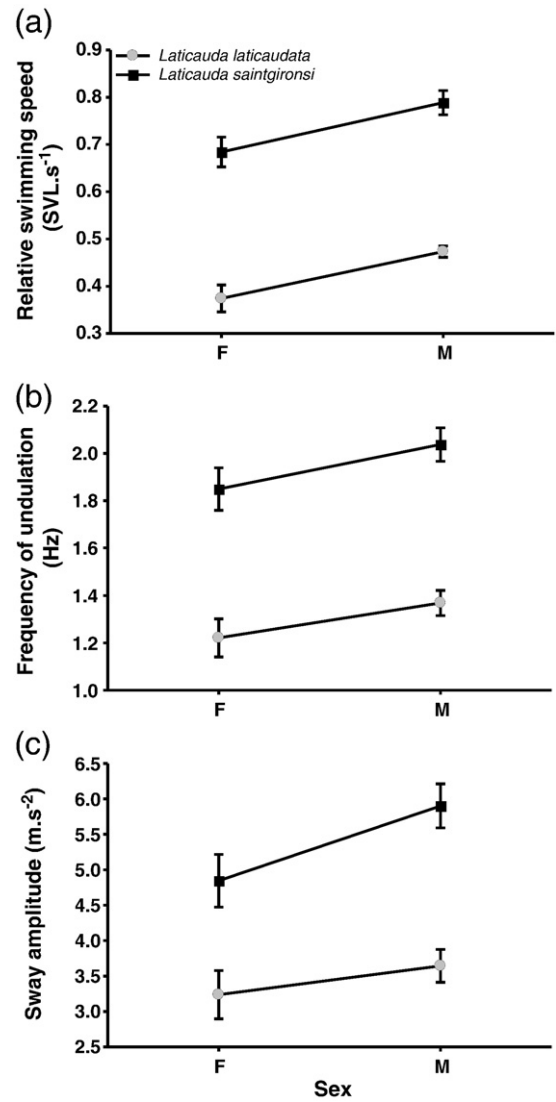
Fig. 3. (a) relative swimming speeds recorded for sea snakes as a function of three alternative positions of the logger (ANT, MID and POST) on the snake's body. (b) frequency of undulations relative to swimming speed for the three positions of the logger. (c) sway amplitude of undulations relative to swimming speed for the three positions of the logger. Means are presented ± SD. See text for details.


Fig. 4. Effects of sex on swimming performance in two species of laticaudine sea kraits. The panels show sex differences in: (a) swimming speed, (b) frequency of undulations, and (c) sway amplitude of undulations. All data were recorded with the logger in the mid-body position. Means are presented ± SD. See text for details.

of locomotor biomechanics do not appear to have been affected. For example, undulation frequency was constant along the snake's length, whereas sway amplitude of the oscillation increased posteriorly (Fig. 3). As documented for unencumbered snakes (Jayne, 1985; Graham et al., 1987; Munk, 2008), the frequency of undulations

Table 1
Summary of the results of statistical tests (GLMM-REML, see text for details) to examine the effect of sea snake species, sex and the interaction between species and sex, on swimming speed (body lengths [SVLs] per second), and the frequency and the sway amplitude of body undulations. Boldface font indicates statistically significant (P<0.05) differences.

	Speed		Frequency		Sway amplitude	
	F	P	F	P	F	P
Species	189.11	**<0.0001**	98.14	**<0.0001**	53.22	**<0.0001**
Sex	11.43	**0.001**	4.08	**0.04**	4.06	**0.04**
Species × Sex	0.01	0.91	0.09	0.75	1.49	0.22
Relative to SVL						
Species	122.17	**<0.0001**	65.35	**<0.0001**	32.13	**<0.0001**
Sex	2.74	0.10	0.89	0.34	1.50	0.22
Species × Sex	0.07	0.78	0.01	0.96	1.05	0.30

Table 2
Summary of the results of statistical tests (GLMM-REML, see text for details) to test for the determinants of the relative swimming speed of two species of sea snakes. SVL: snout-vent length, BCI: body condition index (see text). Boldface font indicates statistically significant (P<0.05) effects.

