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Decreased Sprint Speed as a Cost of Reproduction in the Lizard Scelopours Occidentalis: Variation Among Populations

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DECREASED SPRINT SPEED AS A COST OF REPRODUCTION IN THE LIZARD *SCELOPORUS OCCIDENTALIS*: VARIATION AMONG POPULATIONS

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Summary

Decreased mobility of gravid females is thought to be an important cost of reproduction in lizards. We measured sprint speeds of female western fence lizards (*Sceloporus occidentalis* Baird and Girard) before and after they had oviposited. Females from two California populations were about 20 % slower when gravid, females from an Oregon population were about 30 % slower, and females from a Washington population were about 45 % slower, compared to their speeds after recovering from reproduction. The decrease in sprint speed persisted for several weeks after oviposition, suggesting that reproduction impairs sprint performance by affecting body condition in addition to the burdening effect of eggs.

Oregon and Washington females carried more mass (both somatic and clutch mass) per unit body length than California females. On the shorter bodies of Oregon and Washington lizards, eggs may interfere with the mechanics of running, in addition to their effect on the total mass of the female. In addition, gravid females from Washington had significantly higher reproductive investment (mass of clutch relative to the mass of the female after oviposition) than Oregon and California populations. Greater reproductive investment by Washington females increases the burden carried per unit of body length; we suggest this further impairs sprint performance.

Decrements in sprint speed were not significantly correlated with level of reproductive investment (per unit body mass) among females within any of the study populations. However, the burden carried per unit body length was

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correlated with the sprint speed decrement among gravid females from Oregon. Comparisons within and among populations suggest that differences in morphology among northern and southern populations interact with reproductive investment to produce interpopulation differences in sprint performance for gravid females.

Introduction

Reproduction is thought to entail costs: genetic trade-offs between current *versus* future allocation to reproduction (see Reznick, 1985, for a review). For lizards, authors frequently use relative clutch mass (RCM; clutch mass divided by total mass of the gravid female) as an operational measure of current reproductive investment, and suggest that an increase in RCM carries associated costs of reproduction (Tinkle and Hadley, 1975; Vitt and Congdon, 1978; Shine, 1980). One potentially important cost may result from the reduced mobility of a gravid female: slower lizards may be more susceptible to predation (Vitt and Congdon, 1978; Shine, 1980, 1988; Bauwens and Thoen, 1981; Vitt and Price, 1982).

The ecological correlates of variation in RCM among species of lizards are well documented. Lizards that are active, wide-ranging foragers, or are highly arboreal, tend to have lower RCMs than those that are sedentary or are sit-and-wait predators (Vitt and Congdon, 1978; Vitt, 1981; Huey and Pianka, 1981; Vitt and Price, 1982; Magnusson *et al.* 1985; Anan'eva and Shammakov, 1985). This suggests that there are functional trade-offs between RCM and mobility, such that selection for increased RCM can indirectly select for decreased mobility. However, only a few studies have measured the extent to which mobility is impaired in gravid females, and whether decrements in locomotor ability are correlated with the level of reproductive investment (Shine, 1980; Bauwens and Thoen, 1981).

In this study, we measure how reproduction affects sprint speeds of females from four populations of the western fence lizard, *Sceloporus occidentalis*. We also investigate whether the decrement in sprint speed of a gravid female is correlated with her level of reproductive investment or with other morphological traits. In addition, we describe the time course of recovery of sprint speed following oviposition.

Because the four populations occur at different latitudes and altitudes, they may experience different predation intensities (Pianka, 1970; Tinkle and Ballinger, 1972). Increased predation pressure might cause natural selection for higher sprint speeds, possibly through decreasing reproductive investment. Therefore, we investigated whether reproductive investment and degree of impairment of sprint speed covaried among populations as well as within populations.

Because of methodological problems associated with using RCM (body mass is found in both the numerator and denominator and the allometry between clutch mass and body mass would confound any comparison of animals that differ in size; Packard and Boardman, 1987; Dunham *et al.* 1988), we have used multivariate methods to analyze the relationships between decreased sprint performance and

the burden of a clutch of eggs. Morphological traits that potentially affect performance can be included in these analyses.

