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Evolution of alternative foraging tactics driven by water temperature and physiological constraints in an amphibious snake

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Amphibious predatory ectotherms live and forage in two environments (aquatic and terrestrial) that can drastically differ in temperature means and variance across space and time. The locomotor performance of ectotherms is known to be strongly affected by temperature. However, how differences in water temperature may drive the evolution of alternative foraging tactics in amphibious animals remains poorly understood. Fish-eating Viperine snakes *Natrix maura* occur from high altitude cold water streams to warm shallow lakes, and employ two main feeding strategies: sentinel foraging (underwater sit-and-wait behaviour) and active foraging (fish chasing). Using 272 juvenile snakes we measured: the performance kinetics of diving and swimming in a wide range of water temperatures; basal metabolic levels in relation to body temperature; and the type of foraging mode expressed in water-temperature-acclimated snakes. Individual swimming performances increased with testing temperature (10, 15, 20, 25 or 30 °C). Apnoea time followed an opposite trend however, plausibly reflecting the fact that oxygen demands are related to the metabolic rate of ectotherms. That is, snake heart rates increased with body temperature. Snakes acclimated to 10 °C water mostly displayed sentinel foraging. By contrast, 20 °C and 30 °C water-acclimated snakes were extremely active fish chasers. Individual apnoea times at the various testing temperatures were all correlated; as were individual swimming speeds. There was however no clear relationship between an individual's ability to hold its breath and its ability to swim, suggesting that both performance traits may be the target of different selective pressures. Fast swimming speed and long breath holding abilities are likely key determinants of both foraging success and predatory evasion, although in a context dependent manner. Active swimming foraging is likely to be advantageous in warm water (> 20 °C), while sentinel foraging appears better suited to cold water (< 14 °C). The physiological aspects of foraging tactics of amphibious snakes combined with field and laboratory observations support the idea that physiological and environmental constraints may generate shifts in habitat use and associated foraging tactics in amphibious ectotherms. Avenues for further research are discussed.

Additional Keywords: acclimation – apnoea – foraging tactic – *Natrix maura* – swimming – water temperature.

INTRODUCTION

Locomotor performance is a prime determinant of foraging success in many predators. This is obvious for predators that rely on sheer speed to outperform their prey (e.g. cheetahs – Williams *et al.*, 1997; birds of prey – Hedenström & Rosén, 2001; or whales – Aguilar Soto *et al.*, 2008). But it is also true for many ambush predators where muscle coordination and striking speed is paramount to foraging success (i.e. in pikes – Harper & Blake, 1991; or rattlesnakes – Clark, 2006). One of the key aspects of locomotor performance is that it is, notably in ectotherms, strongly affected by temperature (Huey, 1982; Miller, 1982; Ojanguren & Braña, 2000; Watkins, 2000). Hence, many ectotherms are active thermoregulators that, for instance, bask in the morning sun prior to undertaking further activities, including foraging (Cowles & Bogert, 1944; Casey, 1981; Avery, 1982; Hutchison & Dupre, 1992). Conversely, ectotherms that live in environments that are consistently cold

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*Corresponding author. E-mail: faubret@gmail.com (for instance Artic sea waters), or very hot (such as deep sea hydrothermal vents) have evolved a wide range of physiological adaptations that allow them to function at such extreme temperatures (Dahlhoff *et al*., 1991; Van Dover, 1995; Somero, Dahlhoff & Lin, 1996; Chen, DeVries & Cheng, 1997; Fields, 2001; Jeng, Ng & Ng, 2004; Pakchung, Simpson & Codd, 2006; Bilyk & DeVries, 2011).

Amphibious ectotherms are atypical as they live in two distinct environments: aquatic and terrestrial. Water and air may drastically differ not only in temperature means, but also in temperature variance across space (latitude, altitude) and time (days, seasons or years). Moreover, optimal performance in ectotherms is generally achieved over a relatively narrow range of body temperatures (Hailey & Davies, 1986a; Lillywhite, 1987). In this context, it is inevitable that organisms that, for instance, thermoregulate close to optimal muscle function on land will depart from that optimum when entering water either to forage or escape predators (Seebacher *et al*., 2003a). Although vertebrate amphibious ectotherms are found in a wide range of taxa (i.e. fish, turtles, lizards, amphibians, snakes and crocodiles), the way differences in environmental temperature (and incidentally body temperature) may affect locomotor performances, especially in respect to foraging behaviour, has attracted little attention (Marvin, 2003; Seebacher, Elsey & Trosclair, 2003b; Glanville & Seebacher, 2006; Aubret & Michniewicz, 2010; Aubret & Shine, 2010).

