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Increased Lesser Earless Lizard (Holbrookia maculata) Abundance on Gunnison's Prairie Dog Colonies and Short Term Responses to Artificial Prairie Dog Burrows

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ABSTRACT.—Our studies of the association between the lesser earless lizard (*Holbrookia maculata*) and Gunnison's prairie dogs (*Cynomys gunnisoni*) revealed: (1) the lesser earless lizard was more abundant on prairie dog colonies than off; (2) lesser earless lizard abundance was positively correlated with prairie dog burrow abundance; (3) lesser earless lizards responded positively to artificial burrows created on noncolonized areas; and (4) lesser earless lizards used prairie dog burrows as refuges from predators; however, the relative use of burrows was greatest at high and low temperature extremes. Although prairie dogs alter habitat in many ways, our study suggests that burrows are an important mechanism involved in the association between the lesser earless lizard and Gunnison's prairie dogs.

INTRODUCTION

Although the role of prairie dogs (*Cynomys* sp.) as keystone species is debated (Clark *et al.*, 1982; Whicker and Detling, 1988; Stapp, 1998; Kotliar *et al.*, 1999), prairie dogs do alter areas they inhabit in ways that potentially affect many other members of the plant and animal community. Quantitative studies of the effects of prairie dogs on other community members have focused on birds (O'Meilia *et al.*, 1982; MacCracken *et al.*, 1985), mammals (Ceballos *et al.*, 1999), insects (Agnew *et al.*, 1986) and plants (Whicker and Detling, 1988), and more rarely, reptiles and amphibians. Kretzer and Cully (2001) found that overall abundance of reptiles and amphibians on black-tailed prairie dog (*Cynomys ludovicianus*) colonies did not differ from noncolonized areas, but that species composition did. However, one species they studied, the lesser earless lizard (*Holbrookia maculata*), appeared to be more common in the presence of prairie dogs.

The lesser earless lizard is a small (6 cm SVL) insectivorous iguanid that lives in areas with sparse short vegetation, loose friable soil and relatively level terrain (Degenhardt *et al.*, 1996; Hammerson, 1999). Its abundance is positively associated with cattle grazing and soil disturbance (Ballinger and Jones, 1985; Ballinger and Watts, 1995) and the lesser earless lizard has been noted to use mammal burrows to escape high temperatures (Collins, 1993) and predators (Vaughan, 1961; Gehlbach, 1965).

Several factors might explain the higher abundance of the lesser earless lizard on prairie dog colonies. Changes in vegetation induced by prairie dog activities could create more open habitat and/or alter arthropod abundance and diversity (Agnew *et al.*, 1986; Whicker and Detling, 1988), soil and plant heterogeneity may be increased by burrowing and foraging (Ballinger and Watts, 1995; Ceballos *et al.*, 1999) and/or the burrows could serve as refuges for thermoregulation and predator avoidance (Vaughan, 1965; Collins, 1993; Cooper, 2000).

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To investigate if the lesser earless lizard responds to the presence of prairie dogs and to identify factors that might cause a response, we addressed four questions in a Great Basin Desert grassland colonized by Gunnison's prairie dogs (*Cynomys gunnisoni*). (1) Is the lesser earless lizard more abundant on or off prairie dog colonies? (2) Is its abundance related to prairie dog burrow density? (3) Would its abundance increase on noncolonized transects if artificial burrows were added? and (4) Does the lesser earless lizard use prairie dog burrows as refuges?

METHODS

Three study sites were located in a Great Basin Desert grassland 3 km west of Wupatki National Monument (35°34′41.66″N, 111°31′58.85″W), Coconino County, Arizona. Many prairie dog colonies were present in this area and we selected three sites that were most similar in elevation (1738 to 1784 m), plant community and slope and that were separated by a minimum of 2 km. For each prairie dog colony we selected a nearby (0.5 km) reference site that showed no sign of current or past use by prairie dogs that were again matched as nearly as possible for elevation, plant community and slope. Domestic livestock grazed the entire study area and the sparse vegetation was dominated by nettleleaf goosefoot (*Chenopodium murale*), black gramma (*Bouteloua eripoda*), and blue gramma (*B. gracilis*). Generally, vegetation grew in small clumps (<0.5 m circumference) with relatively open areas of soil between them. The soil was composed of a 1–5 cm deep layer of small particle cinders on top of a sand/clay substrate. At each of the prairie dog and reference sites we established 400 m of permanent transect lines. Because of the irregular shape of prairie dog colonies, we subdivided the 400 m of transects into lengths of 60 to 140 m depending on the shape of the colony. Within a study area each segment of transect line was separated from the next by at least 50 m to reduce the likelihood that individual lizards could move from one transect to another and be counted multiple times during the same census period. Depending on prairie dog colony size, these transects sampled roughly 25–50% of the entire colony. This design yielded three sites (A, B, C), two treatments per site (colonized vs. noncolonized) and 400 m of transects per treatment for a total of 1200 m of transects on colonized areas and 1200 m on noncolonized areas.

