

The diet of the eastern short-horned lizard (*Phrynosoma douglassi brevirostre*) in Alberta and its relationship to sexual size dimorphism

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The diet of *Phrynosoma douglassi brevirostre* in Alberta was investigated and potential prey abundance was examined. The Alberta populations are less strongly myrmecophilous than the average for the species, when the diet is broken down by prey item counts. Breakdown of the diet by prey dry weight shows that ants, nonsilphid Coleoptera, and Orthoptera are the major components of the diet. The range of prey sizes taken is large, but the species concentrates on a small range of prey sizes, from 2.1 to 6.0 mm in length. Arthropod abundances are significantly different between all three study sites, and there is always a significant difference in distribution between the pooled pitfall samples and the pooled gut samples of any one study site. The general dissimilarity in distribution between the pooled gut samples of any two study sites suggests some dietary flexibility. The size range of prey items taken by the large lizards includes and slightly exceeds the size range of prey items taken by medium-sized lizards, and there is a significant positive correlation of average prey size with lizard snout–vent length. There are significant differences in the prey sizes, prey dry weights, and prey item counts between large lizards and medium-sized lizards, indicating intersexual dietary partitioning.

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La diète de *Phrynosoma douglassi brevirostre* en Alberta a fait l'objet d'une étude et l'abondance des proies potentielles a été examinée. L'évaluation de la diète par dénombrement des proies révèle que les populations d'Alberta sont moins strictement myrmécophages que la moyenne des populations de cette espèce. L'analyse de la diète par évaluation de la masse sèche démontre que ce sont les fourmis, les coléoptères autres que les silphidés et les orthoptères qui constituent les principaux éléments de la diète. L'étendue des tailles des proies capturées est grande, mais les lézards concentrent leurs efforts de capture sur une petite étendue de tailles et consomment surtout des proies de 2,1–6,0 mm. L'abondance des arthropodes varie significativement aux trois sites d'échantillonnage et il y a toujours une différence significative dans la répartition entre les échantillons de proies capturées dans les pièges à fosses et les échantillons de contenus stomacaux à un même site. Les différences de distribution entre deux sites différents, telles que révélées par l'analyse des contenus stomacaux, témoignent d'une certaine flexibilité alimentaire chez le lézard. Les gros lézards consomment des proies réparties sur une échelle de tailles qui englobe celle des proies des lézards moyens et la dépasse légèrement et il y a une corrélation positive significative entre la taille moyenne des proies capturées et la longueur du museau à l'anus. Il y a des différences significatives entre les gros lézards et les lézards de taille moyenne en ce qui concerne la taille des proies capturées, la masse sèche des proies et leur nombre; il semble donc s'effectuer un partitionnement alimentaire intersexuel.

[Traduit par le journal]

Introduction

Phrynosoma douglassi, the short-horned lizard, ranges from west central Mexico (Reeve 1952) to southeastern Alberta and southwestern Saskatchewan (Logier and Toner 1961), occupying a variety of high-altitude habitats over this latitudinal range (Smith 1946; Reeve 1952; Montanucci 1981). *Phrynosoma d. brevirostre*, the northern short-horned lizard, has a limited scattered distribution in southeastern Alberta, ranging north to approximately 50° N (and thus representing the northernmost record of the family Iguanidae) and west to approximately 111°45' W. The climate of this area is characteristically dry steppe (Longley 1977) and the climax vegetation is the mixed grass prairie association (Coupland 1950, 1961; North 1976).

Most dietary data available for this species consist of small samples. Ants predominate in the diet of *P. d. ornatissimum* from various locations in Utah (Knowlton 1934, 1942; Knowlton and Janes 1934; Knowlton and Thomas 1936), and Hotton (1955) noted that *P. douglassi* feeds mainly on ants. For the Alberta populations only two brief accounts of the diet have been published (Milner 1979; Laird and Leech 1980).

Taken overall, relatively few accounts of the diets of phrynosomes have been published. The most synoptic account is that of Pianka and Parker (1975), in which the collective diet of the genus is typified as consisting mainly of ants (the proportion varying among the 13 species investigated), although beetles may occasionally dominate. More detailed species-specific

dietary information is available for *Phrynosoma cornutum* (Little and Keller 1937; Hotton 1955; Whitford and Bryant 1979), *P. platyrhinos* (Knowlton 1934, 1942; Knowlton and Janes 1934; Knowlton and Thomas 1936; Hotton 1955; Tanner and Krogh 1973; Pianka and Parker 1975; Rissing 1981), *P. orbiculare* (Montanucci 1981), *P. mcalli* (Norris 1949), and *P. modestum* (Schaffer and Whitford 1981). The predator–prey relationships between phrynosomes and ants have been investigated by Whitford and Bryant (1979, *P. cornutum*) and Schaffer and Whitford (1981, *P. modestum*). Rissing (1981) has described the prey preferences of *P. platyrhinos* and its effect on ant community structure.

In the context of the above, *Phrynosoma douglassi* appears to be aligned with its congeners as a dietary specialist (Hotton 1955; Pianka 1966; Pianka and Parker 1975). The distinction between dietary generalists and specialists can be rather *ad hoc*, however, and definition of the two categories depends upon the taxonomic level under discussion, either of predator or prey (Schoener 1971; Fox and Morrow 1981). “Specialist” in the case of *Phrynosoma* refers to the primarily myrmecophilous diet (Hotton 1955; Pianka 1966; Pianka and Parker 1975); indeed, phrynosomes are regarded as the only North American lacertilian ant specialists. Such specialization is rendered feasible because of the relatively great abundance of ants in North American deserts (Pianka 1966).

In discussing the partitioning of the North American desert environment between 12 lizard species, Pianka (1966) catego-

rized phrynosomes as sit-and-wait predators exploiting the open spaces between bushes. The clumped distribution of ants, as well as the large numbers that must be eaten to satisfy caloric requirements, is most reasonably correlated with such a mode of predation, although Toft (1981) found the opposite to be true of Panamanian litter-foraging anurans. In association with their foraging mode, phrynosomes exhibit a number of morphological and behavioural peculiarities apparently correlated with their dietary habits. Hotton (1955) placed phrynosomes (*P. douglassi*, *P. cornutum*, and *P. platyrhinos*) in his dentition group B, together with two species of *Sceloporus*, an allied genus. This group was characterized by an uncomplicated homodont dentition and categorized as predators upon prey of low activity and "intermediate integument" (chiefly ants).

An additional suite of interrelated features with dietary associations was outlined by Pianka (1966) and Pianka and Parker (1975). The low per-unit caloric value of ants was correlated with the consumption of large numbers of individuals, and this in turn was correlated with the proportionately large stomach volume typical of phrynosomes. Such characteristics, which unite to impose a stocky build, cryptic colouration, and a spiny body are advantageous to a sit-and-wait predator that must spend a great deal of time in the open; the stocky build does not favour rapid retreat as a means of defence. In association with this form and these habits, thermoregulation will tend to become relaxed, since much time must be spent exposed in the open.

