

# Aquatic versus terrestrial locomotion: comparative performance of two ecologically contrasting species of European natricine snakes

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## Keywords

locomotion; niche; temperature; tradeoffs; aquatic; terrestrial; snake.

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Received 10 August 2006; accepted 6 December 2006

doi:10.1111/j.1469-7998.2007.00299.x

## Abstract

One indicator of ecological differences between species is differential locomotory performance in different media. In this study, we compare locomotory speed of two species of natricine snakes on land and in water at a range of temperatures in the laboratory. As expected, both species moved more quickly at higher temperatures and both swam faster than they moved on land. However, the difference between aquatic and terrestrial speed was much greater for the aquatic species, *Natrix maura*, than for the semi-aquatic *Natrix natrix*. Furthermore, although *N. maura* was significantly faster than *N. natrix* in water, the opposite was true on land. In fact, *N. maura* was reluctant to move very far on land at all and would not complete a 2 m terrestrial course. Although we found no evidence of a negative correlation between the aquatic and terrestrial speeds of individual *N. natrix*, this interspecific comparison is consistent with the notion of a tradeoff between performance abilities on land and in water.

## Introduction

The concept of tradeoff is central to evolutionary biology. For example, in life-history theory, tradeoffs are manifest in a wide range of taxa (Gotthard, Nylin & Wiklund, 1994; Golet & Irons, 1999; Schwarzkopf, Blows & Caley, 1999), especially in terms of the allocation of finite resources to competing interests (e.g. growth vs. reproduction, clutch size vs. offspring size). Similarly, in behavioural ecology, there typically are tradeoffs between the need to forage and the need for vigilance against predators (Basey & Jenkins, 1995; Anholt, Werner & Skelly, 2000; Dowling & Godin, 2002). An extension of the idea of tradeoff is that species that are relatively specialized for life in one habitat will 'perform' better in that habitat than in others. For example, in assemblages of lizards, there are strong interspecific correlations among habitat, morphology and locomotory ability, with varying degrees of specialization of taxa (Irschick, 2002). Similarly, in sea snakes, there are tradeoffs in performance between aquatic and terrestrial locomotory abilities (Shine & Shetty, 2001). Locomotory performance, then, is a potentially important indicator of ecological differences between species.

Tests of sprint speed are common in studies of squamate reptiles (Losos, Creer & Schulte, 2002). An implicit assumption of such studies is that a higher speed equals better performance (e.g. for escaping predators or catching prey), although few tests of actual fitness differentials have been

made (but see Jayne & Bennett, 1990). Because of likely tradeoffs in performance abilities (Shine & Shetty, 2001), species that are partly terrestrial and partly aquatic face compromises in their relative performance in the differing media of air and water. On this basis, we predict that the extent to which a species is terrestrial or aquatic should determine its relative locomotory performance on land or in water.

Another factor that influences the performance of ectotherms, such as squamate reptiles, is temperature (Peterson, Gibson & Dorcas, 1993). Temperature can have direct (i.e. reaction rate changes) and/or indirect (i.e. thermoregulatory costs) effects on biological processes (Stevenson, Peterson & Tsuji, 1985; Marsh & Bennett, 1986; Gutzke & Packard, 1987), and most aspects of behaviour and physiology are significantly correlated with temperature (Lillywhite, 1987). Although optimal performance is generally maximized over a relatively narrow range of body temperatures ( $T_b$ 's) (Hailey & Davies, 1986; Lillywhite, 1987), performance variables often have different thermal sensitivities. If thermal sensitivity also varies among species, then comparisons of performance differences among species also need to be made at a range of temperatures.

In this study, we compare the locomotory performance of two closely related, but ecologically contrasting, species of European natricine snakes. The grass snake *Natrix natrix* is one of the most widely distributed snakes in Europe, ranging from southern England and Scandinavia to northern Africa

and from the Atlantic Ocean to western Russia (Gasc *et al.*, 1997). It is a generalist predator, feeding largely on various kinds of anuran prey throughout its range, but also preying on fish, mammals, birds and other reptiles to varying degrees (Gregory & Isaac, 2004a). Although semi-aquatic in its foraging behaviour, it is largely terrestrial otherwise, often basking well away from water (L. A. Isaac & P. T. Gregory, pers. obs.) and making extensive movements overland (Madsen, 1984).

