

Does reproductive state affect a lizard's behavior toward predator chemical cues?

Abstract We examined how reproductive state affected shifts in behavior of adult female *Podarcis sicula* toward chemical cues from a natural snake predator (*Coronella austriaca*). The oviparous *P. sicula* lizards do not experience a major physical burden during reproduction, but gravid females substantially increase duration of basking. Therefore, gravid lizards are likely to experience a greater risk of mortality because they are exposed to predators for longer periods. Both gravid and non-gravid females shifted patterns of locomotion when confronted with snake chemical cues, but the change was notably larger when females were non-gravid. When non-gravid, lizards responded to predator scent by increasing the number of stand-ups and starts, while such a response was not observed when females were gravid. By contrast, gravid lizards clearly reduced the time spent basking in the presence of predator scent, whereas no change in basking behavior was observed when females were non-gravid. Thus, females exhibit differential behavioral responses to predator scents that is dependent on reproductive state.

Keywords Anti-predator behavior · Chemoreception · Lizard · Reproduction · Thermoregulation

Introduction

Models of life history evolution assume that reproduction occurs at a cost, which is a measurable reduction in another component of fitness caused by the allocation

of resources to current reproduction (e.g., Stearns 1992; Roff 1992; Reznick et al. 2000). A decreased probability of survival due to behavioral and physiological changes associated with reproduction is a major manifestation of such costs (see below).

Research on this topic has largely focused on behavioral differences between pregnant and non-pregnant animals due to the physical burden of carrying a clutch. In particular, females can suffer dramatic decreases in running speed, maneuverability and endurance during pregnancy (reviewed in Miles et al. 2000). Thus, in species that flee to escape predators, pregnant animals may experience a greater risk of mortality than conspecifics that are not pregnant (e.g., Shine 1980; Winfield and Townsend 1983; Shaffer and Formanowicz 1996; Olsson et al. 2000; see also Lima and Dill 1990). However, pregnant females might also experience a greater risk of mortality because of behavioral shifts that do not directly reflect increased mass (Cooper et al. 1990; Schwarzkopf and Shine 1992a; see also Svensson 1995). In ectothermic animals, pregnancy is often associated with marked shifts in thermoregulatory behavior, some of which may substantially affect vulnerability. For instance, pregnant female reptiles often bask, and thereby expose themselves overtly, for longer periods and at a greater frequency than do non-pregnant conspecifics (e.g., Braña 1993; Blázquez 1995; Charland 1995; Charland and Gregory 1995). Therefore, in species that remain hidden to avoid being detected by predators, pregnant animals may experience a greater risk of mortality than conspecifics that are not pregnant (reviewed in Schwarzkopf and Shine 1992a, b; Braña 1993; see also Koufopanou and Bell 1984).

Nevertheless, pregnant animals may modify other components of behavior to counteract these potential increments in vulnerability to predation (Andren 1985; Madsen 1987). For instance, pregnant female reptiles behave more cryptically by allowing potential predators to approach more closely before fleeing (e.g., Bauwens and Thoen 1981; Schwarzkopf and Shine 1992a, b). Studies published to date all explore how reproductive state af-

fects behavioral responses of reptiles towards visual stimuli from predators (Bauwens and Thoen 1981; Seigel et al. 1987; Brodie 1989; Cooper et al. 1990; Schwarzkopf and Shine 1992a; see also Shaffer and Formanowicz 1996).

Recent experiments demonstrate that many species of reptiles detect and identify chemical cues of predators (reviewed in Schwenk 1995; Downes and Shine 1998; Mori and Hasegawa 1999). Behavioral responses to predator scent include modifications of tongue-flick rates, of locomotor behavior and of defense tactics, and these shifts can affect vulnerability (see Downes 2002). However, nothing is known about how reproduction may affect a reptile's responses toward chemical stimuli from predators. If reproduction affects a reptile's potential risk of mortality (Shine 1980; Vitt and Price 1982), it is reasonable to expect that females may show differing responses in behavior toward predator scents when they are pregnant versus non-pregnant. We tested this hypothesis for an oviparous lacertid lizard that substantially increases duration of basking when gravid, but does not experience a major physical burden during reproduction (see below).

