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INTRASPECIFIC VARIATION IN HABITAT USE AND MOVEMENT IN LONG-NOSED LEOPARD LIZARDS (*GAMBELIA WISLIZENII*) FROM THE ALVORD BASIN, OREGON

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ABSTRACT—We studied the long-nosed leopard lizard, *Gambelia wislizenii*, in the Great Basin Desert of southeastern Oregon to identify intraspecific patterns of behavioral variation. Sex and body size played an important role in determining intraspecific behavioral differences. Males and females showed different habitat preferences, with males spending more time on hardpan and in the center of shrubs. Males made more long moves and clustered their long moves more frequently than females. Smaller lizards displayed more head turns, tongue flicks, and use of elevated perches. Smaller individuals also spent a higher proportion of time moving.

RESUMEN—Estudiamos el lagarto leopardo, *Gambelia wislizenii*, en el desierto Great Basin del sureste de Oregon para identificar patrones intraspecíficos de variación conductual. El sexo y el tamaño corporal desempeñó un papel importante en la determinación de las diferencias del comportamiento intraespecífico. Los machos y las hembras mostraron diferentes preferencias de hábitat, con los machos pasando más tiempo en la capa dura terrestre y en el centro de arbustos. Los machoshicieron más movimientos largos y agruparon sus movimientos largos más frecuentemente que las hembras. Los lagartos más pequeños giraron más la cabeza , lamieron y usaron perchas más elevadas. Los individuos más pequeños también pasaron una mayor proporción de tiempo en movimiento.

Conspecific males and females can experience a suite of distinct challenges (Shine and Wall, 2005), which in turn can affect their behavior. Body size variation, often present in sexually dimorphic species, could reflect physiological variation and be associated with differences in diet, habitat requirements, and predation threats (Werner and Gilliam, 1984; Shine and Wall, 2007; Dial et al., 2008). Even without obvious morphological variation, there can be consistent behavioral types within a population (Sih et al., 2004). In many sexually dimorphic species, isolating size from sex differences in behavior can be difficult. Judicious selection of study species can provide insight into the factors that contribute to intraspecific variation in behavior. For example, if size is more important than sex, then among related species larger individuals should share behavioral traits, regardless of whether they are of the same sex.

Crotaphytidae is a small family of diurnal North American lizards (~12 species in two genera: *Crotaphytus* and *Gambelia*). *Crotaphytus* lizards often exhibit sex and size differences in behavior and ecology that are said to be related to male-larger sexual dimorphism and to its associated territorial social system (Best and Pfaffenberger, 1987; Baird et al., 1996; Baird and Sloan, 2003). Two of the three described species of *Gambelia*, including the long-nosed leopard lizard (*Gambelia wislizenii*) deviate from the rest of the family by having female-larger dimorphism (both in snout-to-vent length [SVL] and mass; Parker and Pianka, 1976; Tollestrup, 1983). In addition, *G. wislizenii* is not territorial and significant overlap can exist between the home ranges of individual lizards (Tollestrup, 1983). Unlike most crotaphytids, *G. wislizenii* is largely terrestrial rather than saxicolous (McGuire, 1996). The species inhabits desert scrub ecosystems, with varying levels of shrub cover throughout its range, which stretches from southeastern Oregon to portions of northern Mexico (Parker and Pianka, 1976; Tollestrup, 1983; Steffen and Anderson, 2006). Body size varies latitudinally, with individuals in southern populations (Arizona and New Mexico) tending to be larger than individuals in northern populations (Great Basin Desert; Parker and Pianka, 1976). While all species of

Crotaphytidae have been viewed as ambush foragers, *G. wislizenii* makes use of a stalking strategy and has been described as an active forager compared with species of *Crotaphytus* (Lappin and Swinney, 1999; Husak and Ackland, 2003; Anderson, 2007). Foraging by *G. wislizenii* is visually oriented; they consume a diverse diet encompassing arthropods and small vertebrates (Anderson, 2007; McElroy et al., 2011). In southern populations, other lizards (e.g., *Uta*, *Sceloporus*, and *Aspidoscelis* species) constitute the highest proportion of diet by volume, whereas northern populations primarily feed on grasshoppers and beetles, only occasionally consuming lizard prey (Parker and Pianka, 1976).

Researchers have not studied *G. wislizenii* as extensively as some *Crotaphytus* species, but the lack of male-larger sexual dimorphism and the associated territorial social system points to the potential for markedly different patterns of intraspecific behavioral variation. We examined the behavior of *G. wislizenii* in the Great Basin Desert after the mating season, hypothesizing that the sexes would exhibit differences in behavior. Specifically, we tested the null hypothesis that there were no differences between the sexes and minimal size-related variation among adult lizards.