Phenotypic plasticity, either in the form of long term acclimation to water temperature (physiological plasticity) or shorter term thermoregulatory tactics (behavioural plasticity), has long been described as an essential adaptation to an amphibious lifestyle (Johnson & Bennett, 1995; Wilson, James & Johnston, 2000; Johnston & Temple, 2002; Marvin, 2003; Seebacher, 2005; Schaefer & Ryan, 2006; Angilletta, 2009). For instance, Eastern Fox snakes (*Elaphe gloydi*) warm up in the sun prior to entering cold water (MacKinnon *et al*., 2006; see also Aubret and Michniewicz, 2010 for a similar finding). Alligators display seasonal shifts in thermoregulation coupled with physiological adaptations in muscle metabolic enzymes (Seebacher *et al*., 2003a, b). Such physiological and behavioural adjustments allow for the attainment of optimal body temperature and consequently improved locomotor performance (Peterson, Gibson & Dorcas, 1993) while entering an often colder medium. That is, higher speed is assumed to equate to better performance, be it to escape predators or catch prey (Jayne & Bennett, 1990; Kingsolver *et al*., 2001; Le Galliard, Clobert & Ferriere, 2004; Miles, 2004).

Amphibious ectotherms may adjust in a third way by switching between alternative foraging strategies (Fraser, Metcalfe & Thorpe, 1993; Denoël, 2004). Some reptiles switch to mimetic defence tactics at low body temperatures that may not allow for a rapid escape (Hertz, Huey & Nevo, 1982; Weatherhead & Robertson, 1992; Shine *et al*., 2000). Likewise, foraging preferentially on land at times when water temperature is too cold to allow for efficient swimming may be an advantageous strategy. Conversely, active hunting and chasing of fast moving prey might be better suited to warm water, where swimming performance is greater.

In support of this hypothesis, Luiselli & Zimmermann (1997) compared the thermal biology of the Dice snake (*Natrix tessellata*) between populations inhabiting two geographic areas with contrasted climatic conditions (9 °C water, Austria *versus* 18 °C water, central Italy). In Austria, 19% of encountered snakes were found in water, whereas in Italy the proportion of snakes found in water was much higher (77%). Austrian snakes tended to stay in water for very short times (possibly only for foraging), due to low water temperatures. Another study, conducted by Patterson & Davies (1982), found that during the summer months, the vast majority of Viperine snakes *Natrix maura* (Linnaeus 1758) were seen in the water, as opposed to spring where about 70% of the snakes seen were out of the water basking close to the water's edge. The authors suggested that summer water temperatures were high enough for snakes to spend virtually all their time in the water. Presumably, remaining in the water carries advantages in terms of foraging opportunities (i.e. being close to their prey: fish, tadpoles, newts) as well as predatory avoidance (i.e. from aerial and terrestrial predators; Scribner & Weatherhead, 1995; Akani & Luiselli, 2001).

Amphibious snakes display a suite of foraging behaviour that is most likely related to their environment, as well as the type and density of their target prey (Drummond, 1983; Alfaro, 2003). Bilcke, Herrel & Van Damme (2006) demonstrated that prey density, rather than diet, played an important role in the evolution of the different prey-capture strategies and strike velocities of natricine snakes. In *N. maura*, two main types of underwater foraging behaviour were described: sentinel foraging and active foraging (Hailey & Davies, 1986b). Sentinel foraging is an ambush tactic where the snake stays motionless underwater, its tail sometimes coiled around an underwater perch. Sentinel foraging snakes frontally strike at fish passing within reach (Bilcke *et al*., 2006; Van Wassenbergh *et al*., 2010). Active foraging on the other hand refers to a tactic where a snake browses the environment for potential prey. Snakes lunge at and pursue any detected fish. Active foraging may also occur as 'fishing' (Evans, 1942) where snakes swim randomly across the water with their mouth wide open, attempting to make contact with a fish. Sentinel foraging and active foraging (especially as 'fishing') have been respectively associated with low and high prey densities (Drummond, 1983; Alfaro, 2003; Bilcke *et al.*, 2006). However, the effect water temperature may have on the efficiency of each foraging strategy remains unknown.

Given the strong relationships existing between body temperature, activity and oxygen consumption in ectotherms (Huey, 1982; Stevenson, Peterson & Tsuji, 1984; Bennett, 1990), both foraging tactics may be considered as physiological opposites: motionless breath holding *versus* active underwater swimming (Hailey & Davies, 1986b). In this context, we hypothesised that: (1) swimming performance would increase and breath holding performance would decrease with increasing water temperature, (2) sentinel foraging would be observed in cold water and fish chasing in warmer water, and (3) the physiological constraints associated with both hunting modes would have resulted in the evolution of behavioural plasticity in habitat use and foraging tactics in response to water temperature, as observed in numerous amphibious ectotherms (Patterson & Davies, 1982; Fraser *et al.*, 1993; Ikebe & Oishi, 1997; Luiselli & Zimmermann, 1997; Denoël, 2004).

In order to test these hypotheses and obtain insights into the evolution of alternative foraging behaviour in amphibious ectotherms, we used laboratory-born Viperine snakes *Natrix maura* and measured the performance kinetics of diving and swimming in a range of water temperatures, basal metabolic levels in relation to body temperature, and the hunting strategies displayed by water-temperature-acclimated snakes.