Most previous studies of behavior modification in reptiles during reproduction have compared gravid females with other non-reproductive females, whereas other studies have compared gravid female with male performance (reviewed in Miles et al. 2000). However, unless comparisons are made between the same individuals in different reproductive states, factors other than pregnancy may affect performance. We quantified behavior of the same female lizards during non-pregnancy and pregnancy toward a non-predatory scent and toward chemical cues from a snake predator. By selecting a study species that produces several consecutive clutches annually, we were able to observe some lizards first when not pregnant and other lizards first when pregnant and thereby test for habituation to test conditions.

Methods

Study system

Our study animal is the European lacertid lizard *Podarcis sicula*. This medium-sized (adult body length 55–85 mm in our study population) heliothermic lizard is distributed throughout Italy and along the Adriatic coast in Croatia (Arnold and Burton 1978). Females from our study population lay three or four clutches of 4–7 eggs per year, beginning in early May and ending in July (unpublished data). Thus, they must intermittently carry eggs during a substantial part of the activity season. Gravidity may not impose as large a physical burden as in some other lizards, since clutch mass relative to body mass in this species (0.268; unpublished data) is well below the average reported for other lacertid lizards (0.345; Bauwens 1999) and several skinks (0.380–0.541; Shine 1980; Vitt and Price 1982; Vitt and Cooper 1985). However, gravid female *P. sicula* bask for significantly longer periods than do non-gravid conspecifics (see Results). It is possible that basking may be part of a defense strategy that decreases detectability by decreasing movement. However, in our study population, lizards usually bask in open areas that are not immediately close to refuge, and being detected entails a high risk of being captured, at

least by human predators (S. Downes, personal observation). We therefore assume that basking lizards are likely to incur a relatively high risk of predation by actively foraging hunters because they are exposed to predators for longer periods of time.

A recent study (Van Damme and Quick 2002) showed that *P. sicula* detects chemical cues deposited by predatory snakes and distinguishes between chemicals of a predatory and a non-predatory snake. Responses of *P. sicula* towards scents from predatory snakes were qualitatively similar to those exhibited by other species of lacertid lizards (Thoen et al. 1986; Van Damme et al. 1995; Van Damme and Castilla 1996). Studies by Thoen et al. (1986) and Van Damme and Quick (2002) show that lacertid lizards respond differentially to, and hence presumably distinguish between, the scents of predatory and non-predatory snakes. Our study lizards live in an area that contains seven species of actively foraging snake species known to consume lacertid lizards (Arnold and Burton 1978) and several actively foraging bird predators (D. Bauwens, personal observation).

Animals and their maintenance

On 25 and 26 April 2000, we captured 19 adult female lizards of this species from near Novigrad (45°18'N, 13°33'E) in Istra, Croatia, and transported them to Belgium. Two adult smooth snakes (*Coronella austriaca*) were collected on 20 May, near Spontin (50°18'N, 5°00'E) in Namur, Belgium. This species is present near the lizard collection area, but chemical cues from these snakes may differ from those of snakes collected at Belgium. However, a pilot study clearly demonstrated that *P. sicula* perceived scent from the collected snakes as a predator stimulus. Moreover, we compared the relative responses of individual lizards in different reproductive states toward this predator stimulus, rather than the absolute responses of lizards to scent from *C. austriaca* per se. Thus, it was appropriate to use these chemical stimuli in our experiment.

Animals were housed at the Institute of Nature Conservation (Brussels, Belgium). The female lizards were maintained, two to each cage with an adult male lizard, in sand-filled glass terraria (60×35×22 cm) containing leaf litter and rock shelters. House crickets and mealworms were provided ad libitum. As females started to produce clutches, we checked them at least twice daily. The snakes were maintained in another room in a terrarium (60×35×22 cm) that was lined with fine chips of bark (hereafter called "bark chips"). Snakes were not fed during the experimental period. All cages were heated for 8 h/day by one 75-W incandescent light bulb, suspended 30 cm above the substrate. Animals were maintained under the light cycle of the surrounding area, and water was provided ad libitum.

Experimental procedure

Our experiment was conducted in a glass terrarium (60×35×22 cm), the base of which was lined with paper that was covered with sand (2 cm depth). The outside of the glass was covered with brown paper except for one long side that was left unobstructed to enable observations. During the course of the tests, one end of this cage was heated to 38°C by a 75-W incandescent bulb, suspended 30 cm above the substrate. The test room was maintained at 26°C, which is considerably lower than the preferred body temperatures of *P. sicula* from our study population (ca. 32–36 °C; unpublished data). We adopted this procedure because it mimics natural conditions and induces lizards to bask under the heat source to achieve their preferred temperature. At the end of each trial, the sand on the floor of the cage was removed (by raising the sheet of paper lining the cage) and replaced with fresh material.