Phrynosomes display the characteristics of model I predators, as outlined by Schoener (1969a), passively scanning the surrounding terrain from some coign of vantage and pursuing prey items if they satisfy a certain set of size and distance criteria. Considerations of optimal size for solitary model I predators predict that they may display sexual size dimorphism in areas where few or no competitors exist, owing to size-associated dietary niche partitioning (Schoener 1969a, 1977). The theoretical rationale for body-size differences sufficing as a dietary niche partitioning factor has been investigated by Schoener (1969a, 1969b) and Wilson (1975).

In view of the well-demarcated sexual size dimorphism displayed by *P. d. brevirostre* in Alberta (Powell 1982), dietary niche partitioning is to be expected, particularly if these populations are food limited. Such intraspecific competition for food resources could be invoked as the selective impetus that initiated and maintains the dimorphism.

The principal aim of this study was to examine and typify the diet of *P. d. brevirostre* in its northern range-marginal populations in Alberta. To do so, prey abundance at each study site was examined to determine how opportunistic *P. d. brevirostre* is as a predator, and as a basis for comparisons of diet between study sites. It was hypothesized that dietary differences between the size-age groups, and thus between the sexes, would exist and would be associated with the sexual size dimorphism typical of these populations. Variations in diet between populations at each study site, and temporal variation in diet within each population, were also investigated.

Materials and methods

Data collection

Lizards used in this study were hand captured. Snout-vent length (SVL), head length, and head width were recorded for each lizard at the time of capture, regardless of whether it was a recapture or not. Gut contents were sampled by means of a stomach pump (Legler and Sullivan 1979), using a 10-mL syringe with a 3-mL pulse capacity.

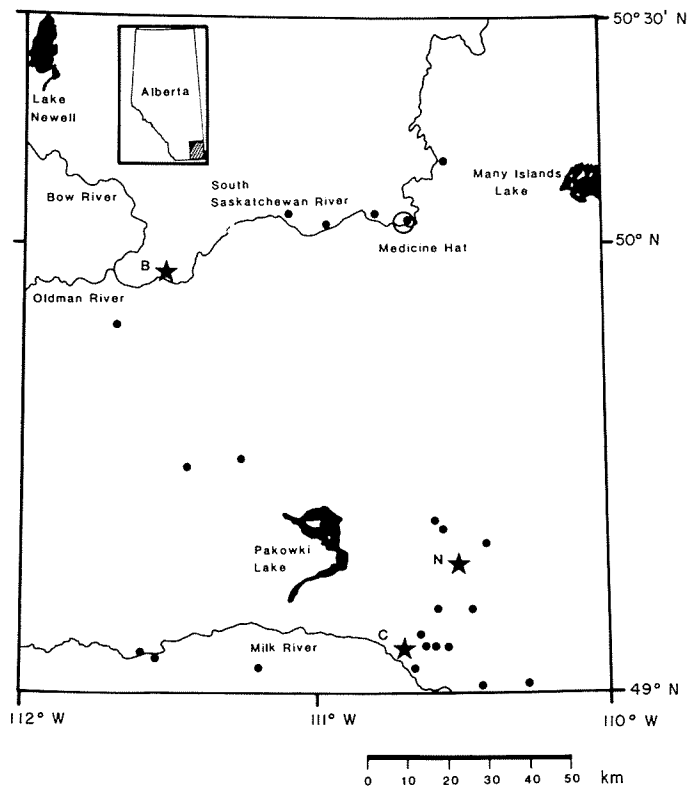


FIG. 1. The range of *Phrynosoma douglassi brevirostre* in south-east Alberta (hatched area of inset map). Locations marked with stars represent study sites discussed in this paper. B, Bow Island; N, Nemiskam; C, Comrey.

In this manner, 97 samples were taken from 76 individuals, with 15 lizards being sampled twice and 3 lizards being sampled on three separate occasions. After gut flushing and a short recovery period, the lizards were released at the capture site.

The mortality rate from gut flushing was 5.2%; those that succumbed were all small lizards, and death was presumably due to excessive pumping pressure causing rupture of the gut. After the occurrence of these initial fatalities, lizards of less than 4.5 g body weight and 40.0 mm SVL were not subjected to gut flushing. The 1980 collecting permit issued by the Alberta Department of Lands and Forests did not allow collection of an adequately large sample for postmortem gut analysis, and none of the populations studied was large enough to withstand great losses, particularly of new recruits. Thus no information could be gathered on the diet of young of the year individuals; the youngest individuals sampled were approaching 1 year in age.

Dietary data were taken at three separate localities within the range in Alberta (Fig. 1). The population at Comrey (49°05' N, 110°41' W) is located in the ecotone between mixed grass prairie and an extensive series of badlands. Phrynosomes were found in a narrow strip along the south-facing edge of the grassland, typified by thin sandy soil, eroded patches of clay hardpan, and exposed bedrock. The scanty uneven vegetation cover consisted mainly of short grasses and forbs, with a scattering of *Artemisia* bushes.

The population at Nemiskam Community Pastures (49°17' N, 110°31' W) is found on a long low (75 m high) ridge, extensively dissected by wide shallow flat-bottomed ravines. The high ground between the ravines, and the upper slopes of the ravines themselves, are covered with plants of the *Bouteloua-Stipa* association, with a scattering of *Artemisia*. The substrate of the lower slopes and bottoms of the ravines consists of finely divided Bearpaw shale, forming extensive regions of 2-m dunes, interspersed with alluvial fans. Creeping juniper (*Juniperus horizontalis*) predominates on the shale, forming extensive mats. Grasses, wild rose (*Rosa* sp.), and *Artemisia* are also

TABLE 1. Gut-sampling periods (1980) with sample size taken at each study site

Study site	Sampling period ^a												
	1	2	3	4	5	6	7	8	9	10	11	12	13
Comrey	6			4			1			5		3	
Nemiskam		6				3		11			12		
Bow Island			9		11				13				13

^aDates for the sampling periods are as follows: 1, 20–21 June; 2, 25–26 June; 3, 28–30 June; 4, 9–10 July; 5, 13–16 July; 6, 18 July; 7, 29 July; 8, 30 July – 4 August; 9, 6–8 August; 10, 10–11 August; 11, 23–26 August; 12, 29–30 August; 13, 31 August – 4 September.

present in small numbers in these areas, but total vegetation cover is not greater than 50%.

The population at Bow Island (49°55' N, 111°30' W) is located on the southwest-facing north side of the South Saskatchewan River canyon. This side of the canyon is 70 m high and extensively dissected by a series of steep gullies extending from the river's floodplain. The upper slopes of these gullies are covered with a thin growth of short grasses, with many bare areas. Phrynosomes were confined to the upper third of these slopes, and were not found on the flat grassland at the top of the canyon.

Sampling at Comrey, Nemiskam, and Bow Island was initiated on June 21, 1980 and continued at intervals until September 4, 1980 (Table 1). Gut contents were stored in 70% EtOH and transported to the laboratory for analysis.

Gut content classification

The blotted wet weight (in EtOH) of each whole gut sample was taken with an analytical balance. The contents of each sample were then categorized. Insects were identified to order, except for ants, which were diagnosed to family; spiders and mites were classed together as Arachnida. The number of individual prey items in each taxon per stomach were determined by counting head capsules. Body length of complete prey items was measured to the nearest 0.1 mm and the resulting data sorted into prey size classes ($i-x_i$), at 2-mm intervals. After these analyses were completed, the individual gut samples were allowed to air dry in plastic petri dishes for 2 months, then further dried at 60°C for at least 24 h in a gravity oven. Each gut sample was then subdivided into prey taxa groups and weighed to the nearest 10^{-4} g.

