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The Influence of Photoperiod and Position of a Light Source on Behavioral Thermoregulation in *Crotaphytus collaris* (Squamata: Iguanidae)

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Temperature selection of male *Crotaphytus collaris* acclimated to 25 ± 1 C was measured over a 24 h period in a thermal gradient with either uniform light over the entire gradient, a point source of light over the hot end of the gradient, or a point source of light over the cold end of the gradient and an 16L/8D, 12L/12D or 8L/16D photoperiod. Both photoperiod and the position of the light source over the gradient significantly influenced the diel cycle of thermal selection. The position of the light also significantly affected mean selected body temperatures. Photoperiod and light position were important both as separate and conjunctional factors influencing behavioral thermoregulation. We concluded that light position, heat, and photoperiod are used as separate cues in behavioral thermoregulation.

PHOTOPERIOD changes throughout a reptile's activity season provide reliable seasonal cues. Reptiles often thermoregulate within narrow limits when provided the opportunity, and some show seasonal differences in temperature preference (Patterson and Davies, 1978; Sievert and Hutchison, 1989a; Van Damme et al., 1986). Photoperiod affects many behavioral and physiological responses including reproduction (Licht, 1971a, 1971b), DNA synthesis in the testis (Noeske and Meier, 1983), temperature selection (Graham and Hutchison, 1979; Rismiller and Heldmaier, 1982, 1988), diel patterns of temperature selection (Rismiller and Heldmaier, 1982; Spellerberg, 1974), and thermal tolerance (Hutchison and Kosh, 1964; Licht, 1968).

Photoperiods with a longer photophase (16L/

8D) caused an elevation of preferred temperatures in painted turtles (*Chrysemys picta*) acclimated at 15 or 25 C and spotted turtles (*Clemmys guttata*) acclimated at 25 C (Graham and Hutchison, 1979). Similar results were found in European green lizards (*Lacerta viridis*) (Rismiller and Heldmaier, 1988) and fence lizards (*Sceloporus undulatus*) in May, but not July (Ballinger et al., 1969). In constant light (LL), blotched water snakes (*Nerodia erythrogaster*) chose higher body temperatures (T_b) than snakes kept on an 12L/12D photoperiod (Gehrmann, 1971).

Light and heat are often treated synonymously in thermal gradient studies, especially in the case of photothermal gradients where a lamp is the source of both heat and light for the gradient. The position of the light source is an important factor in temperature selection in both nocturnal geckonids (Sievert and Hutchison, 1988) and diurnal iguanids (Sievert and Hutchison, 1989a). The position of the light source influences the temporal pattern of thermal selection and in some cases the actual temperatures selected by lizards. The purpose of this study was to examine the effect of both the position of the light source and duration of the light phase of the photoperiod on temperature selection of *Crotaphytus collaris* over diel (24 h) periods. We chose *C. collaris* as a study animal because we had background information on the effects of time of day, sex, season, nutritional status, and the parietal eye on temperature selection in this species (Sievert and Hutchison, 1989a, 1989b; Sievert, 1989).

Because *C. collaris* selects higher T_bs during photophase than during scotophase (Sievert and Hutchison, 1989a) we hypothesized that lizards maintained on long photoperiods would select significantly higher mean T_bs over a 24 h period than lizards maintained on short photoperiods. To test this hypothesis, we monitored T_bs of lizards maintained on 16L/8D, 12L/12D, and 8L/16D photoperiods and determined the effect of photoperiod on: 1) mean T_b selected over a 24 h period; and 2) temporal patterns of temperature selection. We repeated this work with three combinations of light and heat to determine how light position and photoperiod interact to influence behavioral thermoregulation.

Materials and Methods

Male *Crotaphytus collaris* were captured in central Oklahoma and maintained in the laboratory (Sievert, 1987) for at least 6 mo prior to use. After emergence from hibernation in Jan. the lizards were divided into three groups and maintained on either an 8L/16D, 12L/12D, or 16L/8D photoperiod for at least 4 wk before experimentation. In all three groups the photoperiod was centered at 1200 Central Standard Time and air temperature was maintained at 25 ± 1 C. Photophase of the 8L/16D group lasted from 0800–1600 h, of the 12L/12D group from 0600–1800 h, and of the 16L/8D group from 0400–2000 h. Prior to acclimation each lizard was able to elevate T_b by basking under a 60 W incandescent light bulb during photophase. Five days before experimentation each lizard was acclimated to a constant 25 ± 1 C and kept on the same photoperiod on which it had been maintained prior to acclimation. Lizards were provided water ad lib but no food during acclimation to eliminate the possibility of postprandial thermophily (Sievert, 1989).

Late during the photophase of the day before experimentation a single lizard was placed into one of three linear thigmothermal gradients with an aluminum plate (0.3 cm) floor. Each gradient was approx. 210 cm long and had floor temperatures ranging from 10 ± 0.2–50 ± 2 C. Each gradient was covered with a clear acrylic plastic heat shield that prevented heat from the lights from entering the gradient.

