

# Interactive effects of sex and temperature on locomotion in reptiles

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**Synopsis** Males and females from several animal taxa differ in locomotor performance traits such as sprinting and jumping. These performance dimorphisms may be explained at least partially by sexual differences in physiology or morphology. In ectotherms such as reptiles, however, thermal ecology places an additional constraint on realized locomotor performance. I review recent studies on reptiles examining sexual differences in locomotor capacity and related thermoregulatory behavior, and discuss potential causes, constraints, and selective pressures that might drive intersexual divergence in capacity for locomotor performance in reptiles. In several cases where such differences occur, sexual dimorphisms in body size do not account for all the observed variation in performance. However, while sex-specific locomotor capacities might be evident in the laboratory, ecological performance in nature is likely the result of complex interactions among sex, thermal sensitivity, habitat type, and behavioral locomotor compensation. Results from laboratory studies of dimorphisms in maximum locomotor capacity are therefore likely to be poor predictors of realized ecological differences in performance. Nonetheless, sex differences in performance are potentially important modifiers of male and female behavioral strategies and overall fitness, and consequently are deserving of more attention than they have thus far received.

## Introduction

Locomotor performance has long been considered of prime importance in determining overall individual fitness (Huey and Stevenson 1979; Arnold 1983; Irschick and Garland 2001) and a growing number of studies have attempted to quantify the effects of locomotor capacities on various fitness components, including survival and reproduction (Jayne and Bennett 1990; O'Steen et al. 2002; Miles 2004; Husak 2006; Husak et al. 2006). Many of these studies have been conducted on lizards, primarily due to the status of lizards as "model organisms" for the study of whole-organism performance (Irschick and Garland 2001). Additionally, over the last 50 years a rich literature has accumulated evaluating the impact of the thermal environment on aspects of reptilian ecology and life-history, including performance (Huey 1982; Angilletta et al. 2002, 2006, for reviews). For most reptiles, the influence of thermal ecology on locomotor ability in particular is likely to have profound effects on overall fitness in nature, and hence has been rigorously studied at several levels of organization, from cellular (for example, Swoap et al. 1993) to whole-organism (reviewed in Seebacher 2005).

In light of this intensive investigation of both locomotion and temperature in reptiles, it is

surprising that relatively little attention has been paid to intrinsic differences (that is, differences independent of scaling effects) in locomotor capacities between the sexes, the study of the effects of gravidity on locomotor performance in females being a notable exception (for example, Shine 2003). However, even non-gravid females may exhibit realized locomotor abilities different from those of males as a result of intrinsic sex-specific physiological processes or capacities. In humans, for example, the dimorphism in athletic performance between males and females is well-documented (see Pate and Kriska 1984; Wells and Plowman 1983, for reviews). Most notably, maximum sprint speeds are 5% lower in women compared to men of similar body size, as is endurance ability (Wells and Plowman 1983). Males similarly exhibit higher basal metabolic rates than women of the same size, and several other physiological indicators, such as  $VO_2$  max, have also been reported to differ between men and women independent of body size (Pate and Kriska 1984). Given the widespread distribution of sexual size dimorphism (both male-biased and female-biased) in non-human animals (Blanckenhorn 2005), sexual differences in relative locomotor performance may have profound effects on sex-specific behavior, ecology, and ultimately, fitness.