MATERIALS AND METHODS—We conducted our study 1–17 July 2015 in the desert scrub of the Alvord Basin Desert, located in the northern Great Basin Desert, southeastern Oregon (42°18′N, 118°37′W, elevation 1,295 m). The two most abundant plant species on the study plot were basin big sagebrush (Asteraceae: *Artemisia tridentata*) and greasewood (Sarcobataceae: *Sarcobatus vermiculatus*), species whose abundances are inversely proportional to one another (Steffen and Anderson, 2006). Other plants included shadscale (Chenopodiaceae: *Atriplex confertifolia*), littleleaf horsebrush (Asteraceae: *Tetradymia glabrata*), and gray rabbitbrush (Asteraceae: *Ericameria nauseosa*). Several lizard species live in the area, most commonly the long-nosed leopard lizard (*G. wislizenii*), the tiger whiptail (*Aspidoscelis tigris*), and the desert horned lizard (*Phrynosoma platyrhinos*). We conducted the study on a 9-ha plot (300 × 300 m), with a reference grid system of markers at 10-m intervals throughout.

We collected data from 0800 to 1330 h and from 1430 to 1630 h, when lizards were active. We captured lizards by noosing them. After capture, we measured (SVL and mass) and uniquely marked each lizard with nontoxic paint pens on the back and base of the tail. After processing, we returned animals to their initial capture location and did not collect data for 24 h after release. Each day, we systematically searched the plot for lizards by simultaneously walking parallel transects 10 m apart. When we located an unobserved lizard, two researchers observed the animal for 1 h. One researcher recorded data with a hand-held calculator programmed as an event recorder (HP 50g, HP Inc., Palo Alto, California). We recorded the behavioral states of movement duration and amount of time on an elevated perch. Most commonly, elevated perches were rocks or pieces of dead vegetation in which movement by a perching lizard in any direction resulted in the lizard lowering its height. We also recorded head turns (discrete movement of the head), tongue flicks, and the foraging-related categories of jump (all four feet off the ground when attempting to catch prey), pursuit (short sprints), and stalk (body pressed against ground with slow forward movement). The second observer placed markers at the lizard's location every 60 s throughout the observation; to minimize disturbance, we placed markers after the lizard had moved from the vicinity of the point where the marker was to be positioned. During observations, we maintained as great a distance as possible, while maintaining visual contact, sometimes using binoculars. Lizards were generally observed from a distance of >5 m. Marker placement typically occurred only after the lizard was >10 m distant. After observations, we measured the location for each marker relative to the grid system and recorded information on substrate (hardpan, sand, or other), cover (open, plant perimeter, or plant interior), and cover species. We generated 61 locations for each animal: their location at the start (time 0) as well as for each min (1–60). From a weather station at the edge of the study area, we were able to obtain mean, maximum, and minimum air temperatures for each observation period.

We conducted analyses using R and Minitab, with a significance level of $P \leq 0.05$. We present summary statistics as mean ± *SE* (range). We determined percentage of time moving (PTM) and percentage of time on elevated perches for each lizard as well as rates of occurrence for head turns, tongue flicks, jumps, pursuits, stalks, and use of unique perches, in addition to moves per minute (MPM). We tested for sex differences in habitat using χ^2 analyses and used analysis of covariance to examine the relationship between behavioral variables vs. sex, body size, and their interaction. We examined air temperature as a potential covariate. To determine the minimum distances travelled by lizards on two scales (minutes and hours), we used the location markers to determine minute-by-minute displacement distances as well as total displacement distance for each lizard. In addition, we compared movement patterns of males and females by examining the distribution of move durations (time moving) and 1-min displacement distances (distance covered); counts from all individuals were combined and the sexes compared using χ^2 analyses. We also compared the distribution of 1-min displacement distances with the random expectations of a Poisson distribution. Finally, for each individual's 1-h observation, we tallied 2-min displacement sequences, placing movement distances into the categories of none (0 m), small (≤1 m), medium (1–4 m), and large (>4 m). We then used a log-linear model to determine whether the sequence of displacement distances differed from random expectations or between the sexes compared with one-step Markov chains.

