

Ecology and Ontogenetic Variation of Diet in the Pigmy Short-Horned Lizard (*Phrynosoma douglasii*)

MEGAN E. LAHTI¹

Utah State University, Department of Biology, 5305 Old Main Hill, Logan 84322

AND DANIEL D. BECK

Central Washington University, Department of Biological Sciences, 400E. University Way, Ellensburg 98926

ABSTRACT.—To date, the diet of the pigmy short-horned lizard (*Phrynosoma douglasii*) is not known. We report the diet of the pigmy short-horned lizard to determine whether it shows a more generalized diet, similar to other short-horned lizards or a more specialized diet consisting primarily of ants. We compare variation in diet among habitat variables and age/sex classes. We also compare ant head capsules consumed among age/sex classes to determine if lizard groups consume ants of varying size and diversity proportional to their body sizes. Similar to other short-horned lizards, *P. douglasii* consumes relatively lower proportions of ants (71%) than highly myrmecophagous horned lizard species, followed by pebbles (13%) and Coleopteran insects (11%). Aside from terrain, diet varies among all habitat variables measured, but especially among age and sex classes; neonates feed almost exclusively on ants (89%) while adults consume fewer ants (72%) and yearlings consume the lowest proportion of ants (60%). Most ants consumed by adults represent a single ant genus (*Camponotus*), while yearlings and neonates consume multiple ant genera of smaller sizes (*Camponotus*, *Pheidole*, *Tetramorium*). We found a significant positive correlation between lizard SVL and the size of ant heads in the diet of *P. douglasii*. These results are important in understanding variation in diet and ecology of the pigmy short-horned lizard and also in addressing foraging and diet in other insectivorous Phrynosomatid lizards, particularly horned lizards.

INTRODUCTION

Ontogenetic variation in insectivorous lizards is often correlated with prey size, volume and type (Castilla *et al.*, 1991; Herrel *et al.*, 2006; Preest, 1994; Teixeira-Filho *et al.*, 2003). Mechanically, young lizards have reduced gape size and bite force capacity due to an overall reduced body size compared to adults (Herrel *et al.*, 2006). This often results in younger lizards consuming smaller and potentially more soft-bodied insects than adults. For instance, horned lizards show a positive correlation between body size and prey item size (Rissing, 1981; Pianka, 1973; Schoener, 1977; Powell and Russell, 1984; Suarez *et al.*, 2000; Suarez and Case, 2002). However, it is also suggested that the correlation between the sizes of the predator and its prey are influenced by other factors including an innate preference for prey items proportional to lizard size (Whitford and Bryant, 1979), prey availability based on habitat and seasonality (Rissing, 1981; Pianka, 1979) and optimal foraging strategies (Schoener, 1971). Lizards with a preference for or that specialize on a particular prey type are likely to have modified morphologies associated with feeding and foraging habits, life history strategies, or behaviors that reflect this prey preference or specialization.

Horned lizards (genus *Phrynosoma*) are considered dietary ant specialists, yet there is much variation in the degree of myrmecophagy among the 13 currently recognized species (Montanucci, 1989). Some species feed almost exclusively on native ants while others consume higher proportions of other insects and arthropods. For instance, throughout its range *P. platyrhinos* consumes ants in highest proportions (88.7%), followed by beetles

¹ Corresponding author: Telephone: 435.899.9380; e-mail: Phrynosoma@biology.usu.edu

(7.6%) (Pianka and Parker, 1975). In contrast, the diet of *P. hernandesi* (formerly *P. douglassii*) contains nearly equal proportions of ants (48.9%) and beetles (44.9%) at one locality while throughout its greater range, *P. hernandesi* diets contains 81% ants on average (Pianka and Parker, 1975).

Differences in diet among species of *Phrynosoma* correspond to morphologies associated with feeding behaviors and function (Meyers *et al.*, 2006). Most horned lizards from the long-horned lizard clade are considered highly myrmecophagous, having increased cranial morphologies that contrast with species that consume large numbers of non-ant prey (Montanucci, 1989; Meyers *et al.*, 2006). Morphologies associated with myrmecophagy include a more robust skull, a larger and taller coronoid process with a larger posterior area, longer epipterygoid and mandible, greater number of teeth, and a taller and wider head that corresponds to greater bite force (Montanucci, 1989; Meyers *et al.*, 2006). In the short-horned lizard clade (*P. douglasii*, *P. hernandesi*, *P. ditmarsii* and *P. orbiculare*), lizard diets are not typically dominated by ants and cranial morphologies are greatly reduced (Meyers *et al.*, 2006). The divergence in morphologies among lizards in the short-horned lizard clade associated with feeding is likely an adaptation for a generalized insectivorous diet consisting of larger and harder prey items (Meyers *et al.*, 2006; Montanucci, 1981, 1989; Pianka and Parker, 1975; Powell and Russell, 1984).

