

Microhabitat Use and Thermal Biology of the Collared Lizard (*Crotaphytus collaris collaris*) and the Fence Lizard (*Sceloporus undulatus hyacinthinus*) in Missouri Glades

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ABSTRACT.—Collared lizards, *Crotaphytus collaris*, live in isolated populations on Missouri glades. Anecdotal observations suggest that another lizard species, *Sceloporus undulatus*, is rare on glades where *C. collaris* is present. Possible causes of scarcity of *S. undulatus* in the presence of *C. collaris* include competition, predation, and unsuitable thermal conditions. We characterized thermal biology and habitat partitioning in these two species by measuring body and air temperatures, and microhabitat use, at three glades. *Sceloporus undulatus* maintains lower body temperatures than *C. collaris* and shifts from open rock perches to shady tree perches during the middle of its activity season. *Crotaphytus collaris* microhabitats are rockier and more open than those of *S. undulatus*, which tend to have more branches, leaves, and trees nearby. These data indicate that areas of glades hot enough for use by *C. collaris* are too hot for *S. undulatus*. Although we cannot rule out competition or predation, constraints of the thermal environment may be an important factor in the apparent scarcity of *S. undulatus* on glades.

Interspecific competition is often invoked to explain differences in resource use among sympatric species (MacArthur, 1970; May, 1974; Schoener, 1977; Pacala and Roughgarden, 1982; Losos, 1994). Alternatively, other kinds of biotic interactions, such as predation (Holt, 1974; Jeffries and Lawton, 1984) or shared parasites (Settle and Wilson, 1990; Grosholz, 1992; Schall, 1992), may mediate resource partitioning. Many studies have documented resource partitioning among lizard species, and most of these focused on biotic interactions, mainly competition, as the driving forces behind resource partitioning (see reviews by Schoener, 1977; Toft, 1985; Losos, 1994).

Resource partitioning may also result if both species respond to abiotic factors that differ among microhabitats (Grover, 1996). One important factor for ectotherms such as lizards is the thermal environment. Lizards active in nature often exhibit a narrow range of body temperatures that correspond to optima for metabolism, locomotion, and other physiological functions (Huey, 1982; Hertz et al., 1982). Because thermal conditions vary among habitats, an organism with a finite range of thermal tolerances will only be able to exploit a subset of all pos-

sible microhabitats. Thus, species may differ in their resource use for reasons independent of interspecific interactions.

In this study, we document microhabitat resource partitioning by two lizard species, the eastern collared lizard, *Crotaphytus collaris*, and the northern fence lizard, *Sceloporus undulatus hyacinthinus*. *Crotaphytus collaris* is widely distributed throughout the hot and dry regions of the southwestern United States and Mexico; north-eastern-central Missouri marks the northeastern edge of the range of *C. collaris* (Sexton et al., 1992). In Missouri, populations of *C. collaris* are restricted primarily to glades, which are prairie-like habitats characterized by thin soil, rock outcrops, and open, xeric plant communities. Although glades were once widespread throughout Missouri, climatic cooling beginning approximately 4500 years before present and more recent human suppression of natural fires have facilitated forest encroachment (Sexton et al., 1992). Consequently, the plant and animal communities living on glades are now found within isolated patches of hot, dry, open habitat surrounded by forests. Glade habitats are also home to *Sceloporus undulatus*, which, unlike *C. collaris*, is not exclusively limited to the glade habitat. Preliminary observations suggested that *S. undulatus* was scarce on glades where *C. collaris* was present. *Sceloporus undulatus* scarcity could be the result of predation by *C. collaris*, competition with *C. collaris*, or seasonally unfavorable environmental conditions in the glades. We began studies to determine the relative importance of interspecific interactions and abiotic factors in determining patterns of the species' distribution and abundance.

