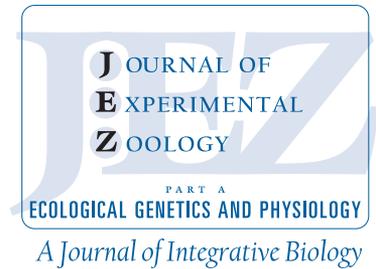# Fast and Furious: Effects of Body Size on Strike Performance in an Arboreal Viper *Trimeresurus* (*Cryptelytrops*) *albolabris*

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ABSTRACT   Body size has a pervasive effect on animal functioning and life history with size dependent changes in performance and physiology throughout ontogeny being common in many ectothermic vertebrates. However, as selection on juvenile life history stages is strong, juveniles often offset the disadvantages of small body size by disproportionate levels of performance. Here, we investigate size-related changes in defensive strike performance in an arboreal pit viper, *Trimerusurus* (*Cryptelytrops*) *albolabris*. Our data show a significant negative allometry in the scaling of head dimensions and head mass to body mass. However, strike velocity and strike distance are independent of body mass, with juveniles in our sample striking as fast and as far as adults. In contrast to model predictions suggesting that acceleration capacity should decrease with increasing body mass, acceleration capacity increases with snake body mass. Our results suggest that this is the result of a negative allometric scaling of head mass combined with an isometric scaling of the dorsal epaxial musculature. Finally, our data show a significant sexual dimorphism in body size and strike velocity with females being heavier and striking faster independent of the dimorphism in body size. *J. Exp. Zool. 315:22–29, 2011.* © 2010 Wiley-Liss, Inc.

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It is well known that size has a profound impact on organisms through its effects on cellular processes, physiology, and the mechanics of movement. By ramification, size also profoundly affects life history, ecological interactions, and ecosystem function and structuring (McMahon, '73; Schmidt-Nielsen, '84; Brown and West, 2000). In terrestrial vertebrates, body size constrains animal function and performance through its effects on the physics of movement in musculo-skeletal systems (Alexander, '83; Biewener, 2003). Consequently, size-dependent changes in performance and physiology throughout ontogeny are common in many terrestrial vertebrates (Carrier, '83, '95, '96; see Herrel and Gibb, 2006, for an overview). However, because selection on juvenile life history stages is strong, juveniles may benefit from investing in the musculo-skeletal system early, to achieve high levels of performance that may offset the disadvantages of small body size. Indeed, in many vertebrates, young animals have levels of performance equaling, or even surpassing, those of adults (e.g. Carrier, '95; Trillmich et al., 2003; Moon and Tullis, 2006; Van Wassenbergh et al., 2009; Roos et al., 2010).

Here, we investigate size-related changes in defensive strike performance in *Trimeresurus (Crypteletrops) albolabris* (Malhotra and Thorpe, 2004), an arboreal pit viper from Southeast Asia (Cox, '91; Gumprecht et al., 2004; Vogel, 2006). Investigating how size affects strike performance in pit vipers is particularly interesting as the extreme sit-and-wait foraging style of these animals likely imposes significant selective pressures on strike performance (Cundall and Greene, 2000; Cundall, 2002; LaDuc, 2002; Young, 2010). Typically, vipers in general, and arboreal pit vipers more specifically, select a foraging site where they lie in ambush and wait for prey to pass by (Tu et al., 2000; Shine et al., 2002a,b). However, in some species juveniles select higher, more open foraging sites as this may give them a thermal foraging advantage (Shine et al., 2002b).This implies that juvenile arboreal pit vipers may be more exposed while foraging, and thus also subjected to high predation pressures (Li, '95; Shine et al., 2002b). Larger individuals, in contrast, tend to forage more in terrestrial environments and typically eat larger prey (Creer et al., 2002; Shine and Sun, 2003; Lin and Tu, 2008). Similar to the different requirements relevant to larger or smaller animals, sexes may also be expected to differ in strike performance capacity if they select different prey types (Vincent et al., 2004), utilize different types of habitats (Saint Girons and Pfeffer, '72), or are simply different in size.