We conducted five censuses of all six sites from 27 June to 16 August 2001 between 0600 and 1830 h. Each pair of colonized and noncolonized sites was censused within 2 h and all sites were censused on the same day. The time of day that each pair was sampled was varied so that data were collected at least once in the morning, afternoon and evening for each pair of sites. Abundance was determined by recording the number of individual lesser earless lizards sighted within 3 m of transect lines by the single researcher walking the transect line. Chi-square was used to compare the number of individuals sighted on prairie dog colonies with the number sighted on noncolonized reference sites. In addition, we divided transects into 20 m segments and counted the number of prairie dog burrows within 3 m of transect lines as an index of burrow abundance. Linear regression was used to examine the relationship between the number of prairie dog burrows on each 20 m segment of transect and the mean number of lesser earless lizards sighted on the same segment at each site.

To determine whether abundances of the lesser earless lizard increased on noncolonized transects if artificial burrows were added, we selected two 20 m segments of transect lines separated by the greatest possible distance at each noncolonized site and used a hand-held Eijkelkamp soil auger (10 cm blade) to create artificial burrows. We created 10 artificial burrows haphazardly spaced along each 20 m transect, all within 1 m of the transect line. This spacing resulted in a burrow density within the natural range of that found on our prairie dog colony sites. Artificial burrows gradually sloped downward from the surface, were cylindrical and approximately 20 cm across and 60 to 75 cm deep. Soil excavated from the burrows was used to build small mounds around the burrow openings. The external

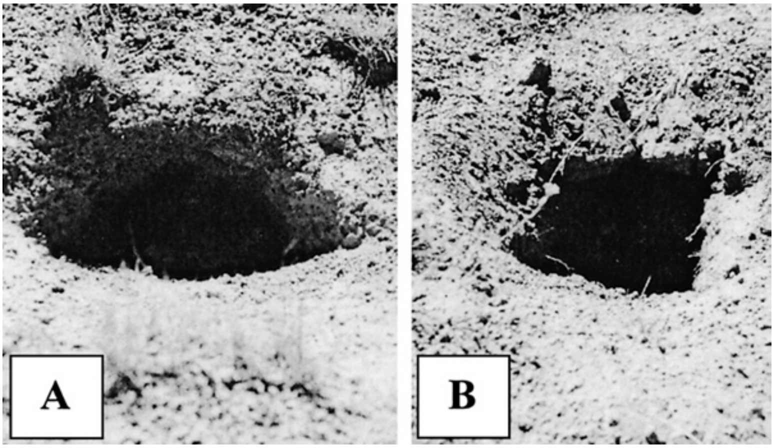

FIG. 1.—Examples of natural prairie dog (A) and artificial (B) burrows used in our study

characteristics of the artificial burrows were indistinguishable from natural burrows to the human eye (Fig. 1). Each 20 m transect segment with artificial burrows was separated from a 20 m reference section by a 20 m "buffer" section to reduce the possibility that individuals attracted to burrows would be censused on reference sections (Fig. 2). Artificial burrows were created on 24 August and censused for lizards on 9, 14, 19, 26 September and 1 October 2001. On each census day individuals were counted on the 20 m artificial burrow and reference sections of transects in noncolonized areas and on a 20 m section of transect on a prairie dog site with a natural burrow density similar to that of the artificial treatments. We compared the mean number of lesser earless lizards observed on each treatment averaged across the five censuses using the Kruskal-Wallis test followed by non-parametric Tukey-type multiple comparisons (Zar, 1984).

