

Do female collared lizards change field use of maximal sprint speed capacity when gravid?

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Abstract Locomotor ability is well-documented to decrease in gravid female lizards. However, no studies have examined what proportion of maximal sprint speed capacity gravid females use in nature or how a reduction in maximal capacity translates to changes in sprint speeds used in nature. Gravid females may compensate for reduced locomotor ability by increasing the proportion of their maximal capacity used in nature, or by changing their antipredator behaviour. I measured maximal sprint speed in the laboratory for female collared lizards (*Crotaphytus collaris*) while gravid and nongravid and then compared those to speeds used in the field while foraging and escaping predators, and also while gravid and nongravid. Females had significantly lower maximal sprint speed capacity while gravid, and they ran slower while foraging and escaping predators. However, gravid females did not increase the proportion of maximal capacity used in those contexts compared to when not gravid. Gravid females compensated for reduced locomotor capacity by staying closer to refugia but not by remaining more cryptic. These results suggest that the costs of reduced locomotor capacity may not be associated with direct

costs while foraging or escaping predators, but instead with potential indirect effects associated with the change in antipredator behaviour.

Keywords Foraging · Locomotion · Performance · Predation · Reproduction costs · Tradeoffs

Introduction

Reproduction may entail costs that result from the tradeoff between current and future reproductive investment (Reznick 1985; Stearns 1989, 1992), and these costs generally take the form of survival or fecundity costs (Bell 1980; Shine 1980; Brodie 1989; Miles et al. 2000). Survival costs can be further divided into those involving metabolic tradeoffs and those involving “ecological”, costs such as increased risk of predation or reduced whole-animal performance (Miles et al. 2000). Among survival costs, reduced locomotor performance in pregnant or gravid females is perhaps the most well-known and studied (e.g. Bauwens and Thoen 1981; Shaffer and Formanowicz 1996; Sinervo and DeNardo 1996; Cuthill and Houston 1997 and references therein). Most of these studies compared maximal sprint speeds of gravid versus nongravid females (Shine 2003) and found reduced locomotor capacity as the result of a “physical” burden associated with increased mass (Shine 1980) and/or a “physiological” burden associated with altered metabolic pathways and hormone profiles (Olsson et al. 2000). Gravidity reduces maximal locomotor capacity as measured in the laboratory, but laboratory measures of performance do not necessarily reflect what animals do in nature. Maximal locomotor abilities could theoretically constrain foraging and

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escape from predators (Bennett and Huey 1990), but there is little evidence to support this proposition (Garland and Losos 1994; Irschick and Garland 2001).

Gravid females with reduced locomotor capacity may compensate in various ways. They may use a greater proportion of their maximal capacity to continue running quickly (Irschick 2003; Husak and Fox 2006). They may rely more heavily on crypsis than on speed, as seen in several lizard species (e.g. Bauwens and Thoen 1981; Brodie 1989; Cooper et al. 1990). They may also increase defensive behaviour, as in scorpions (Shaffer and Formanowicz 1996). Predicting how females will compensate for reduced maximal locomotor performance without knowing the relevance of maximal sprint speed in natural situations is difficult. This uncertainty can be attributed largely to our general lack of knowledge about whether animals use maximal capacity in nature (Irschick 2003). If females do not use maximal capacity in nature, then a reduction in that trait, as measured in the laboratory, may not be relevant and may not impose a cost of reproduction. For example, some female *Anolis* lizards do not utilize near-maximal capacity while foraging, but they do when escaping predators (Irschick 2000; Irschick and Losos 1998), and this pattern is also seen in collared lizards (*Crotaphytus collaris*; Husak 2006). The lack of maximal speeds while foraging implies little if any foraging cost associated with reduced maximal capacity, especially for sit-and-wait foraging species such as anoles and collared lizards. However, there is the potential for a predation cost, and females may compensate by changing their escape behaviour or using a greater proportion of their maximal capacity to attain a sufficient escape speed.