RESULTS—*Population*—We captured and marked 41 adult lizards ($n = 18$ females, 22 males, and 1 undetermined). Females were significantly larger than males in length, though not mass (mean SVL = 101.9 ± 1.4 mm [91–113 mm] vs. 95.0 ± 1.1 mm [84–104 mm], respectively; *t* test: $t = 3.68$, $df = 34$, $P = 0.001$; mean mass = 26.8 ± 1.9 g [17.9–50.4 g] vs. 22.6 ± 0.9 g [14.6–28.3 g], respectively; *t* test: $t = 1.93$, $df = 22$, $P = 0.066$). Sexual-size dimorphism, as represented by the ratio of the largest female SVL divided by the largest male SVL, was factor of 1.086. Many of the females were gravid at the time of capture, reflecting the large range in female mass. We

Table 1—Summary statistics for *Gambelia wislizenii* focal observations. Regression results are for models of snout–vent length (SVL) vs. behavior variable. Initial analysis of covariance indicated that neither sex nor sex × SVL were significant predictor variables.

	Mean ± *SE* (range)	Regression against body size
Moves (min^{-1})	1.32 ± 0.097 (0.2–3.5)	$F_{1,38} = 3.31$, $P = 0.077$, $R^2 = 8.0$
Time moving (%)	5.8 ± 0.5 (0.5–11.8)	$F_{1,38} = 4.95$, $P = 0.032$, $R^2 = 11.5$
Perches (min^{-1})	0.044 ± 0.006 (0.0–0.13)	$F_{1,38} = 10.11$, $P = 0.003$, $R^2 = 21.0$
Time perching (%)	7.1 ± 1.4 (0.0–47.0)	$F_{1,38} = 1.65$, $P = 0.207$, $R^2 = 4.1$
Jumps (min^{-1})	0.028 ± 0.005 (0.00–0.13)	$F_{1,38} = 0.08$, $P = 0.775$, $R^2 = 0.2$
Stalks (min^{-1})	0.050 ± 0.006 (0.00–0.13)	$F_{1,38} = 0.20$, $P = 0.658$, $R^2 = 0.5$
Pursuits (min^{-1})	0.023 ± 0.004 (0.00–0.10)	$F_{1,38} = 0.33$, $P = 0.571$, $R^2 = 0.8$
Head turns (min^{-1})	2.071 ± 0.116 (0.3–3.4)	$F_{1,38} = 3.28$, $P = 0.078$, $R^2 = 7.9$
Tongue flicks (min^{-1})	0.624 ± 0.087 (0.0–1.9)	$F_{1,38} = 8.80$, $P = 0.005$, $R^2 = 18.8$
Distance travelled (m)	65.7 ± 6.7 (3.6–231.6)	$F_{1,38} = 0.08$, $P = 0.780$, $R^2 = 0.2$

cannot be sure how many females were gravid when they were observed.

The air temperature during observations was not related to sex, body size, or their interaction (mean air temperature = 25.1 ± 0.6°C [21.2–30.2°C] vs. 26.9 ± 0.7°C [21.5–34.0°C], respectively; sex: $F_{1,36} = 0.02$, $P = 0.801$; SVL: $F_{1,36} = 0.06$, $P = 0.614$; sex × SVL: $F_{1,36} = 0.12$, $P = 0.730$). Mean air temperature during observations was not significantly correlated with any of our behavioral or habitat use variables.

Behavior—None of the recorded behaviors were significantly different based on sex or the interaction between SVL and sex. The frequencies of the three behaviors associated with foraging (jumps, stalks, and pursuits) were not related to body size (Table 1). However, they were related to levels of activity; rates of stalking and pursuits were positively correlated with PTM and jumping rates were positively correlated with MPM (Table 2). Head turns and tongue flicks were both positively correlated with both MPM and PTM, and tongue flicks tended to occur less frequently with larger lizards (Tables 1 and 2).

Movements—*Gambelia wislizenii* averaged 1.3 MPM and 5.8 PTM (Table 1); the sexes did not differ in MPM or PTM, but these indices did vary inversely with SVL (Table 2). The distribution of move durations differed between the sexes ($\chi^2 = 19.39$, $df = 10$, $P = 0.035$; Fig. 1), with males tending to have more move durations lasting longer than 5 s. Most 1-min intervals were associated with no movement, while at the other extreme individual lizards occasionally travelled >10 m in 1 min. There was no sex difference in the distribution of 1-min displacement distances ($\chi^2 = 11.20$, $df = 7$, $P = 0.129$). Over the course of 1 h, the mean total location displacement distance was 65 m, with some lizards travelling >200 m in 1 h (Table 1; Fig. 2). The three movement indices, PTM, MPM, and total displacement, were all positively correlated (Table 2). Minute-to-minute location displacement sequences differed from random expectations (log-linear model: $G = 226.5$, $df = 18$, $P < 0.00001$) and differed between the sexes ($G = 238.5$, $df = 24$, $P < 0.00001$).