Being able to strike fast and far is likely of importance in both defensive and predatory contexts, as fast and long strikes may deter potential predators before getting too close to the snake, and may also allow snakes to capture elusive prey without these being alerted to the presence of the snake (Greenwald, '74; Cundall, 2002, 2009; Shine et al., 2002c). Theoretical considerations (Hill, '50) suggest that strike velocity should be independent of body size, in which case juveniles should perform equally well as adults. Additionally, in larger animals, a larger mass needs to be displaced during the strike (Young, 2010), and consequently the theoretical prediction is that, all else being equal, acceleration should decrease with body mass to the negative 1 power (Hill, '50). However, limited data on the scaling of the cross-sectional area of the epaxial musculature in an arboreal snake (Jayne and Riley, 2007) indicate a distinct positive allometry, suggesting that larger individuals may be able to generate higher accelerations. Acceleration capacity has been shown to be independent of body size in many systems (see overview in Herrel and Gibb, 2006), and is likely crucial in both a defensive and feeding context as it conveys an element of surprise. In this article, we test how defensive strike performance changes with body size in both male and female *T. albolabris*. Moreover, we test for differences between sexes in morphology and performance and relate observed differences between the sexes and life history stages to published data on the ecology of pit vipers. Even though our data are restricted to defensive strikes only, constraints imposed by body size on maximal performance should be independent of the behavior and may have implications in a feeding-related context as well.

MATERIALS AND METHODS

Animals and Husbandry

We used 18 female and 17 male *T. albolabris*, kept in the snake facility at the Faculty of Science, University of Zagreb, Croatia. The adult animals were obtained 8 years ago from Austria as juveniles. Juveniles used in the experiment were born in the facility. The snakes are maintained individually in plastic cages in a temperature-controlled room (30°C/day, 26°C/night in summer; 27°C/winter, 21°C/night in winter). The photoperiod matched the outside light/dark cycle. Bark mulch was used as a substrate and every snake was provided with the plastic ladder for climbing. Water was provided ad libitum. All snakes were fed freshly killed laboratory mice. Adult snakes were fed at irregular intervals, on average once every 3 weeks. Juveniles were fed at irregular intervals of about 7–10 days.

Thirteen dead snakes preserved in the freezer and ranging in body mass from 1.78 to 262 g were rehydrated overnight and used for morphological analyses. First, the head and tail were separated from the body and weighed separately. Next the body was cut into three segments of equal length, each of which was weighed separately. Finally, the anterior third section of the body was cut midway and the cross sectional area of the entire epaxial muscle mass (semispinalis-spinalis, mutifidus, longissimus dorsi, and illiocostalis; see Jayne and Riley, 2010) was determined. To do so, digital pictures were taken of the section, and the surface area of the epaxial musculature was determined using image J (freely available at: http://rsbweb.nih.gov/ij/).

Morphometrics

Snakes were weighed using a digital scale (Scout Pro, Ohaus, Brooklyn, NY); pictures were taken in dorsal view with a reference grid as background using a Nikon (Tokyo, Japan) digital camera. Images were saved and head length, jaw length, head width, and interocular distance were determined as illustrated in Figure 1 using Image J (freely available at: http://rsbweb.nih.gov/ij/).