One gradient had broad spectrum fluorescent lights (General Electric) suspended over its entire length, which provided uniform light (UL). The second had a point source of light over the hot end (LH) and the third had a point source of light over the cold end (LC). The point source of light was a 60 W broad spectrum incandescent bulb (Westinghouse) with a narrow reflector shade.

Each lizard was allowed to habituate to the gradient overnight. Cloacal temperatures were recorded at 10 min intervals from 0900 h one day until 0900 h the next day with a flexible copper-constantan thermocouple placed in the cloaca with the exiting wire taped to the tail. Details of the gradient and experimental protocol were described by Sievert and Hutchison (1988).

We gathered all data between mid-Feb.–late May. All animals were healthy and alert during the experimental period. We used nine different lizards within each light treatment group in each of the three photoperiod groups.

Data were analyzed with two-way repeated measures ANOVA. Time and either photoperiod or light treatment were the two factors.

This was necessary because we followed individual lizards over time. Each lizard only contributed one to the sample size, not 24. If we treated the number of observations, rather than the number of individuals as the sample size, the sample size would be significantly inflated (Mathur and Silver, 1980). We examined differences in T_bs among the light treatment groups, among T_bs within each group over time, and in temporal patterns of thermoregulation among groups. As required by the ANOVA (SAS, 1982), data missing due to equipment malfunction was replaced with the average of the other lizards' T_bs within the same light and photoperiod treatment group. We used a Tukey's studentized range test (SAS, 1982) to determine if selected T_bs varied over the 24 h time block within each treatment group. Differences were considered significant at $P < 0.05$.

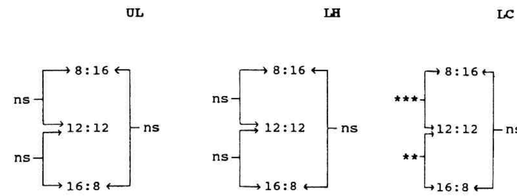

Fig. 1. Comparison of mean 24 h body temperatures of male *Crotaphytus collaris* by photoperiod group within each of the three light treatment groups. UL = uniform light over the entire gradient; LH = light over the hot end of the gradient only; and LC = light over the cold end of the gradient only. Means and SE of each group are shown in Figure 2. Brackets illustrate pairs in each group being compared. ** = $P < 0.01$, *** = $P < 0.001$, and n.s. = $P > 0.05$.

Results

Effect of photoperiod.—The mean 24 h T_bs of the three photoperiod groups (8L/16D, 12L/12D, and 16L/8D) were not significantly different ($P > 0.05$) when compared under the UL or the LH treatment (Fig. 1). There was a significant difference among the three photoperiod groups when compared in the LC treatment ($P < 0.05$). Lizards in the 12L/12D LC group chose significantly higher T_bs than the 8L/16D LC group ($P = 0.0005$) and the 16L/8D LC group ($P = 0.002$). The 8L/16D and 16L/8D LC groups did not select significantly different T_bs ($P = 0.14$) (Fig. 1).

The effect of time of day on temperature selection was significant among the 8L/16D, 12L/12D, and 16L/8D groups when compared under the UL ($P < 0.001$) and LH ($P < 0.001$) treatments, but not the LC treatment ($P = 0.47$). When the treatment and light groups were compared individually among the three UL treatment groups, only the 12L/12D group had a typical cycle of higher T_bs during photophase than scotophase.

All three photoperiod groups compared under the LH treatment displayed significant differences in T_bs over time. The 8L/16D LH group had an unusual cycle where the lowest T_b occurred from 1600–1700 h at the onset of scotophase and the warmest T_b occurred from 1100–1200 h. These lizards also selected T_bs from 2200–2400 that were significantly higher ($P < 0.05$) than those selected from 1600–1700 h.

The 16L/8D LC group lacked a diel cycle of higher photophase T_bs than scotophase T_bs. Statistically the 8L/16D LC and 12L/12D LC groups showed a cycle, but the lizards did not select higher T_bs during photophase than scotophase. In both of these LC groups the lowest and highest T_bs were chosen during photophase (Fig. 2).

The photoperiod regime under which the lizards were examined had a definite impact on the temporal pattern of temperature selection in the UL, LH, and LC groups ($P < 0.01$). The shapes of the temperature selection curves are visibly different (Fig. 2).

Effect of position of light.—The influence of the position of the light on mean T_bs selected over time was a function of the photoperiod in which the comparisons were made. There were no differences among mean T_bs of the three light treatment groups (UL, LH, and LC) when compared within the 8L/16D photoperiod treatment (Fig. 3). The diel patterns of temperature selection over time in the 8L/16D groups were all unusual. The 8L/16D UL group lacked a cycle of preferred T_bs. The 8L/16D LH and LC groups chose different T_bs over time, but did not display a typical cycle of highest T_b during photophase and lowest during scotophase.