Each lizard was tested under two types of scented conditions:

1. Bark chips sprayed the previous day with a 1:10 mixture of commercial cologne ("Confess") and distilled water were haphazardly placed on the floor of the cage. This treatment gauged the responses of lizards to a novel scent that was not related to predation.

2. Bark chips from a snake's home cage were haphazardly placed on the floor of the cage. This treatment gauged the responses of lizards to predator stimuli.

We did not test lizards in cages with bark chips that were not scented because our aim was not to determine whether lizards could distinguish predator stimuli from control scent. Rather, we examined *shifts* in behavior of individual lizards in gravid versus non-gravid states toward predator stimuli and non-predator stimuli. In every trial, care was taken to place bark chips 2-cm deep on the floor of the cage. The chips were 20 mm pine shavings (Pindecor, France). They were discarded after a single use, and were in the cage with a snake for 7–9 days prior to being used in the experiment. New chips were added to the snakes' cage to replace those removed.

Our procedure consisted of introducing a lizard into the test cage and continuously observing its behavior from behind a one-way mirror. The duration of each trial was 15 min. This time period is sufficient to reliably estimate the responses of lizards to chemical cues (unpublished data), but also minimizes the time that animals are exposed to a potentially stressful situation. The same person recorded all observations onto a portable computer (using an event recorder). We scored the frequency (behaviors 1–4) or duration (behaviors 5–9) of the following behavioral acts and locomotor patterns.

1. Tongue-flick: the lizard extrudes and rapidly retracts its tongue, regardless of whether the tongue touches the substrate or is "waved" in the air.
2. Start: sudden jump, most often followed by a brief, short run.
3. Stand up: the lizard stands in an upright position against the wall of the terrarium and performs scratching movements with the forelegs.
4. Tail-vibration: the entire tail, or its posterior, is moved rapidly from side-to-side. A separate event was recorded only if at least 3 s elapsed since the lizard last performed this behavior.
5. Walk: continuous, relatively fast forward movement. This is the locomotor pattern typically observed in unrestrained lizards.
6. Slow motion: the lizard proceeds by slow, stalking movements, sometimes accompanied by jerky movements of the forelimbs.
7. Run: very fast movement, often over a short distance.
8. Stationary: the lizard stands in any part of the cage. Movement of the head, tail or forelimbs usually accompanies this pattern.
9. Bask: the lizard rests under the light bulb with the ribs spread laterally; one or more feet are often tilted upwards.

Trials were performed from 24 May and 24 June between 1000 and 1700 hours. We performed identical tests with the same lizards when they were "non-gravid" (deposited their second clutch of eggs in the previous 3–4 days: mean \pm SE=3.4 \pm 0.2 days) and "gravid" (deposited their second or third clutch of eggs in the following 1–4 days: mean \pm SE=2.4 \pm 0.3 days). We incorporated "reproductive order" as a factor in our experimental design so that we could test for habituation to test conditions. Nine of the 19 lizards were tested when they were gravid with a second clutch and again when they deposited those eggs ("gravid to non-gravid"), whereas the remaining lizards were tested after they had laid their second clutch and again when they were gravid with a third clutch ("non-gravid to gravid"). On average, there were 20.3 days between the deposition of a lizard's second and third clutch of eggs. The mean clutch mass relative to body mass of gravid females during testing was 0.231. Lizards were tested in a counterbalanced order to ensure that each of the two scent types was presented first to one half of the individuals in the different reproductive order treatment groups. This order of scent presentation was maintained during tests with the same lizard when it was gravid and non-gravid. At least 6 h elapsed before we presented lizards with the other scent treatment while in the same reproductive period.

Data analysis

To examine the effect of reproductive condition on behavior toward predatory and non-predatory scent we used each behavioral

act as a dependent variable in repeated measures ANOVA's. Our initial model included as factors the "first scent type" presented and the "reproductive order" of testing, and the repeated measures were "scent type" and "reproductive condition" (i.e., each lizard was tested with both scent types during both states of reproduction). We omitted factors from our model if they did not explain significant variation in the dependent variable (judged as $P > 0.25$ for all main effects and interaction terms involving the factor). With one exception, our analyses detected a significant interaction between "scent type" and "reproductive condition" (see Results). Subsequently, we performed separate ANOVA's on data for each state of reproduction using the model outlined above without the reproductive condition repeated measure. Data were checked for normality and homogeneity of variance before statistical analysis; some variables were log-transformed to normalize variances.