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MATERIALS AND METHODS

Study Sites.—The study was conducted on glade habitats in northeastern-central Missouri. Three glades were selected as study sites based on the presence of rock outcroppings that could serve as lizard perches and refuges, and on similarities in slope and vegetative cover. *Crotaphytus collaris* and *S. undulatus* were already present at Victoria Glade, a Nature Conservancy reserve located in Jefferson County, Missouri. Data collection began at Victoria glade in May 1996. *Sceloporus undulatus* populations were censused in May 1996 by mark-and-recapture methods at the remaining two glades in St. Francois State Park and Hawn State Park, both in St. Francois County, Missouri. *Crotaphytus collaris* was initially absent at both St. Francois and Hawn State Parks. Nine *C. collaris* individuals (three males and six females) were released at both St. Francois and Hawn State Parks in June 1996 as part of a conservation program intended to reestablish the species in restored glade habitats. Trees and brush subdivided St. Francois glade into upper and lower sections. *Crotaphytus collaris* individuals were released only onto the upper glade. We intended to monitor *S. undulatus* in the absence of *C. collaris* on the lower glade. However, *C. collaris* dispersed to the lower glade and could not be removed because the individuals were released as part of reintroduction efforts. Therefore, the lower section could not serve as a control for this study and we treated St. Francois as a single glade. All three glades were visited at least once a week for the duration of the 1996 field season. The study continued at Victoria Glade March–June 1997. Data from May and June at Victoria glade were not different statistically between 1996 and 1997; thus, these data were combined for analyses.

Field Thermal Biology.—We systematically searched for lizards along horizontal transects, varying our point of entry into the glade with each visit. Observations began in the morning and continued until midday heat restricted lizard activity. We attempted to capture every lizard by noose upon sighting. If an animal was captured without a chase, its cloacal temperature (to the nearest 0.1°C) was taken immediately with a Schultheis thermometer. We then measured the ambient air temperature (in the shade, to the nearest 0.1°C) 1 cm above the perch where the lizard was sighted.

Microhabitat.—We measured a range of variables to quantify each lizard's microhabitat use. For every lizard sighting, we recorded the perch type (rock, tree trunk, tree branch, or ground), perch light (full sunlight, filtered sunlight, or shade), distance from the perch to the nearest tree (to the nearest 1 m), and height (to the near-

est 1 m) and basal diameter (to the nearest 0.05 m) of the nearest tree. Only trees greater than 0.25 m tall were considered. Within 1 m of the perch, we summed the number of rocks, plants, dead branches, and trees that intersected each of four perpendicular transects. In addition, we recorded on how many of the four transects gravel and leaf litter were present. Control sites were placed at equally spaced intervals along transects through each glade. The same microhabitat measurements as described above were made at each control site to determine whether the two species were found in nonrandom subsets of the glades.

Statistical Analysis.—Each *C. collaris* and most *S. undulatus* were given unique toe-clip identifications. An unknown number of *S. undulatus* eluded capture and remained unmarked. Because all *C. collaris* and at least some *S. undulatus* were sampled multiply, statistical tests were performed twice, first, using all cases and then, to adjust for repeated observations of the same individual, using for each individual either mean values of continuous variables or frequencies for categorical variables and excluding unmarked individuals. Results were not qualitatively different between the two methods, although, because samples were smaller, significance levels were often lower when using only one case per individual. Because in no case was a result that was statistically significant with all cases rendered nonsignificant when means or frequencies were used, we report only results using all cases.

All continuous variables were log-transformed prior to statistical analysis to meet normality assumptions for parametric tests. We used a two-way analysis of variance (ANOVA) to determine whether cloacal temperature was affected by species, month, or a species-by-month interaction. We used analysis of covariance (ANCOVA) to test for interspecific differences in the relationship between cloacal temperature and perch air temperature. ANCOVA was performed only on all cases because mean values for each individual are meaningless in the context of investigating the relationship between body and air temperature. However, ANCOVA indicated that the relationship between perch air and cloacal temperature varied among *C. collaris* at Victoria glade (difference in slopes, $F_{1,17} = 1292.7$, $P < 0.001$). Consequently, analyses using multiple points from Victoria *C. collaris* may suffer from pseudoreplication and should be interpreted with caution. Unfortunately, we do not have enough data for each individual to allow an analysis in which the relationship between perch air and cloacal temperature could be assessed simultaneously both among individuals and between species. AN-

TABLE 1. Cloacal temperature means \pm 1 SE. Sample sizes are in parentheses.

