Ecology of the Pygmy Short-Horned Lizard [Phrynosoma (Tapaja) douglasii] in Washington

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ECOLOGY OF THE PYGMY SHORT-HORNED LIZARD [*PHRYNOSOMA* (*TAPAJA*) *DOUGLASII*] IN WASHINGTON

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ABSTRACT—We investigated population characteristics, microhabitat use, and activity patterns of *Phrynosoma* (*Tapaja*) *douglasii* (Pygmy Short-horned Lizard) within shrub-steppe habitat in Washington. Females were significantly larger (and more commonly encountered) than were males. Overall, lizards preferred lithosol microhabitat, which is characterized by rocky soils and sparse vegetation. Age, sex, and season, however, affected how lizards used lithosol, loamy, and ecotone microhabitats. Lizard age also affected daily, monthly, and seasonal activity. Adult activity peaked in June, yearling activity in April, and neonate activity in July. During spring and fall, adult activity peaked when daytime temperatures were highest, whereas in summer, the activity peak occurred in early morning and evening. In contrast, neonates remained active during temperature maximums in summer and throughout the day in fall. Although lizards preferred relatively open terrain, they were found closer to shrubs than expected, based on comparisons with random sites. Our results underscore the importance of seasonal variation and age in habitat use and activity patterns of *P.* (*Tapaja*) *douglasii*.

Key words: central Washington, ecology, microhabitat use, natural history, *Phrynosoma* (*Tapaja*) *douglasii*, Pygmy Short-horned Lizard

Temporal and spatial patterns of habitat use by lizards provide critical ecological information and can also clarify various selective forces acting upon the organism (Pianka and Vitt 2003; Stark and others 2005). For instance, Frillneck Lizards (*Chlamydosaurus kingii*) seasonally modify perch site locations in response to natural fire regimes and herbaceous cover; in habitats that experience annual fires, lizards occupy trees with dense foliage and minimal grass cover, whereas in habitats that experience infrequent fires, lizards occupy trees with thin foliage (Griffiths and Christian 1996). Similarly, in the Chihuahuan Desert, Gila Monsters (*Heloderma suspectum*) shift their use of subsurface refugia (shelters) in response to seasonal changes in microhabitat characteristics (Beck and Jennings 2003). Other species within the genus *Phrynosoma* show variation in habitat use and behavior within the active season (Whiting and others 1993; Fair and Henke 1998, 1999; Burrow and others 2001; Moeller and others 2005; Stark and others 2005), yet few studies

have directly assessed the role of seasonality in influencing habitat use over the entire year (Wone and Beauchamp 2003; Mathies and Martin 2008).

Phrynosoma (*Tapaja*) *douglasii* (Pygmy Short-horned Lizard) occurs in Washington and Oregon east of the Cascade Range and into Idaho, northern California, and northern Nevada at elevations up to 2200 m (Stebbins 2003; Lahti and others 2007). Throughout its range, *P.* (*Tapaja*) *douglasii* primarily inhabits shrub-steppe, but also occurs in a variety of other habitats including high-elevation mesic forest, open Pinion-Juniper forest, and grasslands (St. John 2002; Sherbrooke 2003).

Phrynosoma douglasii belongs to a group that includes 3 other species of short-horned lizards [*P.* (*Tapaja*) *hernandesi*, *P. orbiculare*, and *P. ditmarsi*], and is distinguished from all other horned lizard clades by a viviparous reproductive pattern and extremely reduced cranial horns (Leaché and McGuire 2006). *Phrynosoma* (*Tapaja*) *douglasii* is one of the smallest horned lizard species, reaching no more than 6.2 cm snout-vent length (SVL) (Stebbins 2003). These morphological differences likely influence habitat use and activity patterns of *P.* (*Tapaja*)

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douglasii and offer a unique opportunity to explore the implications of reduced body size on habitat use by horned lizards.

