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THERMAL ECOLOGY AND ACTIVITY PATTERNS OF THE SHORT-HORNED LIZARD (*PHRYNOSOMA DOUGLASSI*) AND THE SAGEBRUSH LIZARD (*SCELOPORUS GRACIOSUS*) IN SOUTHEASTERN IDAHO

Craig Guyer^{1,2} and Allan D. Linder¹

ABSTRACT—A mark-recapture study of the short-horned lizard (*Phrynosoma douglassi*) and the sagebrush lizard (*Sceloporus graciosus*) was performed from 1976 to 1977 in southeastern Idaho. Both species had mean cloacal temperatures of approximately 33 C. However, *P. douglassi* had more variable cloacal temperatures, particularly during morning and evening periods. This was caused by differences in sleeping sites chosen by the two species. Adults of both species were active from mid-April through late August, with peak activity in June. Juvenile *P. douglassi* displayed a seasonal activity pattern similar to that of adults. Juvenile *S. graciosus* were most active later in the year (August), when adults were disappearing. In both species, young-of-the-year appeared in early to mid-August. Adult and juvenile *P. douglassi* were active during all daylight hours and displayed no activity peaks, whereas young-of-the-year displayed a bimodal activity pattern. Adult and juvenile *S. graciosus* were active over all daylight hours but had peak activity between 1200 and 1500 h. Ants (*Pogonomyrmex*) were the lizard's principle prey. However, only young-of-the-year *P. douglassi* had activity patterns that paralleled that of ants on their mounds.

This study was conducted to determine aspects of thermal ecology and seasonal, daily, and reproductive activity patterns for the short-horned lizard (*Phrynosoma douglassi*) and the sagebrush lizard (*Sceloporus graciosus*) near the northern edge of their distributions. Thermal activity is a commonly studied aspect of lizard ecology (Brattstrom 1965, Heath 1965, Pianka and Parker 1975, Prieto and Whitford 1971 for *P. douglassi*, and Brattstrom 1965, Burkholder and Tanner 1974, Mueller 1969 for *S. graciosus*), whereas activity patterns are much less commonly reported (Pianka and Parker 1975, for *P. douglassi* and Burkholder and Tanner 1974, and Stebbins 1944 for *S. graciosus*). Our results are compared to studies of *P. douglassi* from Utah (Pianka and Parker 1975) and *S. graciosus* from Utah (Burkholder and Tanner 1974, Woodbury and Woodbury 1945, Tinkle 1973), Wyoming (Mueller and Moore 1969), and California (Goldberg 1975, Stebbins 1944).

METHODS

The study was conducted on the Idaho National Engineering Laboratory (INEL) site in southeastern Idaho during June to October 1976 and April to October 1977. This area is ca 1500 m in elevation, is characterized vegeta-

tively as a sagebrush-desert community (McBride et al., 1978), and is composed geologically of Recent lava flows covered by wind and waterborne deposits. The climate is characterized by short, hot summers (average maximum and minimum temperatures 30.5 and 10.0 C, respectively) and long, cold winter (average maximum and minimum -2.7 and -16.1 C, respectively). The average yearly precipitation is 21.6 cm, mostly in the form of spring rains.

Much of the data were collected on a 1-ha grid system with stakes placed 10 m apart. This grid system and the surrounding area were dominated vegetatively by big sagebrush (*Artemisia tridentata*), rabbitbrush (*Chrysothamnus nauseosus*), halogeton (*Halogeton glomeratus*), and squirreltail grass (*Sitanion hystrix*). Lizards were captured by hand or noose and were marked permanently by toe-clip and for field identification by color marks on their legs. Individuals were sexed and measured snout-to-vent (nearest mm), from which age and sex groups were determined. Five age and sex groups were recognized: young-of-the-year (YOY, 23-30 mm SVL), juvenile males (30-50 mm SVL), juvenile females (30-60 mm SVL), adult males (>50 mm SVL), and adult females (>60 mm SVL). Cloacal temperatures were measured