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The existence of a temperature-limited physiology adds an additional layer of complexity to the ecological utility of locomotor performance in ectotherms such as reptiles. The documented sex differences in life-history (Shine 2005), behavior, and activity (Kerr and Bull 2006) in several reptilian species suggest that males and females might frequently prefer different body temperatures ( $T_b$ ), and hence potentially use different thermoregulatory strategies in a given behavioral or ecological context. Even if the thermal physiology of most reptiles is relatively conservative and adaptive shifts in thermal preferences are therefore unlikely, thermal sensitivity or preferences may still be affected by acclimatization, or otherwise change plastically (Seebacher 2005). Indeed, coadaptation between preferred or selected  $T_b$  and temperature-sensitive behavior is expected to be of central importance in thermal ecology (Huey and Bennett 1987; Angilletta et al. 2006). However, because selected  $T_b$  may be a compromise of several conflicting thermal priorities, as well as environmentally imposed constraints or costs (Huey and Slatkin 1976), realized  $T_b$  in nature may frequently be suboptimal for maximum locomotor ability (Hertz et al. 1988). Thus, preexisting differences in locomotor performance may be exaggerated under natural conditions should the gender with the poorer locomotor capacity be constrained to operate at  $T_b$ s not conducive to maximum performance. Alternatively, intrinsic sex differences in performance might be masked should thermal compromise be forced asymmetrically on the gender with the better locomotor capacity. Yet a further important consideration is that animals may not perform preferentially at their maximum capacities under natural conditions, or may do so only rarely; hence, poorer performers may compensate for any external or intrinsic constraints on locomotor ability by using a greater percentage of their maximum capacity (Carrier 1996; Irschick et al. 2005a; Husak and Fox 2006), or by adopting behavioral strategies that do not depend on locomotor performance (Bauwens and Thoen 1981; Hertz et al. 1982).

In this article, I review recent studies examining sex differences in locomotor performance and thermal ecology in reptiles, and examine the evidence for coadaptation between thermal optima and locomotor performance within each sex, noting potential causal factors and constraints. I primarily deal with factors affecting locomotion, rather than thermoregulation; thus, I do not provide a comprehensive discussion of sex differences in thermoregulation, but rather highlight key studies providing

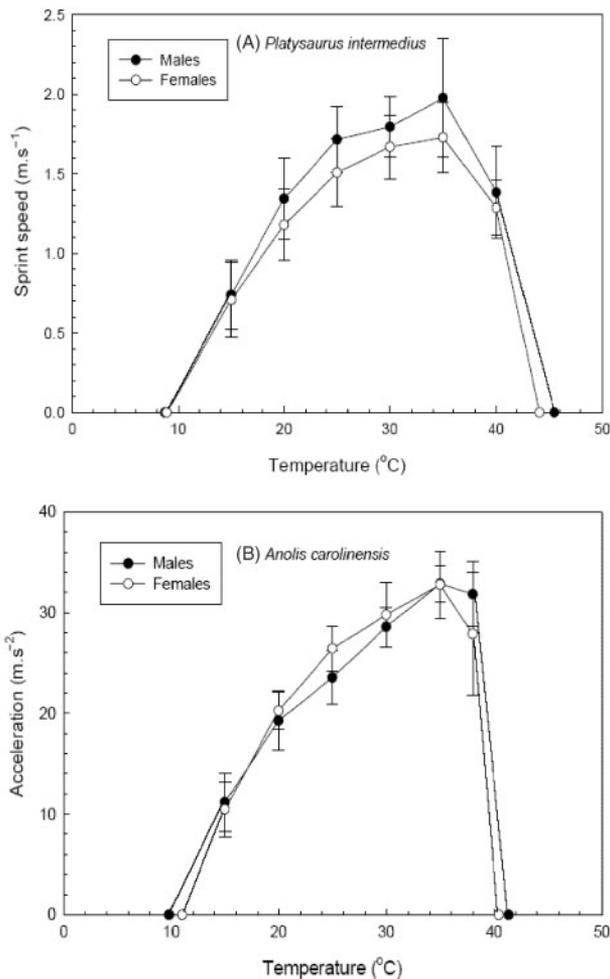
insight into the relationships among sex, locomotion, and temperature. I also do not review in detail the many studies dealing with the effects of gravidity on locomotion in females, as this subject is dealt with by Scales and Butler (2007). Finally, I discuss the ecological implications of such intrinsic sexual differences and highlight promising directions for future research.