Here, we provide information on the ecology of *P.* (*Tapaja*) *douglasii* inhabiting 3 distinct microhabitat types (lithosol, loamy, and ecotone) within the shrub-steppe of central Washington. First, we report population characteristics. We then investigate seasonal patterns of activity and thermal relationships among age and sex classes. Finally, we describe temporal (daily, seasonal) and spatial (microhabitat) variation in habitat use among age and sex classes to better understand the implications of this species' unique body morphology and ecology in the Pacific Northwest.

METHODS

Study Area

The study area is located approximately 32 km east of Ellensburg, in central Washington, at the Quilomene Wildlife Area. This 18,211 ha area was subject to grazing until 1979 (Downes 2003). Fire disturbance has been minimal during the last 30 y and current recreational uses of the area include off-road vehicles, hunting, camping, and hiking.

Summer (June through August) air temperatures average 18.9°C, with maximum temperatures commonly exceeding 38°C (recorded in Ellensburg, WA; Franklin and Dyrness 1988). Air temperatures during fall (September, October) average 9.4°C, while winter month (December through February) temperatures average −1.3°C. Spring (March through May) temperatures are relatively mild, averaging 9.3°C. About 63% of the 226 mm annual precipitation falls during November through March (about 142 mm) and <14 mm of rain, on average, falls during July and August (Donaldson 1979; Franklin and Dyrness 1988; Western Regional Climate Center 2005, period of record: 1901–2005). During the 2 y of this study, precipitation events and climate patterns were similar to these reported values.

The study site is approximately 800 × 400 m in size, extending north from Vantage Hwy. A 4-wheel-drive road bisects the study site north to south and divides into 2 roads near the northern boundary. Elevation ranges from 650 to 700 m. Three broad microhabitat types are present, defined by distinct vegetation and substrate associations: lithosol, loamy soil (loamy), and ecotone (Daubenmire 1988; Taylor 1992; Lahti unpubl. data). Lithosol microhabitat consists predominantly of Stiff Sage (*Artemisia rigida*) and Thymeleaf Buckwheat (*Eriogonum thymoides*). Loamy microhabitat consists predominantly of Big Sage (*Artemisia tridentata*) and Bluebunch Wheatgrass (*Pseudoroegneria spicata*). Ecotone microhabitat is defined by the presence of vegetation from lithosol and loamy microhabitats, as well as Rock Buckwheat (*Eriogonum sphaerocephalum*).

Measuring Lizard Activity and Population Characteristics

We began searching for *P.* (*Tapaja*) *douglasii* on 24 March 2004 to coincide with lizard emergence from hibernation, and we continued searching until 19 October 2004, when lizards were no longer encountered for at least 2 wk. During 2005, we began searching on 1 April and continued until 19 July. A total of 603 h was spent searching for lizards by randomly and haphazardly walking throughout the study site. Random walking was accomplished by walking transects that traversed the length of the study site using randomly-assigned GPS coordinates as transect endpoints; haphazard walking was accomplished by walking linear pathways throughout the length of the study site that were selected arbitrarily using various landmarks as transect endpoints, such as a non-native shrub on the adjacent hillside or small boulders. Searching occurred during all weather conditions except during lightning and heavy rainfall. Searches for lizards on stormy days ceased if no lizards were encountered within 2 h. Search efforts in these instances were not used in this study. Searching occurred opportunistically between dawn and twilight typically for 4 to 6 h/d, 4 d/wk. For this study, we considered "activity" to include lizards encountered on the surface. This measure does not take into consideration potential differences in encounter probabilities among males, females, yearlings, and neonates.

We caught lizards by hand and recorded sex, snout-vent length (SVL; cm), tail length (cm), and mass (g) of each lizard. Annually, we marked lizards ventrally with nail polish for future identification; within and across activity seasons we took dorsal photographs of individ-

ual lizards. Because each lizard has a unique color and pattern, dorsal photographs provide a permanent method of recapture detection. Lizards were assigned to sex and age classes (adult male, adult female, yearling, neonate) using a combination of factors including external reproductive condition (to distinguish males from females as well as adults from yearlings), timing of birthing (to distinguish very small yearlings from neonates), and body size (to distinguish all age classes) (Zamudio 1996).