MATERIAL AND METHODS

Study animals and study site

The Viperine snake occurs in France, Spain, Portugal, south-west Switzerland, north-west Italy and a few Mediterranean islands (Gasc *et al.*, 1997). This species is largely aquatic and individuals are always found in the vicinity of water (Hailey, Davies & Pulford, 1982). The Viperine snake feeds on a wide range of aquatic vertebrates and invertebrates (Castanet & Guyetant, 1989; Arnold, 2002; Santos *et al.*, 2000) and promptly escapes into water when disturbed (Hailey *et al.*, 1982).

Study animals were caught along the banks of the Lez River in south-west Ariège, France. The study site was a 20 kilometre stretch of river between the localities of Moulis (42°57′ 43″ N; 1°05′ 30″ E) and Le Pont (42°52′ 32″N; 0°57′ 19″ E; approximate altitude 800 m). The fish population of the Lez is dominated by trouts (*Salmo trutta*) and minnows (*Phoxinus phoxinus*). The main frog and toad species living in or near the river include *Bufo bufo*, *Alytes obstetricans*, *Rana esculenta* spp., *R. temporaria*, and *R. dalmatina*. Potential prey (as larvae or adults) may also include *Salamandra salamandra* or newts such as *Triturus marmoratus* and *Lissotriton helveticus*. The study site is regularly surveyed as part of a mark-recapture study of *Natrix maura*. In 2011, out of a total of 143 individuals captured, 11 regurgitated a prey while being handled. Prey included nine trouts, one minnow and one frog. Another four snakes were observed in the water carrying a recently captured trout, and successfully dragging it onto land where it was swallowed. Fish are therefore suspected to be the main prey item of Viperine snakes at this site.

Animals used

In total, 28 gravid females were captured in May and June 2011 and brought to the laboratory (Station d'Ecologie Expérimentale à Moulis). They were housed individually in plastic containers (60 × 40 × 15 cm) located in a temperature controlled room (constant 18 °C). A 40 W lamp fitted above each enclosure and set on a 12/12 h day and night timer provided the opportunity to bask. A 5 cm layer of moist peat was used as substrate. Each enclosure also featured a clean water bowl, a shelter (terracotta roof tile) and an egg laying box. The egg laying box was a black plastic container (15 × 10 × 5 cm), containing a 2 cm layer of moist vermiculite, with a 4 cm diameter side opening. Oviposition dates spanned from the 18 June to the 26 July 2011. In total, 318 eggs were obtained (litter size ± SD = 11.41 ± 4.12 eggs). Eggs were collected within 12 h and transferred into an Aqualytic incubation chamber (Dortmund, North Rhine-Westphalia, Germany) set at a constant 28 °C. Eggs were individually marked with a letter (coding for litter of origin) and a number (egg number within each litter) for identification purposes. Eggs were placed on a 2 cm layer of moist vermiculite for the entire incubation period. All females were returned to their exact site of capture within 2 weeks of oviposition. From capture to release, females were fed small dead trouts once a week (frozen trouts were purchased from a local fish farm: Pisciculture des Chutes d'Aston, Les Cabannes, France).

Hatching occurred between the 1 August and the 24 August 2011. Neonates fully emerged from their eggs within 2 days of splitting their egg shells. In total, 282 snakes were born, from which 231 were randomly selected for this study (8.25 ± 4.22 neonates per litter; 100 males and 130 females; one individual was not sexed). All neonates were marked by scale-clipping for identification and measured in body mass (± 0.01 g), snout-vent length (± 0.1 cm) and total length (± 0.1 cm) within 12 h of hatching. Sex was determined by eversion of the hemipenes. Siblings were housed together in plastic boxes (15 × 10 × 5 cm), with a water dish, shelter and paper towel as substrate. All snakes were remeasured in body mass, snout-vent length and total length at 3 weeks of age. During week 4, each individual underwent a series of tests (see below). Snakes were then given their first meal (small dead minnows ranging from 0.5 g to 1 g; supplied by the fish farm Armorvif, Kerpert, France).

To account for differences in condition amongst snakes, a body condition index (BCI; Bonnet & Naulleau, 1994) was calculated for each snake, using the residual values of the linear least-squares regression of Log (body mass) against Log (snout-vent length).

TESTING PROCEDURE

All snakes were subjected to five swimming tests and three apnoea tests. In order to account for potential effects of prior experience, we used a balanced testing design within each litter. On testing day 1, snake 1 did test 1, snake 2 test 2, snake 3 test 3, and so on. On testing day 2, snake 1 did test 2, snake 2 test 3, snake 3 test 4, and so on for 8 different tests and 231 snakes. Individual snakes did one test a day, allowing a 24 h rest between tests.