Materials and methods
Collection and husbandry of gravid females

Gravid female *Sceloporus occidentalis* were collected in May and June 1987 and 1988 from four populations. Two populations are in the San Gabriel Mountains of southern California: one at low elevation (1300 m) on the edge of the Mojave Desert near Pearblossom and the other at high elevation (2200 m) on Table Mountain near Wrightwood. The third population (700 m) is in Oregon near Terrebonne. The fourth population (200 m) is in Washington near Lyle. Further aspects of the ecology of *S. occidentalis* at these study sites are given by Tsuji (1986), Sinervo (1988), and Adolph (1990).

Gravid females were transported to the laboratory (University of Washington) within 4 days of capture. The females were housed individually in plastic terraria with a moist substratum of sand and peat moss. The terraria were kept in an environmental chamber (12 h at 34°C, 12 h at 20°C, 12 h:12 h L:D with full-spectrum illumination). Females were fed crickets [dusted with vitamins (Vionate™) and calcium] every day, and mealworms biweekly. Females were weighed once a week. Terraria were checked twice a day for eggs. Eggs were removed and weighed to determine clutch mass, and each female was weighed to determine her post-oviposition mass. After ovipositing, females were housed in small groups in large terraria (radiant heat, 12 h:12 h L:D, supplemented with ultraviolet light), and given food and water *ad libitum*.

Sprint speed

Gravid females were raced initially within 2 weeks of capture to determine their sprint speed when burdened by a clutch of eggs. On the day of racing the gravid females were held in an environmental chamber at 34°C (the thermal optimum for sprinting in this species; Adolph, 1987). Gravid females were raced on a level 2.4 m×20 cm racetrack to estimate maximum sprint speed. The racetrack had a rough, rubberized substratum that provided excellent traction. Speeds were determined electronically by regularly spaced photocells connected to a computer (Huey *et al.* 1981). Maximum sprint speed was estimated as the fastest 0.5 m interval achieved during four consecutive races held at 1-h intervals. Females were raced again between 10 and 30 days after they had oviposited. The change in sprint speed for each individual (before *vs* after ovipositing) was analyzed using repeated measures analysis of variance (ANOVA), with population as a factor. Further details concerning gravid female rearing and oviposition can be found in Sinervo (1990).

To determine whether sprint performance declines prior to ovipositing, some gravid females were raced twice before ovipositing, once around 14 days before ovipositing and again immediately prior to ovipositing (about 3 days). Similarly, to

determine whether sprint performance increases after ovipositing, another group of females was raced shortly after ovipositing (about 7 days) and re-raced about 14 days after ovipositing. We compared the change in sprint performance in these two groups (paired t-tests). We raced an additional group of females (from the California populations) 1–40 days after they had oviposited (these females had not been raced before they oviposited). This group, which was only raced once, controls for the effect of experience on sprint speed (i.e. training that may occur between successive races by the same individual). We estimated the time course of recovery of sprint speed in this group using regression analysis.

Reproductive investment and morphology

We defined burden as the difference in the mass of each female before and after she oviposited (burden was highly correlated with the total mass of eggs in her clutch). As a measure of reproductive investment we used residuals from the regression of burden against body size, rather than using the ratio of burden to body mass (i.e. RCM). We compared reproductive investment (total clutch mass) among populations by analysis of covariance (ANCOVA) [using post-oviposition mass and snout–vent length (SVL) as covariates in two separate analyses]. We report population differences in total clutch mass (ANCOVA, using mass and SVL) expressed in terms of a difference between low-elevation California females and the other three populations [i.e. dummy variables describing difference between Washington, Oregon and high-elevation California relative to low-elevation California (Draper and Smith, 1981)]. We also measured thigh length (TL, distance from knee to knee when both femurs are held laterally and perpendicular to the body) as another possible morphological correlate of sprint speed (Garland, 1985; Losos and Sinervo, 1989; Sinervo and Huey, 1990). Unless otherwise noted, all variables were log-transformed.