The viperine snake *Natrix maura*, by contrast, has a more limited, southerly distribution, being confined to France, Spain, Portugal, south-west Switzerland, north-west Italy and a few Mediterranean islands (Gasc *et al.*, 1997); Mallorcan populations apparently resulted from introductions by humans about 2000 years ago (Schley & Griffiths, 1998). This species is largely aquatic and is rarely found more than 1–2 m from water (Hailey, Davies & Pulford, 1982) but occurs in various aquatic habitats (Santos *et al.*, 1997). The viperine snake is euryphagous and feeds on a wide range of aquatic vertebrates and invertebrates, although annelids may also be eaten, especially by young snakes (Arnold & Burton, 1978; Castanet & Guyetant, 1989; Santos, González-Solis & Llorente, 2000). Viperine snakes are fairly sedentary compared with grass snakes, and make relatively limited movements (Hailey & Davies, 1987).

We predicted that: (a) both species should be faster in water than on land (Stevenson *et al.*, 1985); (b) *N. maura* should be faster in water than *N. natrix*, but the reverse should be true on land; and (c) the speed of each species in either medium should increase from low to high temperatures.

## Materials and methods

We conducted this study in 2002 and 2003 on the campus of the University of Kent in Canterbury, south-eastern England. We collected *N. natrix* for the experiments from a nearby field site in Fordwich (Gregory & Isaac, 2004b); the *N. maura* we used were captive research specimens maintained by R. Griffiths, University of Kent. We housed snakes in individual plastic cages lined with newsprint, provided them water *ad libitum*, and fed them raw fish every few days. Experiments were performed using only nongravid snakes that had not been fed recently, to avoid the complicating effects of pregnancy or a full stomach on locomotion (Garland & Arnold, 1983; Seigel, Huggins & Ford, 1987).

We conducted three experiments as follows:

(1) In July 2002, we constructed a 2 m long and 0.5 m wide racetrack on a linoleum laboratory floor, with cardboard walls 0.5 m high and a cardboard shelter at the far end as a target for the snakes. To measure crawling speeds, we chased individual snakes down the racetrack while tapping their tails to stimulate movement (i.e. forced, as opposed to voluntary, crawling – Finkler & Claussen, 1999). We measured the time for each trial using a digital stopwatch and then converted the data to speed ( $\text{m s}^{-1}$ ). We ran each snake three times at each of three body temperatures ( $T_b$ ): 16, 21 and 32 °C. Snakes were given a 1 h rest between trials.  $T_b$ 's of snakes were controlled by placing each animal in either a

constant-temperature cooler or incubator about 30 min before each trial;  $T_b$ 's of snakes were confirmed by quickly measuring cloacal temperatures with a digital thermometer. We could not, however, control the ambient temperature of the laboratory in which we conducted the experiment; temperatures varied between 21 and 29 °C. The average snout–vent length (SVL) of the *N. natrix* and *N. maura* used in this experiment was 731 mm (range 480–958; seven males, 21 females) and 436 mm (range 222–557; three males, eight females), respectively.

(2) In August 2002, we tested the swimming speeds of snakes of each species (28 *N. natrix* and 11 *N. maura* – the same snakes as in experiment 1) in a trough constructed from a plastic drain pipe 4 m long, 0.2 m wide and 0.2 m high, with a water depth of 0.2 m. We used a longer track in this case because snakes could swim a short track very quickly (e.g. 2 m in 2–3 s), making measurement error a serious concern. We again tapped snakes' tails to stimulate movement and gave individual snakes a minimum 1 h rest between trials. We measured the time for each trial using a digital stopwatch and then converted the data to speed ( $\text{m s}^{-1}$ ). We ran each snake three times at each of three  $T_b$ 's: 13, 21 and 34 °C. We could not, however, correspondingly vary water temperature, which remained at about 20 °C throughout.