Apnoea time

We used the procedure described in Aubret, Bonnet & Shine (2007). A glass aquarium (25 cm × 15 cm × 20 cm) was filled with 20 cm of water. Water temperature was adjusted immediately prior to testing, and monitored using aquarium thermometers as well as an infrared thermometer (Victor VC303B, ShenZhen Victor Hi-tech Co., Guangdong, China) throughout the testing procedure. For the purpose of the study we needed snake body temperature to equal water temperature prior to testing. The bottom half of a plastic bottle was filled with a few centimetres of water (so that snakes were able to rest on the bottom) and used as an acclimation compartment (5 min), placed within the aquarium. Testing temperatures were 10, 20 or 30 °C. We used four opaque PVC tubes, 10 cm in length and 2 cm in diameter, closed at one end and fitted with small weights to ensure stability under water. Up to four snakes were tested simultaneously. The diameter of the tube was large enough to allow easy movement of the snakes inside it. Snakes were removed from the acclimation compartment, and presented with the open end of a tube. As soon as the snake voluntarily entered the tube, the unit was fully immersed in the water tilted upward to make sure no air bubbles remained trapped within the tube. The tubes were then oriented towards one side of the aquarium, facing the observer, with the tube opening in direct contact with the glass. This allowed the observer to monitor the movement of the snakes inside the tube. Snakes typically remained hidden at the closed end of the tube for a variable length of time, but then invariably moved to the opening, with their snout making contact with the glass tank. At this stage, snakes were encouraged to retreat back down into the tube by the observer making a quick movement or gently knocking the glass with the tip of a finger. Further attempts to exit the tube generally increased in frequency and magnitude, to the extent that snakes would, despite encouragement by the observer to remain in the tube, push back the tube a few millimetres by pressing the snout against the glass, and eventually reach the surface. This stimulus encouraged the animal to prolong the duration of its time underwater, presumably until its need to breathe overcame the perceived risk of predation. The time taken from immersion to surface was recorded with digital chronometers (± 1 s).

Swimming performance

We used a procedure adopted in previous studies (Shine & Shetty, 2001; Aubret, 2004; Aubret *et al*., 2007). A linear 300 cm × 40 cm × 50 cm swimming track was built (wooden frame painted white with black markers drawn every 10 cm, clear coated with Epoxy resin). A high definition wide angle digital camera (30 fps) was fitted above the track and used to record trials (recording section of 260 cm). The tank was filled with 10 cm of water and fitted with a reverse-cycle water chiller (TECO TC15, Ravenna, Italy) and water pump (Aquavie 1264, Connaux, France) that allowed for quick adjustment of water temperature. Testing water temperatures were 10, 15, 20, 25 and 30 °C, encompassing the natural range of water temperature encountered by *N. maura* in the wild, from high altitude streams through to northern African shallow lakes (Gasc *et al*., 1997). Water temperature was regularly checked to ensure it kept the desired temperature.

We used an acclimation pool, consisting of a small glass aquarium (25 × 15 × 20 cm) located at the end of the track and filled with only 3 cm of water taken directly from the pool for temperature consistency. Snakes were left undisturbed for 5 minutes in the acclimation aquarium prior to testing. Snakes were then dropped at one end the track and immediately started swimming towards the opposite end. Maximum speed was maintained by stimulating the snake's tail with an artist's paintbrush. The video was then edited on a computer and swimming speed calculated.

HEART RATES AS A FUNCTION OF BODY TEMPERATURE

Another 12 3-week-old juvenile snakes (five males and seven females) were used in October 2012 to record heart rates (i.e. an estimate of basal metabolism) over a range of body temperatures. These 12 juveniles were the offspring of five different pregnant females, field caught from the same study area (2.40 ± 0.55 neonates were randomly selected per litter). We estimated basal metabolic rate by measuring snake heart rates, owing to the accurate physiological relationship existing between heart rate and oxygen consumption (i.e., an indicator of metabolic rate; Butler *et al*., 2004). Each individual was tested at three different body temperatures (9, 18 or 28 °C) on 3 consecutive days, applying a balanced order design. Snakes were placed inside individual testing bags (made of cotton material) fitted to their size, and into temperature controlled chambers for 30 min in order to reach testing temperature and ensure minimum stress levels at the time of testing (see Aubret and Tort, 2013 for details on method). Each bag was then placed onto the sensor pad of a Buddy digital egg monitor (MK2, Avitronics, Cornwall, England) for heart rate reading (a stable reading was obtained after approximately 30 s; Du, Zhao & Shine, 2010).

INFLUENCE OF WATER TEMPERATURE ON FORAGING TACTICS

Eight gravid female Viperine snakes were captured in June and July 2013. Oviposition dates spanned from the 10 July to the 24 August 2013. In total, 82 eggs (average clutch size: 10.25 ± 5.28 eggs) produced 77 neonates between the 24 August and the 9 October. We kept 41 juveniles snakes (n = 5.13 ± 5.11 neonates per litter) to perform behavioural observations of feeding behaviour in relation to rearing water temperature. Fifteen identical rectangular enclosures (paludarium) were built using wood, and rendered waterproof by Epoxy resin coating (non-toxic once polymerised). The enclosures were housed in a controlled temperature room set at 18 °C at all times. Each enclosure featured a terrestrial area (50 × 20 × 15 cm) joined to an aquatic area (pool of fresh water; 50 × 20 × 40 cm). The water was approximately 20 cm deep in all enclosures. Both compartments were linked by a 30 × 5 cm 'snake ladder' made of artificial plastic grass. This allowed snakes to come and go freely between the two habitats and created a floating platform within the pool on which snakes could rest. A 40 W light globe, set on a 12/12 h timer, fitted at the back of the terrestrial area, provided basking opportunities (hot spot > 45 °C). Several shelters were available in both areas (broken pieces of roof tiles and 10 × 4 cm PVC piping). Underwater hiding spots were used extensively by the snakes.