## Temperature and locomotion

Despite intensive investigation into the thermal ecology of reptiles over the past 50 years, relatively few studies have explicitly investigated sex effects on thermoregulation and thermal physiology in reptiles. In lizards, for example, laboratory measurements of temperature selection and maintenance have shown that males may select similar (Ibargüengoytia 2005), lower (Sievert and Hutchison 1989), or higher  $T_b$ s than do females (Pentecost 1974), depending on the species in question. In those species where sex differences in selected body temperatures ( $T_{sel}$ ) are known, the driving physiological factors are not well understood. However, sex effects on  $T_b$  regulation have been shown to persist even under hypoxic conditions, suggesting that, in those species where they do occur, sex differences in  $T_{sel}$  may be important enough to override other external stimuli (Tattersall and Gerlach 2005). Nonetheless, whereas knowledge of  $T_{sel}$  is both useful and necessary for understanding thermoregulation in reptiles, extrapolating from laboratory measures to a natural context is often problematic. Indeed, the notion of a single selected  $T_b$  may be misleading because of effects of acclimation or plasticity on thermal preferences (Huey 1982; Seebacher et al. 2003). Given this, information on  $T_b$ s maintained by animals in the field, coupled with knowledge of the shape of the thermal performance curves for males and females, may be useful in understanding the extent of the maximum performance capacities that they are able to use in a natural context (for example, Waldschmidt and Tracy 1983; Grant 1990; Huey et al. 2003). While previous studies have shown that males and females may maintain different  $T_b$ s in nature in some lizards (Singh et al. 2002) and several species of snakes (Shine 1993; Brown and Weatherhead 2000; Fitzgerald et al. 2003), few studies integrating laboratory locomotor performance data with field  $T_b$  measurements have considered sex as an explanatory variable.

If  $T_b$  affects performance differently in males and females, then the sexes may exhibit divergence in optimal performance temperatures ( $T_{opt}$ —the  $T_b$  or

$T_b$  range over which performance is maximal) for that particular trait, or in behavioral strategies that may depend on that trait. However, few data are available to test this prediction. Lailvaux et al. (2003) combined field and laboratory data in order to examine how sexual dimorphism in locomotor performance and the thermal sensitivities of sprint speed and maximal exertion (an index of endurance) shape sex-specific antipredatory strategies in the African flat lizard *Platysaurus intermedius*. Males were significantly faster sprinters than females over a range of  $T_b$ s (Fig. 1A), a result that persists following correction for body size. By contrast, males and females did not differ in maximal exertion at any temperature, either before or after correction for body size. However, comparison of  $T_{opt}$  for performance with  $T_{sel}$  measured in a thermal gradient showed that  $T_{sel}$  and  $T_{opt}$  are similar



**Fig. 1** Differences between males and females in thermal performance curves for (A) maximum sprint speed in *Platysaurus intermedius* (redrawn from Lailvaux et al. 2003), and (B) maximum jump acceleration in *Anolis carolinensis* (redrawn from Lailvaux and Irschick, in press).

within each sex for both sprinting and exertion. Males and females also do not differ significantly in  $T_{sel}$  or in  $T_{opt}$  for either performance trait. Thus, both male and female *P. intermedius* appear to select temperatures conducive to optimal performance in the laboratory, suggesting coadaptation between thermal preference and locomotor capacity in both sexes (Angilletta et al. 2006). Field  $T_b$ s for females, however, were lower than either male field  $T_b$ s or female  $T_{sel}$ , and female performance in the field might therefore be expected to be submaximal; in fact, predicted sprint (m/s) and endurance performance (m) at field  $T_b$ s were similar for both sexes. Males and females nonetheless appeared to exhibit sex-specific escape strategies when exposed to predators, one strategy based on speed (males) and the other based on crypsis (females). It is currently not clear whether this difference in escape strategy is driven by sex differences in realized locomotor performance in the field or by conflicting thermoregulatory priorities between males and females.