I examined compensatory behaviour in gravid collared lizards by measuring maximal sprint speed capacity in the laboratory and field-use of maximal capacity. First, I determined whether or not female collared lizards have reduced maximal locomotor performance when gravid. Second, I determined whether nongravid females use maximal capacity in nature, and whether or not this changes when they are gravid. If females use near-maximal capacity when not gravid, do they compensate while gravid by using speeds that are closer to their maximal capacity? Third, do females change their anti-predator behaviour when gravid as an alternative, or additional, means of compensating for reduced locomotor capacity?

Materials and methods

The study site was on Sooner Lake dam in Pawnee County, Oklahoma, where the substrate consisted of

concrete-covered boulders. Lizards were captured by noosing and were permanently marked with toe-clips and a unique pattern of coloured paint spots for visual identification at a distance (after Baird et al. 1996). At two times during the 2003 breeding season, lizards (the same individuals, once while gravid, once when not gravid) were transported to Oklahoma State University and held individually in net bags for one day to encourage the passage of gut contents. The first run was prior to gravidity in late April, whereas the second run was during the first clutch in May–June. Gravidity is easily assessed in collared lizards by palpating their abdomens (Baird 2004). For this study, gravid females had eggs greater than approximately 8 mm maximum diameter with the eggs in the late, round vitellogenic stage or the early, oval shelling stage.

On the mornings of their second and third days of captivity, the lizards were placed inside a lighted incubator set at 37 °C. Three times a day at intervals of at least two hours, each lizard was removed from the incubator and immediately chased down a 3-m race-track into a black bag at the end of the track. The race-track had a high-friction sandpaper substrate. Runs were video taped on Hi8 film (after Braña 2003), and the tapes were later viewed so that the number of frames it took for a lizard to traverse 1-m intervals could be counted. Speeds obtained with this method were comparable to those found for this species by Peterson and Husak (2006) using a racetrack with infrared beams. The quality of each run was classified as “good” or “poor” (van Berkum and Tsuji 1987), and data from “poor” runs (pauses, reversals) were discarded. The single fastest 1-m split for each run was analysed. The best and second-best performances of each individual, regardless of the day on which they occurred, indicated high repeatability for gravid ($r=0.94$, $P<0.001$) and nongravid females ($r=0.92$, $P<0.001$). All lizards were released at their exact point of capture after all trials were completed.

The methods of Irschick and Losos (1998) were used to determine speeds used in nature. Sprint speeds were measured on the same individuals while gravid and while nongravid in two contexts: (1) foraging and (2) escaping a predator. The same generalised procedure for obtaining sprint speeds was used for both contexts. A video camera was used to record the movements of the lizards, and the Hi8 tape was reviewed in the field so that landmarks could be used to measure the distance traversed for each movement. I counted the number of frames per unit of distance measured in the field in order to obtain sprint speeds. If multiple movements occurred during a trial, the fastest speed was used for analysis. All trials were conducted when the

substrate temperature was 30–40 °C, the optimal temperature range for collared lizards in central Oklahoma (Uzee 1990). For the foraging movements, a foraging attempt was staged by tethering a hookless fishing “fly” to the end of a 4-m pole and placing it 3 m away from the lizard and slightly wiggling it (e.g. Husak and Fox 2006). This is an appropriate stimulus, as collared lizards feed opportunistically on available arthropods and small vertebrates (Blair and Blair 1941; Husak and McCoy 2000) using a sit-and-wait foraging style (Cooper et al. 2001). Movements toward the fishing fly were video-recorded, and speeds were calculated in the manner described above. For the predator escape trials, a person (the same person in each case, wearing similar clothing) walked toward a lizard at a constant pace of approximately 40 m/min and from a constant direction, recording where the observer was in relation to the lizard when it ran (approach distance, Cooper 1997) and to where the lizard ran into a refuge (flight distance, a modification of Cooper 1997).

I calculated the proportion of maximal sprint speed capacity used in each context separately for gravid and nongravid females. All data were \log_{10} -transformed for analysis, except proportion of maximal sprint speed used in nature, which was arcsine-transformed. Paired *t*-tests were used to look for differences between gravid and nongravid females in mass, maximal sprint speed, absolute speed used while foraging, absolute speed used while escaping a predator, proportion of maximal sprint speed used in foraging, proportion of maximal sprint speed used in escaping a predator, approach distance and flight distance.