Reproductive investment and morphological traits could affect sprint performance either independently or interactively. Comparing these reproductive and morphological traits among populations that differ in performance can suggest possible functional relationships among these traits, although traits could covary among populations for other reasons. Covariation that is due to functional relationships should be present within populations as well as among populations (Bennett, 1987). Because many physiological and morphological traits are correlated with body size (e.g. Calder, 1984; Schmidt-Nielsen, 1984; Sinervo and Huey, 1990), and hence could covary with one another spuriously, a proper analysis should factor out body size (Bennett, 1987).

We analyzed the relationship between the reproductive investment of a female and her sprint performance after correcting for three different measures of body size and morphology: post-oviposition body mass, SVL and TL. Burden was regressed against each of these measures individually; residuals about the regression were used as variates in subsequent regression analyses of performance. On functional grounds, one would expect a positive correlation between the burden residuals and the magnitude of a female's decrement in sprint speed. For

example, we might expect a female with a relatively large burden for her body mass (large residual) to experience a relatively large decrement in sprint speed when gravid.

Results

Sprint speed

Females from all three populations were slower when gravid than when raced at least 10 days after ovipositing (Fig. 1, Table 1). Sprint speed after ovipositing did not vary among populations, but the females from Oregon and Washington were
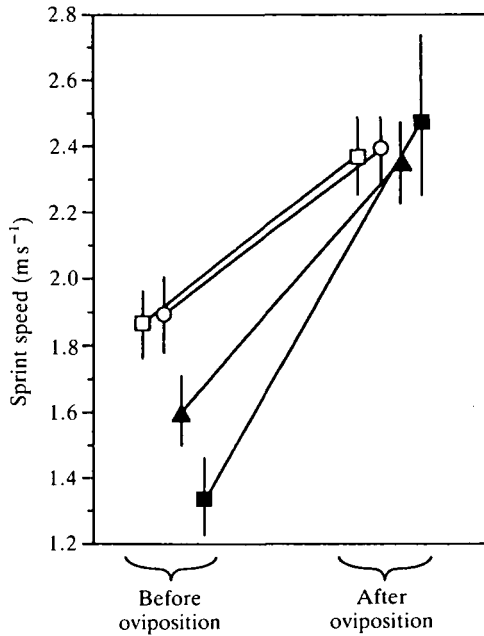

Fig. 1. Sprint speeds (mean±s.e.) of female *Sceloporus occidentalis* lizards before and after ovipositing. California (high elevation) (□), $N=28$; California (low elevation) (○), $N=37$; Oregon (▲), $N=23$ and Washington (■), $N=5$.

Table 1. *Repeated-measure ANOVA (including population as a factor) comparing sprint speeds of female fence lizards* (Sceloporus occidentalis) *before and after laying their eggs*

Source	Sum of squares	d.f.	Mean square	F-ratio	P-value
Population (A)	1.040	3	0.347	0.63	0.60
Subjects within groups	49.371	90	0.549		
Repeated measure (B)	17.323	1	17.323	119.03	0.0001
A×B	1.355	2	0.452	3.10	0.03
B×subjects within groups	13.098	90	0.146		

See Fig. 1 for sample sizes of each population.

slower while gravid than were females from either California population (Fig. 1, Table 1). The mean decrement in sprint speed while gravid was $1.16\,m\,s^{-1}$ for Washington females, $0.76\,m\,s^{-1}$ for Oregon females, $0.48\,m\,s^{-1}$ for females from high elevation in California and $0.53\,m\,s^{-1}$ for females from low elevation in California.

Sprint performance measured on the same individual on two occasions prior to ovipositing was not significantly lower on the second trial (immediately prior to ovipositing; mean sprint performance decrease $=-0.10\,m\,s^{-1}$; paired t-test, $t=-1.04$; $N=11$; $P>0.32$; Fig. 2A). Similarly, sprint performance of individuals from California was not correlated with time before ovipositing (Fig. 2B). Thus, the reduced sprint speed prior to ovipositing probably existed well before females were brought into the laboratory (i.e. more than 3 weeks prior to ovipositing).