Phrynosoma douglasii, the pigmy short-horned lizard, is a recently elevated species, previously grouped as a subspecies (= *P. douglasii douglassii*) belonging to *P. douglassii* along with two other currently recognized species, *P. hernandesi* and *P. ditmarsii* (Zamudio *et al.*, 1997). *Phrynosoma douglasii* (sensu stricto) is unique in having the most reduced body form and horn length of all *Phrynosoma* species and does not occupy any true desert habitat throughout its range. It occurs at elevations up to 2200 m throughout the Pacific Northwest primarily in shrub-steppe habitat but it also occurs in a variety of other habitats including open pinion juniper, mesic forests and farm fields (Dvornich and Petersen, 2005; Lahti *et al.*, 2007; Stebbins, 2003; St. John, 2002).

Little is known about patterns of variation in the diets of horned lizards, especially in the short-horned lizard clade. Zamudio (1996) reported stomach contents for 83 female *Phrynosoma douglasii* in Siskiyou County, California which occurs at the far southwest corner of its current range. The highest frequency of prey items consumed was ants (68.8%) followed by Coleopterans (20.4%); however, diets also consisted of low proportions of Orthopterans (1.0%), larvae (0.2%) and Arachnids (0.1%). Organic and non-organic debris consisted of up to 15.4% of female diets (Zamudio, 1996). Diet data for studies conducted prior to Zamudio (1996) remain inconclusive for *P. douglasii* (sensu stricto) because samples include lizards now considered *P. hernandesi* (Pianka, 1986; Pianka and Parker, 1975; Montanucci, 1989; Stebbins, 1985) and, therefore, obscure possible differences between these taxa.

To gain a further understanding of the unique diet of horned lizards and to investigate the role of age, sex, habitat and season on horned lizard diets, we report the results of a 2-y study on *Phrynosoma douglasii* in central Washington. We address the following questions: (1) does *P. douglasii* specialize on ants or is it a more generalist insectivore as are other *Phrynosoma* species with reduced cranial morphologies and (2) does *P. douglasii* show changes in diet that are associated with ontogenetic/size changes, sex, habitat and/or season.

METHODS

We studied two lizard populations in central Washington: (1) Quilomene Wildlife Area (Quilomene) (650–700 m elevation) located approximately 32 km east of Ellensburg,

Washington and (2) Umtanum Canyon (Umtanum) (800–850 m elevation) located approximately 13 km west of Ellensburg, Washington. Both sites consist of shrub-steppe habitat with three recognized terrain types based on soils and vegetation associations (Daubenmire, 1988; Taylor, 1992). Lithosol terrain is composed of rocky soils overlaying basalt bedrock, sparse vegetation and reduced growth forms of the dominant plant species: stiff sage (*Artemisia rigida*) and thyme leaf buckwheat (*Eriogonum thymoides*). Loamy terrain is composed of deep sandy soils, dense vegetation, and large growth forms of the dominant plant species: big sage (*Artemisia tridentata*) and bluebunch wheatgrass (*Pseudoroegneria spicata*). Ecotone terrain contains soils intermediate between the lithosol and loamy terrains and dominant vegetation includes stiff sage and bluebunch wheatgrass.

We haphazardly searched each study site when lizards were active (May–Aug.) in 2004 and 2005. Quilomene was the primary study site and more effort was spent searching for lizards here than at Umtanum. We recorded sex, snout-to-vent length (SVL in cm) and mass (grams) for each lizard encountered. We held lizards in captivity for up to two days for fecal pellet collection. We then measured the dry mass of each fecal pellet to 0.001 g and examined the contents using a dissecting microscope.

We identified and tallied head capsules from prey items to order (Borror and DeLong, 1964). We counted the presence of a particular insect order as one individual if only body parts other than head capsule from that particular insect order was observed. We verified body part identification either from insects captured at one of the study sites or from museum specimens in the Central Washington University Department of Biological Sciences Entomology Collection. We also recorded organic debris (pieces of leaf or stem vegetation) and pebbles. We treated multiple fecal pellets collected from one individual at one time as one fecal pellet by averaging head capsule counts for each prey item.

We categorized lizards were into four groups based on sex and age: adult male, adult female, yearling and neonate. Adult males and females were greater than 3.80 cm SVL yearlings (lizards entering their first full year of life) were between 2.80 cm and 3.80 cm SVL, and neonates were lizards with SVL less than 2.80 cm. We used analysis of covariance (GLM ANCOVA) to determine variation in fecal pellet mass relative to SVL and body mass for each lizard group (SAS Institute Inc., 2007).