In a related study, Lailvaux and Irschick (in press) examined the effects of sex and temperature on several aspects of jump performance in the lizard *Anolis carolinensis*. Males were generally significantly better performers than were females over a range of  $T_b$ s in *A. carolinensis*. However, the shape of the performance curves was largely similar in males and females. An exception to this pattern was jump acceleration, which exhibited a significant interaction between sex and  $T_b$  independent of body size (Fig. 1B). In addition to acceleration, several measures of jump kinematics, such as time to peak power and time to peak acceleration, also showed significant size-independent interactions between sex and  $T_b$ . Thus, although the overall performance sensitivities to  $T_b$  are similar in males and females,  $T_b$  does appear to have different effects on how males and females jump. Furthermore, these differences are not accounted for by sexual dimorphism in body size. In contrast to *P. intermedius*,  $T_{opt}$  for jumping performance appears to be higher than  $T_{sel}$  in both male and female *A. carolinensis* lizards (Brown and Griffin 2005; Lailvaux and Irschick, in press). Nonetheless, predicted jump performance in the field is similar in male and female *A. carolinensis* lizards, just as was found for *P. intermedius*.

Taken together, the results of these two studies suggest that laboratory findings for sex differences in locomotion are poor indicators of realized locomotor performance in the field (Irschick and Garland 2001; Irschick 2003). An alternative possibility is that the magnitude of the laboratory sex differences, while statistically significant, may not translate into

ecological differences in the field. This does not, however, mean that laboratory studies are not valuable; indeed, laboratory studies may offer insight into the causal factors driving sex differences in performance, such as body size.

### Sex and size

Sex differences in locomotor capacities such as sprint speed have received relatively little attention from researchers, but nonetheless have been reported in several species of reptiles (Table 1). In addition to “traditional” locomotor traits such as sprinting and endurance, the sexes differ in variables such as swimming speed, climbing ability, overall strength, and walking speed in reptiles ranging from tortoises to snakes (Table 1). In many cases, sex differences in performance can be attributed primarily to sexual dimorphism in size, as many locomotor traits tend to scale positively with body size (for example, Miles et al. 2001). However, several cases also exist in which the effects of body size do not explain a significant amount of the variation in locomotor performance between males and females. For example, Cullum (1998) examined several physiological and locomotor performance variables in six species of *Cnemidophorus* lizards. Although global comparisons across all species showed significant sex effects on burst speed and maximal exertion (Cullum 1998), intraspecific comparisons yield few significant differences between males and females for most *Cnemidophorus* species studied (A. Cullum, personal communication). Nonetheless, males exhibited greater maximal exertion than females in two of the six species (Table 1). Indeed, practically none of the variation in maximum exertion could be explained by sex differences in body size in *Cnemidophorus inornatus arizonae*. Similar male-biased sex differences independent of size have been reported for sprint speed in *Platysaurus intermedius* lizards (Lailvaux et al. 2003), and for both walking speed and self-righting in steppe tortoises (*Testudo horsefieldii*; Bonnet et al. 2001). By contrast, Irschick et al. (2005b) found that size-adjusted jumping performance (that is, maximum distance, velocity, and acceleration) was superior in females compared to males in the lizard *Anolis carolinensis*. In most cases, differences in body composition (that is, relative proportions of muscle and fat) may lead to one sex being stronger than the other (Lourdais et al. 2006; see below); for example, the greater climbing ability of laticaudid snakes relative to females of the same body size is attributed to the greater muscularity and strength of the males

(Bonnet et al. 2005). If this is the case, then one might expect males to perform better than females at all ecological tasks requiring burst speed or strength, but not necessarily at tasks involving stamina. Endurance, for example, did not differ between the sexes in *P. intermedius*, in contrast to sprint speed, which did (Lailvaux et al. 2003). Sexual dimorphism in one important locomotor ability therefore does not necessarily imply dimorphism in others. Thus, although effects of body size on locomotion may be important, they do not explain all observed performance dimorphisms in reptiles.