Glade	Month	<i>C. collaris</i>	<i>S. undulatus</i>
Victoria	March	35.2 \pm 0.4 (31)	32.0 \pm 0.7 (13)
Victoria	April	35.9 \pm 0.3 (45)	32.3 \pm 0.4 (25)
Victoria	May	37.8 \pm 0.6 (17)	34.7 \pm 0.4 (15)
Victoria	June	37.9 \pm 0.5 (15)	34.8 \pm 0.3 (18)
St. Francois	June	37.5 \pm 1.1 (3)	35.2 \pm 1.3 (3)
Victoria	July	38.2 \pm 0.6 (10)	35.3 \pm 0.3 (15)
St. Francois	July	37.5 \pm 0.4 (15)	35.6 \pm 0.7 (7)
Victoria	August	38.7 \pm 0.6 (6)	35.9 \pm 0.3 (7)
St. Francois	August	38.9 \pm 0.5 (6)	34.6 \pm 0.6 (9)
Victoria	September	37.8 (1)	32.9 \pm 0.5 (6)
St. Francois	September	36.3 \pm 0.7 (6)	33.7 \pm 0.7 (3)
Victoria	October	34.3 \pm 1.0 (4)	34.2 \pm 0.6 (6)
St. Francois	October	—	34.4 (1)
Victoria	Grand Mean	36.4 \pm 0.2 (131)	33.7 \pm 0.2 (114)
St. Francois	Grand Mean	37.5 \pm 0.3 (30)	34.8 \pm 0.3 (23)
Hawn	Grand Mean	35.9 \pm 0.5 (39)	33.0 \pm 1.1 (9)

COVA did not indicate that the relationship between perch air and cloacal temperature varied among *S. undulatus* at Victoria (slopes, $F_{1,10} = 3.127$, $P = 0.114$; intercepts, $F_{1,15} = 0.677$, $P = 0.789$) or among *C. collaris* at either Hawn (slopes, $F_{1,5} = 0.848$, $P = 0.534$; intercepts, $F_{1,5} = 0.616$, $P = 0.689$) or St. Francois (slopes, $F_{1,3} = 2.430$, $P = 0.103$; intercepts, $F_{1,3} = 0.463$, $P = 0.712$). Our data were insufficient to permit ANCOVA among *S. undulatus* at Hawn or St. Francois.

To compare the frequencies of sightings in the different perch light and perch type categories for the two species, we used chi-square tests on all cases. In addition, we calculated for each individual the proportion of observations in each category. These frequencies were arcsine square-root transformed and used in multivariate analysis of variance (MANOVA) and ANOVA analyses. MANOVA and ANOVA produce results that are qualitatively identical to chi-square tests on all cases, thus only chi-square results are reported here. Microhabitat variables were ordinated using principal components analysis (PCA). We then used ANOVA to assess differences in PCA scores among species and control sites and to assess intraspecific differences in PCA scores across months. Scheffé tests were used to perform posthoc pairwise mean comparisons.

RESULTS

Thermoregulation.—*Crotaphytus collaris* cloacal temperatures were higher than *S. undulatus* cloacal temperatures at all three glades (Table 1). Two-way ANOVA revealed significant effects of species and month on cloacal temperature at Victoria (species: $F_{1,238} = 71.71$, $P < 0.0001$; month: $F_{6,238} = 16.98$, $P < 0.0001$; month \times species: $F_{6,238} = 0.57$, $P = 0.76$). At St. Francois, two-

way ANOVA revealed significant effects of species and marginally significant effects of month on cloacal temperature (species: $F_{1,52} = 30.37$, $P < 0.0001$; month: $F_{3,52} = 2.44$, $P = 0.077$; month \times species: $yF_{3,52} = 1.79$, $P = 0.16$). Small sample sizes at Hawn prevented analysis of the effects of species and month on cloacal temperature.

Interspecific differences in cloacal temperature could be due either to species using thermally different microhabitats or to differences in thermoregulatory behavior. ANCOVA indicated that, relative to air temperature, *C. collaris* had a higher body temperature than *S. undulatus* at Hawn glade (slopes, $F_{1,43} = 17.53$, $P < 0.001$) and at Victoria glade (slopes, $F_{1,236} = 2.41$, $P = 0.12$; intercepts, $F_{1,237} = 32.11$, $P < 0.001$), but not at St. Francois glade (slopes, $F_{1,47} = 2.66$, $P = 0.11$; intercepts, $F_{1,48} = 1.13$, $P = 0.29$).