Microhabitat Measurements

We used a Magellan GPS unit (Thales Navigation Inc., Santa Clara, CA) to record the location, date, and time of each lizard encounter (accuracy within 3 m). We measured microhabitat variables in a 10-m^2 circular area centered at each encounter location including percent cover of perennial plant species, shrub height and width, and ground cover. Cover estimates were measured by subdividing the circular area into quarters and separately estimating percent cover within each quadrant. We recorded percent of ground cover for these features: bare ground, bare rocks, cryptobiotic crust (soils colonized by mosses and lichens), cryptobiotic rocks (rocks covered with mosses, lichens or both), and woody debris.

For each lizard, we measured distance to and height of the nearest plant cover for mature bunch grass or shrub species only. We recorded temperatures at the point of capture for each lizard, at the soil surface, and at 1.0 cm above ground (as a measure of ambient lizard temperature) using a surface-temperature thermometer (0.3°C accuracy; Avinet Inc., Dryden, NY). In 2005, we also recorded lizard cloacal temperatures within 15 s of capture using a quick-read cloacal thermometer (0.3°C accuracy; Avinet Inc., Dryden, NY). To prevent injury, we did not record neonate cloacal temperatures.

To determine the association of lizards with certain microhabitat features, we measured the same microhabitat variables as above from a total of 60 random 10-m^2 circular plots within the study area. The circular plots were divided equally among the 3 microhabitat types.

Analyses

We conducted parametric tests whenever possible using MINITAB14 (v.14, Minitab Inc.,

State College, PA) at significance levels of $\alpha = 0.05$ for 2-tailed t-tests. To assess the suitability of parametric analyses, we used Anderson-Darling Normality tests (Zar 1999).

To estimate the probabilities of initial capture and recapture, as well as lizard abundance, we used mark-recapture data from June 2004 and from 23 May to 22 June 2005. Search efforts were most intense during these periods when lizards were most active. We examined the effects of habitat class, sex and age class, body mass, body size, capture date, and daily search effort on (re)capture probabilities, as well as the derived population abundance parameter, using the Huggins closed capture model in version 5.1 of program MARK (White and Burnham 1999). Because of our relatively small sample size, we did not consider models with more than 1 covariate. For the same reason, we considered a null model in which capture and recapture probabilities were constant and constrained to be equal. Akaike's Information Criterion (AIC) was used to evaluate the statistical support for the various models containing different explanatory covariates (or lack thereof) for (re)capture probabilities and population abundance.

We used an ANCOVA using Tukey honestly significant difference (HSD) test to compare the allometric relationship of lizard mass and SVL. Data were normalized by log-transformation prior to ANCOVA analysis and for lizards upon 1st capture only. To test whether lizards in this population were sexually dimorphic in favor of females (Zamudio 1998) we used a 1-tailed t-test.

To assess microhabitat features associated with lizard capture locations, seasonal variation in habitat use, and differences in habitat use among classes, we used multiple-response permutation procedure (MRPP) and indicator species analysis (ISA) using PC-ORD4 (v4.25, MjM Software, Gleneden Beach., OR). MRPP is a nonparametric equivalent to an ANOVA, while ISA is functionally similar to a post-hoc test in that it identifies variables that significantly vary among treatments.

We used an Anderson-Darling Normality test to determine if the distribution in diel lizard activity was normal across seasons. We used an ANOVA and Tukey HSD to test for differences in activity temperatures (adult, yearling, neonate) and cloacal temperatures (adult, juvenile)

TABLE 1. Lizard population abundance estimates in 2004 and 2005 using Program MARK. Bold indicates models used to estimate population abundance. We considered fewer and less complex models for analysis in 2005 since the sample size and number of recaptures was relatively small.