Statistical analysis

With the exceptions of the estimates of overlap, niche breadth and evenness, the statistical significance of size differences between the two lizard size groups, and tests of difference in distribution of items between groups, all statistical analyses of the data were performed using the subprogrammes of the statistical package for the social sciences (SPSS) (Nie *et al.* 1975). Separate regression analyses were performed on average prey size as a dependent variable against lizard SVL, lizard head width, and lizard head length. The significance of the regression coefficients were tested by means of *F*-tests (Sokal and Rohlf 1969). A probability greater than 0.05 was not considered to be significant.

The lizards were divided into two size classes on the basis of the growth models derived in an associated study (Powell 1982). Group 1 ranged in size from 40.0 to 55.0 mm SVL, and was composed of all yearling females, all yearling males, and all but one of the adult males sampled. Group 2 ranged in size from 56.0 to 76.5 mm SVL, and was made up almost completely of adult females, with one adult male. These two groups do not correspond exactly to the size groups defined in an associated study of thermal biology (Powell 1982), in which group 1 is composed of neonate individuals, group 2 of yearling individuals and adult males, and group 3 solely of adult females. As was explained above, neonates and small yearlings were too small to include in the dietary study. Breeding-age females were divided from males and subadult females both on the basis of size and because the two groups have different energetic demands. Gravid females must satisfy the energetic demand of vitellogenesis (Packard *et al.* 1977)

and gravidity (Guillette 1982), and the added demand of locomotion while gravid, while males and subadult females do not endure these costs. The two lizard size groups were statistically different in SVL ($t_c > t_{0.05}$) as determined by the Minitab two-sample test (Ryan *et al.* 1979). Gut-content data, broken down by prey item count, prey dry weight, and prey size, were pooled for each lizard size class.

In this study, the dietary niche is considered to be the frequency distribution of the range of dietary resources utilized by the species or a portion of the species (Schoener 1977). Since the data presented in this study represent an estimate of the dietary niche, rather than the whole niche, the prey frequency distributions will be considered to be the realized dietary niche.

The diversity of the diet was approximated by the Shannon–Weaver index (H'), using the base of two (Poole 1974). Dietary evenness (the intensity with which the species exploits different parts of the dietary spectrum) was determined by J (Poole 1974). Both statistics were calculated for prey item counts, prey dry weight, and prey size distributions for each lizard size class and for pooled data from all samples. H' and J were also calculated for prey item counts and prey dry weight for samples pooled by sampling period and study site, and for samples pooled by study site alone.

Linton *et al.* (1981) have demonstrated that R_m , Morisita's overlap index as modified by Horn (1966), is a more realistic measure of overlap than R_o , Schoener's overlap index (Schoener 1970) when actual overlap is greater than 85%. Accordingly, dietary overlap between any two pooled groups of gut samples was estimated first by R_o , and if the estimated overlap exceeded 85%, the R_m estimate was calculated. Overlap estimates of prey item counts, prey dry weight, and prey size distribution were calculated between the lizard size classes. Overlap estimates of prey item counts and prey dry weight distributions were calculated for gut samples pooled by sampling period and study site, and for gut samples pooled by study site alone. In all cases, an overlap value of greater than 70% was considered to be high, and an overlap value of less than 50% was considered to be low. Kolmogorov–Smirnov two-sample tests (Siegel 1956) were used to test the statistical significance of differences in distribution of prey size between the lizard size classes. Comparisons of prey item counts or prey dry weight between any two pooled groups were performed by means of chi-square tests (Sokal and Rohlf 1969). A probability greater than 0.05 was not considered to be significant.

Potential prey abundance

The potential prey abundance at each study site was sampled by means of pitfall traps (10.0 cm diameter and 4.5 cm deep, containing approximately 150 mL of 5% formalin). Nine pitfall traps were set at each study site in each sampling period (Table 2). The location of the pitfalls at each study site did not vary between sampling periods. On collection, pitfall contents were preserved in 70% EtOH and later analyzed in the laboratory. Arthropods were identified and counted according to the same criteria as the gut content samples. Blotted wet weights of each taxonomic group present were taken. Silphid beetles, present in large numbers in some samples, were eliminated from the analysis, since they did not appear in any of the gut content samples and their great size and abundance biased the potential prey abundance analyses.

Data were pooled for each sampling period at each study site, and for each study site for all sampling periods. Diversity and evenness for

TABLE 2. Average arthropod number and average weight of arthropods per pitfall trap in 1980. Pitfall trap samples pooled by location and sampling period

	Sampling period ^a							
	1	2	3	4	5	6	7	8
Average arthropod no.								
Comrey	6.272		7.611					6.800
Nemiskam		4.022		18.370		3.610		
Bow Island					25.055		3.944	
Average weight of arthropods								
Comrey	0.102		0.034					0.049
Nemiskam		0.072		0.179		0.103		
Bow Island					0.302		0.158	

^aDates for the sampling periods are as follows: 1, 8–17 May; 2, 20–25 May; 3, 20–24 June; 4, 23–26 June; 5, 28–30 June; 6, 1–4 August; 7, 5–9 August; 8, 10–11 August.

each pooled sample were estimated by H' and J , respectively, calculated on the bases of item counts and wet weights of the pooled samples. Overlap between any two pooled pitfall samples was estimated by R_o or R_m , as described above. Overlaps between pooled pitfall samples and pooled gut samples from the same study site and sampling period were also estimated by these statistics. These overlap values were tested for significance by chi-square tests (Sokal and Rohlf 1969), as above.

Results

Characteristics of the diet

A breakdown of the pooled gut samples by prey item count (Table 3) indicates that ants constitute the majority of the diet (76.93%), with nonsilphid Coleoptera making up the next largest component (13.36%). Dietary diversity by prey item count is relatively small (1.26), and its evenness is low (0.40), owing to the predominance of ants in the diet.

When the pooled gut samples are broken down by dry weight (Table 3), prey distribution is seen to be more equitable. Orthopterans, nonsilphid coleopterans, and ants form the main components of the diet, and ants are not greatly in the majority. Orthopterans and, to a lesser extent, nonsilphid coleopterans, assume a much greater importance by dry weight than they do by item count. The other prey taxa are represented in approximately the same proportions by dry weight and item count. Dietary diversity by prey dry weight is greater than it is by prey item count, as is evenness.

When the pooled gut samples are sorted into size categories (Table 4), a skewed distribution is evident. Prey in the size range of 2.1–6.0 mm constitutes the bulk of the diet, but there are a number of greater prey sizes that are taken with low frequency. The diversity (1.78) and evenness (0.51) of prey sizes taken are greater than the diversity and evenness of the prey item counts (Table 3), but lower than the corresponding statistics for prey dry weights (Table 3).

In general, *Phrynosoma douglassi brevirostre* in Alberta may be said to utilize a fairly broad range of prey types, by taxonomic group or by size class, but only a fraction of these prey taxa comprise the bulk of the diet. This is reflected in the relatively small diversities and relatively low evenness of the pooled prey item count and prey size class breakdowns (Tables 3 and 4). When the dry weights of the prey taxa are considered, dietary diversity and evenness are much higher (Table 3), but three prey taxa constitute 82.51% of the pooled samples by dry weight.