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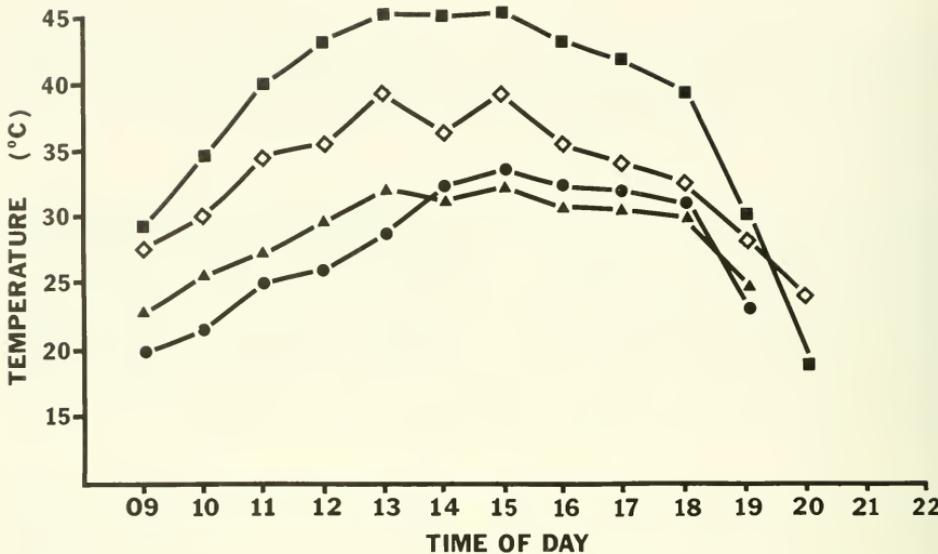


Fig. 1. The relationship between mean environmental temperatures on cloudless days and time of year. Solid squares are soil temperatures in sun, open diamonds are air temperatures in sun, solid triangles are air temperatures in shade, and open circles are soil temperatures in shade.

to the nearest 0.2 C with a Schulteis quick-reading thermometer, except for YOY, which could not accept the bulb without injury. Handling time for individuals was generally less than 5 minutes, and temperatures were taken within the first minute of capture. Time and location where the animals were first sighted were recorded as were the following environmental temperatures: air temperature in sun (ATS), soil temperature in sun (STS), air temperature in shade (ATSh), and soil temperature in shade (STSh). All soil temperatures were taken with the bulb barely covered with loose soil, and all air temperatures were taken with the bulb 1 cm from the soil surface. Each day's observations averaged 5 h and starting times were rotated so that observations occurred during all daylight hours.

Ants (principally *Pogonomyrmex*) were the most abundant insects on the grid. Since ants are important prey of both lizards (Knowlton and Baldwin 1953, Knowlton et al. 1946, Burkholder and Tanner 1974), ant activity was monitored in 1977 to determine if lizard activity paralleled ant activity. All *Pogonomyrmex* mounds on the grid were mapped. During

each grid sampling, each mound was visited. To index ant activity, we recorded active mounds (>20 active ants) and inactive mounds (<20 active ants.)

All data used to analyze activity patterns were from lizards seen on the grid. Temperature data were collected from lizards on the grid as well as lizards marked in surrounding areas (Guyer 1978).

RESULTS

Environmental temperatures increased parabolically from 0800 to 1500 h followed by a parabolic decline from 1500 to 2100 h (Fig. 1). The hottest microenvironment during all hours except 2000 to 2100 h was STS, and STSh was the coolest microenvironment until late afternoon (1400–1900 h), when ATSh was coolest. The peak for STSh was shifted to the right relative to curves of the other three microenvironments indicating a lag period involved with heating and cooling the soil.