Kinematics

Between three and seven defensive strikes were recorded in lateral view for each individual willing to strike using a Redlake MotionPro (IDT, Tallahassee, FL) digital high speed camera set at 400 frames per second. This resulted in 129 strikes for 29 individuals. Room temperature remained between 26 and 29°C throughout the trials, close to the preferred foraging field temperatures in a closely related species of pit viper (Shine et al., 2002d). Six individuals were unwilling to strike or did not strike parallel to the camera, and were thus not included in the kinematic analysis. Snakes were introduced into the experimental arena consisting of a large (100 × 50 × 60 cm; Length × Width × Height) glass aquarium in which a plastic ladder was placed, stabilized by a wooden support at the base. In more than 98% of the cases, snakes struck eagerly at the target (large plush toy frog) while holding on
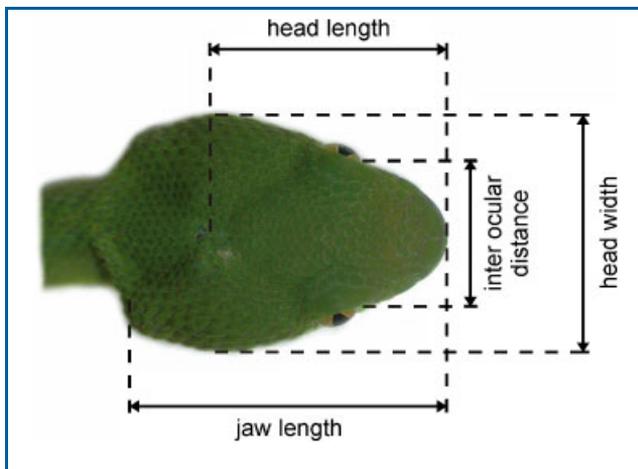
to the ladder with their body and tail. Strikes were nearly always oriented parallel to the long axis of the aquarium and in the horizontal plane as the target was present immediately in front of the snake.

Light was provided by four arrays of custom made ultra bright LEDs. Videos were saved as jpg-sequences and analyzed using Didge (A. Cullum, Creighton University, Omaha, NE). The snout tip was manually digitized frame by frame and coordinates exported to Microsoft Excel. The displacement of the head over time (i.e. the two-dimensional path followed by the snout tip) was calculated and the raw displacement profile was smoothed using a zero phase shift low pass butterworth filter (Winter, 2004), with cutoff frequency set at 50 Hz. Velocities and accelerations were calculated by numerical differentiation of the smoothed

Figure 1. Photograph (dorsal view) of the head of a *Trimeresurus albolabris* illustrating the morphometric measurements taken for each individual. The background grid present on each photo is not shown.

displacement profiles. For each individual, we extracted the single highest instantaneous velocity and acceleration across all strikes recorded (i.e. the fastest velocity and acceleration may thus come from different strikes). Additionally, the strike angle relative to the horizontal plane was quantified for each strike.

Analyses

Morphometric and performance data were $\log_{10}$-transformed before analyses and used as input for regression analyses to investigate the scaling of cranial morphology and strike performance relative to body size. First, we tested for the presence of sexual dimorphism in body size (mass) using an analysis of variance. Next, head shape dimorphism was tested using an ANCOVA with body mass as the covariate. Because no differences in head morphology were detected between males and females, scaling analyses were run on the pooled data set for males and females together. To investigate scaling of head and body dimensions relative to body size, we used reduced major axis (RMA) regressions, as errors on X and Y are likely of the same order of magnitude. For scaling of performance traits vs. body size, we used ordinary least squares (OLS) analyses given the small error in our X (body mass) relative to our Y value (kinematic variables). Our predictions are that velocity should be independent of body size and that accelerations should scale with body mass to the -1 power based on a Hill scaling model. To test whether observed slopes deviated from predictions, we considered observed slopes significant from predicted slopes if the predicted slope fell outside the 95% confidence interval (Table 1). Finally, we tested for differences in strike performance between the sexes using ANCOVA's with body mass as the covariate, and tested for correlations among performance variables using Pearson correlations. RMA regressions were performed using RMA; Software for RMA regression vs. 1.17 (Bohanak and Van

Table 1. Summary of scaling relationships of head dimensions relative to body mass in *T. albolabris.*

Variable	Slope	Intercept	R^2	Confidence limits
Head mass	0.74 ± 0.03	-0.85 ± 0.03	0.98	0.68–0.81[*]
Mass anterior third	1.07 ± 0.09	-0.85 ± 0.12	0.93	0.87–1.27
Mass mid third	1.01 ± 0.05	-0.57 ± 0.07	0.98	0.91–1.11
Mass posterior third	1.03 ± 0.03	-0.53 ± 0.06	0.98	1.02–1.09[*]
Mass tail	0.96 ± 0.08	-1.38 ± 0.09	0.89	0.88–1.26
Muscle surface area	0.63 ± 0.05	0.21 ± 0.09	0.95	0.50–0.75
Head length	0.23 ± 0.02	0.83 ± 0.01	0.92	0.20–0.25[*]
Lower jaw length	0.23 ± 0.01	1.02 ± 0.01	0.97	0.22–0.24[*]
Interocular distance	0.26 ± 0.02	0.58 ± 0.03	0.79	0.22–0.31[*]
Head width	0.22 ± 0.01	0.86 ± 0.01	0.95	0.20–0.24[*]