Relationship between diet and lizard size

Regression analysis of average prey size (PS) against lizard SVL (Fig. 2) indicates an extremely significant linear relationship ($F_c > F_{0.001}$). Regression of PS against lizard head width and against lizard head length yielded similar extremely significant ($F_c > F_{0.001}$) relationships. PS is a function of jaw dimensions, which are a function of SVL. Large lizards tend to eat prey of a greater average size than do small lizards. The greater degree of scatter about the regression line with increased SVL (Fig. 2) indicates that larger lizards, as a group, take a greater range of average prey sizes than do smaller ones.

Examination of the prey item count for both lizard size groups (Table 5) reveals that group 1 and group 2 lizards have very similar diets. Dietary diversities and evenness for the two groups of lizards are very similar (Table 5). Overlap (R_m) between group 1 and group 2 is 0.99, indicating that they are eating the same prey taxonomic groups in almost the same proportions, but the chi-square statistic indicates a significant difference in the distributions.

A breakdown of diet by dry weight of each prey taxonomic category reveals some differences between the two lizard size groups (Table 5). Dietary diversities and evenness are similar for both groups, and larger in each case than they were for the prey item count breakdown (Table 5). Dietary overlap (R_o) is 0.81, and the chi-square test indicates that there is a significant difference in prey weight distributions between the lizard size groups. The main differences between the lizard size groups are that group 2 lizards consume a greater percentage of orthopterans (group 2, 26.48%; group 1, 11.59%) and a lower percentage of ants (group 2, 31.81%; group 1, 45.50%). There is relatively little difference in representation between the two lizard size groups with regard to the other prey taxa.

There are some differences in the distributions of prey sizes taken by the two lizard size groups (Table 4). Group 1 lizards take a smaller size range of prey items (prey size classes $i-ix$) than group 2 lizards (prey size classes $i-xi$). The diversity and evenness of the prey size distribution taken by group 1 lizards are, therefore, slightly lower than those of the prey size distribution taken by group 2 lizards. Dietary overlap between the lizard size groups on the basis of prey size distributions is less than the overlap on the basis of prey dry weights (Table 5). The Kolmogorov–Smirnov two-sample test (Table 4) indicates that large lizards take significantly larger prey than do medium-sized lizards.

TABLE 3. Taxonomic breakdown of dietary data (percentage of diet by item count and dry weight) with diversity (H') and evenness (J) statistics. Data pooled from all gut samples, all locations

	Prey taxonomic group										H'	J
	Arachnida	Orthoptera	Lepidoptera	Coleoptera	Diptera	Hemiptera	Homoptera	Nonformicid Hymenoptera	Formicidae			
Prey item count	1.99	1.65	0.95	13.36	0.34	2.08	0.55	2.14	76.93	1.26	0.3966	
Prey dry weight	2.40	21.66	2.42	24.61	0.92	4.25	0.47	7.03	36.24	2.33	0.7341	

NOTE: Sample size, 3264 items; dry weight, 5.58 g.

Potential prey abundance

Potential prey abundance was sampled during six gut-sampling periods, two at each site (Table 2). Arthropod counts show variation over time at each location. Dipterans, coleopterans, and ants generally constitute the bulk of the arthropods trapped. The arthropod diversity and evenness at each study site increased, to some extent, at successive sampling periods. Bow Island had the greatest diversity (Table 6). The diversities and evenness of the pooled samples from Nemiskam and Comrey increased between June and August. Changes and differences in potential prey abundance are reflected in overlap between study sites and between sampling periods. Overlap between sampling periods at the same study site is generally low; Bow Island has the greatest diversity, and is apparently the most invariant study site, by count, in terms of prey abundance. Comparisons between study sites within the same month show that there is a strong difference between Nemiskam and Comrey in June but high overlap between Nemiskam and Bow Island, and between Bow Island and Comrey, in this month. All three study sites show high overlap between one another in August.

Arthropod diversity and evenness calculated from pooled wet weights at each study site (Table 6) are generally lower than the corresponding statistics calculated from item counts. Beetles and dipterans generally predominate by wet weight.

The diversities and evenness of pitfall sample item counts, pooled by study site only, are not greatly different from one another (Table 6). The major differences between study sites in the pitfall item counts are in the proportion of ants. Pairwise chi-square tests of the pitfall item counts indicate that prey abundance at each locale is significantly different from those at the other two (Table 7). The diversity and evenness of the wet weights of the pooled pitfall contents for Comrey are much greater than the diversities and evenness of the other two pitfall sample wet weights pooled by study site (Table 6). As with pooled pitfall item counts, each study site has a significantly different arthropod wet weight distribution from the other two (Table 7).

Variation between location and sampling periods

The pooled gut-sample data for the populations at each of the three study sites show some differences in prey consumed. Prey item counts (Table 8) show a higher percentage of coleopterans and arachnids and a lower percentage of ants consumed at Nemiskam than at the other two study sites. Dietary diversity and evenness are highest for the population at Nemiskam by prey item counts; the other two populations are similar in dietary composition, niche breadth, and evenness (Table 8). There is no significant difference in pooled prey item distribution between Comrey and Bow Island, but both pooled prey item distributions differ significantly from that of Nemiskam (Table 9).

Prey breakdown by weight (Table 8) reveals a higher percentage of ants and hemipterans and a lower percentage of orthopterans in the diet of the population at Comrey, compared with those of the other two sites. Dietary diversity and evenness in the diet of the population at Comrey are lower than those of the populations at the other two study sites. The population at Bow Island has a higher percentage of orthopterans and non-formicid hymenopterans, and a lower percentage of coleopterans, than those at the other two study sites. The population at Nemiskam has the greatest dietary diversity and evenness of the three study sites. The pooled prey dry weight distribution

TABLE 4. Breakdown of prey by item size (percentage of diet by item count) with diversity (H') and evenness (J) statistics; dietary overlap tested by Schoener's overlap index (R_o) and Kolmogorov-Smirnov two-sample test (χ^2)

	Prey size groups ^a											H'	J	R_o	χ^2
	i	ii	iii	iv	v	vi	vii	viii	ix	x	xi				
Pooled data (all gut samples, all locations)	4.39	39.32	44.96	7.83	1.62	0.78	0.37	0.37	0.16	0.10	0.10	1.78	0.5144	—	—
Lizard size-class data															
Group 1 (40–55 mm SVL)	5.74	50.43	37.13	4.26	1.28	0.53	0.21	0.32	0.10	0.00	0.00	1.64	0.4727	0.7552	76.04 ($p < 0.001$)
Group 2 (56–76.5 mm SVL)	3.08	28.62	52.51	11.28	1.95	1.03	0.51	0.41	0.21	0.21	0.21	1.82	0.5268		

NOTE: Sample sizes (prey items): pooled data, group 1, 940; group 2, 975.
^aPrey size groups represent incremental 2-mm steps, from 0.0–2.0 mm (i) to 20.1–22.0 mm (xi).