Mean cloacal temperatures (± 1 SD) were 33.4 ± 4.4 C for *P. douglassi* (N = 84) and 33.9 ± 2.4 C for *S. graciosus* (N = 61). Since

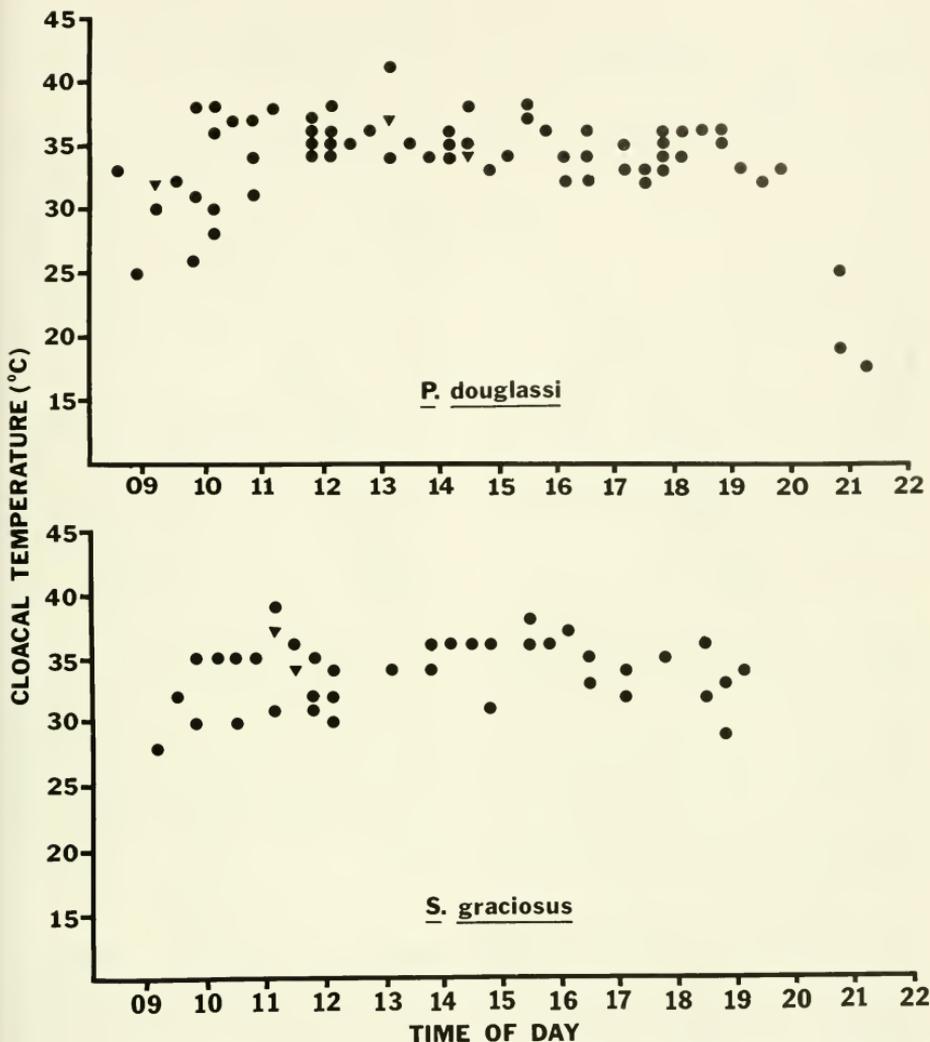


Fig. 2. The relationship of cloacal temperatures of *Phrynosoma douglassi* and *Sceloporus graciosus* and time of day. Circles are single observations, and triangles are double observations.

animals captured on overcast days were much cooler than those captured on sunny days, only lizards caught on cloudless days were used to test for trends among age and sex groups. No differences were found in the distribution of cloacal temperatures among age and sex groups for either species (Kruskal-Wallis test; $p < 0.05$ for both species), so data were pooled within each species.