However, sprint speed did increase with time after ovipositing (Fig. 2). Sprint performance increased significantly in those females (from high elevation in California) that were raced on two different dates after ovipositing (mean sprint performance increase $=0.29\,m\,s^{-1}$; paired t-test, $t=2.79$; $N=16$; $P<0.02$; Fig. 2A). Similarly, the sprint performance of individual females from California (raced for the first time) increased significantly with time after ovipositing (Fig. 2B). Within 2–3 weeks after ovipositing, their sprint speeds were comparable to the sprint speeds of males and females measured well outside the reproductive season (Fig. 2B). These increases in performance suggest that females do not recover maximum sprint performance until about 2 weeks after ovipositing.

Relationships between reproductive investment, morphology and sprint performance

Gravid females from Washington had significantly greater reproductive investment (burden, corrected for body mass differences) than females from the Oregon and California populations (ANCOVA, Fig. 3A). This difference is also reflected by a greater RCM (clutch mass divided by female body mass including clutch mass) for Washington lizards [0.318 (mean) ±0.005 (s.e.)] compared to lizards from Oregon (0.281±0.010), high-elevation California (0.270±0.079) and low-elevation California (0.277±0.077).

When corrected for SVL, burden was significantly greater in both Washington and Oregon females than in California females (ANCOVA, Fig. 3B). Thus, females from northern populations tend to carry more egg mass per unit body mass and/or per unit body length. In addition, the northern lizards had shorter legs (ANCOVA, Fig. 3C).

Populations of *Sceloporus occidentalis* differed in reproductive investment and sprint performance while gravid. This suggests a possible functional relationship between these traits; if so, these traits should covary among individuals within each population (Bennett, 1987). We were particularly interested in the relationship between the sprint speed decrement and the burden carried per unit of body mass and per unit of body length (SVL). We had sufficient data for females from
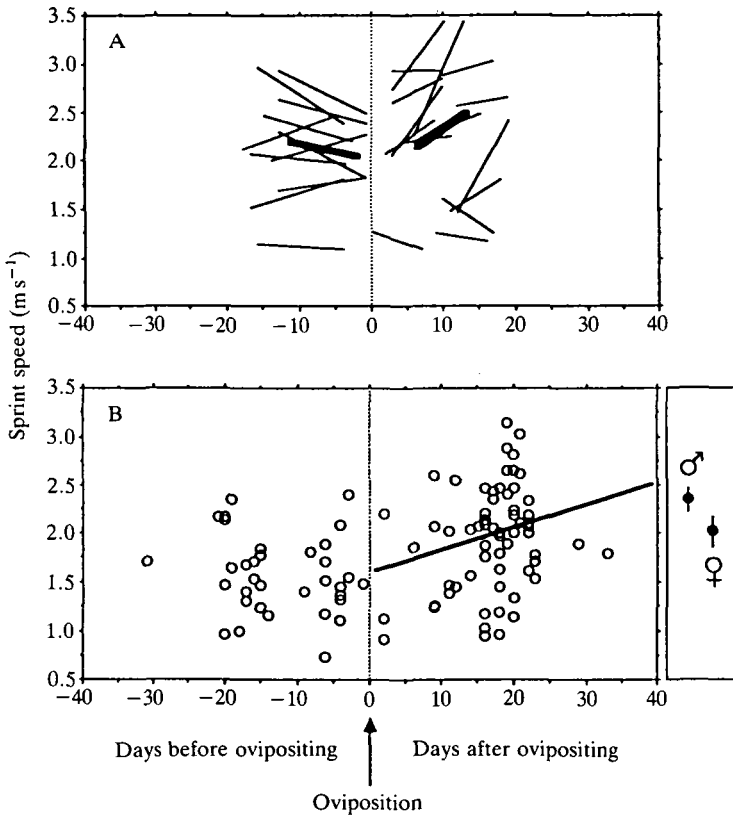
Fig. 2. (A) Changes in sprint speed for individual females from high elevation in California that were raced either twice prior to or twice after ovipositing. The heavy lines describe the mean response for each group from California. Whereas sprint performance did not decline significantly prior to ovipositing, there was a significant recovery in sprint performance after ovipositing (see text). (B) A comparison of sprint speeds among female *Sceloporus occidentalis* lizards from California yields comparable results. Sprint speed before laying did not vary significantly with time ($F_{1,32}=0.757$, $P>0.39$). Sprint speed increased significantly with time after oviposition ($F_{1,62}=4.139$, $P<0.05$; speed $(m s^{-1})=1.548+0.024t$, where t is time in days). The panel on the far right shows sprint speeds (mean$\pm$s.e.) for female ($N=8$) and male ($N=6$) *S. occidentalis* from the California low-elevation population, measured in September (well after the reproductive season ends; S. C. Adolph and F. H. van Berkum, unpublished data).