Microhabitat.—For all months combined, the species differed significantly in both perch type (Victoria, $\chi^2 = 78.60$, $N = 351$, $P < 0.001$; St. Francois, $\chi^2 = 30.57$, $N = 143$, $P < 0.001$; Hawn, $\chi^2 = 16.33$, $N = 104$, $P < 0.001$) and perch insolation categories (Victoria, $\chi^2 = 50.29$, $N = 203$, $P < 0.001$; St. Francois, $\chi^2 = 14.25$, $N = 83$, $P < 0.001$; Hawn, $\chi^2 = 14.58$, $N = 60$, $P < 0.001$). At all glades, *C. collaris* perched almost exclusively on rocks during all months, whereas for *S. undulatus*, use of rock perches decreased and use of tree trunk and branch perches increased during midseason months (Fig. 1a). *Crotaphytus collaris* also perched more frequently than *S. undulatus* in full or partial sun at all glades, although frequency of perching in full sun during midseason months decreased for both species (Fig. 1b).

PCA on the glades were similar, revealing a gradient on PC I from closed microhabitat, with many branches, nearby trees, and more leaf litter, to open microhabitat, with more gravel,

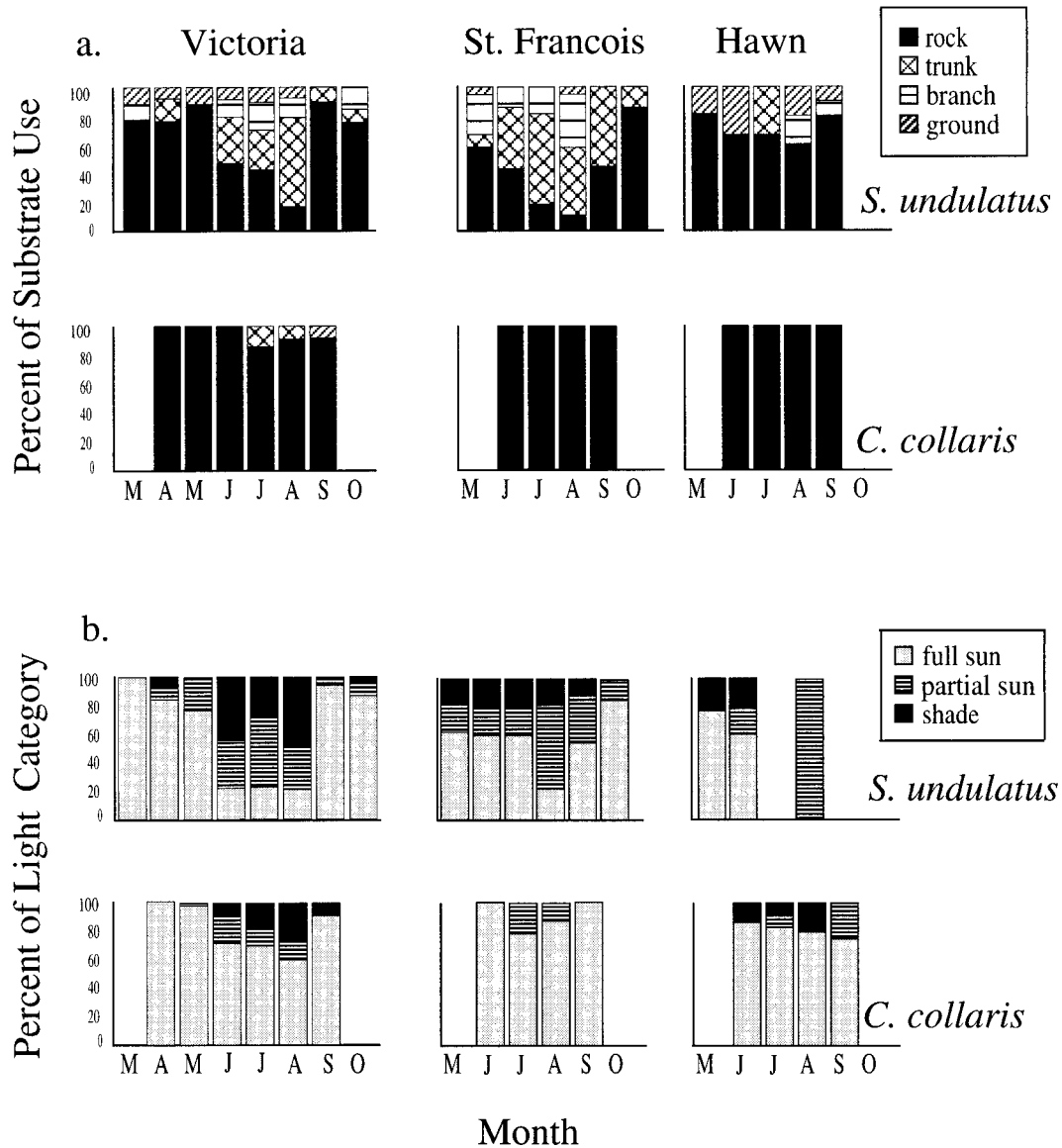


FIG. 1. (a) Monthly variation in frequencies of sightings in different perch substrate categories. (b) Monthly variation in frequencies of sightings in different perch insolation categories. Frequencies for which sample sizes are fewer than three are omitted from the figure.