(3) In May 2003, we repeated the crawling experiment (experiment 1) that was performed in July 2002, because *N. maura* had refused to move down the racetrack in that experiment. Thus, we wanted to test whether this was either a real effect (i.e. do *N. maura* not like to move on terrestrial surfaces?) or whether it was due to the experimental set-up (i.e. did *N. maura* not move because we used an inappropriate type of racetrack or because  $T_b$ 's were too low?). In order to check that the results obtained using this new experimental procedure were comparable to those used in July 2002, we repeated the experiment using *N. natrix* as well. We therefore repeated the experiment using a shorter racetrack with a rougher surface and at a range of higher temperatures that overlapped with the temperatures used in experiment 1. The 1-m-long racetrack was equipped with light sensors that recorded both the start and finish of each trial and automatically displayed a read-out with time and speed. The track was 8.5 cm wide and the walls were 7 cm high; we also provided a hiding place (open pillow case) at the end of the track as a target for the snakes. The floor of the track was cardboard with ribs of masking tape laid across it to improve traction. We tested five new, recently captured *N. natrix* and five *N. maura* from the same group used in experiment 2 three times each at the following temperatures: 25, 30, 34 and 38 °C. Individual snakes were given a minimum of 50–60 min of rest between trials and were given 30–45 min to equilibrate to test temperatures in a constant-temperature incubator. The *N. natrix* in this experiment had an average SVL of 552 mm (range 435–668; five males) and the *N. maura* an average SVL of 505 mm (range 448–575; one male, four females).

In all the experiments, if a snake refused to move down the racetrack or reversed direction either while crawling or

swimming, the trial was stopped and immediately restarted (within 10 s). If this behaviour was repeated more than twice, the snake was taken out of rotation and re-tested at the end of the set of trials. We used data for a given snake only if at least two trials at a particular  $T_b$  were completed. Although we were unable to randomize all trials completely, we did randomize the order in which individuals were tested at a given temperature and the order in which we ran trials at the different temperatures.

We analysed data using SAS 9.1.2. Because individual snakes were tested multiple times in each experiment, we used univariate repeated-measures ANOVAs to compare the mean speed among temperatures and between species, but multivariate repeated-measures ANOVAs gave similar results. The mean speed was highly correlated with the maximum speed in all experiments (e.g. in experiment 2 over all individuals and all temperatures,  $r = 0.98$ ,  $n = 40$ ,  $P < 0.0001$ ) and conclusions using either mean or maximum were similar. Therefore, we present results only for the mean speed (e.g. Finkler & Claussen, 1999); furthermore, this approach allowed us to use all the data and hence also test the differences among individuals at a given temperature. We treated individual snakes as a random factor, and used the RANDOM/TEST option in PROC GLM to determine appropriate  $F$ -tests based on Type III sums of squares. In experiment 1, our initial analysis was simply a temperature  $\times$  individual mixed-model factorial design. However, in experiments 2 and 3, the factors in the initial analysis in each case were species, individuals nested within species, temperature and the interaction between species and temperature (standard univariate repeated-measures design – SAS, 1988; see also Finkler & Claussen, 1999). Depending on whether interaction terms were significant, they were either dropped or analyses were decomposed further, as appropriate. In cases of simple two-way ANOVAs (i.e. no nested factors) with interactions, we decomposed the analysis by slicing (Supplementary Material on CD-ROM accompanying Schabenberger & Pierce, 2001); otherwise, we performed separate analyses of a factor at each level of the other factor. We combined males and females in all analyses because there was no difference between the two sexes and the change in performance with temperature varied consistently between the sexes (i.e. temperature  $\times$  sex interaction always was non-significant). We assessed significance at  $\alpha = 0.05$ . To avoid inflation of overall  $\alpha$ -error in comparisons of speed at different temperatures, we limited our inter-temperature comparisons to orthogonal (i.e. independent) tests between adjacent temperatures (e.g. 25 vs. 30 °C, 30 vs. 34 °C, 34 vs. 38 °C in experiment 2). Finally, for each species at each temperature in each experiment, we tested the correlation between SVL and mean speed ( $n =$  number of individuals in each case). We did this to evaluate whether and how snake size influences locomotory speed.