Since many of the behavioral variables that we measured were necessarily interrelated (e.g., the continuous variables are mutually exclusive), we also used principal components analysis to reduce the number of behavioral variables to a smaller number of mutually independent variables. The raw data used in this analysis were the total duration or frequency scores of the distinct behavioral variables during the 15-min course of the four tests for each individual. The tongue-flick frequency was not entered as a variable since it is considered to be an index of the intensity of examination of the environment by the perception mechanism that discriminates among stimuli and so ultimately induces the behavioral response. Because values of the different continuous behavioral variables (i.e., variables 5–9) necessarily add up to a constant sum, the information provided by one variable is redundant, and the principal component analysis cannot be performed. We therefore omitted from the analysis the variable "run", which was displayed with the shortest overall duration (mean of <40 s in all treatment combinations; Table 2). The principal component analysis was performed on the correlation matrix of the 7 remaining behavioral variables; the principal components were varimax rotated. We retained principal components that had eigenvalues greater than one (Norman and Streiner 1994; but see also Jackson 1993). We used the component scores for each trial in repeated measures ANOVA's using the same models and procedures as outlined above for each separate behavior.

Results

Behavioral responses

The raw data for tongue-flick frequency (Fig. 1) and the behavioral variables (Table 1) are summarized according to reproductive condition and scent treatment. A lizard's reproductive condition affected the expression of a wide range of behaviors but in all but one case the magnitude of this difference varied with scent type (Table 2). Irrespective of reproductive state lizards displayed the run behavior more often during trials with predator scent than they did during trials with non-predator scent (ANOVA: $F=62.12$, $df=1,18$, $P<0.001$).

In several cases, reproductive state did not affect the direction in which a female shifted her behavior toward predator scent, but it did influence the magnitude of the response. In both reproductive states, female lizards displayed significantly different rates or durations of tongue-flicking, tail-vibration, walking and moving slowly during trials with predator scent compared with control scent (Tables 1, 2). The difference in mean number of tongue-flicks emitted towards predator and control scents was substantially higher when females were non-

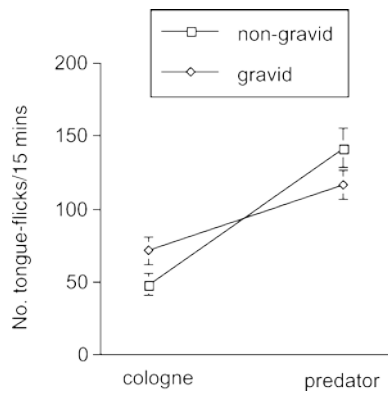


Fig. 1 Mean±SE number of tongue-flicks displayed by female *Podarcis sicula* in gravid and non-gravid states during the 15-min trials. Females were tested under two types of scented conditions: cologne and scent from a common snake predator

gravid (93 flicks) compared with gravid (45 flicks). In response to predator scent female lizards displayed a stronger decrease in average duration of walking when they were non-gravid (112 s) compared with gravid (75 s). Relative to gravid females, in predator-scented trials non-gravid lizards strongly increased the average

amount of time that they moved slowly (72 s and 104 s for gravid and non-gravid females respectively). The females increased tail-vibrations more in response to predator scents when gravid than non-gravid.

In some cases lizards shifted their behavior in response to scented treatments only when they were either gravid or non-gravid. Gravid lizards shortened duration of basking and spent more time stationary during trials with predator scent, whereas the different scented arenas did not induce a significant behavioral response in non-gravid lizards (Table 2). Non-gravid lizards were significantly more likely to stand up against the wall of the test arena and jump forward in a start during trials with predator scent (Table 2). In these two cases, the different scented arenas did not induce a significant behavioral response in gravid lizards (Table 2).