To determine whether the lesser earless lizard used prairie dog burrows as escape sites, we recorded the refuges individuals used when pursued by a human. We defined a refuge as any type of cover (prairie dog burrows, vegetation or rocks) that individuals ran to and paused within or beneath when pursued. We characterized a refuge as "initial" if it was the first location at which an individual chose to stop after running from our approach and as "terminal" if the animal remained in the site even after we reached it. The initial refuge was determined for 327 encounters. The terminal refuge was determined by following individuals ($n = 116$) at a walk to elicit escape behavior until the lizard reached a refuge it refused to leave. To control for behavioral differences caused by variation in temperature, air temperatures were recorded at the beginning and end of each transect and substrate temperatures were recorded at locations where lesser earless lizards were seen basking. The range of substrate temperatures we recorded (23–48 C) was subdivided into 5 categories, each of 5 C. We chose 5 C as the range for each category because this was the smallest increment used in a previous study of temperature-dependent burrow use by a congeneric lizard (Cooper, 2000). A Chi-Square Contingency Table Test was used to compare choice of refuges across substrate temperature categories.

RESULTS

The lesser earless lizard was the dominant reptile at the Great Basin Desert grassland we studied. We recorded 450 observations of lesser earless lizards compared to only 27 reptiles

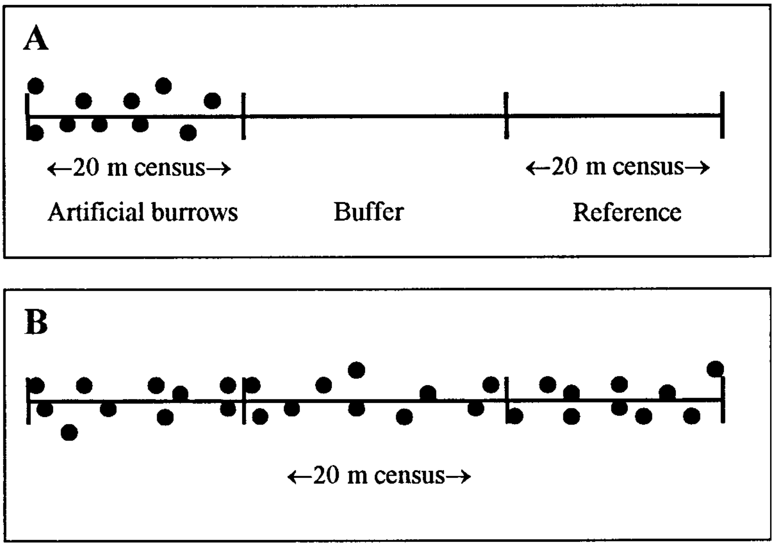

FIG. 2.—Experimental design used to compare lizard abundance on areas with artificial burrows to reference areas without burrows (A) and areas with natural prairie dog burrows (B). Artificial burrows were separated from reference sections by a "buffer" section to reduce the possibility that lizards attracted to burrows would be censused on reference plots

from 2 other genera during our censuses: 23 plateau striped whiptails (*Cnemidophorus velox*) and/or little striped whiptails (*C. inornatus*) (18 on, 5 off colonies) and 4 western rattlesnakes (*Crotalus viridis*) (3 on, 1 off colonies). Of the 450 sightings, 91.6% (412) of lesser earless lizards were associated with natural or artificial burrows.

Total sightings of the lesser earless lizard on prairie dog colonies were nearly 9 times greater (327) than off (37). Although the mean abundance of the lesser earless lizard varied among sites, at each site the total number of lizard sightings was significantly greater on prairie dog colonies than off (Site A: $\chi^2 = 106.52$, df = 1, $P < 0.001$; Site B: $\chi^2 = 32.27$, df = 1, $P < 0.001$; Site C: $\chi^2 = 93.63$, df = 1, $P < 0.001$). Lesser earless lizard abundance along each 20 m section of transect was correlated positively with the number of prairie dog burrows along that section of transect (Site A: $r^2 = 0.797$, $P < 0.05$; Site B: $r^2 = 0.771$, $P < 0.05$; Site C: $r^2 = 0.681$, $P < 0.05$; Fig. 3). Both burrow densities (3 to 19) and mean lesser earless lizard abundances (0.8 to 2.8) varied most at Site A. Burrow density and lesser earless lizard abundance ranged from 1 to 13 and 0 to 1.3, respectively, on Site B and 0 to 10 and 0.4 to 2.0, respectively, on Site C (Fig. 4).