Results

All data were obtained for 15 females. As expected, gravid (mean \pm SE = 29.1 \pm 2.0 g) females were significantly heavier than nongravid (mean \pm SE = 22.8 \pm 1.5 g) females ($t_{14}=10.05$, $P<0.001$). Nongravid females had significantly faster maximal sprint speeds than gravid females ($t_{14}=21.01$, $P<0.001$; Fig. 1). Similarly, nongravid females ran significantly faster than gravid females while foraging ($t_{14}=5.086$, $P<0.001$; Fig. 1) and escaping predators ($t_{14}=9.1$, $P<0.001$; Fig. 1). There was no significant difference between gravid and nongravid females in the proportion of maximal sprint speed capacity used while foraging ($t_{14}=0.20$, $P=0.841$; Fig. 2) or escaping a predator ($t_{14}=2.04$, $P=0.060$; Fig. 2). Gravid and nongravid females also did not significantly differ in approach distance ($t_{14}=1.32$, $P=0.21$; Fig. 3). However, flight distance was significantly shorter in gravid females than in nongravid females ($t_{14}=2.50$, $P=0.025$; Fig. 3).

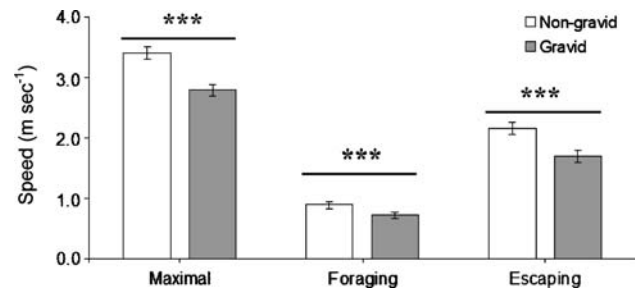


Fig. 1 Sprint speeds (± 1 SEM) attained by nongravid (*open bars*) and gravid (*solid bars*) female collared lizards (*Crotaphytus collaris*) in the laboratory (maximal) and while foraging and escaping a simulated predator in the field. See text for details. Asterisks (***) represent a significant difference with a paired *t*-test at $P<0.001$

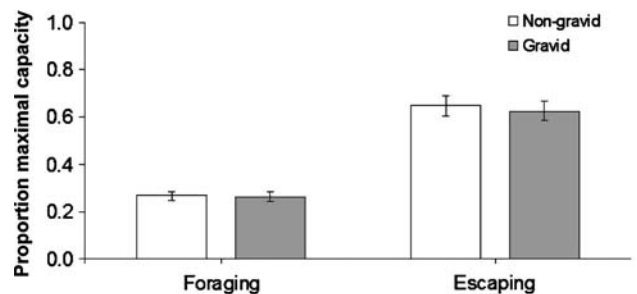


Fig. 2 Proportion of maximal sprint speed capacity used (± 1 SEM) by nongravid (*open bars*) and gravid (*solid bars*) female collared lizards while foraging and escaping in the field. See text for details

Discussion

Life-history traits may reflect tradeoffs among various components of fitness, such as fecundity and survivorship (Stearns 1976; Roff 1992). Such tradeoffs may result in costs associated with reproduction, i.e. reduced locomotor performance. Similar to previous

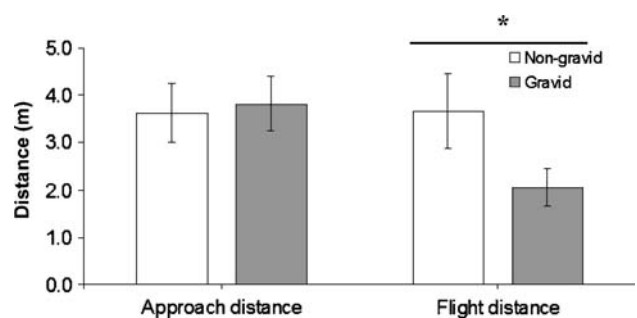


Fig. 3 Antipredator behaviour of nongravid (*open bars*) and gravid (*solid bars*) female collared lizards measured as approach and flight distance (± 1 SEM). Approach distance is the distance between the predator and the lizard when the lizard fled. Flight distance is the distance run after the lizard fled from the predator. The asterisk (*) represents a significant difference with a paired *t*-test at $P<0.05$

studies, I found that gravidity reduced maximal sprint speed capacity of female collared lizards. Gravidity also reduced the speed at which gravid females ran in nature while foraging and escaping predators. Reduced locomotor performance has been interpreted as a cost of reproduction in previous work, but contrary to our expectations, gravid females did not compensate for reduced maximal capacity while gravid by increasing the proportion of maximal capacity used in nature. Instead, they altered their escape behaviour.