2004 Model	AIC	ΔAIC	AIC Weights	Deviance	# Parameters	Model Likelihood
p=c(.)	**210.31**	**0.00**	**0.34**	**208.30**	**1**	**1.00**
p(svl) c(svl)	211.38	1.07	0.20	203.29	4	0.59
p(.) c(.)	212.27	1.96	0.13	208.24	2	0.38
p(TL) c(TL)	212.49	2.18	0.11	204.40	4	0.34
p(ef) c(ef)	212.94	2.63	0.09	204.85	4	0.27
p(sexage) c(sexage)	213.63	3.32	0.06	201.44	6	0.19
p(mass) c(mass)	214.41	4.10	0.04	206.32	4	0.13
p(hab) c(hab)	215.55	5.24	0.02	203.37	6	0.07

2005 Model	AIC	ΔAIC	AIC Weights	Deviance	# Parameters	Model Likelihood
p=c(.)	**130.36**	**0.00**	**0.56**	**128.34**	**1**	**1.00**
p(.) c(.)	130.86	0.51	0.44	126.82	2	0.78

among lizard groups, and for differences between cloacal and microclimate (surface, 1cm above-ground) temperatures. Sex distribution among microhabitat types was tested using a Chi-square contingency table (Zar 1999). We used a t-test to determine whether lizards occurred closer to vegetation than at random, and to determine whether lizards selected vegetation that was of a different height than average.

RESULTS

Population Characteristics

In 2004, 112 observations were made of 86 different lizards (including 26 recaptures of 15 lizards). Of these 86 lizards, 22 were adult males (26%), 36 were adult females (42%), 9 were yearlings (10%), 17 were neonates (20%), and sex was undetermined for 2 adult lizards (2%). The maximum number of observations for any lizard was 4. In 2005, 64 observations were made for 59 different lizards (includes 1 recapture for each of 5 lizards). Of these 59 lizards, 14 were adult males (23%), 27 were adult females (46%), and 18 were yearlings (31%).

The best predictor of population abundance was the simple null model, in which capture and recapture probabilities were constant and equal to each other (Table 1). Based on the null model, estimated lizard abundance for 2004 was 75 lizards (95% CI = 45 to 158 lizards) with a 0.026 probability of initial capture and recapture (95% CI = 0.012 to 0.055). Estimated lizard abundance for 2005 was 115 lizards (95% CI: 45 to 398 lizards) with a 0.015 probability of recapture (95% CI = 0.004 to 0.058).

SVL of males ranged from 3.7 to 5.2 cm ($\bar{x}$ = 4.3, s = 0.06, n = 36) with an average mass of 5.45 g (s = 0.22); whereas SVL of females ranged from 3.8 to 6.4 cm ($\bar{x}$ = 4.8, s = 0.61, n = 63) with an average mass of 7.76 g (s = 0.44). Yearling SVL ranged from 2.3 to 3.7 cm ($\bar{x}$ = 3.1, s = 10.59, n = 27) with an average mass of 2.10 g (s = 0.39). Neonate SVL ranged from 2.1 to 2.7 cm ($\bar{x}$ = 2.4, s = 0.64, n = 17) with an average mass of 0.82 g (s = 0.18). Females were significantly longer in SVL than males (t = 3.60, df = 94, $P <$ 0.0003), although they were not disproportionately longer when scaled to mass (ANCOVA; F = 2.81, df = 93, P = 0.10). Thus, adult males and females were grouped as adults to compare body mass in relation to SVL among age classes. Relative to SVL, adult, yearling, and neonate lizards had significantly different body masses (ANCOVA; F = 346.44, df = 137, $P <$ 0.0001; post hoc $P <$ 0.0001 for all comparisons) (Fig. 1). Adults had the lowest body mass relative to SVL, followed by yearlings, and neonates.

Activity Patterns and Thermal Relationships

Based on unit of search effort, June was the peak activity month for all lizards combined (0.49 lizards/h), followed by July (0.33 lizards/h) (Table 2). Peak activity for males and females occurred in June (0.34 and 0.43 lizards/h, respectively). Yearlings were most commonly encountered during April (0.48 lizards/h) and neonates were most active in July (0.40 lizards/h).

