BEHAVIOURAL ECOLOGY

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Effects of pregnancy on locomotor performance: an experimental study on lizards

Abstract Pregnancy is associated with reduced locomotor performance in many types of animals, but we do not know to what degree this correlation is caused by simple physical burdening, versus physiological changes associated with pregnancy, or to confounding variables (such as season or female body size) that simultaneously influence both reproductive investment and locomotor speeds. To identify causal effects of burden on locomotion, we need to experimentally manipulate the size of the load being carried. Injection of sterile fluid into the peritoneal cavities of 84 garden skinks (*Lampropholis guichenoti*) showed that speeds decreased with increasing burdens. Lizards with a burden equivalent to 25% of their body mass ran about 15% slower, mirroring the situation seen in gravid lizards of this population. Thus, simple physical burdening appears to be the primary causal component of the locomotor cost of reproduction within these animals. A lizard's sex, body size and shape had little effect on its running ability either before or after treatment, but faster lizards showed a greater performance decrement after burdening than did their slower conspecifics.

Keywords Costs of reproduction · Fecundity · Life history · Reproductive effort · Scincidae

Introduction

Reproducing may entail costs as well as benefits, and the extent to which investment in a current reproductive episode reduces the organism's future probable reproductive output ("cost of reproduction") plays a central role in life-history theory (Williams 1966a, 1966b; Roff 1992). Such costs may take many forms, but one of the most straightforward and intuitive involves reduced mobility of reproducing animals due to the physical burden of

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carrying the eggs or offspring. For example, locomotor decrements due to this physical burdening might increase an animal's vulnerability to predation, and thus impose selection for reduced reproductive investment (Schaffer 1974; Bell 1980; Magnhagen 1990, 1991).

There is abundant evidence, from a phylogenetically diverse array of organisms, that gravid animals are indeed slower than their non-reproductive conspecifics. For example, such costs have been demonstrated or inferred in crustaceans (Winfield and Townsend 1983; Berglund and Rosenqvist 1986), scorpions (Shaffer and Formanowicz 1996), insects (Isaacs and Byrne 1998; Gu and Danthanarayana 2000), reptiles (Shine 1980; Seigel et al. 1987; Cooper et al. 1990), birds (Lee et al. 1996; Veasey et al. 2000, 2001), and mammals (McLean and Speakman 2000). This diversity of examples suggests that locomotor "costs" of pregnancy may offer a powerful opportunity for comparisons across disparate kinds of animals.

Unfortunately, the simple observation that reproductive state correlates with locomotor speed does not establish causation. Intuition suggests that the correlation is due to a direct causal effect of physical burden on locomotor capacity, but close analysis reveals a more complex situation. In particular, both the level of reproductive investment and locomotor ability typically display wide variation within a population, and both of these variables are highly correlated with other factors that might modify the relationship between them. For example, a female's health might simultaneously affect her reproductive output and her locomotor speed, generating an artifactual (non-causal) positive correlation between low reproductive output and slow locomotion even in the face of a strong underlying tradeoff (negative correlation) between these traits (van Noordwijk and de Jong 1986). Similarly, female body size or shape might simultaneously affect reproductive investment and locomotion (Sinervo et al. 1991; Sinervo and DeNardo 1996), so that a correlation between the latter two variables was actually generated by their common association with morphology. Lastly, seasonal variation in both traits could generate correlations between reproductive investment

and locomotor speeds, regardless of any causal links between the two (Qualls and Shine 1998).

Available data also suggest that locomotor decrements associated with reproduction may involve more than simply the physical burden of the eggs or offspring. For example, locomotor speeds do not necessarily recover immediately post-parturition, suggesting that physiological or endocrinological changes associated with pregnancy may be more important determinants of locomotor speed than physical burdening (Sinervo et al. 1991; Olsson et al. 2000). Contrariwise, performance of elite human female athletes may be higher soon after giving birth than at any other stage of their careers (Diddle 1984; Potteiger et al. 1993; Foley 1998). This result suggests that physiological modifications associated with reproduction may mask (to some degree) the straightforward effect of physical burden on locomotor ability. The only way to tease apart causal and non-causal influences on the relationship between reproductive burden and locomotor speeds is to manipulate the former variable experimentally (Sinervo and DeNardo 1996; Miles et al. 2000; Veasey et al. 2001). I adopted this approach with an oviparous lizard species, to quantify the effects of differing levels of experimentally induced physical burdening (mimicking oviductal eggs) on locomotor ability. These data enable me to compare the relationship between burden and locomotor decrement between natural (reproductive) and experimental situations.