great distance from trees, and many rocks. PC II at Victoria and St. Francois mainly reflected a gradient from many plants to many rocks, whereas PC II at Hawn loaded strongly for height and diameter of the nearest tree.

Microhabitats used by *C. collaris* were rockier and more open than those used by *S. undulatus*, which tended to have more branches, leaves, and close trees (Fig. 2). At all three glades, species and control sites occupied distinct regions of PC I (Victoria: *C. collaris*, $+0.532 \pm 0.057$, $N = 78$; *S. undulatus*, -0.543 ± 0.081 , $N = 147$;

control: $+0.711 \pm 0.094$, $N = 54$; St. Francois: *C. collaris*, $+0.634 \pm 0.068$, $N = 32$; *S. undulatus*, -0.771 ± 0.155 , $N = 42$; control, $+0.576 \pm 0.102$, $N = 21$; Hawn: *C. collaris*, $+0.486 \pm 0.096$, $N = 54$; *S. undulatus*, -0.628 ± 0.196 , $N = 18$; control, -1.069 ± 0.269 , $N = 14$). Species and control sites also occupied different regions of PC II (Victoria: *C. collaris*, -0.705 ± 0.078 , $N = 78$; *S. undulatus*, $+0.018 \pm 0.072$, $N = 147$; control, $+0.969 \pm 0.123$, $N = 54$; St. Francois: *C. collaris*, -0.610 ± 0.114 , $N = 32$; *S. undulatus*, -0.088 ± 0.135 , $N = 42$; control: $+1.105 \pm$

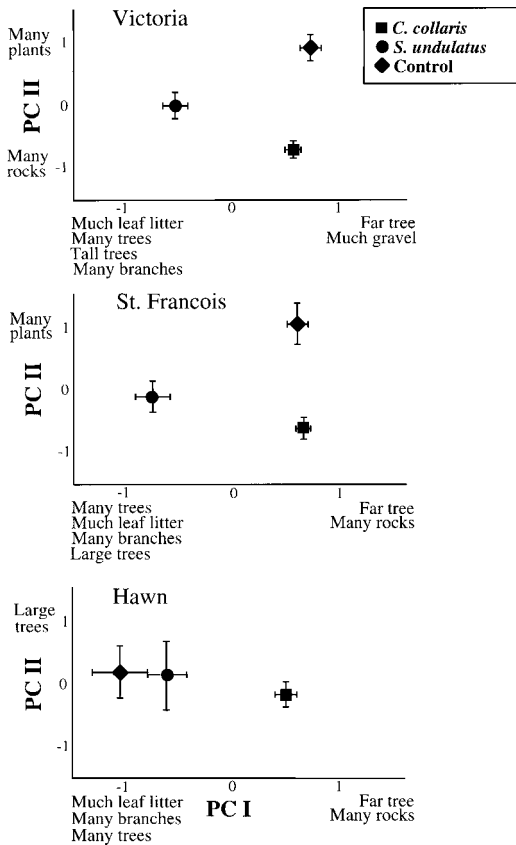


FIG. 2. Mean PC II \pm 1 standard error versus mean PC I \pm 1 standard error for species and control sites at three glades.