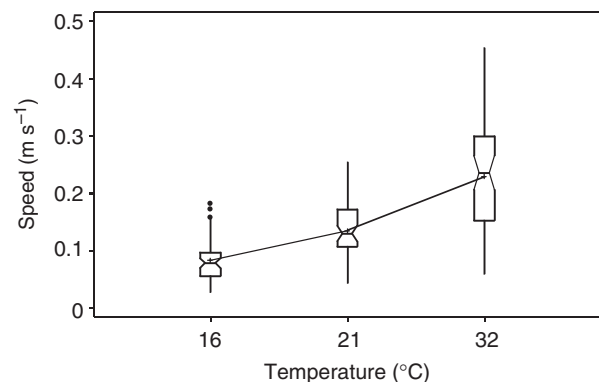
## Results

The effect of body size on the mean speed was highly variable. For example, in experiment 3, the correlations

between SVL and mean speed were all non-significant for *N. natrix* (three of four were negative), but much stronger and positive for *N. maura*, especially at the two lowest temperatures, where  $P = 0.01$  (the effect was also close to significance at the highest temperature,  $P = 0.07$ ). Because body size therefore might influence analyses of speed, we also calculated a size-adjusted speed as body lengths per second (Finkler & Claussen, 1999), where body length equals SVL. However, our results were the same whether we used size-adjusted or unadjusted speeds (e.g. correlation between means in experiment 3 over all individuals and temperatures,  $r = 0.94$ ,  $n = 40$ ,  $P < 0.0001$ ); hence, we consider size-adjusted means no further.

In experiment 1, only 20 *N. natrix* completed sufficient trials at all temperatures to be included in the analysis. Furthermore, *N. maura* were uncooperative in this test situation, either refusing to move or turning back to the start of the track; none completed the 2 m course. There was a significant interaction between temperature and individual *N. natrix* ( $F_{38,119} = 2.24$ ,  $P = 0.0005$ ), but slicing showed that differences in mean speed between temperatures were highly significant in 17 individuals and the trend in virtually all cases was towards increasing speed with increasing temperature. Planned contrasts showed that there was a highly significant difference in mean speed between adjacent temperatures (Fig. 1).

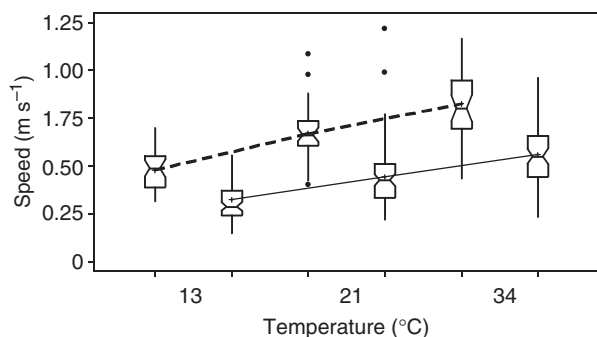
In experiment 2, two *N. natrix* did not complete enough trials to be included in the analysis; hence, the sample for that species was reduced to 26. There were significant interactions between temperature and individuals nested



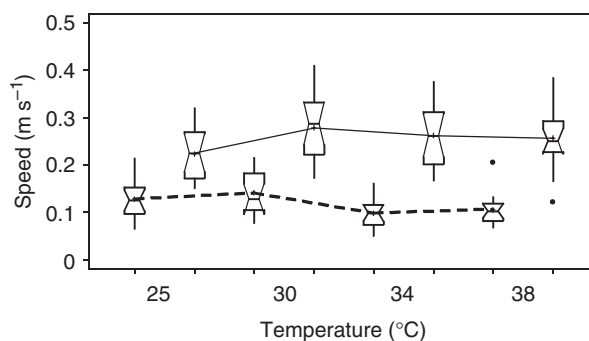
**Figure 1** Box-and-whisker plot comparing the speeds ( $\text{m s}^{-1}$ ) of *Natrix natrix* at three different temperatures on a 2 m track (experiment 1). All replicates for all individuals are included at each temperature, but analyses were performed on means. The upper and lower boundaries of box (hinges) indicate quartiles (25th and 75th percentiles). Whiskers from box reach the most extreme value that does not exceed 1.5 times the distance between the quartiles; more extreme observations than that are represented by dots. Endpoints of the notch in each box represent median  $\pm 1.57(\text{IQR}/\sqrt{n})$ , where IQR is the interquartile range (distance between hinges) and  $n$  is the sample size (Chambers *et al.*, 1983). The horizontal line in each box is the median; means are connected by lines. Average speeds at adjacent temperatures differed significantly in all cases. Note unequal intervals on temperature axis.