Areas with artificial burrows had more lesser earless lizard sightings compared to references after 16 d. By 1 October 2001, the last of the 5 censuses performed after burrows were created, we had recorded 37 observations of the lesser earless lizard (including 7 juveniles) on artificial burrows, 45 (including 3 juveniles) on natural burrows and only 1 on reference transects lacking burrows. Lesser earless lizard abundance on artificial burrow transects did not differ from natural burrow transects but both were significantly greater than noncolonized reference transects [Kruskal-Wallis H (corrected for ties) = 10.3, $P < 0.002$, non-parametric, Tukey-type multiple comparisons: $q = 4.38$, $P < 0.05$ for natural burrows vs. reference, $q = 4.30$, $P < 0.05$ for artificial vs. reference and $q = 0.08$, $P > 0.5$ for

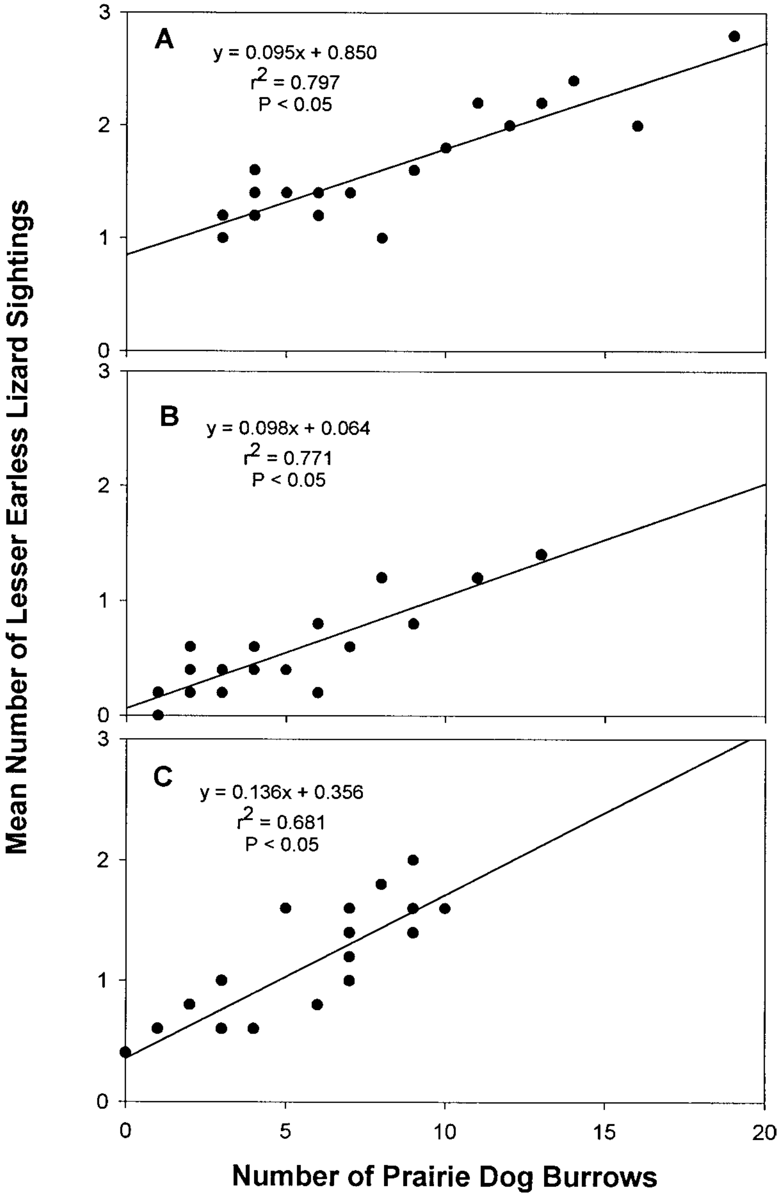

FIG. 3.—Mean abundance of lesser earless lizards versus Gunnison's prairie dog burrow density at three sites (A, B and C) in a Great Basin Desert grassland in northern Arizona

natural vs. artificial]. The mean number of lesser earless lizard sightings on reference and prairie dog transects in the period after artificial burrows were constructed were similar to the numbers recorded during the June–August census (0.667 ± 0.8 SE before vs. 0.17 ± 0.4 after for reference, 5.8 ± 1.3 before vs. 4.7 ± 1.75 after for prairie dog), but the number of