Oregon and the two California populations to test for statistical relationships that might reflect functional relationships.

To determine whether burden might affect sprint performance, we computed residuals from the regression of burden on either measure of body size (performed separately for each population and for each measure), yielding burden residuals for each individual female. Surprisingly, we did not find a significant correlation between burden residuals (factoring out body mass) and sprint speed decrement
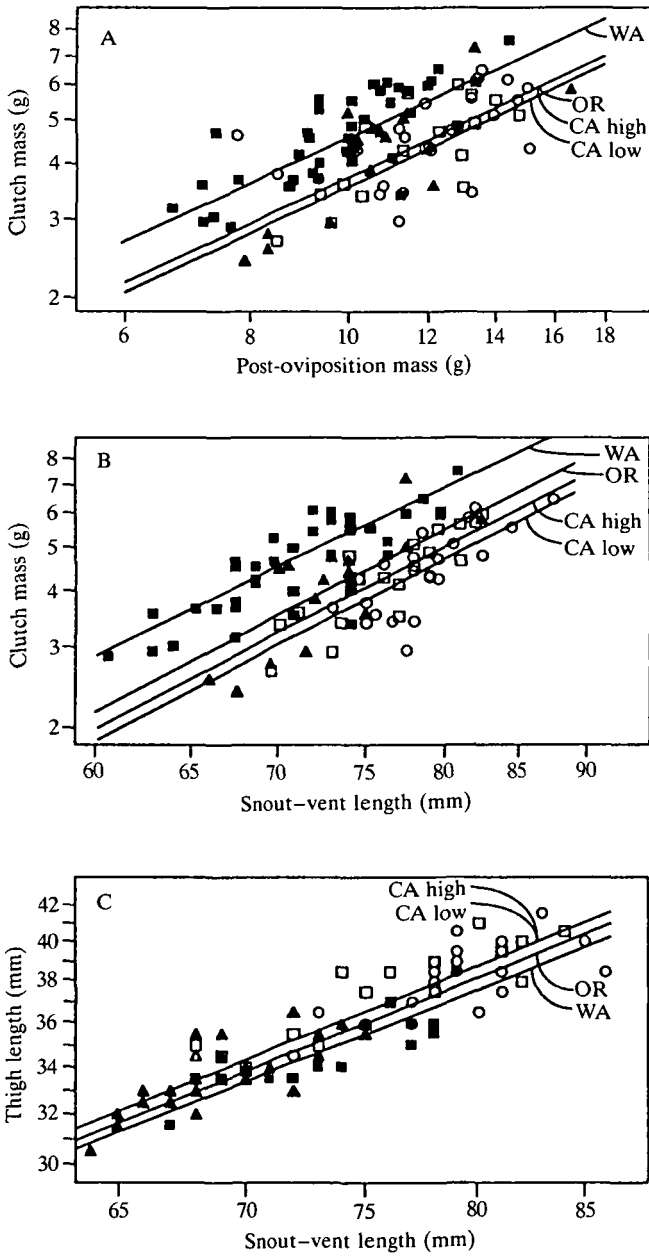
Fig. 3

within any population (California low, $r=0.07$, $P>0.69$, $N=36$; California high, $r=0.15$, $P>0.44$, $N=27$; Oregon, $r=0.195$, $P>0.37$, $N=22$). Similarly, sprint speed decrement and burden residuals (factoring out SVL) were not significantly correlated within either of the California populations (California low, $r=0.10$, $P>0.57$, $N=36$; California high, $r=0.12$, $P>0.54$, $N=27$; Fig. 4B,C). However, in Oregon females, SVL-corrected burden was positively correlated with sprint