within species ( $F_{70,216} = 2.86$ ,  $P < 0.0001$ ) and between temperature and species ( $F_{2,216} = 6.39$ ,  $P = 0.002$ ); hence, we again performed separate analyses for each temperature and for each species. In the former, *N. maura* swam significantly faster at each temperature than *N. natrix* (all  $P$ 's  $< 0.0001$ ; Fig. 2). In the latter, there was still a significant interaction between temperature and individuals for each species (*N. natrix*,  $P < 0.0001$ ; *N. maura*,  $P = 0.001$ ), so we sliced the analysis in each case. In *N. natrix*, there was a significant effect of temperature on the mean swimming speed for 18 of 26 snakes (although another two were at  $P = 0.07$  and  $0.08$ ), and for nine of 11 *N. maura*. For both species, however, there was a significant increase in swimming speed with an increase in temperature (all planned comparisons,  $P < 0.0001$ ; Fig. 2). The two species swam differently down the track: *N. maura* swam with their heads completely underwater, whereas *N. natrix* typically swam with their heads out of the water. Only occasionally did *N. natrix* swim with their heads under water.

In experiment 3, the interaction between individual snakes (nested within species) and temperature was not significant; hence, we dropped that factor from our analysis. However, there was a significant interaction between species and temperature ( $F_{3,104} = 4.56$ ,  $P = 0.005$ ; Fig. 3); hence we decomposed the analysis into two separate analyses, one for each species, using the same model as in experiment 1. In neither case was the individual  $\times$  temperature interaction significant (i.e. individuals did not differ in relative performance at different temperatures), so we dropped that term from each analysis. In both cases, there was significant variation among temperatures (*N. maura*:  $F_{3,52} = 7.94$ ,  $P = 0.0002$ ; *N. natrix*:  $F_{3,52} = 3.68$ ,  $P < 0.02$ ), but planned comparisons showed that significant differences were limited to 25 versus 30 °C for *N. natrix* ( $F_{1,52} = 10.46$ ,  $P = 0.002$ ) and to 30 versus 34 °C for *N. maura*



**Figure 2** Box-and-whisker plot comparing the swimming speeds ( $\text{m s}^{-1}$ ) of *Natrix maura* and *Natrix natrix* at four different temperatures in a 4 m trough (experiment 2). All replicates for all individuals are included at each temperature, but analyses were performed on means. Interpretation of symbols is as in Fig. 1. The solid lines connect the means of *N. natrix* and dashed lines connect the means of *N. maura*. *Natrix maura* was significantly faster than *N. natrix*, on average, at every temperature. The average speeds at adjacent temperatures differed significantly in all cases. Note the difference in vertical scale compared with Figs 1 and 3.



**Figure 3** Box-and-whisker plot comparing the speeds ( $\text{m s}^{-1}$ ) of *Natrix maura* and *Natrix natrix* at four different temperatures on a 1 m track (experiment 3). All replicates for all individuals are included at each temperature, but analyses were performed on means. The solid lines connect the means of *N. natrix* and the dashed lines connect the means of *N. maura*. Interpretation of symbols is as in Fig. 1. *Natrix natrix* was significantly faster than *N. maura*, on average, at every temperature. Significant differences between adjacent temperatures were restricted to 25 vs. 30 for *N. natrix* and to 30 vs. 34 for *N. maura*.