Cloacal temperatures of *P. douglassi* during daylight hours could be separated into three thermoregulatory periods (Fig. 2): a morning period (0800–1100 h), a midday period (1100–1800 h), and an evening period (1800–2200 h). The morning period was characterized by rising temperatures at each successive hour and wide variability. The midday period was characterized by relatively stable temper-

atures and reduced variability, and the evening period was characterized by falling and widely variable temperatures. During midday *P. douglassi* were found more frequently in shade than in direct sun (68 of 158 in direct sun), whereas during morning (58 of 70 in sun) and evening (23 of 36 in sun) periods lizards were found more often in direct sun. There was a significant association between thermoregulatory period and location of *P. douglassi* (Chi-square test of association; $p < 0.05$). However, there was no difference in location of individuals between morning and evening periods (Chi-square test; $p > 0.05$). One thermoregulatory period was found in *S. graciosus*, corresponding to the midday period of *P. douglassi* (Fig. 2). No major shifts in cloacal temperature occurred during daylight hours. Because *S. graciosus* escaped at distances prohibiting the determination of original microhabitat, locations with respect to sun or shade could not be analyzed.

Adult *P. douglassi* were first sighted 12 April 1977, and juveniles were first sighted 23 April 1977. Fieldwork was begun too late in the season to determine time of emergence in 1976. Seasonal patterns of activity were similar between years so these data were pooled. Adults and juveniles had similar seasonal activity patterns, with greatest activity occurring from June to July and declining activity from July to September (Fig. 3). Adults were last seen 29 August 1976 and 3 September 1977, and juveniles were last seen 18 September 1976 and 11 September 1977.

One copulation of *P. douglassi* was observed 10 May 1977. Young-of-the-year of this species were first seen 5 August 1976 and 10 August 1977. This group was encountered increasingly more often until their sudden disappearance in mid- to late September (Fig. 3). Individuals from this age class were last sighted 25 September 1976 and 12 September 1977.

The earliest emergence of *S. graciosus* adults was 16 April 1977, whereas juveniles were first seen 31 May 1977. Again, seasonal patterns of abundance did not differ, so data for the two years were pooled. Monthly activity of adults and juveniles differed in that adult activity peaked during May and declined from June through September, whereas juveniles peaked in August and declined through Sep-

tember (Fig. 3). Adults were last seen 29 August 1976 and 28 August 1977, whereas juveniles were last seen 29 August 1976 and 17 September 1977.

We estimated time of mating for *S. graciosus* using the intensity of orange, the nuptial coloration in females that indicates ovulation (Burkholder and Tanner 1974). In 1977 orange color was most intense 3–8 June 1977 with some color persisting through 21 June 1977, implying an early June mating season. Young-of-the-year were first seen 28 August 1976 and 14 August 1977. This group was active throughout August and September (Fig. 3) and was last seen 25 September 1976 and 1 October 1977.

Daily activity patterns of adult and juvenile *P. douglassi* were uniform throughout all daylight hours (Fig. 4). This pattern did not shift during the study period so data for all months and both years were pooled. Daily activity of young of the year followed a bimodal pattern with decreased activity during the hottest part of the day (Fig. 4). Because insufficient captures were made of *S. graciosus* juveniles and YOY, their daily activity patterns were not analyzed. Adults showed uniform daily activity patterns, with peak activity occurring from 1100 to 1500 h (Fig. 4). The daily activity of *Pogonomyrnx* on their mounds was bimodal (Fig. 4), with activity depressed during the hottest part of the day. This pattern was similar for all months sampled, so data were pooled.