There were three experimental treatments. Water temperature was set at a constant 10 °C in five enclosures (using a water conditioner TECO TC15, Ravenna, Italy – Cold treatment), 20 °C in another five (using water heaters JBL ProTemp S50 50W, Neuhofen, Rheinland-Pfalz, Germany – Warm treatment), and 30 °C in the remaining five enclosures (using water heaters as above – Hot treatment). We used a split-clutch design to account for maternal effects: 2 or 3 snakes from each clutch were allocated to each dual environment. Twelve juveniles were allocated to the Cold treatment, 14 to the Warm treatment and 15 to the Hot treatment group. Data collection started after 118.00 ± 13.32 days of acclimation and lasted 71 days. Food was offered every 2 days and foraging tactics recorded only for snakes feeding in the water (snakes that were hiding or basking in the terrestrial area were fed, but their feeding behaviour was not recorded). Fish (dead small minnows ranging from 0.3 to 0.5 g) were presented at the end of 30 cm long metal tweezers a few centimetres in front of the snake's snout and slowly moved away in order to try and elicit chasing. We noted individual foraging behaviour observed during the feeding events: sentinel foraging or active foraging. Once the prey had been captured, the snake was briefly handled for identification. Between four and eight feeding events were recorded for each individual snake (5.54 ± 0.98 per snake on average).

All snakes were returned to their mother's capture site after completion of the experiments.

DATA ANALYSIS

The assumption for normally distributed data was tested on all variables. Where not normal, requirements were met by Log-transforming the relevant data prior to analysis. Where the assumption for normal distribution could not be met by Log-transforming the data, non-parametric tests were performed using non-transformed data.

ETHICAL NOTE

All experiments complied with the CNRS animal ethics committee requirements and were approved by the Préfecture de l'Ariège (Arrété #2012-11), the Direction Régionale de l'Environnement, de l'Aménagement et du Logement (DREAL Midi-

Pyrénées) and the Conseil Scientifique Régional du Patrimoine Naturel (CSRPN Midi-Pyrénées). Individual snakes were monitored for a given period following all experiments. In respect to the apnoea time experiment, while the tubes were rested against the glass, the materials used, and the set up was such that with minor effort, snakes were able to push the tubes away from the glass to exit. No snakes suffered any detrimental consequences during, or subsequently, from any of the experiments.

RESULTS

Apnoea time and water temperature

There was no effect of sex on individual apnoea time at any testing temperature (repeated measures design ANOVA with sex and temperature as factors, and individual apnoea time at each temperature as the repeated measure; interaction term $F_{2,\ 456} = 1.27$, $P = 0.28$; effect of sex $F_{1,\ 228} = 0.13$, $P = 0.72$). There was however a strong effect of water temperature on individual apnoea time ($F_{2,\ 456} = 1082.2$, $P < 0.0001$; Fig. 1 left axis). While the average apnoea time increased three-fold from 30 °C to 20 °C testing temperature, the average performance in 10 °C water was over 15 times higher than in 30 °C water. Maximum individual values were 159.8 min in 10 °C water, 58.2 min in 20 °C water and up to 23.3 min at 30 °C.

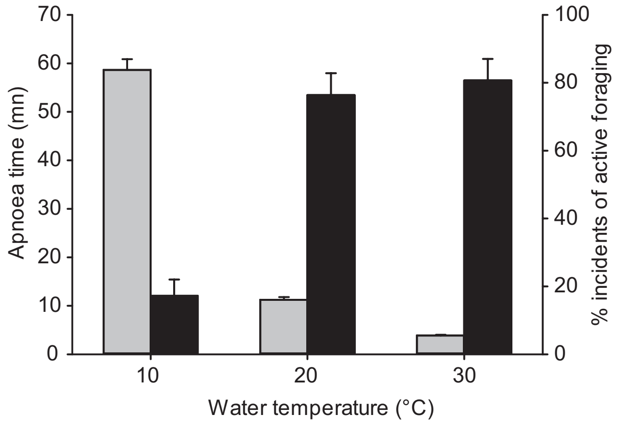

Figure 1. Breath-holding abilities and foraging tactics as function of water temperature in juvenile Viperine snakes. The left Y axis shows the breath holding abilities (i.e. apnoea time; grey bars) of 3-week-old Viperine snakes in different water temperatures (10, 20 or 30 °C). The right Y axis shows the percentage of active foraging (black bars) in 4-month-old juvenile Viperine snakes acclimated to three water temperatures (10, 20 or 30 °C). Observed foraging tactics (active *versus* ambush foraging; see text for details) were strongly affected by acclimation to water temperature. Means + SE are plotted.