We compared proportions of each insect order from fecal pellets collected at Quilomene between years, seasons, terrain types and lizard age and sex classes using multi-response permutation procedure (MRPP) and indicator species analysis (ISA) (PC-ORD4, 1999). MRPP is essentially a nonparametric version of the MANOVA test; differences among multiple groups are calculated based on a Euclidian distance matrix (McCune and Grace, 2002). The chance-correlated within-group agreement (A) indicates the difference between groups compared to random where $A = 0$ corresponds to no difference and $A = 1$ corresponds to complete difference. Indicator species analysis discriminates which variables detected by the MRPP analysis are statistically significant (McCune and Grace, 2002).

To determine if there is ontogenetic variation in prey item size among lizard age and sex classes, we analyzed a sub-sample of ant head capsules from Quilomene lizard fecal pellets. Five ant head capsules were haphazardly selected from fecal pellets of each of 10 different adult male, adult female, yearling and neonate lizards. An ocular micrometer was used to measure each ant head width and length to the nearest 0.1 mm. Length was measured along the median longitudinal line from the forehead apex to the anterior tip of the clypeus and width was measured at the widest distance between the distal portion of the eyes (Fig. 1). We used ANCOVA to test for differences in head capsule size among lizard groups and linear regression to investigate relationships between SVL and body mass relative to ant head

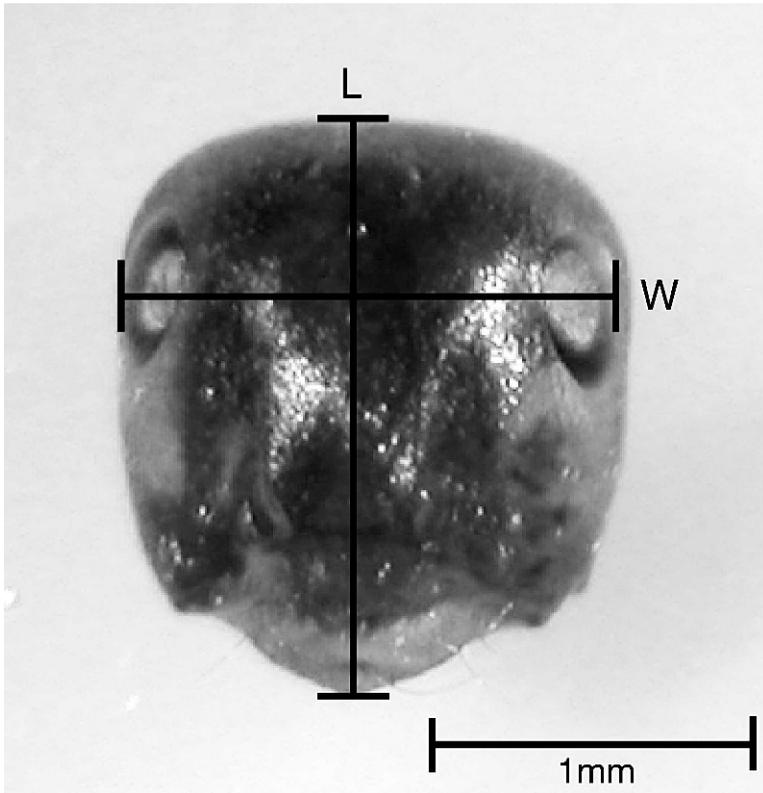


FIG. 1.—Ant head capsules were measured along two perpendicular axes. Head length was measured along the median longitudinal line from the forehead apex to the anterior tip of the clypeus and head width was measured from the widest distance between the distal portion of the eyes

capsule size for each lizard group. We used Chi-square analysis (Zar, 1999) to test for differences in proportions of ant species consumed by each lizard group and for differences in proportions of *Camponotus* soldiers and worker ants consumed. Because ant head size varies continuously (not discretely) between worker and soldier ants, we divided ant head capsules into five size classes (length*width) prior to Chi-square analyses. Soldier ants were differentiated from workers based on head shape; soldiers have a more pronounced squared head with prominent incisors while workers have a more rounded head with reduced incisors.

RESULTS

We collected a total of 157 fecal pellets from 117 lizards; 132 fecal pellets from 102 lizards were from Quilomene and 25 fecal pellets from 15 lizards were from Umtanum. We did not encounter any neonate fecal pellets from Umtanum during either year.

Overall, females had the greatest fecal pellet mass (0.088 ± 0.059 g), followed by males (0.062 ± 0.042 g), yearlings (0.031 ± 0.020 g) and neonates (0.010 ± 0.006 g). Fecal pellet mass did not vary among lizard groups relative to SVL (ANCOVA GLM: $F = 1.33$, $df = 3$, $P = 0.27$) or body mass (ANCOVA GLM: $F = 1.87$, $df = 3$, $P = 0.14$).