DISCUSSION

Mean cloacal temperatures of both species agree with those reported from other populations (Brattstrom 1965, Pianka and Parker 1975 for *P. douglassi*, and Brattstrom 1965, Burkholder and Tanner 1974 for *S. graciosus*). *Sceloporus graciosus* had similar cloacal temperatures throughout the daylight hours. However, *P. douglassi* temperatures differed during the day, with reduced temperatures during early and late hours of the day. This difference appears to be related to daily activity patterns and sleeping sites utilized. *Phrynosoma douglassi* were never observed using rodent burrows or burrowing under loose soil. Several individuals were followed

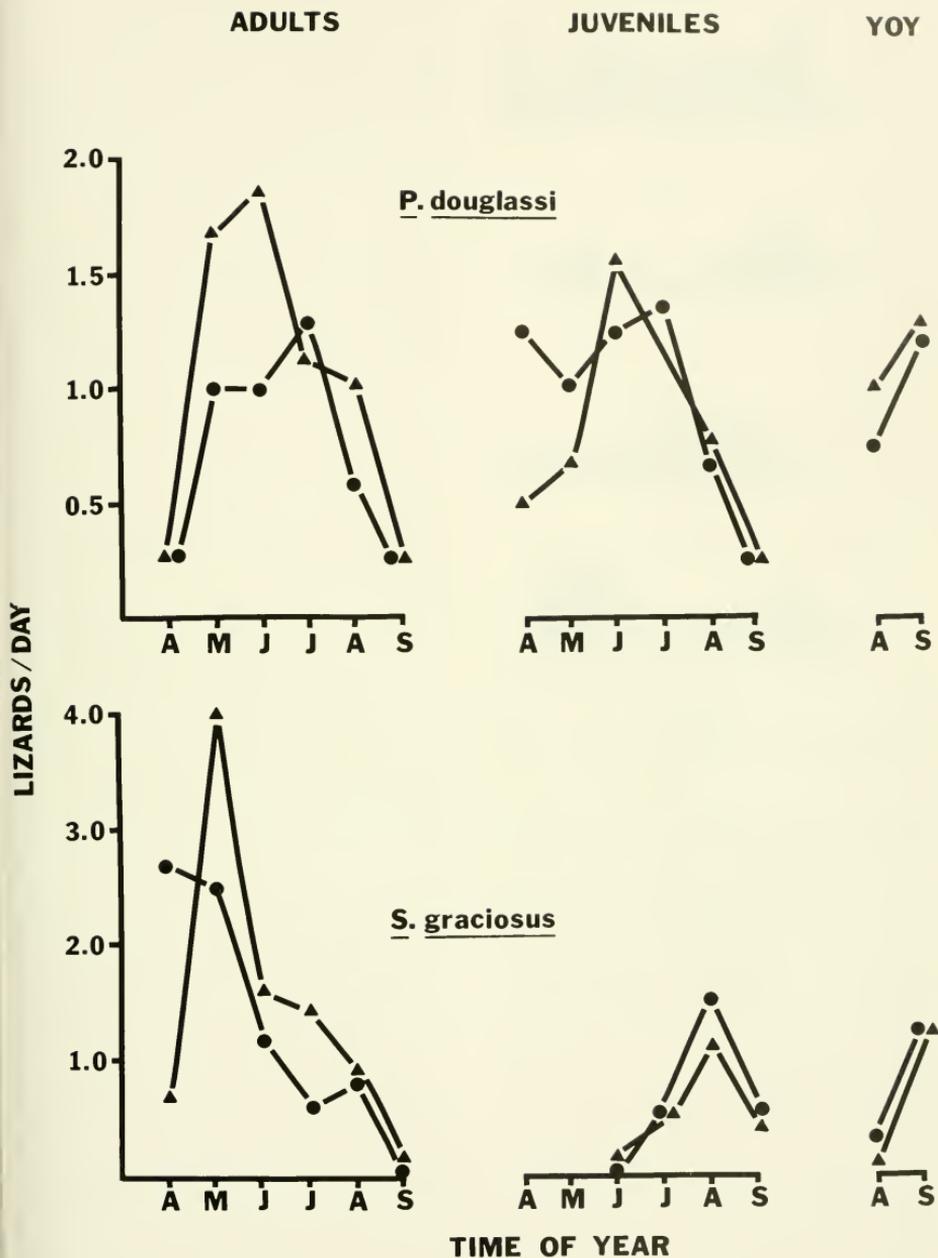


Fig. 3. The relationship between mean number of lizards seen per sample period and time of year. Circles are males, and triangles are females.