Apnoea time was not correlated with any morphological traits at any of the testing temperatures: Linear regression of Log (apnoea time) against Log (body mass) yielded all $P > 0.07$; $0.001 < \text{all } R < 0.12$; against Log (total length): all $P > 0.29$; $0.04 < \text{all } R < 0.07$; against BCI: all $P > 0.07$; $0.08 < \text{all } R < 0.12$.

Swimming performance and water temperature

There was no significant effect of sex on maximum swimming speed (in cm.s^{-1}) across testing temperatures (Repeated Measures ANOVA; interaction term $F_{4,\ 772} = 1.19$, $P = 0.31$; effect of sex $F_{1,\ 193} = 1.27$, $P = 0.26$) nor on maximum swimming speed relative to snake length (in number of body length swum per s): interaction term $F_{4,\ 772} = 1.89$, $P = 0.11$; effect of sex $F_{1,\ 193} = 0.002$, $P = 0.96$. Water temperature however had a strong effect on both individual maximum swimming speed ($F_{4,\ 772} = 500.36$, $P < 0.0001$; Fig. 2) and maximum swimming speed relative to snake length ($F_{4,\ 772} = 497.99$, $P < 0.0001$).

The maximum swimming speeds for each testing temperature were significantly and positively correlated with body mass (Linear regression of Log [swimming speed] against Log [body mass]; all $P < 0.005$; $0.19 < \text{all } R < 0.53$); total length (all $P < 0.00018$, $0.25 < \text{all } R < 0.47$) and BCI (with the exception of 10 °C water testing, $P = 0.37$; all other temperatures: all $P < 0.0025$; $0.20 < \text{all } R < 0.35$).

As with apnoea time, the relationship between temperature and swimming performances was not

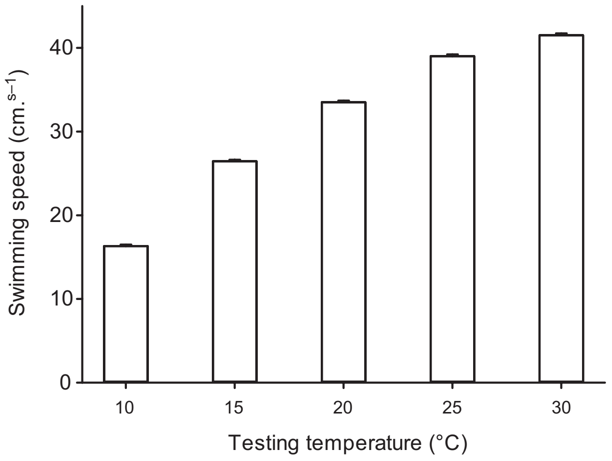

Figure 2. Swimming performance and water temperature in juveniles Viperine snakes. Snakes were tested for maximum swimming speed across a range of water temperatures (10, 15, 20, 25 or 30 °C). Individual maximum swimming speed increased as a function of water temperature. Means + SE are plotted.

linear: for each 5 °C increment from 10 to 30 °C, maximum swimming speed increased 62, 27, 16, and 6% respectively.

ANALYSIS OF PERFORMANCE TRAITS AND POTENTIAL CONSTRAINTS

We tested for potential correlations amongst individual apnoea times and amongst swimming performances at the various testing temperatures. Spearman Rank Order correlations amongst the three apnoea values Log (time at 10 °C), Log (time at 20 °C) and Log (time at 30 °C) all yielded positive, significant, but weak relationships (All $P < 0.037$; $0.14 <$ all $R < 0.31$). Maximum swimming speed results were similar: individual performances at the various testing temperatures were all well correlated: Spearman Rank Order correlations; all $P < 0.0002$, $0.30 < R < 0.46$.

Then, we looked at potential correlations between apnoea times and swimming performances at the various testing temperatures. Out of the 15 cross-correlations performed, only one was statistically significant: apnoea time at 10 °C was correlated with maximum swimming speed at 20 °C ($N = 230$, $t_{228} = 2.84$, $R = 0.18$, $P < 0.0049$; for all other tests, all $P > 0.076$, $0.004 <$ all $R < 0.12$).

HEART RATES AS A FUNCTION OF BODY TEMPERATURE

Heart rates were repeatedly recorded in 12 *Natrix maura* ranging from 1.69 g to 3.36 g in body mass and 14.0 cm to 16.5 cm snout-vent length. Heart rates strongly increased with body temperature (Friedman ANOVA $\chi^2_{2,12} = 24.00$, $P < 0.00001$; Fig. 3).

INFLUENCE OF WATER TEMPERATURE ON FORAGING TACTICS

Observed foraging tactics were strongly affected by acclimation to water temperature: the proportions of active foraging averaged 17.22 ± 16.69 % (Cold) *versus* 76.36 ± 24.08 % (Warm) *versus* 80.70 ± 24.51 % (Hot – Kruskal–Wallis test: $H_{2,\,41} = 21.77$; $P < 0.0001$; see Fig. 1 right axis).