Lizards showed differences in daily activity times per month and across seasons (Fig. 2). During April, more adults (72%) were found in early afternoon (13:00 to 16:00), while in May
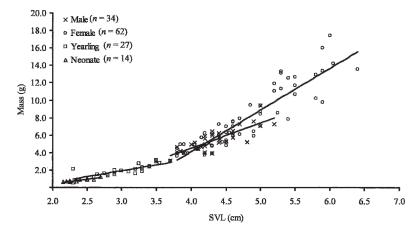
FIGURE 1. Snout-vent length (SVL) and mass comparisons among lizard age and sex classes.

most adults (55%) were found before noon (09:00 to 12:00). The abundance of lizards throughout spring showed a normal distribution with an activity peak in the early afternoon (Anderson Darling; $A^2 = 0.44$, $P = 0.24$). This trend of early afternoon activity was driven by yearling lizards, where 75% were active from 11:00 to 15:00, whereas only 46% of adults were active during this time period (Fig. 2). During summer, there was a shift in adult activity; 49% of adults were encountered from 09:00 to 11:00 and from 17:00 to 19:00. In contrast, most yearlings (89%) and neonates (62%) were encountered between 11:00 to 14:00.

Accordingly, neonates were active during significantly higher surface temperatures than adults during summer (neonate = 43.5°C, s = 1.7; adult = 36.7°C, s = 0.9; ANOVA F = 4.84, df = 147, P = 0.01; Tukey HSD $P < 0.05$ for adult vs. neonate only), while surface temperatures for yearlings did not differ significantly from those of adults or neonates (38.2°C, s = 1.8) (Fig. 3). Moreover, neonates and yearlings were active during significantly higher temperatures 1 cm above ground in summer than adults (neonate = 37.8°C, s = 0.9; yearling = 32.9°C, s = 1.7; adult = 31.7°C, s = 0.6; ANOVA F = 6.81, df = 147, P = 0.002; Tukey HSD $P < 0.05$ for adult vs. neonate and yearling vs. neonate).

Within lizard groups, cloacal temperatures showed significant deviation from environmental temperatures. During spring, adult cloacal temperatures (32.1°C, s = 1.1) were significantly higher than temperatures at 1 cm above the surface of the ground (24.9°C, s = 1.5) but not surface temperatures (30.5°C, s = 1.7), and surface temperatures were significantly higher than temperatures at 1 cm (ANOVA; F = 13.38, df = 28, $P < 0.0001$; Tukey HSD $P < 0.05$ for 1 cm vs. cloacal, and $P < 0.01$ for surface vs. 1 cm). During summer, adult lizard cloacal temperatures (35.7°C, s = 0.6) did not significantly vary from temperatures at the surface or at 1 cm, although temperatures between the surface and 1 cm did vary significantly (surface = 36.0°C, s = 2.0; 1 cm = 31.2°C, s = 1.7;

TABLE 2. Lizard captures (including recaptures) per month from 2004–2005 at Quilomene Wilderness Area in central Washington.

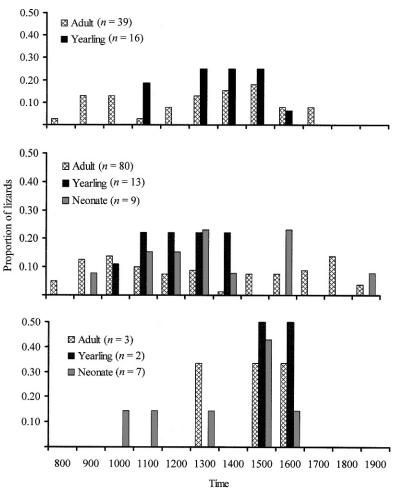|	Adult male	Adult female	Yearling	Neonate	Unknown	Total search hours	Total lizards	Lizards/ search hour
April	11	12	15	0	0	147.0	38	0.26
May	4	13	5	0	0	83.5	22	0.24
June	16	33	9	0	1	120.0	59	0.49
July	10	15	0	8	1	108.0	34	0.33
August	4	2	0	5	0	65.0	11	0.17
September	2	1	2	7	0	62.5	12	0.19
October	0	0	0	0	0	17.0	0	0.00
TOTALS	47	76	31	20	2	603.0	176	

FIGURE 2.   Hour of day when lizards were encountered during the 2004–2005 field season in spring (March–May), summer (June–August), and fall (September–October).