Relationships among behaviors

We extracted three principal components that accounted for 27.1%, 27.0% and 25.3% of the after station variation in our data (total explained variation = 79.4%). The alignment of the experiments along the component axes was studied by considering the projections (i.e., scores)

Table 1 Raw scores (frequency * or duration ^) of distinct behavioral acts, and projections of the behavioral scores on the principal components, in gravid versus non-gravid adult female *Podarcis sicula* in cages covered with non-predatory scent (cologne) and predatory scent (from a snake predator) (mean±SE, n=19, test duration =15 min)

	Non-gravid		Gravid	
	Non-predator	Predator	Non-predator	Predator
Walk^	147.5±18.5	35.5±7.4	107.9±10.5	32.4±8.0
Slow motion^	1.6±0.7	106.5±12.9	30.8±8.6	103.2±13.5
Run^	3.9±1.5	20.7±5.9	8.4±2.9	40.9±10.1
Bask^	237.1±31.1	202.8±29.2	307.8±23.4	191.4±32.1
Stationary^	510.0±31.6	534.5±31.6	445.3±27.9	532.1±36.5
Stand up*	2.2±0.5	9.4±1.6	1.8±0.5	2.4±0.5
Start*	0.2±0.1	2.1±0.1	0.5±0.1	0.3±0.2
Tail vibration*	0.1±0.1	1.1±0.3	0.3±0.1	1.7±0.3
Component 1	-1.32±0.11	0.78±0.17	-0.35±0.13	0.91±0.18
Component 2	0.11±0.23	0.12±0.23	-0.43±0.19	0.20±0.30
Component 3	-0.22±0.10	0.89±0.37	-0.33±0.30	-0.35±0.35

Table 2 Summary statistics for ANOVA's on each behavioral act recorded during the study. With one exception (see below), our analyses detected a significant interaction effect between the two repeated measures used in the model, "scent type" and "reproductive condition" (statistics are indicated in the left hand columns). Subse-

quently, we performed a separate ANOVA on data for each state of reproduction using the model outlined above without the reproductive condition repeated measure (statistics are indicated in the right hand columns). The exception was "run"; summary statistics for this variable are reported in the main body of the Results; *df*=1,18

	Interaction effect		Main effects			
	F value	P value	Non-gravid		Gravid	
			F value	P value	F value	P value
Tongue-flick*	13.01	<0.01	54.87	<0.01	40.02	<0.01
Walk^	5.37	0.04	29.12	<0.01	54.84	<0.01
Slow motion^	5.65	0.03	66.90	<0.01	38.27	<0.01
Bask^	4.68	0.05	0.94	0.35	19.69	<0.01
Stationary^	6.03	0.04	0.36	0.56	10.58	<0.01
Stand up*	18.79	<0.01	17.86	<0.01	2.05	0.17
Start*	5.25	0.04	5.44	0.03	3.17	0.09
Tail-vibration*	5.93	0.03	47.10	<0.01	17.87	<0.01