Fig. 3. Allometric relationships of clutch mass and thigh length with body size. Regression lines with pooled slope are plotted for each population. All axes are logarithmic in scale. Populations did not differ significantly in slope for any of the comparisons, but there were differences in the intercept in each case (ANCOVA). California (high elevation) (□), California (low elevation) (○), Oregon (▲), and Washington (■). (A) Clutch mass *versus* post-oviposition mass (pooled allometric slope of ln-transformed variables=1.06 for all four populations, t=11.28, P<0.0001, intercept for low-elevation females, −1.112). Females from the Washington population had a significantly greater clutch mass per unit of body mass than females from low elevation in California (difference in intercept=0.200, t=4.20, P<0.0001), whereas females from low elevation in California did not differ from females from Oregon (difference in intercept=0.028, t=0.50, P>0.62) or high elevation in California (difference in intercept=−0.033, t=0.59, P>0.55). (B) Clutch mass *versus* snout–vent length (pooled allometric slope in ln-transformed variables=3.44; t=13.442; P<0.0001, intercept for low-elevation females=−13.512. Females from both the Washington population (difference in intercept=0.396, t=8.085, P<0.0001) and the Oregon population (difference in intercept=0.172, t=3.09, P<0.003) had a significantly greater clutch mass per unit of body length than females from low elevation in California, whereas females from low elevation in California did not differ from females from high elevation in California (difference in intercept=0.067, t=1.32, P>0.19). (C) Thigh length versus snout–vent length (pooled allometric slope of ln-transformed variables=0.776; t=12.62; P<0.0001, intercept for low- and high-elevation females from California=0.259. Females from both the Washington population (difference in intercept=−0.048, t=5.06, P<0.0001) and the Oregon population (difference in intercept=−0.026, t=2.64, P<0.01) had significantly shorter thighs than females from California.

speed decrement: females with a relatively large burden for their length experienced a greater decline in sprint speed when gravid (Fig. 4A, r=−0.56, P=0.006, N=22).

Discussion

Sprint speed of gravid females

Sprint speeds of female fence lizards while gravid were consistently lower than after they had oviposited. Sprint speeds were reduced by about 20 % in gravid females from both California populations, by about 30 % in gravid females from Oregon, and by about 45 % in gravid females from Washington (Fig. 1). Similarly, running speeds are reduced by 20–30 % in several species of gravid skinks (Shine, 1980) and by 26 % in gravid *Lacerta vivipara* (Bauwens and Thoen, 1981). Whereas previous studies determined the decrement in sprint speed of gravid females by comparing them to either non-gravid females or males, our study compared the change in sprint speed of the same individuals before and after ovipositing (Table 1). A similar study comparing the speed of gravid snakes before and after reproduction found a 20 % reduction in locomotor ability (Seigel *et al.* 1987).