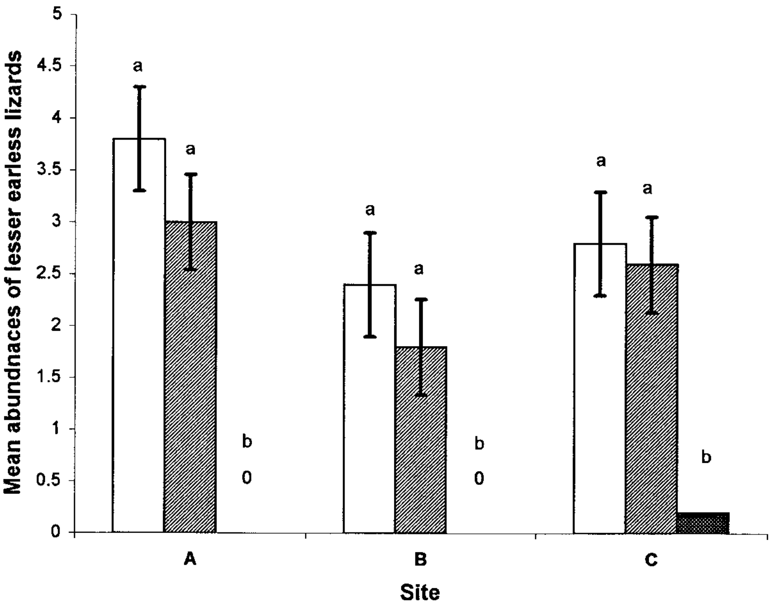

FIG. 4.—Mean abundance (total # sightings/5 censuses ± SE) of lesser earless lizards on Gunnison's prairie dog colonies (open bars), artificial burrow treatments (shaded bars) and references (dotted bars). Although data from each site were analyzed independently, they were combined in this figure. Abundances are based on 40 m transects at each site. Bars with the same letter are not significantly different; bars with different letters are significantly different at $P < 0.05$ [Kruskal-Wallis H (corrected for ties) = 10.3, $P < 0.002$]

sightings on transects with artificial burrows increased almost 6 fold (1.17 ± 0.8 before vs. 6.0 ± 2.0 after).

The lesser earless lizard responded differently in its selection of initial and terminal escape refuges. During initial escape responses ($n = 327$), individuals moved into the open more often (59.3% of observations) than either into a clump of vegetation (27.2%) or a burrow (13.5%) ($\chi^2 = 108.7$, df = 2, $P < 0.001$). When selecting a terminal refuge ($n = 116$), individuals chose either vegetation (55%) or prairie dog burrows (45%) ($\chi^2 = 0.68$, df = 1, n.s.).

The choice of vegetation versus burrows as terminal refuges varied depending upon substrate temperature across our five temperature categories (Chi-Square Contingency Test; $\chi^2 = 36.97$, df = 4, $P < 0.001$; Fig. 5). Burrows were selected by 67% of lesser earless lizards when substrate temperatures were coolest (23–28 C) and by 75% when warmest (43.1–48 C). In contrast, 67% and 92% of individuals chose vegetation at intermediate substrate temperatures, 28.1–33 and 33.1–38 C, respectively. Lesser earless lizards chose vegetation and burrows with equal frequency when substrate temperatures were 38.1–43 C.

DISCUSSION

Our results demonstrated that the lesser earless lizard was more abundant on Gunnison's prairie dog colonies than in nearby areas without prairie dogs. A similar relationship was suggested in previous studies of the lesser earless lizard in other grasslands occupied by the black-tailed prairie dog (*Cynomys ludovicianus*) (Knight and Collins, 1977; Clark *et al.*, 1982; Kretzer and Cully, 2001). Both prairie dog species modify their habitat in ways that could