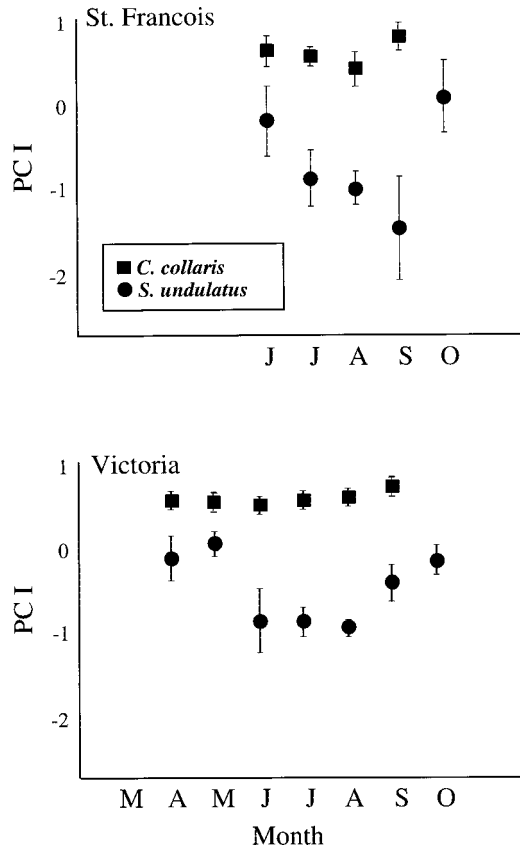


FIG. 3. Monthly variation in mean PC I score \pm 1 standard error at St. Francois and Victoria glades. Means for which sample sizes are fewer than three are omitted from the figure.

0.179, $N = 21$; Hawn: *C. collaris*, -0.113 ± 0.118 , *S. undulatus*, $+0.174 \pm 0.334$, control: $+0.211 \pm 0.264$, $N = 14$). ANOVA on PC I and PC II scores revealed that differences existed among species and controls (PC I: Victoria, $F_{2,276} = 69.07$, $P < 0.001$; St. Francois, $F_{2,92} = 41.82$, $P < 0.001$; Hawn, $F_{2,83} = 30.29$, $P < 0.001$; PC II: Victoria, $F_{2,276} = 65.61$, $P < 0.001$; St. Francois, $F_{2,92} = 31.08$, $P < 0.001$; Hawn: $F_{2,83} = 0.93$, $P = 0.400$). Posthoc contrasts of differences in PC scores indicated that all interspecific differences were statistically significant except for the second PC axis at Hawn (Victoria: PC I, $P < 0.001$; PC II, $P < 0.001$; St. Francois: PC I, $P < 0.001$; PC II, $P = 0.02$; Hawn: PC I, $P < 0.001$; PC II, $P = 0.577$). Each species differed from control locations on at least one axis (with the exception of *S. undulatus* at Hawn, where sample sizes were low), indicating that both species were using nonrandom subsets of the glades (*C. collaris*: Victoria, PC I, $P = 0.466$; PC II, $P < 0.001$; St. Francois, PC I, $P = 0.962$; PC II, $P < 0.001$; Hawn, PC I, $P < 0.001$, PC II, $P = 0.562$; *S. un-*

dulatus: Victoria, PC I, $P < 0.001$; PC II, $P < 0.001$; St. Francois, PC I, $P < 0.001$; PC II, $P < 0.001$; Hawn, PC I, $P = 0.28$; PC II, $P = 0.955$).