ANOVA $F_{2,48} = 4.4$, $P = 0.025$; Tukey HSD $P < 0.05$). Cloacal temperatures of yearlings did not vary from surface or 1 cm temperatures during spring (31.8°C, $s = 1.7$), although temperatures between the surface and at 1 cm did vary significantly (surface = 33.8 °C, $s = 4.0$; 1 cm = 27.5°C, $s = 2.2$; ANOVA $F = 5.71$, $df = 18$, $P = 0.04$; Tukey HSD $P < 0.05$ for surface vs. 1 cm). Too few samples were obtained for yearlings during summer to conduct statistical analyses ($n = 3$); however, yearling mean cloacal temperature was 38.0°C ($s = 2.6$), while mean temperatures at 1 cm and at the surface were 35.3°C ($s = 3.4$) and 36.3°C ($s = 3.6$), respectively.

Microhabitat Use

Overall, most lizards were encountered at lithosol (61%), followed by ecotone (31%) and loamy (8%) microhabitats. The highest proportion of male, female, and yearling lizards all occurred in the lithosol microhabitats (adult males = 67%, adult females = 56%, yearlings = 74%) (Table 3). Neonates occurred almost equally in ecotone (53%) and lithosol microhabitats (47%), and were absent from loamy microhabitats.

Microhabitat use differed significantly among males and neonates compared to random plots (MRPP $A = 0.287$, $P < 0.001$); males were associated with Stiff Sage (ISA IV = 23.9, $P =$
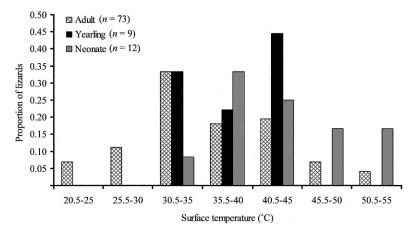
FIGURE 3.   Ground surface temperatures during summer activity (June–August). Adult mean = 36.7 ± 0.9°C; yearling = 38.2 ± 1.8°C; and neonate = 43.5 ± 1.7°C.

0.076) and cryptobiotic rock (ISA IV = 23.4, P = 0.058), whereas neonates were associated with significantly more Thymeleaf Buckwheat (ISA IV = 17.3, P = 0.050), Rock Buckwheat (ISA IV = 12.5, P = 0.029), and cryptobiotic crust (ISA IV = 29.9, P = 0.003) than any other lizard group. Big Sage (ISA IV = 21.9, P = 0.010) and Bluebunch Wheatgrass cover (ISA IV = 24.4, P = 0.007) were significantly greater in areas where lizards were typically not observed.

Lizards also showed seasonal variation in microhabitat use (MRPP A = 0.008, P = 0.05). During spring, lizards were observed more often in microhabitats having more bare rock (ISA IV = 30.9, P = 0.034); in summer, lizards were more often observed in microhabitats with more Bluebunch Wheatgrass (ISA IV= 30.3, P = 0.084); and during fall, lizards were associated with microhabitats with higher proportions of cryptobiotic crust (ISA IV= 43.3, P = 0.028).

Lizards, particularly those inhabiting lithosol microhabitats, typically did not retreat to shrub cover until approached within 1 m. Most lizards (68%) retreated to the nearest vegetative cover; this trend was especially noticed in females (68%), while only 50% of males did the same. *Phrynosoma* (*Tapaja*) *douglasii* sightings were significantly closer to vegetation than random locales (t = 2.46, df = 111, P = 0.016). On average, lizards were found within 0.52 m (s = 0.05) of a shrub, whereas random points were within 0.72 m (s = 0.09) of a shrub. Lizards also were captured adjacent to shrubs that averaged 11 cm (s = 1.4) shorter than surrounding shrub height (t = 3.07, df = 76, P = 0.003). This association with shorter shrubs was most pronounced in loamy microhabitats, where lizards were captured adjacent to shrubs that averaged 18 cm (s = 9.3) shorter than surrounding shrubs.