( $F_{1,52} = 18.76$ ,  $P < 0.0001$ ; Fig. 3). We also compared the mean speed between species at each temperature (nested ANOVA, individuals within species) and found *N. natrix* to be significantly faster than *N. maura* at all temperatures ( $P$ 's ranging from 0.003 to 0.007, d.f. = 1,8; Fig. 3). An additional four *N. maura* were tested in pilot trials before this experiment, but they would not complete the 1 m course. Although snakes were more restless when held at 38 °C than at other temperatures, they tolerated that temperature well and apparently suffered no adverse effects.

Although the temperatures in experiments 1 and 2 were not identical, they were very similar. Therefore, because we used the same *N. natrix* in each experiment, we could test for potential tradeoffs between terrestrial and aquatic locomotion among individuals. We tested the correlation between mean speeds in each experiment for each temperature level, again using data for snakes only if they completed at least two trials at the particular temperature. This resulted in sample sizes of 20, 19 and 18 at low, medium and high temperatures, respectively. However, none of these correlations approached significance and were positive, rather than negative as predicted, at low and high temperatures. As in the other analyses, taking SVL into account (via partial correlation) did not change this result, nor did substituting maximum speeds for means.

## Discussion

The locomotory performance of semi-aquatic snakes is influenced by a complex array of environmental and organismal factors such as body size, temperature and substrate (Finkler & Claussen, 1999). We found strong and significant effects of temperature, especially at lower temperatures, on locomotory performance, but the effect of body size was different between species. However, because the relative performance of different individuals did not vary among

temperatures in either species, the effects of size (or other individual characteristics) were irrelevant for intraspecific comparisons of crawling speed. The large differences in speed between the two species also obviated any confounding effect of body size on interspecific comparisons.

Regardless of temperature and body-size effects, our results clearly distinguish major performance differences between these two European natricines: *N. maura* were much faster swimmers than *N. natrix*, but the reverse was true for locomotion on land. In short, the relative performances match the known ecology of these two species very well. In fact, we could not even stimulate *N. maura* to complete the terrestrial course in experiment 1; perhaps, the unnatural, smooth linoleum substrate, as well as the length of the course, inhibited them, but pilot trials in experiment 3 also indicated that almost half of the *N. maura* tested would not complete the shorter course used in that experiment. Thus, *N. maura* were not only slower on land, but less willing to continue moving forward, further emphasizing the difference between them and *N. natrix*. Although one might argue that the *N. maura* simply were more habituated to captivity and therefore less motivated to move than the 'wilder' *N. natrix*, this cannot explain the reversed results in the swimming tests.

*Natrix maura* is apparently an aquatic specialist, feeding mainly on aquatic prey. According to Hailey *et al.* (1982), viperine snakes basking on land are usually within 2 m of water (similar to the largely aquatic *Nerodia sipedon*; Scribner & Weatherhead, 1995) and usually escape into water by diving; syntopic grass snakes, by contrast, swim across the surface of water to escape (Hailey *et al.*, 1982). Our observations of swimming behaviour of the two species parallel these results.

In terms of its habitat use and feeding habits, *N. natrix* is also a much more generalist species in terms of both habitat and diet. These differences mirror those observed between species of natricines in North America. Scribner & Weatherhead (1995) found that the more aquatic *Nerodia* swam farther and dived more often than two less aquatic species of *Thamnophis*. Some species of *Thamnophis* are aquatic specialists and feed mainly on aquatic prey (Macias Garcia & Drummond, 1995), whereas other species have much more catholic diets (Gregory, 1984; Gregory & Nelson, 1991), feeding in both water and on land, and are much less tied to water in general. *Thamnophis* species that are aquatic specialists are also much more efficient predators in water than are more generalist species (Drummond, 1983; Drummond & Macias Garcia, 1989), but we know of no comparable studies of *Natrix*.

Typically, in snakes, the swimming speed is greater than the crawling speed at a given temperature (Stevenson *et al.*, 1985; Scribner & Weatherhead, 1995; Finkler & Claussen, 1999; Shine & Shetty, 2001). Our data support this conclusion for both species. Grass snakes swam faster than they crawled at the same set of temperatures (Fig. 1 vs. Fig. 2) and viperine snakes swam much faster, even at low temperatures, than they crawled at high temperatures (Fig. 2 vs. 3). This aquatic–terrestrial difference might be due to factors

such as friction with the substrate (Scribner & Weatherhead, 1995) or how much of the snake's surface area is in contact with the substrate (Finkler & Claussen, 1999). Overall, in our study, the difference between speed in water versus speed on land was greater for *N. maura*, the aquatic specialist (compare values around 25–30 °C in Figs 1–3). This parallels the results obtained by Shine & Shetty (2001) when they compared terrestrial elapids with aquatic laticuadids.