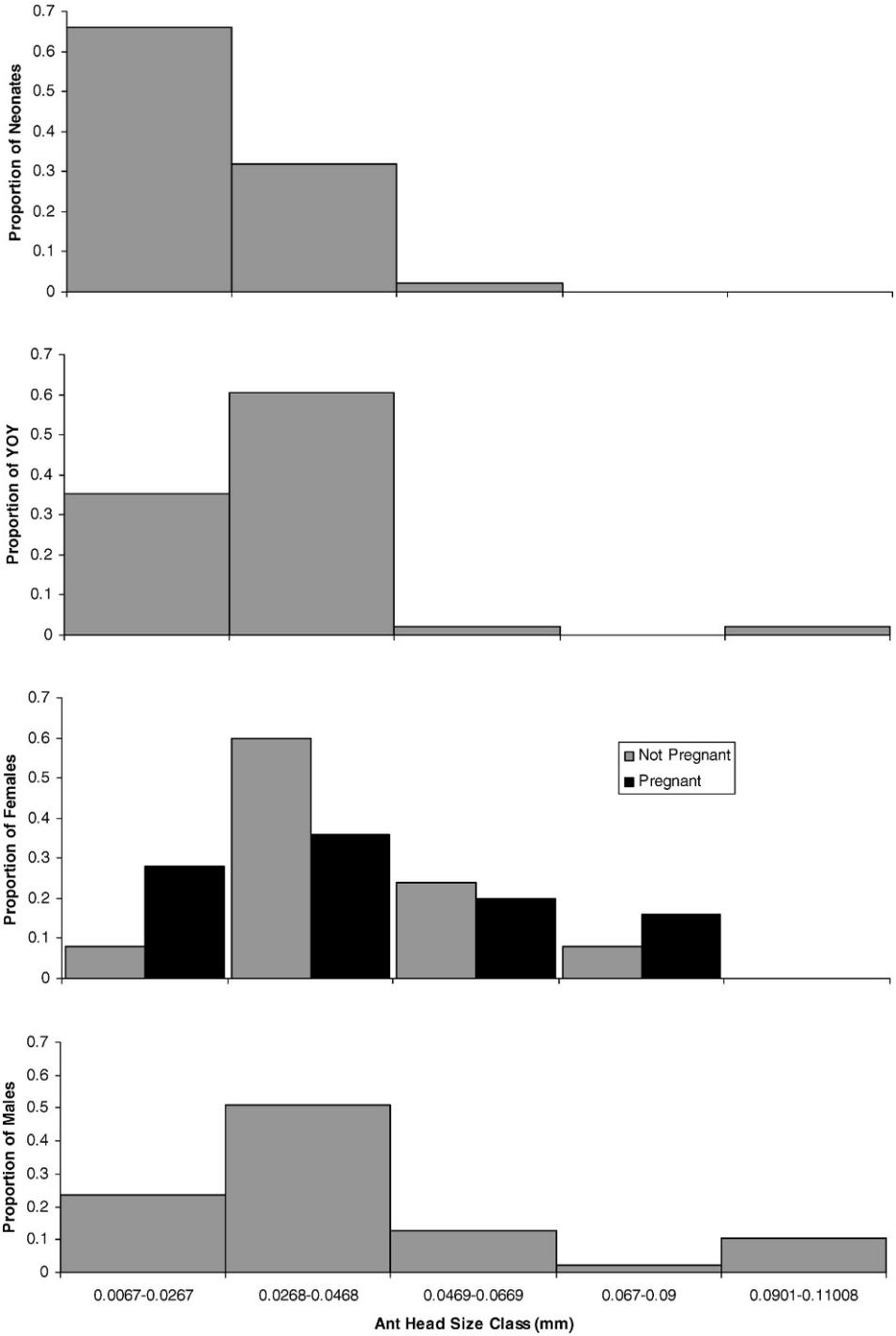
TABLE 1.—Diet composition consumed by *Phrynosoma douglasii* at Umtanum and Quilomene. Terrain, season and year represent lizards from Quilomene only. Insect prey items are represented by head capsule counts. Insect counts from multiple fecal pellets obtained during one collection event from one individual are averaged. Percentage (italicized) indicates proportion of diet consumed within each lizard group