DISCUSSION

Population Characteristics

In most horned lizard species, females are larger than males (Pianka and Parker 1975; Guyer and Linder 1985; Montgomery and Mackessy 2003) and typically reach sexual maturity a year after males (Guyer 1978; Powell and Russell 1985; Zamudio 1998). Selective forces driving the early onset of sexual maturity

TABLE 3.   Lizard observations (excluding recaptures) across microhabitats.

Microhabitat	Lizards Observed				
	Male	Female	Yearling	Neonate	Totals
Lithosol	24	35	20	8	87
Loamy	2	8	2	0	12
Ecotone	10	20	5	9	44
Totals	36	63	27	17	143

in males likely contribute to overall body size reduction (Zamudio 1998). Zamudio (1998) suggests that smaller-sized males are most advantageous in populations where females occur at low densities and are dispersed across the terrain. Horned lizards are generally considered low-density species (Pianka and Parker 1975), although relatively high population densities have been reported in *P.* (*Tapaja*) *douglasii* (14.3 to 14.6 lizards/ha in eastern Idaho) (Guyer and Linder 1985). However, the density of lizards at the Quilomene Wildlife Area (<2 lizards/ha) is more characteristic of other horned lizard species including *Phrynosoma cornutum* (1.6 lizards/ha, Worthington 1972) and *Phrynosoma* (*Doliosaurus*) *platyrhinos* (1.0 to 2.5 lizards/ha, Medica and others 1973; 5.0 lizards/ha, Tanner and Krough 1973).

The sex ratio of captured lizards was female-biased (1.7:1.0), which is higher than reported for other horned lizards, such as 1.5:1.0 (Whiting and others 1993), 1.34:1.0 (Moeller and others 2005), and 1.4:1.0 (Montgomery and Mackessy 2003) for *P. cornutum*. Given the high number of search hours (n = 603) and lizard encounters (n = 176), it is unlikely that the sex ratio is an artifact of search effort or sample size. Instead, this disproportionate ratio of females to males may indicate a higher mortality rate for males or a higher proportion of female offspring (Guyer and Linder 1985).

As with other ectotherms that inhabit higher latitudes and elevations, the reproductive strategy of *P.* (*Tapaja*) *douglasii* includes viviparity and higher numbers of smaller offspring (Pianka 1986; Hodges 2004). Although there may be as many as 15 offspring produced from 1 reproductive event for 1 female (Nussbaum and others 1983), only 17 neonates were observed during this study. It is likely that in our population females might not reproduce annually (Zamudio 1996). Additionally, although not assessed in this study, Quilomene Wildlife Area lizards may have a relatively low reproductive rate (Zamudio 1996); our observations of a relatively low population density and few neonates support this hypothesis.

Activity Patterns

At Quilomene Wildlife Area, lizard thermal preferences mirror what has been found in other horned lizards; during spring and fall lizards are mostly found during peak daily temperatures, while during summer lizards become more crepuscular (Pianka and Parker 1975; Henke and Montemayor 1998; Hernandez-Ibarra and Ramirez-Bautista 2002; Montgomery and Mackessy 2003). Neonates, and to a lesser degree yearling lizards, maintain activity during peak summer temperatures and remain active later in the season. In other lizard species, ontogenetic variation in activity can correlate with intraspecific competition (Stamps 1983). However, *P.* (*Tapaja*) *douglasii* is non-territorial (Zamudio 1998). Thus, it is unlikely that neonate activity during temperature extremes is a result of habitat or foraging displacement. As temperature and food resources are considered to have significant effects on lizard growth rates (Sinervo and Adolph 1989), a more likely scenario is that neonates are active throughout the day, especially during peak temperatures, to maximize energy intake and subsequent growth and energy reserves needed to survive overwintering, which lasts approximately 7 mo at Quilomene Wildlife Area. Following birth, *Sceloporus graciosus* neonates occurring at high elevations have a relatively high increase in mass compared to length. This trend, common to Quilomene Wildlife Area neonates, is thought to be due to a greater investment in energetic reserves than somatic growth in an environment with both limited thermal period available prior to hibernation and a long overwintering period that exceeds 6 mo (Sinervo and Adolph 1989). Survival through overwintering is most critical for a neonate lizard, and chances of survival are greatly increased when energy reserves are sufficient for overwintering conditions (Gregory 1982; Smith and Fretwell 1974). This trade-off of resource allocation to mass compared to growth in neonates also correlates with a higher chance of survival as juveniles (Olsson and Shine 2002; Warner and Andrews 2002).