Although *N. maura* is a relatively warm-climate species, its locomotory performance in water is superior to that of *N. natrix*, even at lower  $T_b$ .

Hailey *et al.* (1982) described *N. maura* as a thermal generalist because it was active both day and night at their study site (unlike syntopic *N. natrix*, which was seen only in the daytime) and because it was active at a wide range of  $T_b$ . In the temperate zone, swimming snakes frequently encounter cool conditions (Nelson & Gregory, 2000; MacKinnon *et al.*, 2006). In our experiment, we could not easily modify the water temperature, and the high heat capacity of water presumably affected snake  $T_b$ 's during swimming trials. Nonetheless, as expected, swimming speed increased significantly with increases in  $T_b$  at the start of the trial.

Hailey *et al.* (1982) found that  $T_b$ 's of *N. maura* captured on land were significantly higher than those of snakes captured in water at the same time of year. If so, acceptance of temporarily low  $T_b$  might simply be a cost of foraging aquatically. At higher latitudes, where natricine snakes sometimes forage in quite cold water, access to higher temperatures on land for basking and digestion may be a key determinant of their activity patterns (Nelson & Gregory, 2000); similarly, Manjarrez & Drummond (1996) concluded that foraging activity of a Mexican garter snake was limited by water temperature. However, aquatic foraging snakes might be less disadvantaged by low temperature than those foraging terrestrially. For example, Stevenson *et al.* (1985) determined that the swimming speed of a temperate-zone garter snake was less sensitive to temperature than crawling speed (see also Finkler & Claussen, 1999) and that snakes were less reluctant to swim at low temperatures than they were to crawl.

Our findings are inconsistent with respect to the hypothesis that there are tradeoffs between terrestrial and aquatic locomotion in snakes (Shine & Shetty, 2001). Although the difference between *N. natrix* and *N. maura* was supportive of such a tradeoff, variation among individual *N. natrix* was not. However, revealing tradeoffs by simple correlations among individuals is difficult (van Noordwijk & de Jong, 1986), especially if other variables are correlated with those involved in the tradeoff (i.e. individuals vary in 'quality'). For example, in life-history studies, the expected tradeoff between litter size and offspring size is often apparent only if the body size of the mother is taken into account (e.g. Gignac & Gregory, 2005). Thus, if there is a tradeoff in the effectiveness of terrestrial and aquatic locomotion in *N. natrix*, we may need to measure additional variables (e.g. muscular strength – Bonnet, Ineich & Shine, 2005) to demonstrate it (and match temperatures more closely as well). Presumably, tradeoffs show up more readily in

interpopulation or interspecific comparisons because these other influential variables also differ more strongly.

Alternatively, the differences between *N. natrix* and *N. maura* in their relative locomotory abilities on land and in water may not be due to a performance tradeoff, but due to other factors. For example, crypticity presumably plays an important role in the anti-predation repertoire of snakes (Greene, 1988) and there is evidence of correlation between colour patterns and escape responses of snakes (Jackson, Ingram & Campbell, 1976). Thus, species that are more cryptic on land may rely less on speed to escape, especially if escape habitat (e.g. water) is always close by. Our sample admittedly confounded the effects of species and geography, but the body patterns of the *N. natrix* and *N. maura* that we used differed substantially, the latter being more blotched and presumably more disruptive. The extent, if any, to which these kinds of factors contribute to performance differences between these and other species awaits further study.

## Acknowledgements

We thank R. Griffiths (University of Kent) for advice, logistic support and loan of specimens of *N. maura*. Doug Schneider helped us collect *N. natrix* in the field and assisted in the laboratory. This work was supported by a Research Grant from the Natural Sciences and Engineering Research Council of Canada to P.T.G.

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