DISCUSSION

Our study confirmed that swimming performances increased with testing temperature in semi-aquatic snakes (Hailey & Davies, 1988; Isaac & Gregory, 2007). The increase in performance was sharp at the lower end of the temperature spectrum but tended to plateau above 25 °C. Swimming speeds were on average 2.5 times faster at 30 °C than at 10 °C. There was no difference between sexes in swimming performances, nor in absolute terms or relative to body length. With regard to apnoea time, there was no effect of sex at any of the testing temperatures (as in other reptile species; see Brischoux *et al.*, 2008 for a review). Apnoea time was however strongly related to testing temperature; most likely reflecting the fact that oxygen demands are related to the metabolic rate of ectotherms (itself related to body temperature; Pough, 1980). While a 2.5-fold change in swimming performance was measured from 10 °C to 30 °C, apnoea time in 10 °C water was over 15 times higher than in 30 °C water, reflecting differing physiological kinetics (Fig. 4). Moreover, heart rates (as an estimate of basal metabolism) increased with body temperature, suggesting that apnoea time largely reflects temperature-related oxygen consumption (Stevenson *et al.*, 1984). Several studies have also demonstrated that diving freshwater snakes were capable of bradycardia (Johansen, 1959; Jacob & McDonald, 1976), potentially lengthening diving bouts.

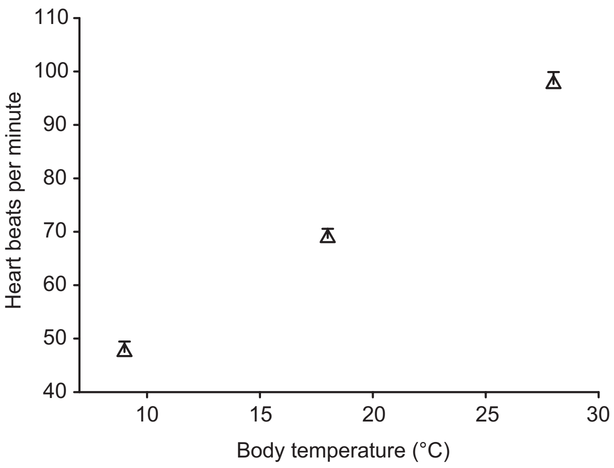

Figure 3. Heart rates as a function of body temperature in juvenile Viperine snakes. Heart beats were recorded in 12 juvenile *Natrix maura* at three different testing temperatures as surrogate estimates of basal metabolism using a Buddy digital egg monitor. Means + SE are plotted.

Swimming performance and apnoea time therefore were inverse functions of the water temperature snakes were tested in (Fig. 4). It is likely that faster swimming speed is a key determinant of predator evasion from a range of amphibious and aquatic predators such as large fish, otters, or herons (Scribner & Weatherhead, 1995; Akani & Luiselli, 2001). Faster swimming may also be an important determinant of foraging success for snakes that are actively foraging (i.e. random open-mouthed ‘fishing’, or active prey chasing; Evans, 1942; Hailey & Davies,

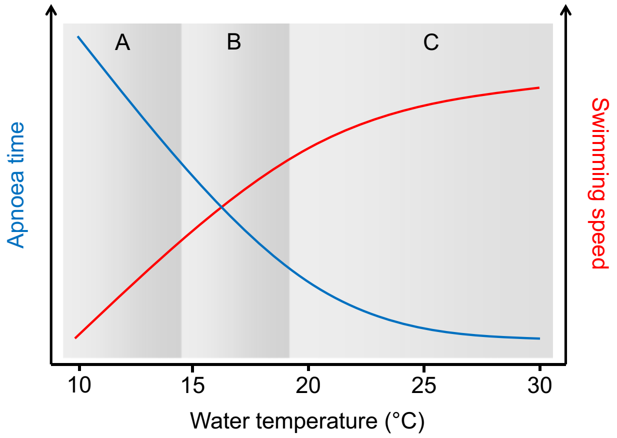

Figure 4. Representation of swimming performance and capacity for apnoea in relation to water temperature. In cold water (zone A), apnoea times favour sentinel foraging, whereas warmer water (zone C) are better suited to active chasing due to enhanced swimming performances. In between these extremes may exist a range of water temperature where both techniques are efficient enough to be relied on for catching fish and escaping predators (zone B).

1986b; Bilcke *et al*., 2006). In the context of costs and benefits (i.e. low *versus* high foraging success; low *versus* high risk of predation), one can expect foraging tactics based on active swimming to be advantageous in warmer water (>19 °C; in the warmest parts of the species range, or during summer months; Fig. 4 zone C) rather than in colder water (<14 °C). As late summer is also the time when large schools of young fish gather in shallower and warmer waters (Mills, 1991), active foraging appears particularly well suited to warm water and high prey densities (Bilcke *et al*., 2006). Along the same lines, foraging tactics involving underwater breath holding abilities (i.e. sentinel foraging) appear better suited to parts of the range where water is coldest (elevated latitudes and altitudes; early spring; Fig. 4 zone A). Long-lasting sentinel foraging may allow snakes to remain undetected by potential prey (or predators) for longer periods (i.e. where taking a breath will reveal the snake's presence), potentially increasing capture success rate. Likewise, long apnoea time may allow snakes to outperform predatory animals (provided they are holding their breath too) or remain long enough in an underwater hide for a predator to abandon the hunt (Scribner & Weatherhead, 1995). Can these physiological and environmental constraints have shaped the evolution of foraging tactics in amphibious ectotherms such as *Natrix maura*?