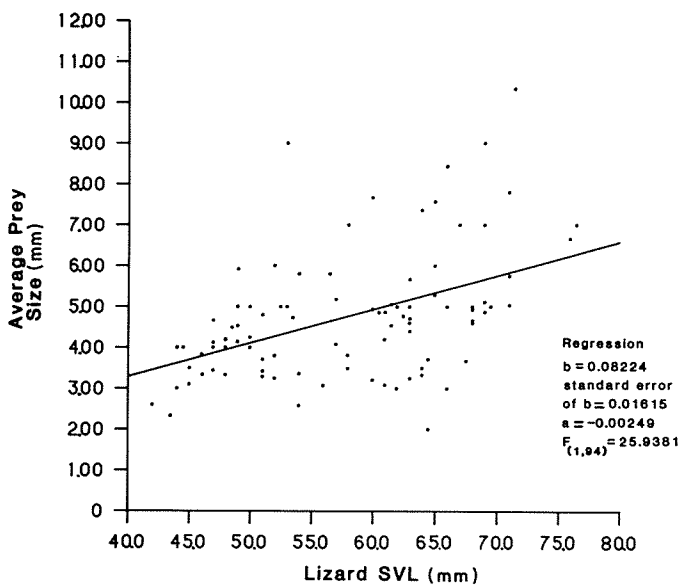


FIG. 2. Plot of average prey size against lizard SVL, with regression line and relevant regression statistics.

of the population at each study site is significantly different from those of the populations at the other two study sites (Table 9).

Pooled gut-sample variations over time for the populations of each study site are best considered in terms of diversity and evenness. All three populations show changes in diversity and evenness for both prey item counts and prey dry weight breakdowns over the study period, but these bear little relation to the statistics for pitfall samples at the corresponding location. Prey item count and pitfall sample item count pooled by study site only are consistently significantly different when compared pairwise (Table 10). Variations in arthropod populations over time at any one study site may be related to fluctuations in weather (Dunham 1980) and conclusions concerning dietary differences between study sites are best drawn from pooled data (Tables 8 and 9).

Discussion

Potential sources of bias

There are obvious drawbacks to the methods of gut content analysis used here. Lack of data on gut passage time makes it difficult to estimate how representative head capsule counts are

of true predation rates. The amount of chitin in an arthropod's cuticle, and the degree to which the cuticle is tanned, will affect the rate at which the cuticle is digested, as well as the degree to which it is digested (Skoczylas 1978). Thus, it is possible that, for example, larval lepidopterans may be proportionately underrepresented owing to their relatively thin cuticles, whereas ants may be proportionately overrepresented owing to the durability of their head capsules. The ease with which the cuticle is breached by the digestive enzymes will in turn affect the rate at which the rest of the tissues are digested, if the prey item is swallowed whole. Thus, it is possible that lightly armoured prey items are more quickly digested and less frequently found in gut samples. This argument also applies to the dry weights obtained for each prey category. Soft-bodied forms could well be underrepresented by weight, and heavily armoured forms overrepresented. Similarly, forms with easily digestible cuticles will be prone to disarticulation in the gut, and large items, such as most orthopterans, may be dealt with violently when captured (Milne and Milne 1950; Laird and Leech 1980), tending to be dismembered and difficult to measure. Usually not all of the prey items in a given gut sample were complete and measurable.

All of these problems are intrinsic to gut content analysis, in the absence of controlled experiments on gut passage time and digestion rates. By using three gut content classifications simultaneously (item count, dry weight, and item size), the bias inherent in each might be offset by one or both of the others.

A further problem with the sampling method used is that it does not obtain any material from points beyond the pyloric valve. Schoener (1967) observed that the upper small intestine frequently contains identifiable insect remains, and that this area should be examined in any dietary study. However, the size of the sample employed here makes it unlikely that any particular prey taxon or prey size group consistently escaped notice by having passed beyond the pylorus, although differences in gut passage time between prey taxa or prey size groups may have biased the results somewhat. Such a potential disadvantage is, however, offset to some extent by the potential for sampling any individual lizard more than once. Gut flushing is also superior to postmortem examination for a study such as this because of collection limitations imposed on populations categorized as threatened (Roberts 1982). The examination of faecal pellets is unsatisfactory because they are not easy to find, and their true identity is doubtful unless the lizard is actually observed in the act of defecation. In addition, the condition of prey items in a gut-flushing sample is better than the condition

TABLE 5. Taxonomic breakdown of dietary data (percentage of diet by item count and dry weight) of the two lizard size groups, with diversity (H') and evenness (J) statistics. Dietary overlap tested by Morisita's and Schoener's overlap indices (R_m and R_o , respectively) and chi-square tests

	Prey taxonomic group										H'	J	Overlap	χ^2
	Arachnida	Orthoptera	Lepidoptera	Coleoptera	Diptera	Hemiptera	Homoptera	Nonformicid Hymenoptera	Formicidae					
Prey item count														
Group 1 (40–55 mm SVL)	2.31	1.09	0.58	13.39	0.38	1.54	0.96	2.11	77.64	1.22	0.3838			
												0.9995 (R_m)	25.45 ($p < 0.005$)	
Group 2 (56–76.5 mm SVL)	1.70	2.17	1.29	13.33	0.29	2.58	0.18	2.17	76.28	1.28	0.4045			
Prey dry weight														
Group 1 (40–55 mm SVL)	2.68	11.59	3.34	23.36	1.18	2.89	1.05	8.41	45.50	2.26	0.7130			
												0.8127 (R_o)	2396.63 ($p < 0.005$)	
Group 2 (56–76.5 mm SVL)	2.27	26.48	1.98	25.21	0.80	4.64	0.20	6.37	31.81	2.31	0.7272			

NOTE: Sample sizes (prey items): group 1, 1561; group 2, 1703. Prey dry weights (grams): group 1, 1.8083; group 2, 3.7735.

TABLE 6. Taxonomic breakdown by item count and wet weight of pitfall samples pooled by location (silphid beetles excluded), with diversity (H') and evenness (J) statistics

	Arthropod taxonomic group												H'	J
	Orthoptera	Lepidoptera	Coleoptera	Diptera	Hemiptera	Homoptera	Nonformicid Hymenoptera	Formicidae	Araneae and Acarina	Opiliones	Scorpiones	Chilopoda		
% of items														
Comrey	1.01	1.26	7.58	26.26	1.52	1.01	1.77	52.57	6.06	0.00	0.25	0.25	1.97	0.5508
Nemiskam	0.00	0.48	5.11	29.39	0.16	0.32	0.80	13.58	49.84	0.48	0.00	0.00	1.80	0.5025
Bow Island	0.84	0.34	7.76	31.03	0.34	1.18	1.67	38.62	18.21	0.00	0.00	0.00	2.08	0.5789
% of wet weight														
Comrey	13.89	1.35	16.42	32.08	1.51	1.49	4.32	24.51	5.16	0.00	1.52	0.33	2.65	0.7387
Nemiskam	0.00	0.65	54.17	36.11	0.05	0.05	2.55	2.89	3.00	1.05	0.00	0.00	1.57	0.4384
Bow Island	3.03	0.10	74.92	11.25	0.27	0.27	0.74	6.72	2.69	0.00	0.00	0.00	1.33	0.3710

NOTE: Sample sizes (prey items): Comrey, 393; Nemiskam, 627; Bow Island, 493. Sample weights (grams): Comrey, 2.1278 g; Nemiskam, 8.6513 g; Bow Island, 11.1431 g.