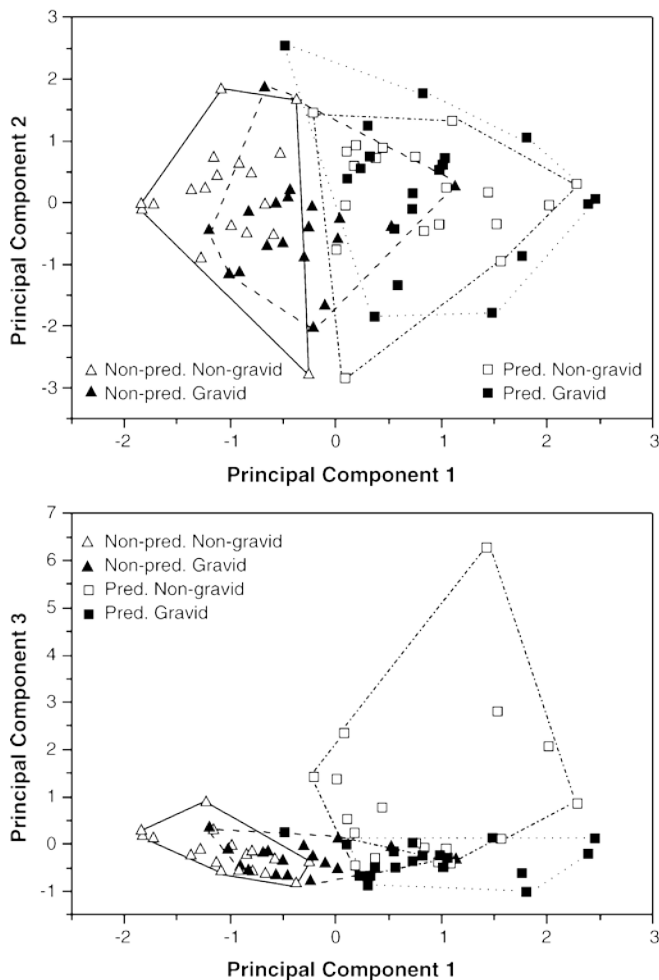


Fig. 2a, b Broad shifts in behavior of female *P. sicula* during pregnancy and non-pregnancy as depicted by the scores of the individual tests on the first three dimensions extracted by principal components analysis. Females were tested under two types of scented conditions (cologne and predator scent), and the same females were used in all four tests. **a** Plot of scores on principal component 1 versus scores on principal component 2. **b** Plot of scores on principal component 2 versus scores on principal component 3

of the individual tests on these axes (Fig. 2a, b). The r values indicated below are the factor loading of the original (raw) variables on the extracted principal components.

The first principal component represents a behavioral gradient characterized by a transition of extensive periods of walking ($r=-0.75$) toward the use of slow motion ($r=0.81$) and frequent displays of tail vibration ($r=0.78$). Scores on this first component differed according to reproductive condition, but this variation was dependent on the type of scent covering the test cage (ANOVA: scent type ξ reproductive condition, $F=5.92$, $df=1,18$, $P=0.026$). In both reproductive states, lizards scored higher during trials with predator scent than control scent (ANOVA: $F=15.35$, $df=1,18$, $P<0.001$). However, the difference in PC1 scores between trials with predator

and control scent was higher when lizards were non-gravid versus gravid (average PC1 scores = 1.80 vs 1.26 for non-gravid vs gravid lizards).

The second principal component was negatively correlated with the duration of basking ($r=-0.92$) and positively correlated with the duration of remaining stationary ($r=0.98$). Hence, it represents a behavioral shift from the extensive use of basking to remaining stationary for long periods. The positions of the projections on the second principal component also demonstrated variation according to reproductive condition. When lizards were non-gravid they displayed relatively high PC1 scores that did not differ significantly between both scent conditions (ANOVA: $F=0.028$, $df=1,18$, $P=0.987$). However, when lizards were gravid they displayed relatively low PC1 scores on this component during trials with control scent compared with predator scent (ANOVA: $F=9.75$, $df=1,18$, $P=0.006$). Thus, when lizards were gravid they basked longer during control scent trials than in the presence of predator scent, and than they did in both scent conditions when they were non-gravid (Table 2).

The third principal component depicts a progressive increase of displaying starts ($r=0.90$) and stand ups ($r=0.92$). Scores on the third principal component differed according to reproductive condition but this variation was dependent on the type of scent covering the test cage (ANOVA: scent type ξ reproductive condition, $F=9.29$, $df=1,18$, $P=0.007$). When lizards were non-gravid they displayed significantly higher scores on this component during trials with predator scent compared with control scent (ANOVA: $F=8.29$, $df=1,18$, $P=0.010$). However, when lizards were gravid they exhibited low and non-significantly different scores in the two scent conditions (ANOVA: $F=0.07$, $df=1,18$, $P=0.794$). Additionally, gravid lizards that were first presented with non-predatory scent displayed significantly lower scores on this component than did gravid lizards that were first presented with predatory scent (ANOVA: $F=10.15$, $df=1,17$, $P=0.005$).

Discussion

Podarcis sicula detects chemical cues deposited by a predatory snake. This is evident from an increased tongue-flick rate, the prolonged use of the “slow motion” locomotor pattern and the display of behavioral acts that are typically associated with stress-situations (tail vibrations, fast starts). These responses are qualitatively highly similar to those exhibited by other species of lacertid lizard in analogous experimental conditions (Thoen et al. 1986; Van Damme et al. 1990; Van Damme and Castilla 1996; Van Damme and Quick 2002).

Our results demonstrate that reproductive state affects behavioral responses by female *P. sicula* to predatory chemical cues. Both gravid and non-gravid females shifted patterns of locomotion when confronted with snake chemical cues, but the change was notably larger when

females were non-gravid. When non-gravid, lizards responded to predator scent by increasing the number of stand-ups and starts, while such a response was not observed when females were gravid. By contrast, gravid lizards reduced the time spent basking in the presence of predator scent, whereas no change in basking behavior was notable when females were non-gravid.