	Formicidae		Diptera		Hemiptera		Coleoptera		Pebbles		Organic debris	
	n	%	n	%	n	%	n	%	n	%	n	%
Umtanum (n = 15)	223	75.6%	1.5	0.5%	13.5	4.6%	27.5	9.3%	19	6.4%	10.5	3.6%
Male (n = 7)	96	77.1%	0	0.0%	0	0.0%	8.5	6.8%	16.5	13.3%	3.5	2.8%
Female (n = 7)	125	75.5%	1.5	0.9%	13.5	8.2%	17	10.3%	1.5	0.9%	7	4.2%
Yearling (n = 1)	2	40.0%	0	0.0%	0	0.0%	2	40.0%	1	20.0%	0	0.0%
Quilomene (n = 102)	1906.6	71.2%	21	0.8%	43	1.6%	295.6	11.0%	353.3	13.2%	58	2.2%
Male (n = 20)	287.5	72.4%	1	0.3%	7.5	1.8%	41.5	10.5%	46.5	11.7%	13	3.3%
Female (n = 45)	1103.6	72.4%	19	1.2%	25.3	1.6%	164.1	10.8%	180	11.8%	33.3	2.2%
Yearling (n = 25)	329.5	60.4%	1	0.2%	8	1.5%	84	15.4%	113.5	20.8%	9.5	1.7%
Neonate (n = 12)	186	88.8%	0	0.0%	2.2	1.0%	6	2.9%	13.3	6.3%	2.2	1.0%
Terrain (n = 102)												
Lithosol (n = 66)	952.3	66.7%	16	1.1%	24.7	1.7%	194.3	13.6%	210.8	14.7%	31.5	2.2%
Loamy (n = 6)	187.5	79.0%	0	0.0%	6	2.5%	18.5	7.8%	19.5	8.2%	6	2.5%
Ecotone (n = 30)	766.8	75.9%	5	0.5%	12.3	1.2%	82.8	8.2%	123	12.2%	20.5	2.0%
Season (n = 102)												
Spring (n = 46)	920.6	73.5%	9	0.6%	14.8	1.2%	171.1	13.7%	128.5	10.3%	8.3	0.7%
Summer (n = 48)	915	68.8%	12	0.9%	25.7	1.9%	120.5	9.1%	208.8	15.7%	48.2	3.6%
Fall (n = 8)	71	74.8%	0	0.0%	2.5	2.6%	4	4.2%	16	16.8%	1.5	1.6%
Year (n = 102)												
2004 (n = 53)	717.6	70.4%	3	0.3%	22	2.2%	88.1	8.6%	163.3	16.0%	25	2.5%
2005 (n = 49)	1189	71.7%	18	1.0%	21	1.3%	207.5	12.5%	190	11.5%	33	2.0%

At Quilomene, season influenced diet ($A = 0.016$, $P = 0.070$) (Tables 1, 2); lizards consumed higher amounts of Coleopteran insects during spring ($P = 0.010$) and more organic debris during summer ($P = 0.022$). During 2005, lizards consumed significantly greater proportions of ants ($P = 0.004$), Coleopteran ($P = 0.041$) and Dipteran ($P = 0.001$)

TABLE 2.—Indicator Species Analysis of significant differences in *Phrynosoma douglasii*'s diet among years, seasons and lizard groups. No significant differences in diet were found across terrain types

Variable	Food item	Indicator value	p-value	Significant group
Year (2004, 2005)	Formicidae	64.2	0.004	2005
	Diptera	14.1	0.041	2005
	Coleoptera	65.9	0.001	2005
Season (spring, summer, fall)	Coleoptera	34.4	0.010	Spring
	Organic Debris	19.3	0.022	Summer
Sex/Age (male, female, yearling, neonate)	Formicidae	35.5	0.091	Female
	Diptera	14.7	0.060	Female
	Coleoptera	32.1	0.070	Female
	Pebbles	16.8	0.077	Yearling



insects than lizards in 2004 (Tables 1, 2). Lizards showed no differences in diet composition among the lithosol, loamy or ecotone terrains.

For all lizards at Quilomene, ants were consumed in highest numbers ($n = 1906.6$ prey items), followed by Coleopterans ($n = 295.6$ prey items) (Table 1). Neonates consumed the highest proportion of ants (88.8%), whereas yearlings consumed the highest proportion of Coleopterans (15.4%). Hemipteran and Dipteran insects occurred in low numbers across all lizard diets ($n = 43$ and 21, respectively). Hemipterans consisted of less than 2.0% of lizard diets for all age/sex classes while dipterans, although consumed in low proportions by all lizards, were consumed at least four times greater by females (1.2%) than males, yearlings or neonates (Tables 1, 2). We stomach-flushed five lizards from Quilomene and expelled soft-bodied Dipterans, a caterpillar larva ~ 2.5 cm length, a juvenile grasshopper and a tick. However, we did not include these data in our analyses and we acknowledge that certain soft-bodied prey may have gone undetected in our analyses of fecal samples.

At Umtanum, ants were also consumed in the highest numbers ($n = 223$), followed by Coleopterans ($n = 27.5$) (Table 1). At Umtanum, ants were consumed by adults in nearly equal proportions (females = 75.5%, males = 77.1%) while yearlings consumed only 40% ants. Although only two fecal pellets from one yearling individual were obtained, yearlings consumed the highest proportion of Coleopterans (40%). Only female fecal pellets contained Hemipteran (8.2%) or Dipteran (0.9%) insects.