Materials and methods

Study species

Garden skinks, *Lampropholis guichenoti*, are small (to 70 mm total length) oviparous scincid lizards abundant in coastal and montane regions of eastern Australia (Cogger 2000), including in highly modified suburban habitats (Swan 1990). Females lay one to three clutches in the warmer months of the year (Shine 1980; Joss and Minard 1985); clutches contain one to five eggs (Qualls 1996; Qualls and Shine 1997). Relative Clutch Masses (clutch mass divided by maternal body mass) vary spatially and temporally, but generally average around 0.25–0.30 (Pengilley 1972; Qualls 1996). The extent to which pregnancy influences maternal locomotion varies geographically; running speeds of gravid females in the population I studied are slower during pregnancy than soon after oviposition [14–15% decrease in Qualls and Shine 1997 (based on my reanalysis of raw data); 18% in Shine, unpublished data]. In other populations of *L. guichenoti*, females show either greater (25% slower: Shine 1980) or lesser (8% faster: Qualls and Shine 1997) changes in running speeds during pregnancy.

Methods

Adult *L. guichenoti* were collected by hand from suburban gardens in Sydney during summer 2001–02. The animals were maintained until trials commenced in July 2002 (midwinter), outside the reproductive period (Greer 1989), to ensure that none of the females were vitellogenic or gravid. Sex of the skinks was determined by manual eversion of hemipenes. Captive lizards were maintained in large outdoor enclosures (2.5×1 m) containing ad libitum water, shade, and basking sites. Food (live crickets) was provided twice weekly. One week before the experimental trials, the animals were transferred to separate plastic lunchboxes

(22×13×8 cm) containing a 1 cm substrate of commercial potting mix, a plastic shelter and a water dish. These cages were then arranged on timer-controlled heating racks allowing the skinks to control their own body temperatures (range in cage from 22.7±0.34 to 32.0±1.14°C). In previous field studies, body temperatures of active skinks averaged 26.8°C (range 21.1–34.7°C: Greer 1989). Heating was provided from 0800 to 1700 hours. Outside these hours, cage temperatures fell to ambient temperature (20°C). Timer-controlled lighting in the room provided a light: dark photoperiod of 12L:12D (lights on 0700–1900 hours). Lizards were fed on crickets twice weekly, and water was provided ad libitum.

Three days after they were last fed (to allow time for gut clearance), the lizards were measured [snout-vent length (SVL), tail, axilla-groin] and weighed, and injected with reptile ringer's solution equivalent to 10, 15, 20, 25 or 30% of their post-absorptive mass into the peritoneal cavity using a 1 ml insulin syringe. Seven male and seven female skinks were randomly allocated to each treatment, with another seven males and seven females sham-injected. That is, the needle of an empty 1 ml insulin syringe was inserted into the peritoneal cavity for approximately the same length of time as it had taken to inject the ringer's solution into the other lizards. I used males as well as females to expand the morphological variation within the sample, especially with respect to sexually dimorphic attributes such as relative axilla-groin length (Greer 1989). Each lizard was used in only a single treatment.

All lizards were reweighed to check the accuracy of the injected mass of fluid, then transferred to a constant-temperature room at 25°C, where they were given 30 min to recover from the handling and injection. They were then transferred directly from their containers to the starting area of the 4.5 cm-wide raceway and allowed to run 1 m along the raceway (within the 25°C room). Animals that refused to run were lightly touched on the tail with an artist's paintbrush. Infra-red photocells located at 25 cm intervals along the runway recorded the cumulative time taken for lizards to cross each successive infra-red beam. I used these data to calculate maximal running speed over 25 cm and mean running speed over 1 m for each lizard. Upon completion of these trials, lizards were returned to their original cages and fed. All injected animals urinated copiously over the next 24 h and returned to their original mass.