Table entries are based on reduced major axis regressions of each variable against $\log_{10}$-transformed body mass. Linear distances are in millimeters, masses in grams, and surface areas in millimeters[2].
[*]Indicates significant allometry.

der Linde, 2004); analyses of variance and OLS analyses were performed using SPSS V15 (Statsoft Inc., Tulsa, OK).

RESULTS

Strike Behavior and Performance

Snakes readily struck at the target presented and all strikes included in the analysis involved fang erection and biting of the target. Strikes were predominantly horizontal, deviating less than $10°$ from the horizontal (Fig. 2). Coils in the anterior half of the body were used to propel the head of the snake forward but were rarely fully extended, suggesting that snakes waited to strike the object until it was comfortably within reach (Fig. 2). Strike profiles were characterized by a rapid initial acceleration causing an increase in head velocity until right before or up to prey contact (Fig. 3). At prey contact, the head of snake decelerated strongly and the velocity dropped to zero (Fig. 3). All strikes continued, however, after initial prey contact, resulting in a considerable impact with the target often causing it to be displaced posteriorly.

Strike speeds in the animals tested here ranged from 1.11 to $1.92 \, ms^{-1}$ for males (mean: $1.45 \pm 0.23 \, ms^{-1}$) and from 1.12 to $2.4 \, ms^{-1}$ for females (mean $1.6 \pm 0.36 \, ms^{-1}$). The longest strikes in both sexes were of similar length and approached 20 cm (males: 18.2 cm; females: 19.9 cm). Mean strike distances were similar in males (11.8 ± 3.8 cm) and females (12.1 ± 3.3 cm). Accelerations were relatively high and reached $91.4 \, ms^{-2}$ in males ($56.8 \pm 17.7 \, ms^{-2}$ on average) and $119 \, ms^{-2}$ in females ($67.7 \pm 27.0 \, ms^{-2}$ on average).

Scaling

Head dimensions and head mass scaled with significant negative allometry relative to body mass (Table 1; Fig. 4), indicating that larger animals have relatively small heads for a given body mass. The mass of the anterior and middle body section, tail mass, and the cross-sectional area of the epaxial muscles in the anterior third of the body scaled with isometry relative to overall body mass (Table 1). The mass of the posterior third of the body scaled with slight but significant positive allometry relative to overall body mass. Among the performance traits measured, strike distance and strike velocity did not scale with snake size (distance: $P = 0.57$; $R^2 = 0.01$; velocity: $P = 0.53$; $R^2 = 0.02$; Fig. 5A). Strike acceleration, however, showed a small albeit significant ($P = 0.03$; $R^2 = 0.17$; slope $= 0.11$; see Fig. 5B) increase with body mass in T. albolabris.

Sexual Dimorphism

An ANOVA testing for differences in body mass between the sexes detected a significant difference ($F_{1,33} = 8.19$; $P = 0.007$), with females being heavier than males. Analyses of covariance testing for differences in head shape between males and females detected no differences (all $P > 0.05$). ANOVA's testing for differences between the sexes in strike distance and strike acceleration were nonsignificant (distance: $F_{1,27} = 2.92$, $P = 0.10$; acceleration: $F_{1,27} = 4.00$; $P = 0.06$). An analysis of covariance testing for differences in strike velocity between the sexes did, however, detect a significant difference ($F_{1,26} = 4.95$, $P = 0.04$), with females striking faster than males independent of their body mass.
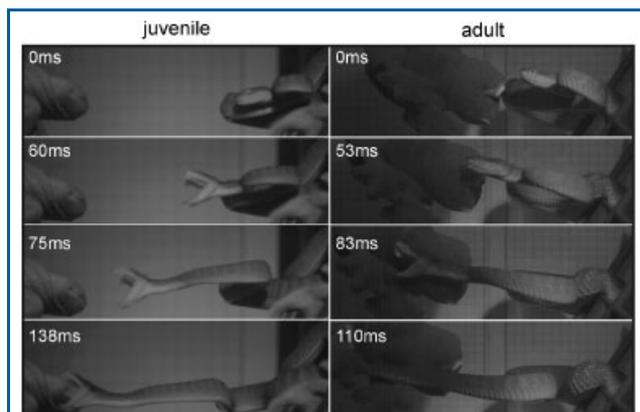