Organic debris and pebbles were also consistently found in fecal pellets from both sites. At Quilomene, organic debris accounted for 2.2% of all items found ($n = 58$) and pebbles accounted for 13.2% of all items found ($n = 353.3$). At Umtanum, organic debris consisted of 3.6% of all items found ($n = 10.5$) while pebbles consisted of 6.4% of all items found ($n = 19$). At both sites, 20% of yearling diets consisted of pebbles which tends to be higher than males, females and neonates ($P = 0.067$) (Tables 1, 2). Organic debris was consumed in highest proportions at Quilomene by males (3.3%) and at Umtanum by females (4.2%). Neonates consumed the least amount of organic debris (1.0%) and pebbles (6.3%). In the field, we tossed pebbles within proximity of foraging adult lizards and if the pebble landed within ~ 0.5 m of the lizard, the lizard would almost always lunge toward the pebble. Often, lizards would lick the pebbles into their mouths and spit them out or swallow them; other lizards approached the pebble but lost interest.

The average head capsule size (length*width) of ants consumed by adult males was 0.419 ± 0.269 mm, 0.415 ± 0.169 mm for adult females, 0.274 ± 0.155 mm for yearlings and 0.199 ± 0.129 mm for neonates. Although ant head capsule size varied significantly between lizard groups (ANOVA: $F = 3.67$, $df = 3$, $P = 0.021$), ant head capsule size did not vary significantly among lizard groups relative to SVL (ANCOVA: $F = 0.52$; $df = 3$; $P = 0.67$). Adult males and females consumed higher proportions of larger ant head capsules, whereas neonates consumed higher proportions of smaller ant head capsules and yearlings showed an intermediary preference for ant head sizes ($X^2 = 63.19$, $df = 12$, $P < 0.0001$) (Fig. 2).

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Fig. 2.—Proportion of ant head capsule sizes (length*width) consumed by male ($n = 50$), non-pregnant female ($n = 25$), pregnant female ($n = 25$), yearling ($n = 50$) and neonate ($n = 48$) lizards. Lizards consume higher proportions of larger ants with increasing age/size. Adult lizards also consume primarily ants ranging from 0.0268–0.0468 mm; however, they consume ants ranging within the two largest size classes. Compared to non-pregnant females, male lizards consume the largest ants. Non-pregnant females consume greater numbers of ants from larger size classes ($X^2 = 20.4$, $df = 3$, $P < 0.001$)

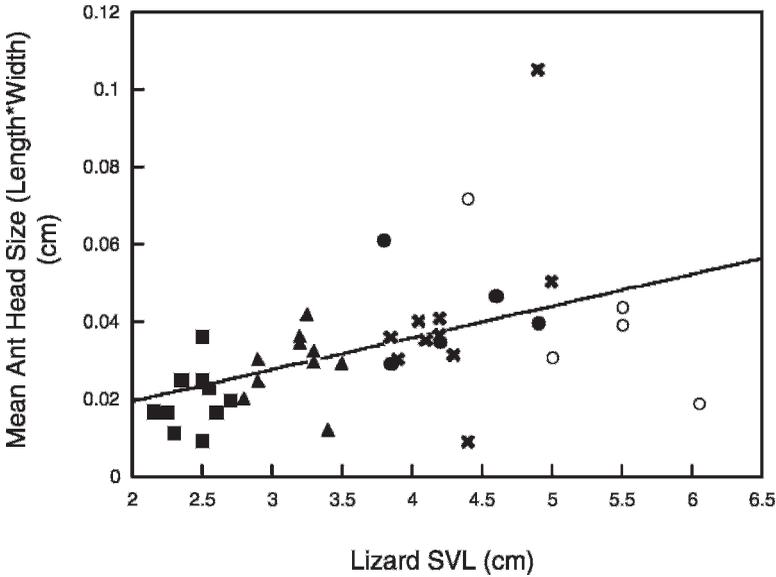


FIG. 3.—Mean ant head capsule sizes consumed by lizards based on SVL. Squares represent neonates, triangles represent yearlings, crosses represent males, filled circles represent females and open circles represent pregnant females. There is a significant positive correlation of lizard body size (SVL) with mean ant head capsule size ($n = 40$, $R^2 = 22.6\%$, $F = 11.08$, $P = 0.002$). No significant correlations were observed within lizard age/sex classes ($P > 0.05$)

Mean ant head size (length*width) showed an overall positive correlation with lizard SVL when all lizard classes were pooled ($R^2 = 22.6\%$, ANOVA: $F = 11.08$, $P = 0.002$) however, the within group correlations for male, female, yearling and neonate lizards were not significant (Fig. 3). Adult pregnant females showed a strong negative correlation of mean ant head size compared to SVL ($R^2 = 70.6\%$; ANOVA $df = 4$, $F = 7.19$, $P = 0.075$), adult non-pregnant females showed no correlation ($R^2 = 1.8\%$; ANOVA $df = 4$, $F = 0.05$, $P = 0.831$), adult males showed a strong positive correlation ($R^2 = 34.2\%$; ANOVA $df = 9$, $F = 4.15$, $P = 0.076$), yearlings showed no correlation ($R^2 = 1.6\%$; ANOVA $df = 9$, $F = 0.13$, $P = 0.730$) and neonates showed a weak positive correlation ($R^2 = 5.1\%$; ANOVA $df = 9$, $F = 0.43$, $P = 0.532$).