To compare the degree and spatial distribution of bodily distension due to injection to that due to pregnancy, I also quantified abdominal shapes. Digital calipers (±0.1 mm) were used to measure axilla-groin length, and the body width and depth at each of three points along the body (at the pectoral girdle, the pelvic girdle, and halfway between) for ten unfed female lizards. Another ten unfed females were injected with a volume of ringer's solution comprising 20% of their original body mass, and then measured in the same way as above. These data were compared to those for unfed gravid females, measured earlier in the year during the reproductive season.

Results

Table 1 shows that the random allocation of lizards to treatment groups successfully removed any significant variation in body lengths among groups (two-factor ANOVA with sex and treatment group; $F_{5, 72}=0.57$, $P=0.72$) although males (mean SVL 41.1 mm) were shorter-bodied than females (mean 43.5 mm: sex, $F_{1, 72}=20.08$, $P<0.0001$; interaction sex × treatment, $F_{5, 72}=0.56$, $P=0.73$). Mean body masses prior to injection did not differ either between sexes or among treatment groups (sex, $F_{1, 72}=0.84$, $P=0.36$; treatment, $F_{5, 72}=0.31$, $P=0.90$; interaction, $F_{5, 72}=0.68$, $P=0.64$), nor did pre-injection running speeds (m/sec) over distances of either 1 m (sex, $F_{1, 72}=0.31$, $P=0.58$; treatment, $F_{5, 72}=0.41$,

Table 1 Mean values and associated standard errors for body sizes, locomotor speeds and speed decrements due to intraperitoneal injection of saline in garden skinks*Lampropholis guichenoti* from four treatment groups differing in the volume of saline injected. Each lizard was used in only a single treatment; n=7 lizards of each sex in each treatment. See text for statistical analysis of these data