Sprint speeds could decline because the weight of the clutch hampers locomotion (Shine, 1980; Bauwens and Thoen, 1981; Vitt and Price, 1982). On a finer
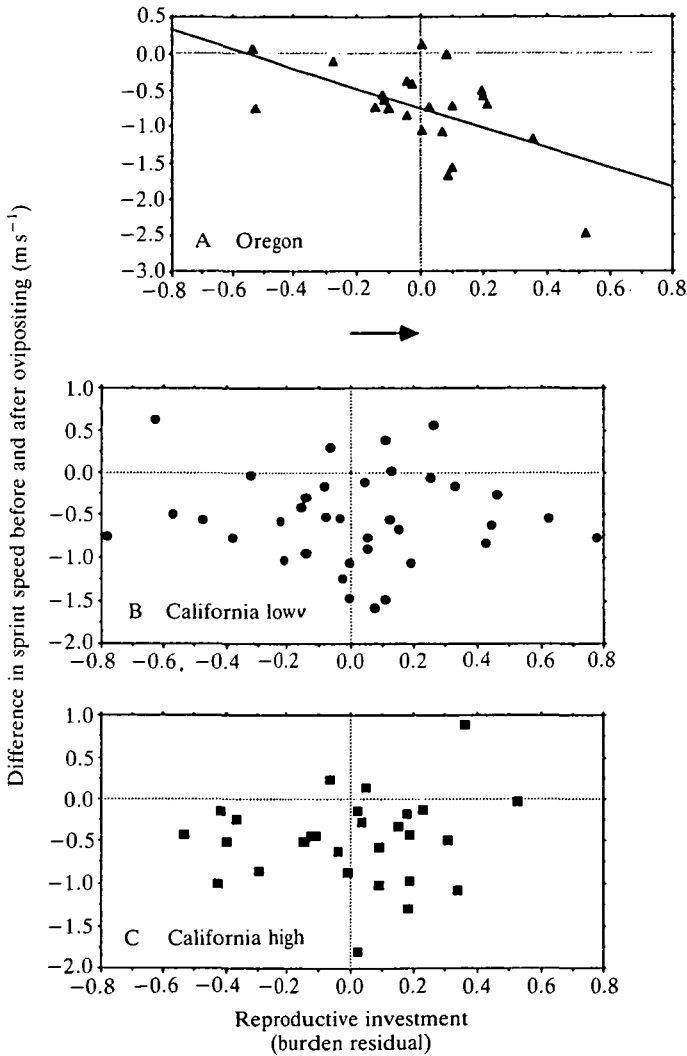
Fig. 4. Relationship between the sprint speed decrement while gravid (difference between pre- and post-oviposition sprint speed) and burden carried per unit of body length (residuals from regression of burden on SVL). The offset (arrow) between the panel describing data from Oregon females (A) and the panels describing data for low-elevation (B) and high-elevation (C) females from California reflects the among-population difference in burden per unit of body length (derived from ANCOVA, see text).

scale, variation in reproductive investment among females within a population could covary with the degree of locomotor impairment. Indeed, sprint speed decreases with RCM in two species of scincid lizards (Shine, 1980). In our study, we did not find a significant correlation between the level of reproductive investment (relative to body mass) and sprint speed decrement among individuals

within a population. However, the effect of reproductive investment was statistically significant in one of our populations (Oregon) if morphology – burden carried per unit of body length – was incorporated in the analysis (see below). This morphological effect could explain the larger sprint speed decrements experienced by the stockier northern lizards.

An alternative cause of the decline in sprint speed could be a temporary deterioration of the body condition of gravid females. Indeed, our results show that the sprint speed of a female immediately after ovipositing is as low as when she is burdened, and that she requires several weeks to recover her maximum ability. This suggests that reproduction not only impairs locomotion because eggs are a physical burden but that it also exacts a physiological toll on females. The poor body condition of females immediately after ovipositing supports this view (B. Sinervo and S. C. Adolph, personal observation in the laboratory and field). Thus, the disadvantage of decreased sprint speed does not end at oviposition, but persists for several more weeks.

Regardless of its causal mechanism(s), the reduced sprint speed is potentially an important cost of reproduction, particularly if it increases the risk of predation (Shine, 1980; Bauwens and Thoen, 1981; Christian and Tracy, 1981). Indeed, Shine (1980) found in laboratory trials that gravid female skinks (*Leiolopisma coventryi*) were more vulnerable to predation by a snake than were non-gravid individuals (males). In addition to the potential risk of greater predation, reduced sprint speed could entail other costs for gravid female lizards. For example, foraging success (Avery *et al.* 1982) may depend in part on sprint speed.