Both field and laboratory behavioural observations seem to support this hypothesis. In the current study, young snakes maintained in the Cold treatment mostly displayed sentinel foraging. Snakes would stay motionless, the anterior part of the body coiled in an S shape and wait for a fish to be presented close enough to their snout to strike frontally at it (Herrel *et al*., 2008; Van Wassenbergh *et al*., 2010). By contrast, snakes in the Warm (20 °C) and Hot treatment (30 °C water) would often enter a 'foraging frenzy' during feeding events, where snakes were frequently observed swimming frantically with their mouth wide open ('fishing'; Evans, 1942), crossing the pool several times in a seemingly random pattern and sweeping the head from side to side through the water. Bilcke *et al*. (2006) described feeding behaviour in laboratory maintained *Natrix maura*: upon detecting a fish, snakes initiated a sit-and-wait strategy or started pursuing the prey by moving their head (and body) towards it, mostly in an unsteady manner (i.e. in short, discrete bouts of movement). Snakes, according to Bilcke *et al*. (2006), frequently switched from one type of behaviour to the other. These tests were performed in 25 °C water and seem to correspond to our current observations of mixed feeding tactics at temperatures >20 °C (approximately 25% sentinel foraging). Field observations made by Patterson & Davies (1982) in water bodies ranging from 18.5 to 25.9 °C also agreed with a mixture of sentinel foraging and active foraging (respective proportions were not given) within this temperature range. However, the foraging behaviour observed in 10 °C water acclimated snakes rarely included active swimming, and consisted mostly of sentinel foraging associated with frontal striking (Fig. 4 zone A). It is also remarkable that the percentage of active foraging observed in water-acclimated snakes perfectly mirrors apnoea times in naïve juvenile Viperine snakes (Fig. 1). According to Hailey & Davies (1986a), 25 °C is the average temperature at which *N. maura* forages in nature, with 14 °C being the minimum temperature for foraging (Hailey & Davies, 1988). Both our experimental and field observations seem to indicate that *Natrix maura* from our study area are capable of foraging in water as cold as 8 °C (field observation) and as warm as 30 °C (experimental observation). Although 20 °C and 30 °C water-acclimated snakes readily engaged in active foraging in the laboratory, such behaviour was never observed in wild snakes at our field site, perhaps due to much colder water and associated poor swimming performances. In conclusion, the physiological aspects of foraging tactics of amphibious snakes combined with field and laboratory observations collectively support the idea that physiological and environmental constraints may generate shifts in habitat use and associated foraging tactics observed in amphibious ectotherms (Patterson & Davies, 1982; Fraser *et al*., 1993; Ikebe & Oishi, 1997; Luiselli & Zimmermann, 1997; Denoël, 2004).

With respect to performance trait correlations or constraints, individual apnoea times were all correlated, as were individual swimming speeds at the various testing temperatures. That is, good breath holders were good at all temperatures and good swimmers were consistently good swimmers, and vice versa. There was however no clear relationship between an individual's ability to hold its breath and its ability to swim; this was seen across the range of testing temperatures. In other words, good swimmers did not tend to be poor, or good breath holders, and vice versa. This suggests that both performance traits may be the target of different selective pressures, perhaps due to the different physiological pathways involved (i.e. anaerobic versus aerobic metabolism; Hailey & Davies, 1986b).

The plasticity in foraging tactics observed in the acclimation experiment is likely advantageous in mid-range water temperatures (Fig. 4 zone B) where snakes can switch from one strategy to the other based on fish density, water depth, or water temperature (Bilcke *et al*., 2006). In areas where water temperature falls at the physiological extremes however (Fig. 4 zones A and C), one would expect natural selection (i.e. co-adaptation hypothesis; Blouin-Demers, Weatherhead & McCracken, 2003) to respectively lead to the evolution of snakes capable of fast active swimming in relatively colder water (i.e. high altitude populations) and, at the other extreme, snakes capable of holding their breath for longer at relatively higher temperatures (*N. maura* populations from northern Africa). Future studies may test this hypothesis over a range of naturally occurring populations of freshwater snakes, and allow us to tease apart local physiological and behavioural adaptations from general physiological and mechanical constraints associated with the various foraging tactics.

Finally, although river water remains cold year round at our study site (between 5 and 12 °C), it is remarkable that laboratory-born snakes displayed strong behavioural plasticity in foraging tactics when reared in alternative water temperatures (Himes, 2002). This flexibility will offer opportunities to test for the potential cost associated with the maintenance of behavioural plasticity in foraging tactics in a seemingly homogenous and predictable environment (DeWitt, Sih & Wilson, 1998; Relyea, 2002), as well as the importance of such plasticity in the face of climate change and potential warming river temperatures (Arnell & Reynard, 1996; IPCC, 2007).

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