Treatment	Sex	Snout-vent length (mm)	Axilla-groin length (mm)	Pre-injection mass (g)	Speed (m/s) over 1 m	Speed (m/s) over 25 cm	Speed decrease over 1 m (%)	Speed decrease over 25 cm (%)
10%	f	43.71 (0.99)	25.11 (0.49)	1.42 (0.11)	0.52 (0.02)	0.72 (0.05)	1.4 (1.1)	5.8 (3.7)
10%	m	42.43 (1.21)	22.76 (0.48)	1.39 (0.06)	0.58 (0.03)	0.78 (0.03)	-0.1 (1.2)	0.8 (3.9)
15%	f	43.29 (0.68)	25.50 (0.91)	1.38 (0.08)	0.55 (0.03)	0.72 (0.07)	5.8 (1.1)	11.4 (5.3)
15%	m	40.57 (1.07)	22.73 (0.59)	1.38 (0.10)	0.57 (0.02)	0.81 (0.06)	4.8 (1.4)	10.9 (4.5)
20%	f	43.71 (0.84)	25.80 (0.84)	1.41 (0.07)	0.58 (0.03)	0.75 (0.04)	4.9 (1.7)	6.2 (4)
20%	m	39.86 (0.71)	22.51 (0.57)	1.31 (0.09)	0.57 (0.04)	0.77 (0.06)	6.7 (2.1)	5.4 (3.2)
25%	f	43.43 (1.04)	25.74 (0.78)	1.46 (0.11)	0.58 (0.02)	0.84 (0.04)	10.4 (1.7)	24.7 (2.5)
25%	m	41.71 (0.52)	22.90 (0.58)	1.43 (0.06)	0.56 (0.03)	0.81 (0.06)	6 (1.1)	14.2 (3.1)
30%	f	43.86 (0.94)	25.36 (1.00)	1.49 (0.05)	0.59 (0.04)	0.80 (0.06)	8.7 (1.9)	14.4 (2.4)
30%	m	41.00 (1.05)	23.40 (0.64)	1.31 (0.05)	0.57 (0.04)	0.72 (0.05)	11.3 (2.5)	10.1 (2.3)
Sham	f	42.86 (0.83)	25.37 (0.72)	1.32 (0.07)	0.54 (0.04)	0.68 (0.06)	1.7 (1.2)	-2.9 (3)
Sham	m	41.14 (0.83)	23.36 (0.21)	1.41 (0.09)	0.55 (0.04)	0.81 (0.09)	2.2 (1.6)	2.4 (-3.5)
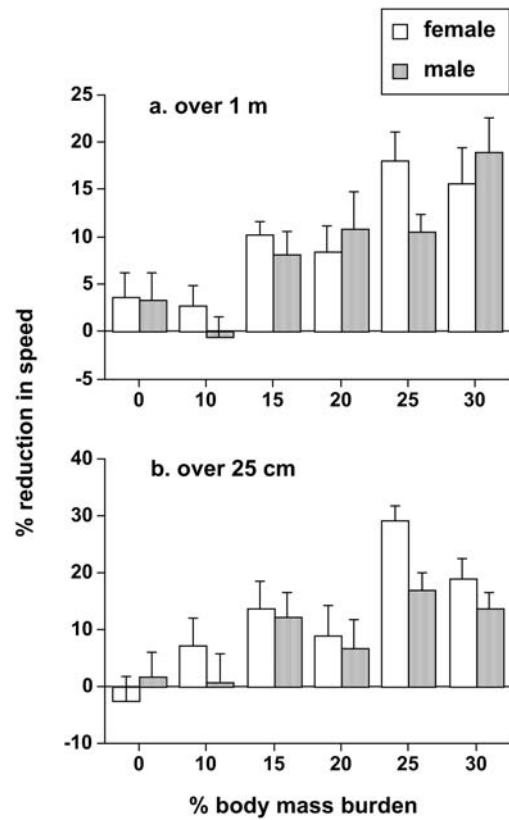
Fig. 1 Effect of injection of intraperitoneally-injected fluid on running speeds of male and female garden skinks, *Lampropholis guichenoti* (n=7 in each group). Reptile ringers' solution equivalent to 0 (sham-injected), 10, 15, 20, 25 or 30% of the lizards' original body mass was injected. The Y-axis shows the percent reduction in speed after injection compared to the same lizards' speeds prior to injection. Histograms show mean values and one standard error

P=0.84; interaction, $F_{5,\,72}$=0.49, P=0.79) or 25 cm (sex, $F_{1,\,72}$=0.99, P=0.32; treatment, $F_{5,\,72}$=0.51, P=0.77; interaction, $F_{5,\,72}$=0.90, P=0.49). Body lengths were not correlated with running speeds prior to injection in either sex (over both distances, both sexes have P>0.05).

Reweighing lizards immediately after injection showed that we had successfully introduced close to the desired masses of fluid. Mass change averaged 0.9% for sham-operated animals, and 8.6, 13.8, 19.1, 22.1 and 28.3% for the nominally 10, 15, 20, 25 and 30% groups respectively. The mass of fluid injected into the peritoneal cavity had strong and consistent effects on locomotor speeds. Lizards that were sham-injected or received an injection weighing only 10% of their body mass ran almost as quickly post-treatment as before (Fig. 1). However, higher burdens substantially reduced running speeds over both of the distances that I measured (Fig. 1). Two-factor ANOVA (as above) on these data confirms that running speeds were affected by treatment but not by sex, nor by any interaction between treatment and sex (over 1 m—sex, $F_{1,\,72}$=0.57, P=0.45; treatment, $F_{5,\,72}$=9.91, P<0.0001; interaction, $F_{5,\,72}$=1.02, P=0.41;
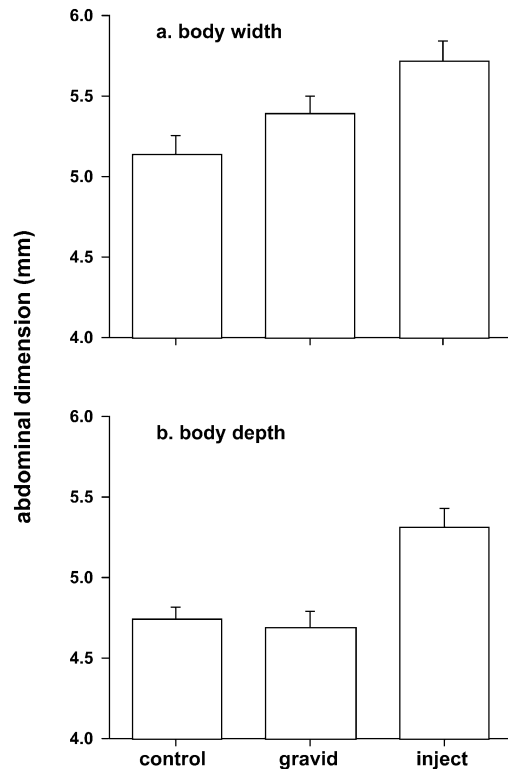
Fig. 2 Abdominal dimensions of adult female skinks, *Lampropholis guichenoti*, from three treatment groups (*n*=10 in each group). All lizards were unfed; one group were controls, others were gravid, and the remainder (non-gravid) were injected intraperitoneally with fluid comprising 20% of their original mass. Body widths and depths were measured at three points along the trunk (behind the forelegs, anterior to the hind legs, and in the middle of the trunk); these were combined to generate mean values for the graphs. Histograms show mean values and one standard error