### Sex and substrate

As well as employing different physiological capacities (for example, aerobic capacities for endurance and anaerobic capacities for sprint speed) or gaits appropriate to the various forms of terrestrial locomotion, reptiles may also move frequently in different habitat types, or even different media, which may affect locomotor ability (see also Snell et al. 1988; Losos and Sinervo 1989; Spezzano and Jayne 2004). Some species of snakes, for example, are semiaquatic, and may forage or disperse both terrestrially and aquatically (Vincent et al. 2004; Shine 2005). Despite the different locomotor challenges and selection pressures posed by aquatic and terrestrial environments, size-free sexual dimorphisms have been reported in both crawling and swimming speed within several snake species. Shine et al. (2003) conducted a comparative study of terrestrial and aquatic locomotion in laticaudid sea snakes, and noted that the sexual dimorphism in relative locomotor ability (that is, males faster than females) is likely a general feature of laticaudid biology. Similarly, in the natricine snake *Seminatrix pygaea*, males are faster than females both on land and in water, although overall speeds are greater on land (Winne and Hopkins 2006). This pattern of snakes attaining higher velocities during terrestrial crawling compared with aquatic swimming is common amongst semiaquatic and amphibious snakes, despite swimming being an overall more efficient mode of locomotion (Seymour 1982; Lillywhite 1987).

In addition to an effect of sex on speed, speed may also be affected by the medium of locomotion, such that the differences in velocity of locomotion between males and females are exaggerated for terrestrial compared with aquatic situations. In the case of sea snakes, this substrate effect has been attributed to the necessity of terrestrial locomotion in males for finding mates (for example,

**Table 1** Studies on locomotion in reptiles including sex as an explanatory variable

Species	Locomotor trait	Sex difference	Reference
Tortoises			
<i>Testudo horsefieldii</i>	Walking speed	A	Bonnet et al. 2001
	Righting ability	A	
Snakes			
<i>Seminatrix pygaea</i>	Swimming speed	SI	Winne and Hopkins 2006
	Crawling speed	SI	
<i>Laticauda colubrine</i>	Swimming speed	A, SI	Shine and Shetty 2001; Shine et al. 2003
	Crawling speed	A, SI	
	Climbing ability	A	
<i>Laticauda frontalis</i>	Swimming speed	A	Shine et al. 2003
	Crawling speed	A	
<i>Laticauda laticaudata</i>	Swimming speed	A	Shine et al. 2003
	Crawling speed	A	
	Climbing ability	A	
<i>Emydocephalus annulatus</i>	Swimming speed	A	Shine et al. 2003
	Crawling speed	A	
<i>Notechis ater occidentalis</i>	Swimming speed	N	Aubret 2001
<i>Epicrates cenchria maurus</i>	Climbing ability	A, SI	Lourdais et al. 2006
<i>Thamnophis elegans</i>	Crawling speed	A	Kelley et al. 1997
Lizards			
<i>Amphibolurus nuchalus</i>	Sprint speed	N	Garland 1985
<i>Microlophus albemarlensis</i>	Endurance	A	Miles et al. 2001; Snell et al. 1988
	Sprint speed	A	
<i>Crotaphytus collaris</i>	Sprint speed	N	Husak and Fox 2006; Peterson and Husak 2006
Ecological performance			
<i>Platysaurus intermedius</i>	Sprint speed	SI	Lailvaux et al. 2003
Exertion			
<i>Anolis carolinensis</i>	Jump acceleration	SI	Lailvaux and Irschick, in press
	Jump kinematics	SI	
<i>Cnemidophorus burti</i>	Sprint speed	N	Cullum 1998
	Exertion	A	
	Endurance	N	
<i>Cnemidophorus inornatus arizonae</i>	Sprint speed	N	Cullum 1998
	Exertion	A, SI	
	Endurance	N	
<i>Cnemidophorus inornatus heptogrammus</i>	Sprint speed	N	Cullum 1998
	Exertion	N	
	Endurance	N	
<i>Cnemidophorus septemvittatus</i>	Sprint speed	N	Cullum 1998
	Exertion	N	
	Endurance	N	
<i>Cnemidophorus tigris punctilinealis</i>	Sprint speed	N	Cullum 1998
	Exertion	N	
	Endurance	N	

Continued

Table 1 (continued)

Species	Locomotor trait	Sex difference	Reference
<i>Cnemidophorus tigris marmoratus</i>	Sprint speed	N	Cullum 1998
	Exertion	N	
	Endurance	N	
<i>Takydromus walteri</i>	Sprint speed	N	Chen et al. 2003
	Exertion	N	
<i>Lacerta bedrigae</i>	Sprint speed	N	Vanhooydonck et al. 2000
	Climbing speed	N	
	Maneuverability	N	
	Endurance	N	
<i>Podarcis sicula</i>	Sprint speed	N	Vanhooydonck et al. 2000
	Climbing speed	N	
	Maneuverability	N	
	Endurance	N	
<i>Podarcis tiliguerta</i>	Sprint speed	N	Vanhooydonck et al. 2000
	Climbing speed	N	
	Maneuverability	N	
	Endurance	N	

A, absolute performance; SI, size-independent performance; N, no performance difference.