	Relative swimming speed	
	F	P
Species	80.04	**<0.0001**
Sex	3.00	0.09
Species × Sex	0.19	0.66
SVL	1.34	0.25
Relative tail length	1.33	0.25
BCI	0.75	0.39
Frequency	77.47	**<0.0001**
Sway amplitude	164.35	**<0.0001**
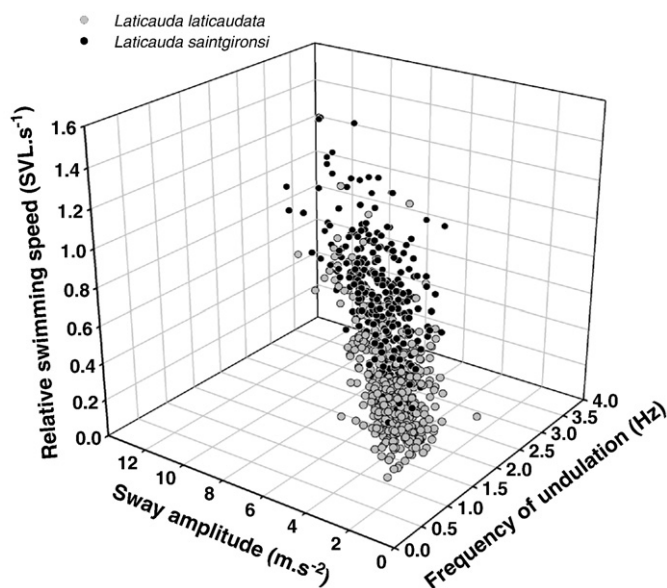
Fig. 5. Relationships between relative swimming speed of sea snakes and the frequency and sway amplitude of their lateral undulations, recorded with the logger in mid-body position. Equations of the multiple regressions are: Swimming Speed $(SVL \cdot s^{-1}) = 0.0866 + 0.0234$ Sway amplitude $(m\ s^{-2}) + 0.2079$ Frequency (Hz) for *L. laticaudata* and Swimming Speed $(SVL \cdot s^{-1}) = 0.1474 + 0.0285$ Sway amplitude $(m \cdot s^{-1}) + 0.2084$ Frequency (Hz) for *L. saintgironsi*. See text for details.

remained constant along the body, but their amplitude progressively increased from head to tail. These data imply that the speed of propagation of the propulsive wave (and thus its sway amplitude) also increases from head to tail. Mean values of undulatory sway amplitude and frequency (and the resulting swimming speed) shifted consistently with snake sex, size and species (Fig. 4). Importantly, undulation frequency and sway amplitude were robust predictors of swimming speeds (see validation of the predictive equations). Below, we discuss the implications of our results for (a) the determinants of locomotor speed in seasnakes, and (b) emerging opportunities for studies on locomotor activity of free-ranging snakes in the field.

Our results show that the swimming speed of seasnakes is mainly determined by a combination of the frequency and sway amplitude of undulations (see also Munk, 2008). Within species, a snake's size affects the undulation parameters, whereas interspecific differences in undulation parameters do not seem to be related to body size. Two hypotheses (not mutually exclusive) can explain both the interspecific and intraspecific differences we detected using accelerometers, and thus, clarify the determinants of swimming speed in seasnakes. First, the fastest species (*L. saintgironsi*) is heavier-bodied (Bonnet et al., 2005; see Fig. 2) and has more muscular strength than *L. laticaudata* (Bonnet et al., 2005). Within both species, males are stronger than females (Bonnet et al., 2005). Clearly, a stronger snake should be able to put more energy into each undulation, thereby resulting in greater speed for any given set of undulation parameters. Although this hypothesis is compelling for the interspecific difference we observed, it is less satisfactory at explaining the intraspecific variation in swimming speed or undulation parameters. Although males are stronger than females (Bonnet et al., 2005), both the undulation parameters and the resulting swimming speeds were similar (relative to body size) between sexes.

Our second hypothesis involves the body shapes of aquatic snakes. Highly aquatic species exhibit a laterally compressed body during swimming (Hydrophiids: Heatwole, 1999; Acrochrodids: Shine and Houston, 1993; Colubrids: Pattishall and Cundall, 2008; Laticaudines: personal observations). A laterally compressed body presumably allows a more efficient thrust against the water than a cylindrical one (Shine, 1988). Accordingly, higher bodies present more surface area

per unit length, and the thrust generated will be linearly correlated with this surface area. The two sea krait species differ significantly in overall body shape. Although relative body height and width are not a direct quantification of the ventral keel, these measurements are related to the potential for lateral flattening (the greater the relative diameter, the greater the potential extent of lateral flattening). The direction and magnitude of this difference between species accord well with the difference in swimming speed. Future investigations of seasnake locomotor mechanics could usefully consider variations of body shape linked to activities (e.g., feeding and reproduction) that impose significant bodily distension (Brischoux et al., in press) and hence exert selective forces on morphology in aquatic snakes (Shine, 1988).

Our experimental data suggest that bio-loggers may be able to record physiologically and behaviourally relevant data on seasnakes (see also Brischoux et al., 2007c). Deployment of accelerometers on free-ranging individuals has revolutionized our understanding of the ecology of air-breathing marine vertebrates (Yoda et al., 2001; Ropert-Coudert et al., 2004; Kato et al., 2006; Sato et al., 2007). Internal implantation of such bio-loggers in seasnakes would facilitate studies on the behaviour and physiology of marine snakes when the animals are at sea, and thus are unobservable by most methods of study. Finally, miniaturized accelerometers in seasnakes may help to clarify the locomotor challenges faced by these organisms in the course of their evolutionary transition to marine life.

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