Contrary to some previous studies (Bauwens and Thoen 1981; Brodie 1989; Cooper et al. 1990), gravid females do not rely more on crypsis and decrease the distance between themselves and an approaching predator before fleeing, perhaps because crypsis is not an option for lizards as large as collared lizards. Instead, female collared lizards decreased the distance they ran when a predator approached. This suggests that either (1) gravid females are closer to refugia than nongravid females, or (2) that nongravid females are more likely to risk running a longer distance when a predator approaches. The first hypothesis predicts that gravid females would not need to attain a high speed to escape, because they can enter a refuge close to where they are perched. Such females may be using the familiarity of their home range to escape potential predators efficiently. Baird and Sloan (2003) argued for the first hypothesis in a population of collared lizards in central Oklahoma where females defended core areas surrounding a perch rock with a refuge underneath it. The second hypothesis implies that nongravid females lack one or another cost associated with being gravid, for example reduced locomotor capacity, physiological costs associated with egg production, or reduced body temperatures due to gravidity.

In many lizard species that are diurnal, gravid females typically have lower body temperatures than nongravid individuals (Beuchat 1986; Mathies and Andrews 1997; Le Galliard et al. 2003 and references therein, but see Labra and Bozinovic 2002). Similar to how lower body temperatures in gravid females can result in a behavioural shift when responding to a predator (Cooper 2000), the reduction in field speeds of gravid females may reflect generally lower body temperatures as a result of gravidity. Sprint speed in many species is temperature-dependent (Huey and Kingsolver 1989), but without data on the body temperatures of field-active lizards during the activities measured in this study it is difficult to comment on this hypothesis. However, basking perches are abundant and ambient temperatures are typically well above preferred temperatures during the breeding season at the study site (J. Husak, unpublished data), suggesting that

body temperatures are not lower due to limitations imposed by escape behaviour.

Many other species of lizards compensate for reduced locomotor capacity by relying more on crypsis (Bauwens and Thoen 1981; Brodie 1989; Cooper et al. 1990). Why did female collared lizards not compensate in a similar manner? Unlike other lizards that have been found to rely more on crypsis while gravid, female collared lizards are visually more conspicuous in their environment when gravid due to the presence of large orange markings on the dorsolateral portion of the trunk (Ferguson 1976; Baird 2004). Even if the visual systems of collared lizard predators are different to those of human observers, which they most likely are, the intensity contrast alone would make gravid female collared lizards conspicuous against the grey rocks of Sooner Lake (Macedonia et al. 2004). Future work may find a general pattern across lizard species, where species with females that exhibit conspicuous gravid colouration compensate by perching closer to refugia instead of relying on crypsis.

The results of this study have interesting implications for whether or not reduced locomotor capacity is costly to gravid females. For female collared lizards, gravidity likely does not impose a foraging cost in the sense that gravid females cannot attain speeds to capture prey; nor does it likely impose a direct predation cost where females cannot attain speeds to escape predators. Although females ran significantly slower while gravid in these contexts, the fact that they did not increase the proportion of maximal capacity used suggests that slower speeds may not be detrimental during predator escape. However, “close calls” where predators manage to get very close to a female may represent a situation in which fast sprint speeds are important. In such cases, gravid females perhaps cannot attain speeds fast enough to reach a refuge even if it is close. Thus, costs may manifest themselves when gravid females move far from known refugia in order to forage, or when they re-emerge after seeking refuge from a predator, and when, with lower body temperatures, they may have even more reduced sprint speed capacity. Future studies that simultaneously address the interplay of gravidity, body temperature, field use of sprint speed, and antipredator behaviour would aid our understanding of reproductive costs.

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