Shine and Shetty 2001), although the proximate factors affecting this difference are unclear. In semiaquatic snakes such as natricines, however, evidence for effects of the habitat or medium on sex performance is mixed, with interactions between habitat and sex reported in some species (Scribner and Weatherhead 1995) but not in others (Winne and Hopkins 2006). In a study measuring locomotion in areas of dense and sparse vegetation in the exclusively terrestrial snake *Thamnophis elegans*, no interaction was found between sex and substrate type for either crawling speed or head-to-tail distance (HTD), an index of lateral bending, although males crawled faster than females at all but the lowest vegetation densities (Kelley et al. 1997). Further studies on the interaction between sex and substrate in other snake groups are required to test comparative hypotheses regarding the relationship between terrestrial and aquatic locomotion.

In contrast to snakes, studies of sex differences in locomotor performance within different habitat or substrate types in lizards and other reptiles are fewer. Irschick et al. (2005b) examined habitat use and performance in male and female *Anolis carolinensis* lizards, but found no evidence for an interactive effect of sex and habitat type on performance. Nonetheless, the effects of substrate or habitat type on performance in male and female lizards may be potentially important in driving the evolution of sex

differences in locomotion if males and females differ in habitat use (Snell et al. 1988); however, surprisingly few data are available on sex differences in habitat use in lizards or other reptiles (see Losos et al. 2003 for a discussion).

### Proximate causes of sexual dimorphism in performance

Although reports of sexual dimorphisms in performance independent of body size are increasing, numerous cases also exist in which either body size has little effect on maximum laboratory-measured sprint speed or locomotion in either sex, or in which males and females exhibit similar performance capacities following correction for size (Table 1). This similarity between the sexes likely reflects either a lack of differential selection for locomotor capacities in males relative to females for those particular species, or some constraint preventing males and/or females from responding to sex-specific selection (alternatively, sexual size dimorphism itself may be a response to differential selection on locomotor capacities). In cases where males and females clearly do differ in relative performance, the causal factors affecting sex differences are generally thought to be physiological, such as sex differences in androgen levels leading to different proportions of muscle and fat in males and females (Cullum 1998;

see also Lourdais et al. 2006). Indeed, differences between the sexes have been noted for a number of physiological variables, in addition to hormone levels, that might affect locomotion in reptiles and related taxa. For example, activity of mitochondrial enzymes is significantly higher in male *Alligator mississippiensis* compared to females, possibly facilitating sex-specific seasonal demands for locomotor performance (Seebacher et al. 2003). Sex differences in the nervous systems of reptiles are also well documented (Godwin and Crews 1997). Gravity has long been known to affect locomotor performance in females, although in some cases it is unclear whether the effect is physical (that is, due to the weight of the eggs), or physiological (that is, changes associated with gravity) (Olsson et al. 2000). The greater jumping ability of males relative to females is correlated with higher metabolic rates in females from several species of desert fleas (Krasnov et al. 2004); however, comparable detailed studies of the proximate physiological causes (as opposed to patterns) in sexual performance dimorphisms in reptiles are currently lacking.