Habitat Use

Horned lizards are generally sedentary and rely on cryptic coloration and mimicry of habitat features to avoid predators and to assist in their sit-and-wait foraging tactics (Sherbrooke and Montanucci 1988; Sherbrooke and Middendorf 2001; Sherbrooke 2003). Thus, open microhabitat with moderately-spaced vegeta-

tion is an optimal habitat type for horned lizards because dense vegetation restricts their foraging, locomotive, and thermoregulatory options (Blackshear and Richerson 1999; Newbold 2005). On the other hand, vegetation is important because it functions as an important refuge for lizards from temperature extremes and predators. *Phrynosoma* (*Tapaja*) *douglasii* was most often observed in lithosol microhabitat, which had the sparsest vegetative cover and was the most open habitat, suggesting that *P.* (*Tapaja*) *douglasii* microhabitat use is at least partially influenced by shrub cover.

Neonates were almost always encountered closest to Thymeleaf Buckwheat and would often retreat toward this plant as we approached. Thymeleaf Buckwheat has the smallest and most compact growth form of any perennial plant at Quilomene Wildlife Area. In contrast, adults would usually retreat to either Stiff Sage or Rock Buckwheat, both of which have larger growth forms. This suggests that lizards use vegetation cover proportional to their sizes.

Because there is an uneven distribution of males, females, and neonates across each terrain type, the age and sex classes may be actively segregating to microhabitats that best meet their specific needs. Male horned lizards are known to increase their home ranges during the mating season and return to smaller ranges thereafter (Stark and others 2005). Male horned lizards might occur in greater numbers at lithosol sites because this habitat type offers the greatest capacity for movement and sighting ability via low vegetation density. Location is presumed to be even more critical for pregnant females, because there are obligations to both mother and developing fetuses (Shine 1980; Cooper and others 1990, 2003). As all neonates were encountered at ecotone or lithosol microhabitats, and females are the 2nd highest proportion of lizards found at the ecotone microhabitat, females might migrate to these microhabitat types during parturition. All neonate *P.* (*Tapaja*) *douglasii* were observed within 10 m of their original capture locations throughout the remainder of their activity season (pers. obs.). However, since neonates occur most often in the ecotone microhabitat and few yearling or adult lizards occupy this microhabitat type, it can be inferred that neonates likely migrate out of the

ecotone microhabitat upon entering their 1st full year (as yearling) and possibly into their 2nd.

Conclusion

Phrynosoma (*Tapaja*) *douglasii* occur at low densities in the shrub-steppe of Washington where females are both larger and more abundant than males, neonates are rare, and reproductive output appears low. Younger lizards maintain activity into hotter periods and remain active later in the activity season than do adults, a trait likely related to the importance of garnering sufficient energy to emerge in good condition after a long winter. *Phrynosoma* (*Tapaja*) *douglasii* are most commonly encountered in shrub-steppe habitats, but within that system these lizards show considerable spatial and seasonal variation in use of microhabitats. Age and sex classes appear to select different microhabitat types that best meet their specific needs. As one of the few species of horned lizards that has extremely reduced horns, *P.* (*Tapaja*) *douglasii* must rely more on crypsis and escape to refugia (rather than cranial horns) as a primary defense against predators. These lizards also are most often observed in relatively open habitats where they blend in well with their surroundings; although they also use microhabitats that allow ready access to shrub refugia, where they often flee when encountered.

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