Figure 2. Representative strikes for a juvenile (left) and an adult (right) female Trimeresurus albolabris striking at the target. Note how part of the body remains coiled even after prey contact. The background grid visible in the images was not used for scaling purposes.
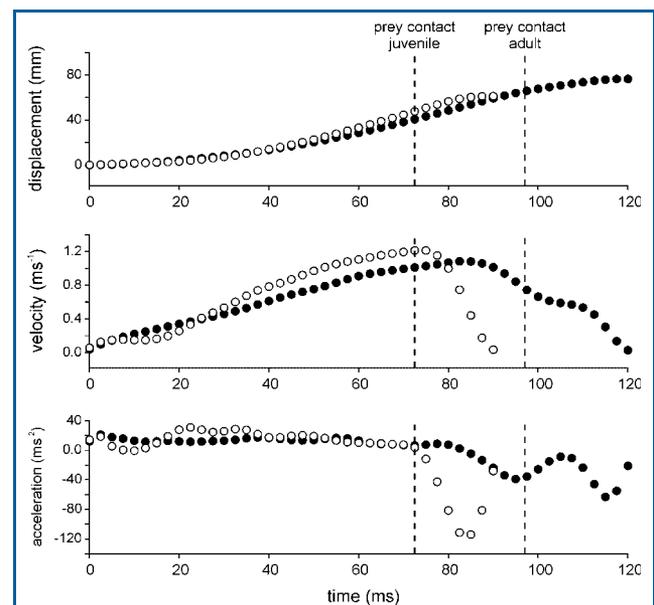
Figure 3. Representative kinematic profiles illustrating the displacement, velocity, and acceleration during the strike in a juvenile (open symbols) and an adult (closed symbols) female Trimeresurus albolabris. Dashed lines indicated the moment of prey contact.
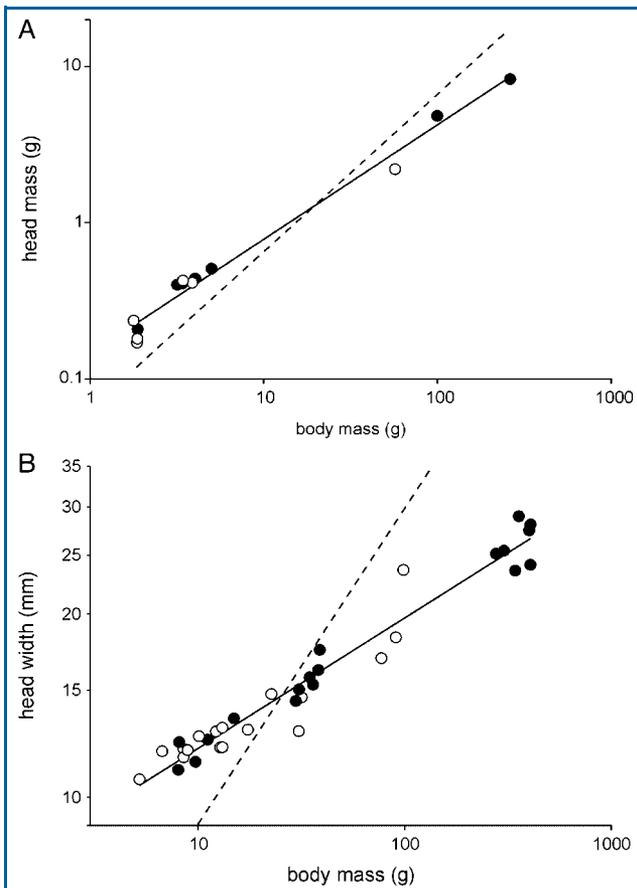
Figure 4. Scatterplots illustrating the scaling of head mass (A) and head width (B) relative to body mass. Filled