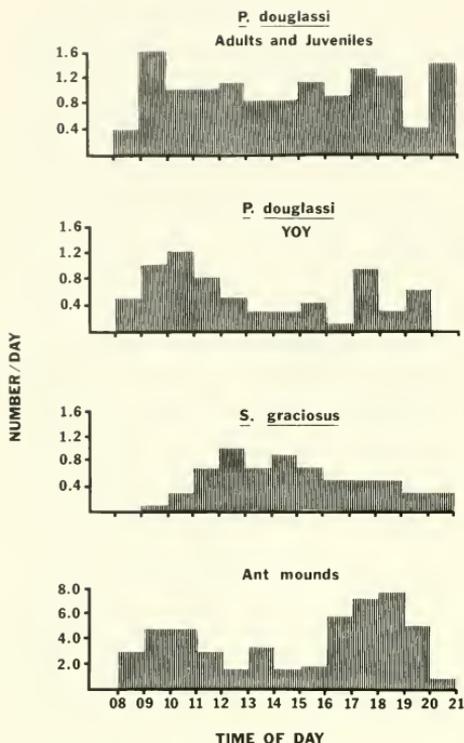


Fig. 4. Mean number of lizards and active ant mounds seen per sample period and time of day.

until they became inactive during evening hours and were relocated early the next morning before becoming active. All were observed to spend the night above ground. On several occasions sluggish individuals were captured during cool, early-morning hours. In contrast, *S. graciosus* were often observed using rodent burrows for escape and were found at burrow entrances during early-morning hours. These sites were apparently used overnight. Sluggish individuals were never observed. The fact that cloacal temperatures of *S. graciosus* were uniform throughout all daylight hours over which lizards were observed indicates that this species does not emerge until body temperatures reach levels at which activity takes place and that this level is maintained throughout the hours over which activity occurs. The morning and even-

ing periods of low cloacal temperatures seen in *P. douglassi* apparently result from the location of these animals above ground during all hours of the day. *Phrynosoma douglassi* expedite their morning rise in cloacal temperature by locating in the warmest and fastest heating microhabitat (STS), a conclusion supported by Heath (1965). Maintenance of a relatively constant cloacal temperature throughout midday hours, when environmental temperatures continue to fluctuate, is probably accomplished by shuttling between sun and shade and may indicate the level preferred for daily activity. Cloacal temperatures were maintained until STS dropped below this preferred level. Cloacal temperatures then decreased at a rate similar to STS. This cooling during evening hours may be delayed by relocating in sunny areas.

Pianka and Parker (1975) found variability of cloacal temperature in *Phrynosoma* to be greater than that of any other North American iguanid. They attribute this to relaxed thermoregulation. In this study both species had approximately equal mean cloacal temperatures, but the variation about the mean was approximately two times greater in *P. douglassi* than in *S. graciosus*. However, the increased variability of *P. douglassi* was due to lizards captured during morning and evening periods, when few *S. graciosus* were observed. If *S. graciosus* could have been captured at these times, it is likely that similar variability would have been seen. During midday hours both species maintained relatively constant and similar cloacal temperatures. Thus, during comparable periods of activity *P. douglassi* probably does not exhibit wider thermal variability than *S. graciosus*.