Habitat Use—The amount of time spent on elevated perches was not significantly related to sex or body size, but the rate of perch use (perches min^{-1}) was negatively correlated with body size (Tables 1 and 2). Substrate use varied significantly by sex ($\chi^2 = 59.9$, $df = 2$, $P < 0.0001$) with males making greater use of hardpan (25.2 vs. 14.2% of intervals). Cover also varied by sex ($\chi^2 = 16.7$, $df = 2$, $P < 0.001$) with males spending less time in the open and more time in the center of bushes (open: 55.0 vs. 59.8% of intervals; center: 5.7 vs. 2.6% of intervals). The species of plant used for cover did not vary with sex ($\chi^2 = 3.73$, $df = 2$, $P = 0.176$).

Discussion—Our study revealed size- and sex-related variation in *G. wislizenii* behavior, including tongue flicks, movement patterns, and habitat use, differences that are not necessarily isolated from each other. Body size can contribute to variation in behavior and ecology in a number of ways, including diet, predation risk, and the nature of conspecific interactions (Werner and Gilliam, 1984; Shine and Wall, 2007). Smaller *G. wislizenii* tended to be more active and alert; they had a higher PTM and used more elevated perches and tongue flicks. The use of elevated perches can serve multiple functions related to monitoring the environment (Stamps, 1977). Lizard tongue flicking can be used to detect predators, prey, and conspecifics (Cooper, 2007). Although ambush predators might not use tongue flicks for prey recognition (Cooper, 2007), *G. wislizenii* displayed higher tongue flick rates in prey capture events (McElroy et al., 2011). In ambush-foraging lizards, tongue flicks commonly follow movements (Cooper et al., 1994; McElroy et al., 2011); in our study, tongue flick rates were correlated with movement rates, which could allow the lizard to assess new microhabitats as they are entered. In the related lizard *Gambelia silus*, tongue flicks allow for recognition of (snake) predators and are part of conspecific interactions (Montanucci, 1965). *Crotaphytus collaris,* a close relative of *Gambelia*, tongue flick fecal pellets, possibly to discriminate between conspecifics (Wilgers and Horne, 2009).

TABLE 2—Pearson correlation coefficients *r* (*P*) for analyses examining the relationships between body size and behavior in *Gambelia wislizenii*. SVL = snout–vent length, MPM = moves per minute, PTM = percentage of time moving.

	SVL	MPM	PTM	Perch rate	Perch percentage	Jump rate	Stalk rate	Pursuit rate	Head turn rate	Tongue flick rate
MPM	−0.283 (0.077)	—	—	—	—	—	—	—	—	—
PTM	−0.340 (0.032)	0.667 (0.001)	—	—	—	—	—	—	—	—
Perch rate	−0.458 (0.003)	0.561 (0.001)	0.450 (0.004)	—	—	—	—	—	—	—
Perch percentage	−0.204 (0.207)	0.311 (0.051)	0.214 (0.185)	0.691 (0.001)	—	—	—	—	—	—
Jump rate	−0.047 (0.775)	0.348 (0.028)	0.167 (0.304)	0.383 (0.015)	0.134 (0.410)	—	—	—	—	—
Stalk rate	0.072 (0.658)	0.025 (0.880)	0.344 (0.030)	0.134 (0.411)	0.288 (0.072)	0.077 (0.636)	—	—	—	—
Pursuit rate	−0.092 (0.571)	0.122 (0.453)	0.341 (0.031)	0.139 (0.391)	0.153 (0.347)	0.125 (0.440)	0.558 (0.001)	—	—	—
Head turn rate	−0.28 (0.08)	0.619 (0.001)	0.475 (0.002)	0.412 (0.008)	0.204 (0.207)	0.331 (0.037)	0.058 (0.721)	0.228 (0.157)	—	—
Tongue flick rate	−0.434 (0.005)	0.534 (0.001)	0.429 (0.006)	0.429 (0.006)	0.133 (0.412)	0.320 (0.044)	−0.039 (0.809)	0.029 (0.861)	0.474 (0.002)	—
Total displacement	−0.045 (0.780)	0.601 (0.001)	0.589 (0.001)	0.335 (0.034)	0.100 (0.540)	0.010 (0.952)	−0.017 (0.918)	0.018 (0.912)	0.517 (0.001)	0.038 (0.817)

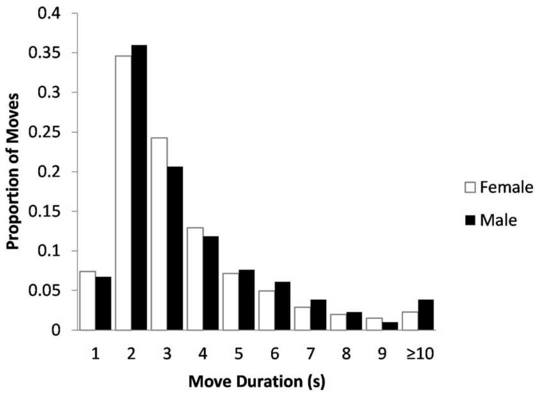

FIG. 1.—Frequency distributions for movement durations of male (*n* = 21; 1,826 moves) and female (*n* = 18; 1,301 moves) *Gambelia wislizenii*.