Gravid lizards might be expected to compensate behaviourally for their reduced mobility. For example, gravid female *Lacerta vivipara* rely more on camouflage and less on flight than do males or non-reproductive females (Bauwens and Thoen, 1981). Similarly, unpublished field observations (B. Sinervo and S. C. Adolph) suggest that, during the reproductive season, gravid female *S. occidentalis* choose perches that are less conspicuous, and closer to shelter, than do males. Outside the reproductive season, however, males and females do not differ in microhabitat use (Adolph, 1990).

Interactions between reproductive investment, morphology and sprint performance

Washington females were both much slower when gravid and had greater reproductive investment (burden *versus* post-laying mass) compared to females from other populations. This suggests a functional trade-off between these two traits. However, differences in reproductive investment are clearly not the only cause of differences in sprint speed decrement among populations of *S. occidentalis*. For example, gravid females from Oregon were also slower than those from California, yet they carried the same clutch mass for their body mass.

Gravid Oregon and Washington females may be slower because they have a shorter, stockier frame (Figs 3B, 4). Indeed, we found a significant correlation between the sprint speed decrement and burden per unit body length (SVL) in

females from Oregon. Quadrupedal locomotion in lizards involves both horizontal flexion of the vertebral column and rotation of the pelvis (Snyder, 1952, 1962), and the presence of a clutch of eggs may interfere with this motion. Similarly, other researchers have suggested that the presence of food (Ford and Shuttlesworth, 1986) and eggs or developing young (Shine, 1988) may interfere with lateral undulation during locomotion in snakes. In *S. occidentalis*, this effect could be greater in Oregon and Washington females because of their shorter bodies. The effect on sprinting performance might be further exacerbated in Washington females because of their increased level of reproductive investment.

In addition to their shorter bodies, females from the more northern populations have shorter thighs (relative to SVL) compared to the faster California females (Fig. 3C). This difference could contribute to the greater sprint speed decrement experienced by gravid northern females (Fig. 1). However, we found no significant correlation between thigh length and sprint performance within each population. Thus, the possible functional relationship between thigh length and sprint performance while gravid remains unclear.

The evolution of reproductive investment and morphology

Several workers have suggested that predation pressure decreases with increasing latitude (Pianka, 1970; Tinkle and Ballinger, 1972). If so, we would expect to see more highly evolved anti-predator defenses in California populations of *S. occidentalis*, compared to Oregon and Washington populations. For example, higher predation might select for faster overall sprint speeds or for lower levels of reproductive investment. We found some evidence of such a difference in the present study: the higher sprint speeds of gravid California lizards could be interpreted as an adaptation to greater predation pressure. Conversely, the larger decrement in sprinting performance of gravid females from northern populations could reflect relaxed selection ón performance which, in the case of Washington lizards, may also have permitted the evolution of increased reproductive investment and correlated changes in morphology.

Indeed, the ecological correlates of RCM among species include evolved changes in morphology. Lizard species that are active, wide-ranging foragers, or are highly arboreal, tend to have lower RCMs than those that are sedentary or sit-and-wait predators; these differences are associated with changes in body shape and limb proportions (Pianka and Parker, 1975; Vitt and Congdon, 1978; Vitt and Price, 1982). In the present study, differences in morphology and reproductive investment among northern and southern populations of *S. occidentalis* are also associated with the degree of arboreality: fence lizards in California are highly arboreal (especially at low elevation; Adolph, 1990) compared with lizards from Oregon and Washington (J. S. Tsuji, personal communication; Sinervo and Losos, 1991).

Our study documents variation in reproduction and morphology that may be responsible for differences in sprint performance of gravid females among populations of a single species. Interestingly, among-population variation in

reproductive investment did not fully explain the differences in sprint performance of gravid females: the interaction between morphology and reproductive investment appears to be important as well. The results from our among-population comparison of a single species imply that differences in RCM among species may not be the only cause of performance differences but that morphological evolution is also likely to play a strong role in shaping the association between reproductive investment and its ecological correlates in squamates (also see Shine, 1988). Finally, we advocate a multivariate approach to the analysis of reproductive investment within and among species (see also Dunham *et al.* 1988). Multivariate analysis of morphology can lead to useful insights into the biomechanical basis of decrements in performance associated with reproduction.

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