Studies of thermal ecology suggest that sex-specific thermal tolerance ranges might potentially drive sex differences in performance in reptiles, particularly over a wide range of  $T_b$ s. For example, *A. carolinensis* males and females exhibit differences in the shape of the thermal sensitivity curve for several aspects of performance [jump acceleration and several aspects of jump kinematics (see above)]. Females of this species also exhibit significantly narrower thermal tolerance ranges compared to males (that is, higher  $CT_{min}$  and/or lower  $CT_{max}$ , where  $CT_{min}$  and  $CT_{max}$  represent low and high endpoints respectively on the thermal performance curve such that locomotor performance = 0) (Lailvaux and Irschick, in press; see also Lailvaux et al. 2003). This narrower tolerance range for females relative to males results in a concurrent overall narrower thermal performance curve for females, possibly because muscle function becomes compromised first in females, then in males as the upper or lower tolerance limits are approached. The ecological relevance of such differences is likely to be minimal at best because reptiles typically approach the limits of their tolerance range only rarely, if ever (Huey and Stevenson 1979; Huey 1982), and because the difference in thermal tolerance range, though statistically significant, is small. Nevertheless, differences in tolerance range may have important implications for the evolution of the shape of the thermal performance curve in males and females (although selection on performance breadth driving

thermal tolerance ranges is equally plausible). Indeed, although little is known regarding the heritability of  $CT_{min}$  or  $CT_{max}$  in reptiles, and thermal tolerances are possibly affected by body size, upper thermal tolerance is known to be heritable in the rainbow trout (*Oncorhynchus mykiss*) (see also Gilchrist and Huey 1999; Baer and Travis 2000; Perry et al. 2005). Furthermore, upper thermal tolerance is also linked to sex-limited quantitative trait loci in *O. mykiss* (Perry et al. 2005), suggesting a possible constraint on the evolution of thermal tolerance and, potentially, the shape of this species' sex-specific thermal performance curves. If thermal tolerance limits are similarly sex-limited and subject to selection in reptiles, then the potential exists for differential indirect selection on the shape of thermal performance curves in males and females. Whether such selection has occurred, or is even an important pressure affecting the evolution of thermal performance curves, is a question ripe for further study.

### Ecological performance and sex

Although the proximate causes of sexual differences in performance are unclear, researchers are nonetheless able to infer ultimate patterns of selection on males and females from examination of ecological performance (that is, the extent of locomotor capacities used by free-ranging animals in the field) (Irschick and Garland 2001; Irschick 2003). In particular, by noting whether males and females in different ecological contexts compensate for poor maximum laboratory locomotor performance by moving at close-to-maximum locomotor capacity (Carrier 1996; Irschick 2003), one is able to determine in which context selection is likely to be important for each sex (Irschick 2003; Husak and Fox 2006). In the lizard *Crotaphytus collaris*, for example, males and females exhibit differences in patterns of ecological performance depending on context; females use the greatest proportion of their maximal speed during escape from predators, whereas males move closest to maximum speed when responding to an intruder in their territory (see also Braña 2003; Husak and Fox 2006). Thus, selection for sprinting performance is likely stronger for females than for males in the context of predator escape, as revealed by female locomotor compensation. Similarly, female *Anolis lineatopus* lizards are not significantly worse sprinters (at either relative or percentage speeds) than are adult males during escape or feeding in the field, despite females having an average 11% lower maximal sprinting capacity than males (Macrini and Irschick 1998),

suggesting that females utilize more of their maximum capacity in the field. Locomotor compensation therefore appears to be an important strategy used by both males and females, although the generality of such a strategy is questionable, as some species are known to routinely utilize less than their maximum locomotor capacities in nature (Irschick et al. 2005a). These findings highlight the importance of measuring realized ecological performance in the field, as opposed to extrapolating from maximum laboratory data (Irschick et al. 2005a); for example, sex differences have been found in *Crotaphytus collaris* ecological performance, in contrast to laboratory studies of sprint performance which find no evidence for a sex effect on sprinting in this species (Peterson and Husak 2006).