Female *P. sicula* are likely to experience an increased vulnerability to predators due to behavioral changes associated with reproduction. Similar reports have been made for several other reptile taxa that exhibit substantially slower locomotor performance because of the physical burden of carrying a clutch (Bauwens and Thoen 1981; Brodie 1989; Cooper et al. 1990). Clutches are not likely to impose as large a physical burden on gravid female *P. sicula* as in some other lizards (see Study System subsection of Methods). However, even over short periods (i.e., a 20-min trial) lizards exposed to non-predatory stimuli basked for around 20% longer when they were gravid versus non-gravid. Although we did not directly test whether increased duration of basking heightens the probability that predators will detect lizards, it probably does. *P. sicula* is a surface-active lizard that remains hidden to avoid being detected or attacked by predators (S. Downes, personal observation). It basks in open areas that are not close to refuge, where being detected entails a high risk of being captured (S. Downes, personal observation). Studies on other lizards with similar habits demonstrate that increased exposure to predators via basking may result in greater probability of detection and subsequent capture (Schwarzkopf and Shine 1992a; S. Downes, unpublished data).

The increased duration of basking by gravid *P. sicula* in predator-free conditions is in agreement with observations on numerous other species of reptiles (e.g., Blázquez 1995; Charland 1995; Charland and Gregory 1995). Longer basking times during pregnancy are presumably induced by the effects of developmental temperature on the rate of embryogenesis and offspring characteristics (reviewed in Schwarzkopf and Shine 1992b; Shine and Harlow 1993; Mathies and Andrews 1997), and hence the demands of precise maternal thermoregulation. If basking results in increased exposure and vulnerability to predators, females should adopt a basking strategy that strikes a balance between the thermoregulatory demands of the developing embryos and survival probabilities of the female. This balance is likely to be affected by changes in perceived risks of predation. Thus, upon exposure to snake chemical cues that reveal the potential presence of a predator, gravid *P. sicula* curtailed duration of basking to levels similar to those exhibited during non-pregnancy.

During pregnancy *P. sicula* also shifted the expression of several other behaviors in ways that may reduce probabilities of being detected while exposed to predators. For instance, by remaining stationary for longer periods when out of retreat-sites, active female lizards may decrease chances of encountering predators (Sih 1992; Anholt et al. 1996; Rodd and Reznick 1997). Additional-

ly, reduced mobility, as well as slower locomotion while moving and the display of fewer fast starts, may lessen rates of detection and attack by visually oriented snake predators (Skelly 1994; Downes and Shine 2001). By employing tail vibration more frequently, female lizards may encourage stalking predators to attack their dispensable tail rather than their main body (Congdon et al. 1974; Cooper 1998a, b; Downes and Shine 2001). Thus, we speculate that *P. sicula* compensates for the increased exposure to predators during gestation by decreasing the probability of being detected and captured.

The effect of reproductive state on lizard mobility could explain the differences in tongue-flick rates during pregnancy versus non-pregnancy (Fig. 1). Studies on a range of lacertid lizards demonstrate that animals usually tongue-flick more often when they are mobile than when they are stationary (e.g., Thoen et al. 1986; Van Damme et al. 1990, 1995). Therefore, the higher rate of tongue flicking by non-gravid female lizards may reflect their greater mobility.

Gravid females shift some types of behavior even in the absence of high perceived risk of predation. This finding may indicate differences in the costs of performing certain behaviors during pregnancy: tactics incurring high costs should only be employed under high risk conditions (Maynard Smith 1982). Although we did not directly test this hypothesis, our data provide some support. For instance, jumping forward (fast start) may draw the attention of nearby visual predators, and gravid females only increased their use of this tactic in the presence of predator scent. Similarly, the degree to which females move in slow motion may affect rates of foraging, but this is unlikely to impose a large cost because reptiles often eat less while gravid (Gregory and Skebo 1998; Gregory et al. 1999). Accordingly, differences in the expression of slow motion were observed in predator-free conditions.

The order in which females in different reproductive states were tested did not significantly affect the expression of behavior. However, we cannot assess whether this finding is generally applicable among systems. We recommend that future experiments on this topic be designed to enable order of testing to be used as a factor in statistical analyses or to be statistically controlled. Furthermore, our study indicates that the order in which scents are presented to females may affect the expression of some behavior (see also Cooper 1990).

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