95% confidence limits for these slopes were indeed <1.0 both over distances of 1 m (0.63–0.90) and over 25 cm (0.54–0.83).

Morphological data confirmed that body shapes differed significantly among the three groups of female lizards (control, injected, and gravid). ANOVAs revealed that SVLs were similar ($F_{2, 27}$=1.96, P=0.16) but that body widths and body depths (averaged across the three points where these variables were measured) differed (width—$F_{2,2 7}$=6.74, P<0.004; depth—$F_{2, 27}$=12.55, P<0.0001). Post hoc Fishers PLSD tests showed that injected lizards differed from controls (P<0.05) in both respects, and that gravid and injected lizards also differed in mean body depth (see Fig. 2). To clarify this result, I calculated the ratio of mean body width to mean body depth and conducted an ANOVA on this ratio measure. Again, the three groups differed significantly ($F_{2, 27}$=7.57, P<0.003), with post hoc tests showing that the injected lizards were relatively deeper-bodied than either the control or gravid animals. That is, the injected fluid was distributed differently from eggs. Gravid lizards retained the same body depth as controls, increasing only in width, whereas the injected lizards also increased in body depth.

Discussion

The running speeds of skinks were substantially reduced by physical burdens comprising >20% of their body mass (Fig. 1). Sham-operated animals, and lizards receiving lighter burdens, did not show significant shifts in locomotor performance, suggesting that the mass or volume of the injected fluids (rather than the experimental procedures) were responsible for this effect. The physical burdening generated by injection of fluids was not identical to the physical burden due to carrying a clutch of eggs; eggs constituting >20% of maternal body mass were accommodated inside the female's body without as much distension as an equivalent mass of fluid (Fig. 2). Undoubtedly, the experimental injection procedure failed to exactly mimic other aspects of pregnancy also. For example, females may adapt to this longer-term burden by gradually modifying aspects such as their stride lengths to compensate for the extra load, whereas the injected lizards had little time to compensate for a suddenly imposed burden. Nonetheless, the experimental procedures provided an approximate simulation of the physical burdening due to pregnancy.

The fact that a heavy physical burden substantially impairs the mobility of a lizard is not surprising. More interesting is the form of this effect (e.g. is it linear?), its magnitude (how much slower is a burdened animal?), and its determinants (e.g. does the effect depend upon an animal's sex, size, shape, or prior speed?). Most importantly, how does the form and magnitude of the locomotor decrement compare to that seen in gravid lizards of the same population? Below, I address these issues.

over 25 cm—sex, $F_{1, 72}$=2.58, P=0.11; treatment, $F_{5, 72}$=8.29, P<0.0001; interaction, $F_{5, 72}$=0.86, P=0.51).