Lizard groups consumed significantly different proportions of ant genera ($X^2 = 221.8$, $df = 8$, $P < 0.001$); adult male and female lizard consumed almost exclusively on the largest ant species, *Camponotus* (94% and 96%, respectively). Pregnant females consumed minimal numbers of *Tetramorium* (8%), which are of intermediate size, while non-pregnant females consumed *Camponotus* species exclusively. Yearlings consumed mostly *Camponotus* species (75%), but also the smallest ant species, *Pheidole* (21%), while neonates consumed almost equal proportions of *Pheidole* (53%) and *Camponotus* (45%) species. *Tetramorium* species were absent from adult male diets and consisted of 5% or less in diets of all other lizard classes.

Soldiers and workers of *Camponotus* ants were consumed in significantly different proportions among lizard groups ($X^2 = 20.6$, $df = 4$, $P < 0.001$). Typically soldiers are larger-sized than adults however, soldiers do overlap in size with workers. Adult males consumed nearly equal proportions of workers (49%) and soldiers (51%) and adult females consumed more workers (61%) than soldiers (39%). However, pregnant females consumed more workers (77%) than soldiers (23%) while non-pregnant females consumed equal

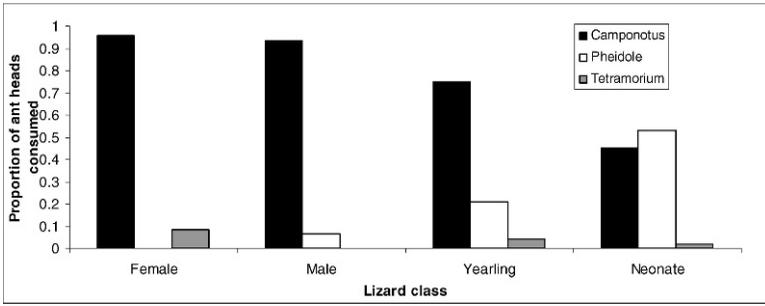


FIG. 4.—Proportion of ant species consumed by lizard group. Lizards show ontogenetic variation in proportions of ant species consumed ($X^2 = 50.15$, $df = 6$, $P < 0.001$). Neonate and yearling lizards consume a higher amount of different ant species than adults that feed primarily on *Camponotus*

amounts of workers and soldiers (50%). Yearling lizards consumed only 22% workers and 78% soldiers while neonates consumed 32% soldiers and 68% workers (Fig. 5).

DISCUSSION

In many lizard species diet composition is influenced by environmental variables including prey availability, season and habitat (Pianka, 1973), and by ontogenetic variation (Castilla *et al.*, 1991; Preest, 1994). *Phrynosoma douglasii* shows variation of its diet in response to year, season and age/sex classes. Because prey populations are subject to seasonal changes and microhabitat differences, it should not be surprising that the diet of an insectivorous predator also shows variation over time and within different habitats. Similarly, many insects and all insect larvae remain undetectable in fecal pellets because they lack chitin and are digested beyond recognition. However, this information, in addition to diet data from Zamudio (1996) suggests that *P. douglasii* consumes a variety of other, non-chitinous invertebrates.

Although adult, yearling and neonate lizards occupy the same habitat and, thus, likely experience the same prey resource availability, these age classes show differences in diet composition; neonates feed almost exclusively on ants, whereas adults consume fewer ants and greater proportions of Coleopteran and Hemipteran insects. Similarly, neonate and

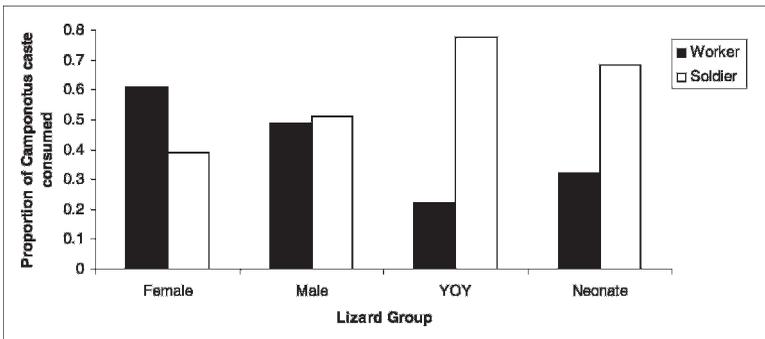


FIG. 5.—Proportion of *Camponotus* spp. ant castes consumed by lizard groups. Lizards consume workers and soldiers in significantly different proportions ($X^2 = 13.47$, $df = 3$, $P = 0.004$)