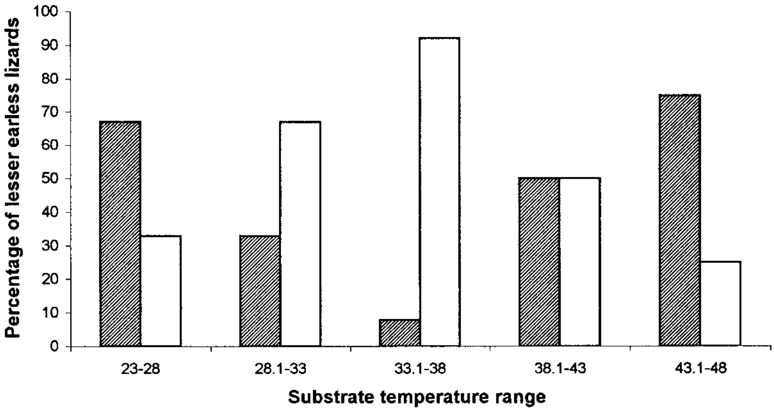

FIG. 5.—Percentage of lesser earless lizards observed using Gunnison's prairie dog burrows (shaded bars) versus vegetation (open bars) as terminal refuges in five substrate temperature ranges (n = 116) ($\chi^2 = 36.97$, df = 4, $P < 0.001$)

affect lesser earless lizard abundance. Vegetation shifts and soil disturbance caused by prairie dogs could create more open habitat and/or alter arthropod abundance and diversity. Open spaces of bare soil have been argued to be critical to the survival of populations of the lesser earless lizard in other grassland areas (Ballinger and Watts, 1995), and Gunnison's prairie dogs increase the amount of bare open soil (Bangert and Slobodchikoff, 2000). Likewise, the lesser earless lizard could benefit from prairie dog burrows by using them to escape predators, reduce solar input during hot summer months and/or as over-winter hibernacula. In addition, the soil mounds around burrow openings could be used as basking sites, as they are by other lizard species (Hager, 2000).

Two lines of evidence from our study indicate that prairie dog burrows are an important resource for the lesser earless lizard. First, within each prairie dog colony, lesser earless lizard abundance along each 20 m section of transect was correlated positively with the number of prairie dog burrows along the same section of transect. Second, the number of lesser earless lizards sighted in reference areas where we constructed artificial burrows was significantly higher than in nearby reference areas without artificial burrows. The significant correlation between burrow density and lizard sightings on natural prairie dog colonies could have been due to prairie dog-induced changes in vegetation or insect prey abundance in colonized areas. However, the artificial burrow experiment was done in areas that had not been modified by prairie dogs, so the positive response by the lesser earless lizard was due to attributes of the artificial burrows alone. In this respect, prairie dogs may be especially important in the areas we studied because no other burrowing rodent in our area creates burrow densities as great as those of prairie dogs.

The rapid colonization (16 d) of artificial burrows was unexpected given that they were created in areas of low lesser earless lizard density relatively far (0.3–0.5 km) from the nearest prairie dog colonies and suggested that burrows may be a limiting resource that individuals can locate quickly. In contrast to the differences in lesser earless lizard abundance between prairie dog colonies and noncolonized areas, the short-term response to artificial burrows we documented late in the season was unlikely to be due to increased reproduction, but rather was a shift of existing animals into areas with artificial burrows. Adult lesser earless lizards are territorial (Collins, 1993; Degenhardt *et al.*, 1996;

Hammerson, 1999), and the higher abundances on both artificial and natural burrows indicate that either territory size is smaller in areas with burrows or that areas without burrows are not saturated.

Our observations of lesser earless lizard escape behavior were consistent with previous work indicating that rodent burrows act as refuges from predators (Vaughan, 1961; Gehlbach, 1965; Cooper, 1997). When initially startled by a human, lesser earless lizards ran to burrows in 13% of our observations, but, when pursued further, burrows became the terminal refuge in roughly half of our observations. However, this use of burrows as terminal refugia was temperature dependent, with greater use of burrows at high and low temperatures. A similar result was described in a study of escape behavior of a closely related species, the keeled earless lizard (*Holbrookia propinqua*; Cooper, 2000). Our findings are consistent with the hypothesis that burrows become increasingly important as refuges as the threat of predation increases and at temperature extremes, when physiological function and mobility of ectotherms are most compromised (Bennett, 1980; Huey, 1982; Downes and Shine, 1998; Cooper, 2000).

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