The magnitude of the locomotor decrement due to the experimental injection (% reduction in speed) was not significantly correlated with the lizard's body sizes (SVLs) or body shapes (sexes combined, all *n*=84; over 1 m—vs SVL, *r*=0.03, P=0.76; vs axilla-groin as % of SVL, *r*=0.15, P=0.19; vs tail as % SVL, *r*=0.02, P=0.86; mass relative to SVL, *r*=0.19, P=0.08; over 25 cm—vs SVL, *r*=0.19, P=0.08; vs axilla-groin as % of SVL, *r*=0.09, P=0.42; vs tail as % SVL, *r*=0.02, P=0.86; mass relative to SVL, *r*=0.05, P=0.63). However, lizards that ran faster prior to injection showed a greater % reduction in speed after injection (over 1 m, *n*=84, *r*=0.22, P<0.05; over 25 cm, *n*=84, *r*=0.26, P<0.02). Although intuitive, this comparison is statistically flawed because ratio measures can be artifactually correlated to their component variables (Atchley et al. 1976). A more robust method is to regress post-injection speeds against pre-injection speeds for each lizard, and examine the slope of the resulting least-squares linear regression. A slope <1.0 would indicate that the injection reduced speeds more in faster-running lizards than in their slower conspecifics.

Linearity

Mathematical models of optimal reproductive effort suggest that any nonlinearity in the relationship between reproductive output and associated costs create differing cost-benefit ratios with differing levels of investment, and thus modify predicted levels of reproductive investment (Bull and Shine 1979; Schwarzkopf 1996). My study did not reveal any strong nonlinearities, although there was substantial scatter in the data (especially with data for speeds over 25 cm: see Fig. 1). In the only previous manipulative study on effects of reproductive burden on locomotor abilities in lizards, Miles et al. (2000) reduced clutch mass of *Uta stansburiana* by ablation of ovarian follicles and measured effects on maternal endurance (rather than velocity) as well as survival. Consistent with my data on *L. guichenoti*, female *Uta* with experimentally reduced clutches exhibited higher endurance; this advantage persisted after oviposition. Surprisingly, however, a 32% decrease in reproductive burden eliminated the entire endurance reduction caused by "normal" pregnancy (in Fig. 3 of Miles et al. 2000, endurance of gravid yolkectomised females was similar to that of post-oviposition controls and sham-operated animals). Also, reproductive burden was correlated with the reduction in endurance only when the sample included females with large as well as small clutches (Table 3 in Miles et al. 2000). In combination, these results suggest a strong nonlinearity in the effects of reproductive burden on maternal endurance, with relatively small clutches having no measurable impact on maternal locomotor ability. Hence, relationships between reproductive investment and performance decrements may be linear in some species but not others.

Even if locomotor decrements are linearly related to burden, there may be threshold speeds that influence vulnerability to predation (i.e. an animal can outrun predators at any speed above some fixed level, but not at any lower speed). Thus, nonlinearities are likely to be widespread in the broader relationship between reproductive investment and "costs", even if they are not apparent in the relationship between burden and locomotor impairment.

Magnitude

It is easy to imagine a situation where burdens reduce running speeds, but do so to such a minor degree that organismal performance is affected in only a trivial way (i.e. the effects are statistically but not biologically significant). This was not the case for my study: locomotor speeds were depressed by about 20% in the most heavily burdened animals (Fig. 1). Whether or not such a decrease is biologically important will depend upon how (or if) shifts in speed translate into shifts in vulnerability to predation (see above). For example, some species may not depend upon speed very often; or predators may be quicker than even the fastest lizard. *L.*

guichenoti is an active searching forager often found far from shelter, and relies upon speed to escape predation (Greer 1989); thus, locomotor abilities are likely to influence fitness. In some cases, however, even a 20% decrement in speed will be irrelevant because speed does not influence the outcome of predator-prey encounters (e.g. Schwarzkopf and Shine 1992) whereas such a decrease may be critical in other cases (even for the same species with a different predator: e.g. Shine 1980; Downes and Shine 2001). Field studies are essential to clarify this question (e.g. Sinervo and DeNardo 1996).