yearling lizards consume ants, that are significantly smaller and more taxonomically diverse than adults. We cannot say whether this pattern reflects a preference of neonates (or yearling lizards) for smaller ant taxa (e.g., *Pheidole* and smaller individuals of *Camponotus*) and/or morphological limitations of smaller lizards. The latter limitation, if present, might represent an instance of constraints from morphology (reduced jaw size and gape, proportional head size relative to body size), physiology (reduced bite force and tongue capture ability), less experience with handling larger prey items than adults, dietary niche partitioning (intraspecific competition reduction), differences in food nutrient and energy assimilation and/or increased success rates of preying on smaller insects (i.e., costs of increased prey handling time) (Rutsche, 2004; Suarez *et al.*, 2000).

Thus, the trend for *Phrynosoma douglasii* appears to be that neonate lizards gradually shift from a diet of high proportions of smaller ants towards a diet of more Coleopterans and fewer, albeit, larger ants, as adults. However, yearling lizards do not align with this trend; yearling lizards consume the lowest proportion of ants and the highest proportion of Coleopterans and pebbles. Interestingly, yearling lizards are not always larger or heavier than neonates, particularly upon emergence from their first hibernation. At Quilomene, yearlings overlap in SVL and mass with neonates, however, no fecal pellets from these small yearling lizards were collected and thus the composition of their diets and sizes of prey items is not known.

Ontogenetic variation in resource allocation is a function of life history variation and directly affects individual fitness (Dudycha and Lynch, 2005). The high proportion of pebbles and Coleopterans in yearling diets might be a result of yearling lizards attempting to capture larger prey items, independent of the energetic costs associated with capturing and ingesting a large prey item. In the absence of reproduction, immature organisms primarily allocate energy towards maximizing growth. Hence, the energetic cost of consuming larger prey items is reduced. As adults, particularly pregnant females, *Phrynosoma douglasii* might return to consuming a higher proportion of small prey items that require less energy to capture and ingest since more energy is allocated towards reproduction and energy storage (Tracy, 1998). This might also explain the greater variety of prey item sizes consumed by adult lizards, particularly by pregnant females where sizes of ants consumed shows a negative correlation with SVL.

Based on the amount of organic debris and pebbles consumed, in addition to responses elicited by tossing pebbles at actively foraging lizards, lizards might also be selecting prey items based on movement rather than type. This foraging behavior is described by Schoener (1969) as a Type I predator whereby lizards passively seek out and evaluate the prey potential based on size and distance and is typical of horned lizards (Powell and Russell, 1984). Milne and Milne (1950) noted that movement is likely the primary determinant of prey consumption; Weese (1907, 1919) also noted *Phrynosoma modestum* ingesting a lead shot rolling downhill and windblown sand grains. Wind is common at both Quilomene and Umtanum where gusts exceed 30 mph, especially during spring and early summer. Foraging lizards might consume higher numbers of pebbles and vegetation in response to the wind blowing the objects. Yearlings also consume the highest proportion of pebbles and it is likely that behaviors associated with foraging techniques and optimization of those, are likely an effect of this.

Although lizards belonging to the short-horned lizard clade have more robust morphologies, including a greater bite force, compared to all other horned lizard species, morphological data for *Phrynosoma douglasii* were not included in Meyers *et al.*'s (2006) study because no diet data were available for this species. Thus, it is not known whether *P. douglasii*

has reduced morphologies congruent with other lizards from the short horned lizard clade. Though, based on its phylogenetic relatedness in addition to diet data from this study, *P. douglasii* is likely congruent with *P. hermandesi*, *P. ditmarsii* and *P. orbiculare* in its broad dietary niche and generalist feeding habits (Meyers *et al.*, 2006).

In light of its dietary composition, *Phrynosoma douglasii* does not appear to be as highly myrmecophagous compared to other horned lizard species, particularly those outside of the short horned lizard clade. Variation in *P. douglasii*'s diet across seasons and years, in addition to the foraging behavior and diversity and quantity of non-ant prey items consumed, suggests that *P. douglasii* is a generalist feeder compared to other horned lizard species. Ontogenetic differences in its diet also support generalist feeding behaviors; although neonates consume primarily ants, adults and especially yearling lizard diets, include high proportions of non-ant prey items. Similarly, body size is not a limiting factor of prey items consumed by lizards, particularly yearling and females, further suggesting that optimal foraging in lizards is associated with variables other than prey item size exclusively.

Even though *Phrynosoma douglasii* is not an ant specialist relative to other highly myrmecophagous horned lizard species, ants are obviously an important component of their diet, especially for neonates. At least three different ant genera, in a diversity of sizes, were represented in the diets of *P. douglasii*. Our results suggest that management efforts aimed at protecting *P. douglasii* populations and habitats should also consider maintaining the biodiversity of the invertebrate taxa on which this lizard depends.

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