Patterns of seasonal shifts in PC position mirrored those seen for use of rocks and perch isolation. ANOVA indicated that the position of *S. undulatus* on PC I varied significantly with month at Victoria ($F_{4,142} = 4.24$, $P = 0.003$) and at St. Francois ($F_{4,37} = 2.89$, $P = 0.035$) but not at Hawn ($F_{4,13} = 0.91$, $P = 0.486$). By contrast, the position occupied by *C. collaris* along PC I varied significantly only at Victoria (Victoria, $F_{4,73} = 2.91$, $P = 0.027$; St. Francois, $F_{4,27} = 0.78$, $P = 0.551$; Hawn, $F_{3,50} = 1.96$, $P = 0.131$). Overall, *S. undulatus* showed a greater shift in mean PC I score during midseason months than did *C. collaris* (Fig. 3). PC II scores did not vary significantly across months for either species.

DISCUSSION

Sceloporus undulatus used open rock perches in Missouri glades early and late in the year but occupied trees, generally at the periphery of

glades, during the middle of the year. Because *S. undulatus* has a longer activity season than *C. collaris*, this shift by *S. undulatus* from rocks to trees and then back to rocks coincides with the appearance and disappearance of *C. collaris*. This concordance suggests the possibility of a causal relationship: competition with or predation by *C. collaris* may be responsible for the habitat shift by *S. undulatus*. Both species are insectivorous, sit-and-wait predators that probably overlap substantially in the prey that they take, although *C. collaris* can undoubtedly eat prey that are too large for *S. undulatus*. Moreover, *C. collaris* is known to eat smaller lizards, including *S. undulatus* (e.g., Blair and Blair, 1941; Fitch, 1956; McAllister, 1985). Thus, both interspecific competition and predation are plausible possibilities and should be tested directly, perhaps by removal experiments.

Another possibility, however, is that both species are responding to changes in temperature. Previous laboratory and field studies on other (non-Missouri) populations of *C. collaris* indicate that these lizards maintain body temperatures averaging 36–38°C, with some animals attaining temperatures as high as 43°C (Fitch, 1956; Dawson and Templeton, 1963; Brattstrom, 1965; Firth et al., 1989). By contrast, previous studies on other populations of *S. undulatus* report body temperatures averaging 34°C and generally ranging from 32–36°C (Brattstrom, 1965; Crowley, 1985). Indeed, the genus *Sceloporus* is thermally conservative, with all species exhibiting a similar thermal profile despite substantial differences in habitat use, geography, and altitude (Bogert, 1949; Crowley, 1985; Adolph, 1990). Our observations indicate that lizards on Missouri glades conform to previous studies of the thermal biology of these species. Both species show a gradual increase in body temperature from spring to summer, followed by a corresponding decrease in the fall, but mean temperatures correspond exactly to those reported for the species in other localities.

Examination of microhabitat use and seasonal activity patterns of the species illustrates how these differences in temperature might be attained. Early in the year, *S. undulatus* spends most of its time in rocky areas, which are usually in the open sun. As the season progresses, the lizards move to trees and other shaded habitats, thus allowing them to maintain the same temperatures even as the weather gets hotter. By contrast, when active, *C. collaris* stayed in the rocky areas all season and was usually observed in the sun even in the middle of the summer. As a result, *C. collaris* maintained higher temperatures than *S. undulatus*. Even in the early spring, however, the species differed in body temperature although they both primarily used

rocky habitats at this time. These differences probably resulted both from the greater use of shade by *S. undulatus* and subtle differences in microhabitat use between the species.

Given that the thermal biology of *S. undulatus* on Missouri glades does not differ from conspecifics elsewhere, or from congeners that occupy vastly different habitats and localities, we hypothesize that the shift in habitat use exhibited by this species may be primarily a response to the changing thermal environment, rather than to the presence of *C. collaris*. Indeed, similar seasonal shifts in habitat use have been reported for other *Sceloporus* (Smith, 1997). Nonetheless, predation, competition, and thermoregulation are not mutually exclusive hypotheses, and ecological interactions—both competition and predation—are likely to occur between these two species. Because many Missouri glades do not contain *C. collaris*, comparison of *S. undulatus* on different glades with and without *C. collaris* can assess the role that thermal biology and interspecific interactions play in determining microhabitat use. Moreover, reintroductions of *C. collaris* as part of conservation efforts may allow experimental tests of these hypotheses.

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