The role of tongue flicks needs to be more thoroughly investigated.

Male and female *G. wislizenii* differed in both their movements and habitat use. The standard measures of lizard movement (MPM and PTM) and 1-min displacement distances did not vary by sex, but MPM and PTM have increasingly been found to be inadequate for describing the range and adaptive characteristics of movement patterns (Eifler and Eifler, 1999*a*, 1999*b*; Butler, 2005; McElroy et al., 2011). Using different metrics, we found a significant difference between the sexes in displacement sequences and in the distribution of movement durations. *Gambelia wislizenii* males made more moves of long durations and tended to string long displacements together more than females. These differences in movements are likely to be related to foraging and habitat use.

Foraging is likely to have played a role in shaping the movement patterns we observed. Foragers can adjust their move durations to accommodate external changes in prey density, prey type, and prey detectability (Pietruszka, 1986; Evans and O'Brien, 1988; Ehlinger, 1989; Eifler and

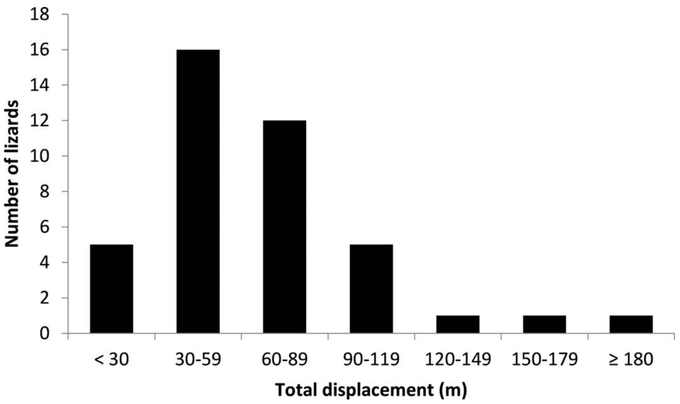

FIG. 2.—Frequency distribution for total displacement by *Gambelia wislizenii* observed for 1 h (*n* = 41 lizards: 18 females, 22 males, 1 undetermined sex).

Eifler, 1999*a*). Lizard foraging can also vary depending on intrinsic factors such as gender (Durtsche, 1992; Lister and Aguayo, 1992; Eifler and Eifler, 1999*b*) and age or size class (Paulissen, 1987; Perry, 1996; Greeff and Whiting, 2000; Eifler et al., 2007). Among *G. wislizenii*, foraging movements can be influenced by prey availability (Anderson, 2007). We do not know whether the sexes differ in diet at our site. In southern (Mojave) populations of *G. wislizenii*, females have more lizards in their diet than males (Tollestrup, 1983). Reproductive condition might also contribute to our observed sex differences. Our study was conducted after the mating season. Most females were gravid or had been so recently. Gravid lizards are likely to be more vulnerable to predation than males (Shine, 1980; Schwarzkopf, 1994) and might adjust their movements because of their limited ability to move.

Intraspecific variation in habitat use has been observed repeatedly in lizards, both between sexes (Hebrard and Madsen, 1984; Eifler et al., 2007) and among size or age classes (Stamps, 1983; Wikelski and Trillmich, 1994; Eifler, 1995). Variation in habitat use can be associated with social activities, foraging, predation risk, and physiological considerations (Stamps, 1983), potential interconnections that are not necessarily mutually exclusive (Andrews, 1971; Scott et al., 1976; Stamps, 1977). Among the differences we found, habitat could influence movement patterns. For example, male *G. wislizenii* in our study occurred more often on hardpan, which is an open habitat where scanning large areas might be easier, enabling lizards to take long moves that were characteristic of males while effectively assessing their surroundings. Shine and Wall (2005) have shown that gravid female lizards spend more time basking to thermoregulate than males, which could help explain why we more often found females in the open in our study rather than in the center of plants, where males were more common. Our results might point to seasonal differences in movement patterns or habitat use that are linked to time in the breeding cycle (Shine and Wall, 2005).

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