TABLE 7. Overlap statistics between pitfall samples pooled by location. Chi-square statistic for difference in distribution and its significance for each pairwise comparison given

	Nemiskam		Bow Island	
	R_o	χ^2	R_o	χ^2
Item counts				
Comrey	0.5307	296.03 ($p < 0.005$)	0.8311	82.59 ($p < 0.005$)
Nemiskam	—	—	0.6784	109.17 ($p < 0.005$)
Wet weights				
Comrey	0.5614	31 790.79 ($p < 0.005$)	0.4021	30 795.99 ($p < 0.005$)
Nemiskam	—	—	0.7164	23 756.70 ($p < 0.005$)

of prey items from a faecal sample, the latter being generally disarticulated and reduced to exoskeletons. Thus dry weights of faecal samples would be even more subject to the bias towards heavily armoured forms outlined above.

The method of sampling potential prey abundance is unavoidably biased in that it sampled crawling and cryptic arthropods preferentially. Arthropods found on vegetation or those whose behavioural repertoires precluded them from wandering under the lid of a pitfall trap will be proportionately under-represented. Conversely, those that tend to seek out sheltered situations would be disproportionately abundant in the pitfall samples. Thus dipterans constitute a large proportion by number of the pooled pitfall samples (Table 6). Additionally, pitfall traps will sample arthropods active at times when phrynosomes are not, leading to a further bias. Nonetheless, the pitfall data give some indication to the potential prey pool. As Dunham (1980) points out, any method of arthropod sampling has its drawbacks and will bias estimates in one way or another.

Characteristics of the diet

Laird and Leech (1980) reported that captive specimens of *P. d. brevirostre* from Alberta would accept orthopterans, coleopterans, ants, and homopterans. Milner (1979) reported that *P. d. brevirostre* in Alberta feeds mainly on ants, but also takes small dipterans and immature grasshoppers. His data were gathered from faecal pellets and were unquantified. The percentage of ants (Table 3) in the diet of *P. d. brevirostre* in Alberta by prey item count is somewhat lower than that (81.0%) given for *P. douglassi* by Pianka and Parker (1975).

Hotton (1955) characterized the prey of phrynosomes as being arthropods of low activity, but the evidence for *P. d. brevirostre* in Alberta suggests otherwise. The prey types vary widely in activity, although all are mobile and thus likely to come to a phrynosome's attention, prey activity being the stimulus for predatory action (Milne and Milne 1950; Laird and Leech 1980). This is to be expected of a sit-and-wait predator which, by the nature of its foraging method, tends to encounter prey more active than itself (Pianka 1977).

The breakdown of diet by prey dry weight probably reflects the true relative importances of the prey taxa more accurately than does the prey item count, owing to the differing sizes of the prey types. In this breakdown of the samples (Table 3) ants are not the predominant prey type, and coleopterans and orthopterans combined form a much larger part of the diet than item counts would indicate. Once again, the prey types taken

TABLE 8. Taxonomic breakdown of prey data (percentage of diet by item counts and dry weights) pooled by location, with diversity (H') and evenness (J) statistics

	Prey taxonomic group											H'	J	
	Arachnida	Orthoptera	Lepidoptera	Coleoptera	Diptera	Hemiptera	Homoptera	Hymenoptera	Nonformicid	Formicidae				
Item counts														
Comrey	0.82	1.64	1.48	7.88	0.32	3.28	0.66	1.80	82.10	1.11	0.3492			
Nemiskam	4.02	1.20	0.60	26.09	0.09	1.97	0.94	2.14	62.96	1.54	0.4845			
Bow Island	0.94	2.01	1.01	5.57	0.54	1.68	0.20	2.55	85.49	0.96	0.3033			
Dry weights														
Comrey	0.46	11.10	2.64	27.70	0.55	9.01	0.61	3.39	44.54	2.12	0.6699			
Nemiskam	4.54	21.99	3.22	28.76	0.05	3.02	0.82	5.89	31.70	2.69	0.8479			
Bow Island	1.64	25.93	1.72	20.19	1.73	3.10	0.16	9.44	36.08	2.28	0.7206			

Note: Sample sizes (prey items): Comrey, 609; Nemiskam, 1169; Bow Island, 1486. Dry weights (grams): Comrey, 1.0988; Nemiskam, 1.9174; Bow Island, 2.5656.

TABLE 9. Overlap statistics between gut samples pooled by location. Chi-square statistic for difference in distribution and its significance for each pairwise comparison given

	Nemiskam		Bow Island		
	R_o	χ^2	R_m	R_o	χ^2
Item counts					
Comrey	0.7799	110.88 ($p < 0.005$)	0.9985	—	14.80 (NS)
Nemiskam	—		—	0.7538	275.40 ($p < 0.005$)
Dry weights					
Comrey	0.8068	3324.20 ($p < 0.005$)	—	0.7676	2291.49 ($p < 0.005$)
Nemiskam	—		0.9720	—	1486.05 ($p < 0.005$)

NOTE: NS, not significant.

TABLE 10. Overlap statistics between gut sample and pitfall sample item counts, pooled by location. Chi-square statistic for difference in distribution and its significance for each pairwise comparison given

		Gut sample item counts					
		Comrey		Nemiskam		Bow Island	
		R_o	χ^2	R_o	χ^2	R_o	χ^2
Pitfall item counts	Comrey	0.6772	213.17 ($p < 0.005$)	—	—	—	—
	Nemiskam	—	—	0.2452	1107.77 ($p < 0.005$)	—	—
	Bow Island	—	—	—	—	0.3728	993.46 ($p < 0.005$)

in greatest proportions are active forms. It is evident from Table 3B that *P. d. brevirostre* is not as much of a myrmecophage as the prey item counts would indicate. The greater dietary diversity and evenness for the dietary breakdown by prey dry weight than for the dietary breakdown by prey item count (Table 3A) indicates that this species is more generalized in its feeding habits than horned lizards are generally held to be (Hotton 1955; Pianka and Parker 1975). Unfortunately there are no comparable prey dry weight data for this species from the rest of its range, or for any of its congeners. However, dietary diversity and evenness for prey breakdown by volume for *P. douglassi* in Mexico ($H' = 2.70$, $J = 0.61$; statistics calculated from data in Montanucci 1981) are similar to the values for dietary breakdown by prey dry weight for the Alberta populations. Dietary breakdowns by prey item count are available for some populations of *Phrynosoma douglassi ornatissimum* in Utah (Table 11). Diversity and evenness of these samples are generally lower than those estimated for any Alberta population at any sampling period. The Utah data indicate a much higher proportion of ants and lower proportion of coleopterans than the Alberta data, although on the whole the same range of prey taxa are taken. There are a number of other lizard species present in the areas of Utah where these samples were taken, including one congener (*P. platyrhinus*). It is not clear, however, if this congener is syntopic with the *P. d. ornatissimum* sampled (Knowlton 1934, 1942; Knowlton and Janes 1934; Knowlton and Thomas 1936). When *P. douglassi* is syntopic with a congener it displays a dietary shift away from ants and towards coleopterans and orthopterans (Pianka and Parker 1975; Montanucci 1981). A similar dietary

profile is typical of the species in Alberta. Broadening of the dietary niche in this way, in the absence of reptilian competitors in this province, could be the result of ecological release, or a response to latitudinal decrease in total food abundance (Schoener 1974, 1977). There is insufficient evidence to decide between these two alternatives at present.