Determinants

Because a female reptile's abdominal volume imposes an upper limit on her clutch volume, her body size and shape can influence her reproductive output (Vitt and Congdon 1978; Shine 1992). Biomechanical models predict that maternal morphology can also affect the mother's speed and potentially, her ability to carry a physical burden (Gans 1974). Hence, correlations between reproductive output and running speeds may reflect this common correlation with morphology, rather than (or as well as) a direct causal influence of burden on speeds. This hypothesis predicts associations between a lizard's morphology and its locomotor performance, but I found no such associations. This was true even when males as well as females were included in the analysis. I expected that male *L. guichenoti* would be less capable of carrying a heavy physical burden than females, because male morphology has not been under strong selection for this task in the same way as has been true for females. In practice, even the wide range of morphological variation introduced by including both sexes did not generate any significant relationships between morphology and speed. Thus, the locomotor decrements displayed by gravid *L. guichenoti* (e.g. Shine 1980; Qualls and Shine 1997) cannot be attributed to confounding effects of variables such as maternal body size and shape.

Although a lizard's morphology did not predict its decrement in speed when burdened, its initial speed (prior to injection) played a significant role. Faster lizards lost a significantly higher proportion of their initial speed after injection. A similar tradeoff between initial speed and response to a locomotor-impairing treatment (dosage with newt toxin) has been reported for garter snakes (Brodie and Brodie 1999). These authors interpreted the pattern as evidence for a tradeoff, whereby morphological features that facilitated rapid locomotion were also more sensitive to disruption. It may generally be true that high-performance systems are more easily disrupted. The obvious inference from this result is that females that are intrinsically very swift runners might benefit differentially from lower-than-average reproductive investment.

Comparison with field data

Is the locomotor reduction during pregnancy in *L. guichenoti* (Shine 1980; Qualls and Shine 1997) simply due to physical burden of the eggs? If so, the decrease in running speeds of gravid lizards should be about the same as that observed when lizards are injected with a mass of fluid similar to the mass of the eggs. This comparison is slightly weakened by the fact that the bodily distension due to fluid injection did not exactly mimic that due to pregnancy, but the broad magnitude of comparisons is still worthwhile. Speed decrements reported for gravid female *L. guichenoti* from Sydney averaged 14% and 18% (Qualls and Shine 1997; Shine, unpublished data). Data in Fig. 1 predict a speed decrease of around 18% from a burden as large as the observed mean relative clutch mass in this species (0.25–0.30: Pengilley 1972; Qualls 1996). The locomotor decrease observed with a clutch-sized injection thus is equal to or greater than the observed decreases in locomotor speeds of gravid lizards from this population (see above). That is, an experimentally generated physical burden equal in mass to a clutch of eggs decreased running speeds of lizards by about the same amount as did pregnancy. This broad similarity suggests that simple physical burdening can explain most of the effects of pregnancy on running speeds within this species. Indeed, the strong hint (especially from the Blue Mountains lizards, that did not reduce speeds when gravid: Qualls and Shine 1997) is that reproductive females somehow adapt to the burden of the clutch and manage to maintain higher speeds than expected from the injection trials.

The conclusion that much of the locomotor decrement of gravid females is due to simple physical burdening runs counter to results and inferences from some previous work. For example, it does not explain why lizards sometimes do not recover their full locomotor capacity for a considerable time after parturition (Sinervo et al. 1991), nor why captive animals maintained fast running speeds despite carrying fat-body masses equivalent to clutches (Olsson et al. 2000). As noted above, females may adjust to long-term loads by modifying stride patterns; quantitative analysis of this possibility would be of interest. Also, interspecific variation may be important: for example, viviparous squamates may undergo more profound modifications to maternal physiology during gestation than do oviparous taxa. Wide intraspecific variation in morphology, running speeds and locomotor costs of pregnancy (Sinervo et al. 1991; Qualls and Shine 1997, 1998), suggests that such traits may be highly labile. Hence, generalisations about the causal basis of locomotor decrements due to reproduction will need to wait until both experimental and observational data are available on additional taxa.

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