symbols represent females, open symbols represent males. Both lower jaw length and head mass scale with significant negative allometry are relative to body mass. Dashed lines indicate the expected slopes of 1 and 0.33 under conditions of isometry.
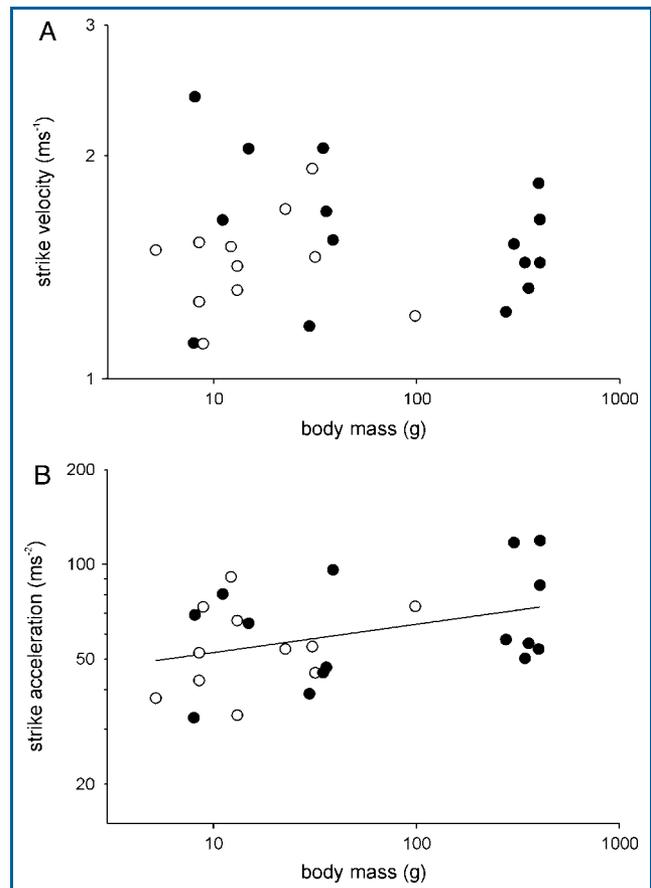
Figure 5. Scatterplots illustrating the scaling of strike velocity (A) and acceleration (B) relative to body mass. Whereas strike velocity is independent of body size, strike acceleration increases significantly with body size. Filled symbols represent females, open symbols represent males. Note how females strike faster for a given body mass than males on average.
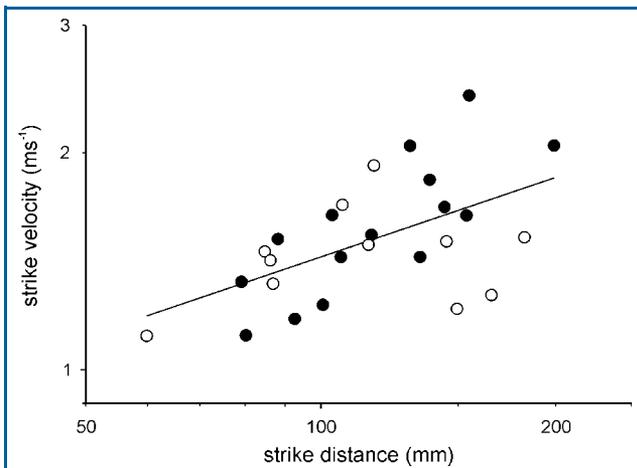
Correlations Among Performance Traits