In the absence of data on prey abundance it is not possible to draw firm conclusions, but these dietary shifts suggest that *P. douglassi* may be more of a dietary generalist than the congeners with which it comes into syntopy. Possibly *P. douglassi* cannot exploit ants as a food source as well as these and is forced, by competition, into a dietary shift. Ants are frequently clumped in distribution and so can be considered as a patchy resource. Competition can result in habitat patches being dropped from a predator's feeding itinerary if a competitor is exploiting them to a sufficient degree (Schoener 1974). Whatever the case, it appears that *P. douglassi* may more readily broaden its dietary repertoire than other members of the genus.

The size distribution of prey items (Table 4) indicates that *P. d. brevirostre* preys heavily upon a rather small range of prey sizes, 85.28% of the prey items of the pooled gut samples being between 2.1 and 6.0 mm in length. Lack of information on the availabilities of the various prey sizes, and of experimental data concerning prey size preference, precludes characterization of this prey size range as the optimal prey size range. For the sake of discussion, it may be taken to be the realized optimal prey size range for the size range of lizards examined. It is to be expected that the optimal prey size range will be determined by the size of the predator's jaws (MacArthur

1972), but the realized optimal prey size range of *P. d. brevirostre* is considerably smaller in length than the measured head dimensions of even the smallest of the lizards examined. Foraging method may also affect optimal prey size, however. Small prey items are more common than large ones (MacArthur 1972) and a sit-and-wait predator, taking prey items as they come by, would be expected to feature more small items than large ones in its diet, particularly if it has the rather indiscriminating predatory response of a horned lizard (Milne and Milne 1950). It is possible that a sit-and-wait predator can afford to preferentially take larger prey, owing to its low search costs, but observations of foraging phrynosomes indicate that they attempt to catch any arthropod that comes by (personal observation). In addition, horned lizards have a simple weak dentition (Hotton 1955), and this might account, to some extent, for their concentration on small prey items of a variety of taxa, since they may find larger prey items difficult to handle. Iguanids, such as *Holbrookia*, that eat large active prey have sharper, more cusped teeth (Hotton 1955). Large *P. d. brevirostre* in captivity will stalk adult crickets over some distance, but even in confined circumstances their capture success at first attempt is not great (personal observation).

Relatively few prey items belonging to prey size group *i* are taken (Table 4). There is undoubtedly a lower prey size limit below which the energetic expense of pursuing and capturing a prey item is not repaid by its calorific value, and prey items of prey size group *i* may be below this lower limit for lizards of the size range represented by the pooled sample.

From the foregoing it is evident that subadult and adult *P. d. brevirostre* in Alberta can be said to concentrate upon a particular prey size range rather than on a particular prey taxon. This dietary opportunism was noted in *P. douglassi* in Mexico by Montanucci (1981). Guyer (1978) found no evidence that the daily activity of *P. d. douglassi* is timed to coincide with the activity of the ant *Pogonomyrmex* sp. (the commonest insect on his study site), while Baharav (1975) found that the activity of *Phrynosoma solare* tracked ant activity. This further illustrates the dietary opportunism of *P. douglassi* relative to its congeners and may also reflect the differing degree of myrmecophagy between the species (Pianka and Parker 1975).

Variations between study sites

The lack of similarity between pitfall item counts and pitfall wet weights pooled by location (Table 7) suggests that the phrynosome populations at these three study sites are preying upon different arthropod faunas, and this is borne out by the generally significant differences between gut samples pooled by location (Table 9). Only Comrey and Bow Island are similar in terms of prey item counts (Table 9), and the prey dry weight distributions are significantly different between any two pooled gut samples (Table 9). It may be that the phrynosomes at these three study sites have specialized in diet to some extent, probably because of the different arthropod faunas at the three sites. However, they are not sampling arthropods with regard to their abundances, as is shown by the significant differences between all three gut samples pooled by location and the corresponding pitfall samples pooled by location (Table 10). The main differences between the prey distributions (Table 8) and the arthropod distributions (Table 6) at the same locale are in the proportions of ants and dipterans. Phrynosomes take the first in greater proportion than they occur in the pitfall samples, and the latter in much lesser proportion.

Differences in diet between study sites are, to a large extent,

TABLE 11. Breakdown of prey item counts (percent), with diversity (H') and evenness (J) statistics, for four samples of *Phrynosoma douglassi ornataissimum* from Utah

Source	Prey taxonomic group														Sample size
	Arachnida	Orthoptera	Lepidoptera	Coleoptera	Diptera	Hemiptera	Homoptera	Hymenoptera	Nonformicid	Formicidae	Neuroptera	H'	J		
Knowlton 1934	0.18	1.07	1.07	2.50	0.36	1.60	0.36	3.20	89.32	0.36	0.78	0.2339	27		
Knowlton and Jones 1934	0.00	3.64	0.00	9.09	0.00	0.00	0.00	1.82	85.45	0.00	0.79	0.3938	3		
Knowlton and Thomas 1936	0.00	1.08	0.54	0.54	0.00	0.00	1.08	2.15	94.62	0.00	0.42	0.1613	11		
Knowlton 1942	0.00	0.93	0.00	7.72	0.31	7.10	0.62	1.23	82.10	0.00	1.00	0.3569	3		

reflective of differences in the degree to which ants are utilized (Table 8). Dietary diversity and evenness are greatest in the population at Nemiskam, for both prey item counts and prey dry weight. This implies that *P. d. brevirostre* is somewhat less specialized in diet at Nemiskam than at Bow Island and Comrey. Possibly the more heterogeneous physical environment at Nemiskam provides more habitat patches within which the lizards can forage. It is also possible that weather conditions before and during the field season at each study site affected the arthropod faunas differently (Tanner and Krogh 1973), although this is not evident from the data at hand.

Variation in dietary diversity and evenness over time at one study site could be due to differing degrees of dietary specialization within the population as the season progressed (caused presumably by weather fluctuations) or perhaps to sample size differences. Laird and Leech (1980) noted that feeding activity in captive *P. d. brevirostre* from Alberta seemed to vary according to the amount of insolation. The phrynosomes did not feed readily on cloudy days, even when the air temperature was high. This sort of reaction could account for much dietary variation over time.

The relationship of diet to lizard size

The size-related dietary differences found in the Alberta populations of *P. d. brevirostre* display some interesting features. There is a significant positive relationship between lizard SVL and average prey size (Fig. 2), and the prey size range taken by adult females includes and exceeds that taken by adult males and yearling females (Table 4). This is a common phenomenon in size-dimorphic predators (Schoener 1969a; Wilson 1975). It is to be expected that large individuals of a predatory species will take a prey size range including and exceeding that of smaller individuals, since prey handling time increases with increasing prey size more slowly for large predators than it does for small predators. Thus, large predators do not incur heavy costs in prey handling time by taking prey items over the prey size range taken by the smaller predators, as long as the smaller prey are easy to obtain, and in addition the larger predators can deal with larger prey items that would be uneconomical prey for the smaller predators (Schoener 1969a; 1969b; Schoener and Gorman 1968).