The 12L/12D LC group selected significantly higher ($P = 0.02$) T_bs than the 12L/12D UL and LH groups (Fig. 3). In this photoperiod treatment, both the UL and LH groups displayed normal diel cycles, although the amplitude of T_bs in the LH cycle was small. The LC group had an unusual T_b cycle where both the high and low T_bs occurred during photophase.

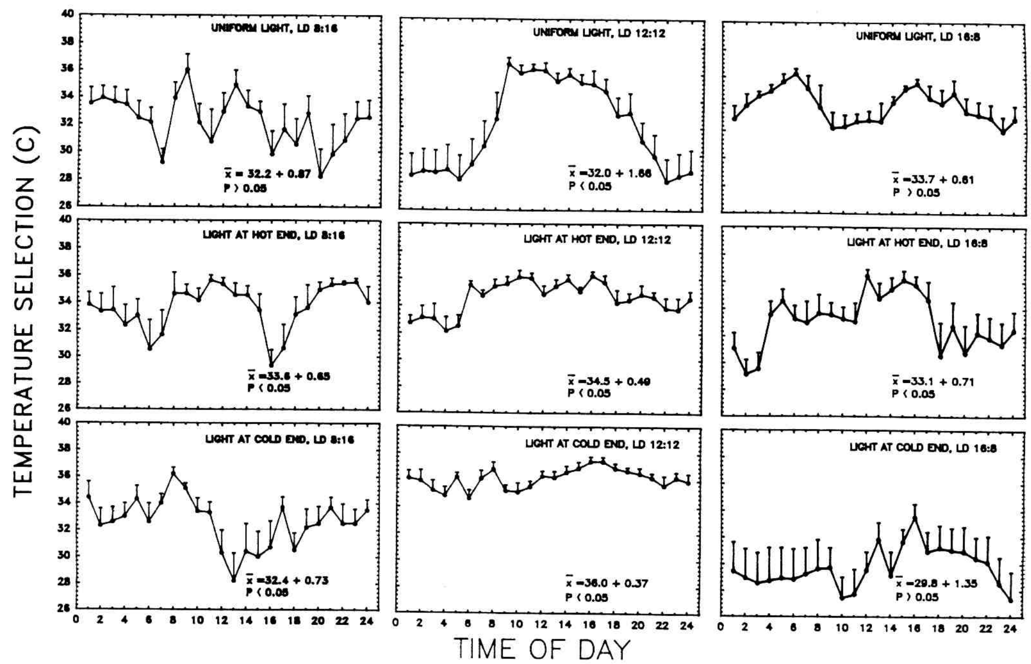

Fig. 2. Temperature selection of male *Crotaphytus collaris* in a thermal gradient over a 24 h period. Lizards were acclimated to 25 ± 1 C and either an 8L/16D, 12L/12D or 16L/8D photoperiod. Mean T_bs are plotted at 1 h intervals. Vertical lines represent 1 SE above the mean. The 24 h mean and SE and *P* values of the Tukey's studentized range test are given for each group.

The 16L/8D UL group selected significantly higher ($P = 0.04$) T_bs than the 16L/8D LC group (Fig. 3). With the 16L/8D treatment only the LH group displayed a normal diel cycle of T_bs. Both the UL and LC groups lacked cycles with higher photophase T_bs than scotophase T_bs.

The light treatment (UL, LH, or LC) had a definite impact on the temporal pattern of temperature selection in the 8L/16D and 12L/12D ($P < 0.0001$) groups, but not in the 16L/8D group ($P = 0.08$). The three UL and three LH groups differed significantly ($P < 0.05$) in the shapes of their selected T_b over time curves when compared within the same photoperiod (8L/16D, 12L/12D, or 16L/8D) treatment even though the mean T_bs selected over the 24 h period did not differ in any photoperiod condition.

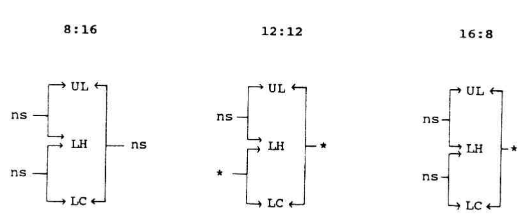

Fig. 3. Comparison of mean 24 h body temperatures of male *Crotaphytus collaris* by light treatment group within each of the three photoperiod treatment groups. Abbreviations are the same as in Figure 1. Means and SE of each group are shown in Figure 2. Brackets illustrate pairs of groups being compared. * = $P < 0.05$ and n.s. = $P > 0.05$.

Discussion

Our initial hypothesis that collared lizards maintained on long photoperiods select higher T_bs than those on short photoperiods was not supported. In all cases the 16L/8D treatment groups selected T_bs that were equal to or significantly lower than the 8L/16D and 12L/12D treatment groups. This is in direct contrast to observations on *Lacerta viridis* (Rismiller and Heldmaier, 1982) and *Chrysemys picta* and *Clemmys guttata* (Graham and Hutchison, 1979). Days with long photophases would not be encountered by *C. collaris* immediately after hibernation. In March or April when the lizards emerge from hibernation in Oklahoma, the photophase of the natural photoperiod is between 12–13 h.