Pearson correlations demonstrated significant correlations between strike distance on the one hand and strike velocity ($r = 0.85$; $P < 0.001$; Fig. 6) and strike acceleration ($r = 0.47$; $P = 0.011$) on the other hand, with longer strikes being both faster and being associated with higher accelerations. Moreover, faster strikes were also associated with higher accelerations ($r = 0.55$; $P = 0.002$).

DISCUSSION

Strike Performance in an Arboreal Pit Viper

Strike velocity in *T. albolabris* (mean: 1.5–1.6 ms^{-1} for males and females, respectively) is somewhat lower than that reported in some other studies on vipers and pit vipers (Van Riper, '54;

Young et al., 2001; LaDuc, 2002; Young, 2010), but similar to that reported for cottonmouths and some vipers of similar size (around 1.5 ms^{-1}; see Janoo and Gasc, '92; Kardong and Bels, '98; Vincent et al., 2005). Although unclear at this point in time whether the lower strike velocity is associated with the arboreal habits of our study species, this may also be owing to the significantly larger body sizes in rattle snakes and puff adders included in other studies. As strike velocity is linearly related to strike distance, larger snakes showing greater strike distances can be expected to reach higher peak velocities. Both mean and peak strike velocities recorded here for *T. albolabris* were, however, significantly greater than those reported for a closely related species, *G. shedaoensis* (Shine et al., 2002c). This is not all that surprising given that the data for *G. shedaoensis* were average velocities over an entire strike rather than peak instantaneous

Figure 6. Scatterplot illustrating that longer strikes are also faster. Strike distance was, however, independent of body mass. Filled symbols represent females, open symbols represent males.

observed for typical terrestrial vipers and pit vipers (e.g. see LaDuc, 2002; Young, 2010). Yet, it should be noted that we likely did not elicit maximal strike distances from the adults in our sample, and thus these results should be interpreted with caution.

Contrary to our predictions, our results show that larger animals reach higher peak accelerations than do smaller animals (Fig. 3B). One potential explanation for why larger individuals can reach higher strike accelerations may be the negative allometry of head size and mass coupled with the isometric scaling of epaxial muscle mass observed in this species. Indeed, larger animals have relatively smaller heads and, as a consequence, need to move a relatively smaller mass toward the target.

Sexual Dimorphism in Relation to Ecology

As in most snakes studied to date including other pit vipers, female *T. albolabris* in our study were heavier than males (Shine, '93; Tu et al., 2000). However, whereas there were no differences in head shape, strike distance, or acceleration capacity, the sexes did differ in peak strike velocity with females striking faster than males. This is, however, not a consequence of differences in body mass as results remained significant when taking this difference into account. Why would females have higher strike velocities than males? Although this question currently remains unanswered, in many species of arboreal pit vipers including *T. albolabris*, females become more terrestrial during the breeding season (Saint Girons and Pfeffer, '72) exposing them to a different suit of predators and potential prey items. However, given the paucity of data available on the ecology of this species, we cannot address this issue in detail. In summary, although our data suggest interesting differences between the sexes in strike performance, both the generality and ecological relevance of this result need to be investigated further.

velocities as reported here (Shine et al., 2002c). Peak accelerations, on the other hand, are more similar to data reported for other vipers and pit vipers (e.g. 72–74 msec^{-2}; see Vincent et al., 2005; Young, 2010), and much higher than those reported for colubrid snakes (Greenwald, '74; Alfaro, 2002; Bilcke et al., 2006). The striking difference in acceleration performance between viperids and colubrids is in itself not unexpected, given the larger cross-sectional area of the epaxial musculature in viperids giving them their typical stocky body shape and appearance (Moon and Candy, '97).

Scaling in Relation to Ecology and Mechanics

Our data show that strike velocity and strike distance are independent of body size in *T. albolabris*. Thus, juveniles included in our sample struck as fast and as far as adults. These data are in contrast to data reported for the closely related pit viper, *G. shedaoensis*, where adults strike faster than juveniles (Shine et al., 2002c). Achieving strike velocities comparable to those observed in adults is likely important for juveniles, given the larger predation pressure they typically experience (Li, '95) and the fact that they may compete with adults for similar prey (*T. albolabris* juveniles and adults feed principally on frogs; see Orlov et al., 2002). Mechanically, it is not unexpected that juveniles can reach similar strike velocities as, theoretically, this is predicted by scaling models (Hill, '50). More surprising is, however, that juveniles struck over similar distances as adults despite their smaller absolute body lengths. This can potentially be explained by the arboreal nature and prehensile tails of these animals. As they can hold on to the substrate with their tails while striking, this allows them to extend their bodies to more than 50% of body length during the strike, in contrast to what is

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