Schoener (1977) pointed out that it is difficult to isolate the causes of intraspecific phenotypic variation, and rash to ascribe it immediately to intraspecific competition. The Alberta populations of *P. d. brevirostre* display well-marked sexual size dimorphism (Powell 1982), the female:male SVL ratio being 1.3189 (calculated from estimates of asymptotic SVL). It was thus considered possible that this sexual size dimorphism may be associated with dietary niche partitioning.

Sexual size dimorphism in a predator may be accompanied by a bimodality in feeding efficiency, adults of the two sexes spending equal amounts of time feeding, despite the disparity in their sizes, and displaying greater feeding efficiencies than would adults of intermediate sizes (Schoener 1969a). This would add the advantage of equal adult feeding efficiencies to that of the decrease in dietary overlap between adults of the two sexes due to the difference in body size (Schoener 1969a), and so would, under certain circumstances, act as an additional selective force favouring sexual size dimorphism. Schoener (1969a) demonstrated that the advantages of dietary resource partitioning, when permitted by equal feeding efficiencies of two adult size classes, can explain sexual size dimorphism in solitary predators, that is, predators that have no similar com-

peting species within their habitat or geographic range.

Sexual size dimorphism should be more common in solitary model 1 predators, owing to the greater likelihood of such predators having feeding efficiency curves that are bimodal over a large body size range (Schoener 1969a). Ectothermic predators are more likely to display sexual size dimorphism, owing to their low energy requirements, which makes equal predatory efficiencies of two adult size classes more likely (Schoener 1969a). Sexual size dimorphism is also more likely in predators that have small trophic appendages (jaws) in relation to body size, since this entails greater prey handling time and consequent greater probability of a bimodal feeding efficiency curve (Schoener 1969a).

Sexual size dimorphism associated with dietary niche partitioning has been documented in a number of West Indian *Anolis* lizards (Schoener 1967, 1968; Schoener and Gorman 1968). This phenomenon can be most reasonably explained in these lizards as a result of intraspecific competition, although conformity to the predictions of the optimal foraging hypothesis (Schoener 1969a) and (or) sexual selection cannot be ruled out as alternative explanations (Ghiselin 1974; Trivers 1976; Schoener 1977).

On the basis of the above, the *P. d. brevirostre* populations in Alberta would be predicted to display sexual size dimorphism and associated dietary niche partitioning by prey size for a number of reasons. As ectothermic model 1 predators, they would be predicted to have a bimodal feeding efficiency curve over a large adult size range. Head size is small relative to body size implying that prey handling time will increase rapidly with increasing prey size. There is a significant difference in head length between the sexes, and adult males can be distinguished from adult females on the basis of relative head proportions (Powell 1982). Finally, there are no other lizard species in Alberta. If intraspecific dietary competition affects sexual size dimorphism in lizards, then the Alberta populations of *P. d. brevirostre*, in the absence of competing saurian species, would be expected to display greater sexual size dimorphism than populations in areas with saurian competitors, as a result of the effect of species packing on within-species phenotypic variation (Roughgarden 1974).

Females would be at an advantage if these populations divide the dietary niche by prey size. As the larger of the two sexes, adult females would be able to exploit a larger range of prey sizes (Schoener 1969a; Wilson 1975), as in fact they do (Table 4). Thus they have a prey size range which is not exploited by males, as well as exploiting the common prey size range differently from males. This "predatory refugium" could be important to adult females during vitellogenesis and gravidity, since they incur energetic costs at these times (Packard *et al.* 1977; Guillette 1982) that males are not subject to.

A hypothetical case can thus be made for the explanation of the sexual size dimorphism of the Alberta populations of *P. d. brevirostre* by intraspecific dietary niche partitioning, either as a result of intraspecific competition or as a result of the ecological release expected in a solitary model 1 predator. The significant differences in the distributions of prey item counts, prey dry weights (Table 5), and prey size (Table 4) between the lizard size groups provide evidence for this hypothesis. However, it is by no means certain that the dietary niche partitioning evident from these tables is the selection force producing the sexual dimorphism typical of these populations.

The 1.32 average female:average male SVL ratio closely

approximates the ratio in body or jaw size regarded as sufficient to reduce dietary competition between two syntopic species of predator (Hutchinson 1959; MacArthur 1972). This body size ratio is also associated with intersexual dietary niche partitioning in some species of *Anolis* (Schoener 1967, 1968; Schoener and Gorman 1968). Other studies have indicated that a body or jaw size ratio of approximately this magnitude is not necessarily associated with dietary niche partitioning, either between species (Rose 1976; Simberloff and Boecklen 1981) or within species (Weins and Rotenberry 1980; Schoener *et al.* 1982; Floyd and Jenssen 1983). This suggests that care must be taken in implicating dietary competition as the selectional force producing and maintaining size dimorphism when it is associated with dietary niche partitioning.

In the case at hand, it is possible that male dispersal competition (Ghiselin 1974) and viviparity have acted in concert to produce the sexual size dimorphism typical of these populations (Powell 1982), and the associated dietary niche partitioning is merely a by-product of this dimorphism rather than the selectional force producing it. The size difference between the two lizard size groups has some thermoregulatory implications (Powell 1982) which in turn are correlated with a significant difference in microhabitat use between the size groups ($\chi^2 = 16.72$, $p < 0.005$). This difference in microhabitat use could account for the significant difference in prey distributions between the two size groups (Tables 4 and 5). The arthropod sampling technique used here is not sensitive enough to discriminate between any possible differences in the potential prey abundances of different microhabitats, and so no firm conclusions can be drawn on this issue.

On the other hand, the significant difference in prey size distributions between the lizard size groups assumes greater importance when the actual size range of males and non-breeding females that breeding-age females would be competing against is considered. The 1.32 ratio of female to male SVL is based on the asymptotic SVLs of the two sexes, derived from logistic growth models (Powell 1982). The distributions of SVLs within each size group would insure that the female: male SVL ratio of the phrynosome sample as a whole is somewhat less than 1.3. Thus, a breeding-age female of any size would be competing for prey against the total SVL range of group 1 lizards. The 1.3 ratio would be too large in the greater proportion of these cases. The dietary differences between the two lizard size groups are significant despite this, which implies that dietary competition may be an important selectional force in producing sexual size dimorphism.

In conclusion, it can be stated that sexual size dimorphism is associated with dietary niche partitioning in the Alberta populations of *P. d. brevirostre*, and that this relationship conforms to the predictions of theory (Schoener 1969a). However, it is not clear whether dietary competition between breeding-age females and males and subadult females produces and maintains sexual size dimorphism, or if dietary niche partitioning is a corollary of a sexual size dimorphism produced by some other selective force, presumably a more straightforward intrasexual selection. A reasonable assumption is that dietary competition works with other selectional forces to produce the sexual size dimorphism typical of these populations, but there is insufficient data to assess this properly. A concurrent study of growth in the Alberta populations of *P. d. brevirostre* has helped clarify the role that intrasexual selection plays in the production of sexual size dimorphism. The details of this will be presented elsewhere. Data on diet and sexual size dimor-

phism in *P. douglassi* in areas where it has saurian competitors, particularly congeners, would also be valuable in assessing the importance of dietary competition in the production of sexual size dimorphism in this species.

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