Seasonal activity of juveniles differed between the two species. Activity of *P. douglassi* juveniles was similar to that of adults, whereas activity of juvenile *S. graciosus* was inversely related to that of adults. The reduced activity of juvenile *S. graciosus* early in summer was due primarily to the low numbers of juveniles encountered, but this was confounded by poor capture success of smaller lizards. These results differ from those of Burkholder and

Tanner (1974), who found activity patterns to be similar for *S. graciosus* adults and juveniles in Utah. These authors did show that the level of activity maintained by juveniles was below that of adults until August, when adults began hibernating. Whitford and Creusere (1977) showed an inverse relationship between adult and juvenile activity for *P. cornutum* and *S. magister* in New Mexico.

Seasonal activity patterns for adults of both species were similar, with emergence occurring in mid-April and hibernation beginning in late August to early September. Peak activity of adults occurred approximately one month earlier in *S. graciosus* (May) than in *P. douglassi* (June). The duration of adult seasonal activity was shorter than that reported for southern populations of the same two species (Goldberg 1971, 1975, Burkholder and Tanner 1974) due to later emergence and earlier hibernation. The active season reported for *S. graciosus* adults in this study is similar to that reported for northern populations (Stebbins 1944, Mueller and Moore 1969). A similar pattern of adult seasonal activity has been found for *P. douglassi* in Alberta, Canada (G. Larry Powell, personal communication).

Mating occurred at different times of the year in the two species. This is probably due to the difference in reproductive method of the two species. *Phrynosoma douglassi* is ovoviviparous and gestation is approximately three months (Goldberg 1971), whereas *S. graciosus* is oviparous and gestation is approximately two weeks (Goldberg 1975). The time of mating predicted or observed in this study compares favorably with that found by Goldberg (1971) for *P. douglassi* and by Burkholder and Tanner (1974) for *S. graciosus*.

Young-of-the-year appeared at approximately the same time of year (early August) in both species. The time of hatching is similar to that reported by Goldberg (1971) and Pianka and Parker (1975) for *P. douglassi* and by Woodbury and Woodbury (1945), Mueller and Moore (1969), Tinkle (1973), Burkholder and Tanner (1974), and Goldberg (1975) for *S. graciosus*. Because these studies were done

in a variety of geographic locations, there seems to be little geographic variation in timing of the first clutch in either species.

Bimodal activity patterns, particularly in the hot months of July and August, have been reported commonly for southern populations of *Phrynosoma* (Parker 1971, Tanner and Krogh 1973, 1974, Baharav 1975) and *S. graciosus* (Burkholder and Tanner 1974). This pattern was observed only in *P. douglassi* YOY during this study. Bimodality seen in southern populations appears to provide an escape from high midday temperatures. In this study at least one microhabitat was available at all times that was lower than and one that was higher than or at least equal to the cloacal temperature maintained by the two species. This may explain the absence of bimodality seen in this study. Because of this absence of midday decline in activity, northern populations may have a longer daily activity pattern than southern populations. The bimodal pattern of *P. douglassi* YOY may be a result of more rapid heating and cooling of small ectotherms (Brattstrom 1965). Because the duration of seasonal activity is much longer in southern than in northern populations, it has been suggested that southern populations are exposed to predation for longer periods of time. This is thought to be an important factor causing the short life span of southern populations (Tinkle 1973). However, because southern populations may have reduced daily activity compared to northern populations, the effects of seasonal and daily activity may cancel each other between northern and southern populations. Thus, speculation about the relative role of predation in northern versus southern lizard populations must account for not only the effect of differences in seasonal activity patterns (Nussbaum and Diller 1976) but the effect of daily activity patterns as well.

Ant activity on the grid was bimodal. However, activity patterns of both lizard species were not directly related to that of ants. This differs from the observations of Baharav (1975), who found that *P. solare* in Arizona tracked ant activity. The fact that *P. douglassi*

activity did not track that of ants may be related to the broader diet of this species compared to *P. solare* (Pianka and Parker 1975), or it may indicate that the relationship between *Phrynosoma* activity and ant activity in Arizona is not a causal one. Instead both lizards and ants may require escape from high mid-day temperatures in Arizona, whereas lizards in Idaho require no such escape.

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