### Conclusions and future directions

Despite the vast literature dealing with performance and temperature effects on performance in reptiles, studies have frequently been carried out on only one sex, usually males. However, numerous examples exist where either the sex of individuals was noted but results pooled for analysis without testing for sex effects, or (less often) there was no determination of the sex of the animals used. The literature on sex differences in locomotion and thermoregulation in reptiles is therefore spotty, and few attempts have been made to comprehensively examine differences between males and females in the context of thermal performance sensitivity. Consequently, our understanding of the factors driving such differences and the relevance of sex-specific locomotor capacities to ecology and fitness remains incomplete. Nonetheless, some tentative patterns can be discerned among the few published studies on this topic. First, sex differences in locomotion appear to be more prevalent in snakes than in other reptiles, although this may change as data from more reptilian taxa are gathered. Second, in those species in which dimorphisms in locomotion do occur, sexual dimorphism in body size is not always sufficient to explain all or even most of the variation in performance between the sexes. In many snakes, for example, males and females differ in locomotor performance even after controlling for body size. In these cases, dimorphisms in performance are likely driven by differences in body composition between males and females, although this has seldom been tested in a rigorous manner (but see Lourdais et al. 2006). Third, aspects of locomotor performance can respond differently to changes in  $T_b$  in males and females, such as jump acceleration and kinematics in

*A. carolinensis*. Finally, a potential mismatch exists between measured dimorphisms in locomotion in the laboratory and realized dimorphisms in ecological performance in the field, limiting the usefulness of extrapolating laboratory results to ecological contexts within either or both sexes. Nonetheless, studies of ecological performance also show that males and females do indeed differ in locomotor ability in the field depending on ecological context. Male and female locomotor capacities may therefore be subject to different patterns of selection in nature, and understanding the factors affecting the expression and use of sex-specific performance capacities should therefore be of high priority.

### Future directions

The study of sex differences in locomotor performance is clearly in its infancy. An obvious fruitful avenue for future research is therefore to simply document sex differences in ecologically relevant performance traits, habitat use, and  $T_b$  in other reptilian groups, particularly in taxa that have received relatively little attention in this regard, such as crocodylians. However, further consideration of the proximate and ultimate causes of sexual dimorphisms in performance would be instructive in understanding the implications of such differences for the ecology of males and females. Experimental studies might play an important role in this respect. For example, although physiological factors such as sex-specific androgen levels have been posited as causal factors driving observed size-free dimorphisms in reptiles (Cullum 1998; Lailvaux et al. 2003), to my knowledge no experimental studies have attempted manipulations of androgen levels in both males and females to address this hypothesis. In addition to physiological variables, a further potential explanatory variable for sex differences in locomotion is shape. Males and females frequently differ not only in body size, but also in numerous other morphological variables, such as stockiness (Cullum 1998) or limb length (Irschick et al. 2005b), either of which might potentially affect locomotor performance. Males of some sexually dimorphic lizard species, for example, have particularly large heads relative to those of females (possibly related to male combat; Herrel et al. 2001), which may hinder locomotion. Conversely, females may be slower than males if they exhibit pelvic girdle adaptations for giving birth or laying eggs. Indeed, intersexual differences in morphology constitute a more likely explanation than physiological causes for observed sex differences in jump kinematics in *A. carolinensis*. A multivariate

ecomorphological approach to the functional factors affecting performance in males and females should therefore be explored wherever possible before invoking more indirect explanatory variables for sex differences in performance.

The role of acclimation and plasticity in affecting thermal physiology is an important frontier for further exploration, not only in the context of sex differences in locomotion, but in reptilian thermoregulation generally. In particular, reports of sex-limited expression of thermal tolerance in some ectotherms represent a possible alternative hypothesis to the null expectation of plasticity in tolerance (Seebacher 2005). Thus far, this area has received relatively little attention from researchers, but might be important in understanding both the evolution of thermal performance curves and the relationship between selected field and optimal body temperatures in both males and females.

A further impediment to our understanding of the ecological relevance of dimorphisms is the lack of data pertaining to ecological performance in males and females. Although a few studies exist, these have not been conducted with the explicit aim of comparing laboratory and field performance. Quantifying rates of performance attributes for individual sexes both in the lab and in the field offers considerable empirical challenges, but nonetheless is essential if one is to understand potential selection pressures on each sex, as well as sex-specific responses (if any) to those pressures. As a final caveat, it is important to note that physiological and performance traits may change seasonally (Irschick et al. 2006), and hence sex differences in performance traits might be evident only at certain times of year (Cooke 2004).

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