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THE UNIVERSITY OF OKLAHOMA

GRADUATE COLLEGE

PARIETALECTOMY AND THERMAL SELECTION IN THE LIZARD

SCELOPORUS MAGISTER

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degree of

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BY

GUSTAV A. ENGBRETSON

Norman, Oklahoma

1975

PARIETALECTOMY AND THERMAL SELECTION IN THE LIZARD

SCELOPORUS MAGISTER

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PARIETALECTOMY AND THERMAL SELECTION IN THE LIZARD

SCELOPORUS MAGISTER

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The effects of parietectomy, photoperiod, and thermal acclimatization on thermal selection by Sceloporus magister were investigated in the laboratory. Parietalectomized, sham operated and control lizards were acclimatized to temperature and photoperiod regimes (15°C-LD=08:16, 15°C-LD=16:08, 35°C-LD=08:16, and 35°C-LD=16:08) and placed in light-proof thermal gradients under the same photoperiod employed in acclimatization. The lizards body temperatures were monitored 24 hours per day for periods of up to 15 days. Daily rhythms of thermal selection were evident with higher temperatures selected in late photophase and lower temperatures selected in scotophase. Parietalectomized animals chose higher body temperatures than shams or controls. Temperature and photoperiod acclimatization had little or no effect on the thermal preferendum. The preferred body temperature of controls was $33.2^{\circ}\text{C} \pm 3.59$. Length of time in the gradient tended to change thermal preference, especially in lizards acclimatized to 15°C. Through interactions with the pineal gland the parietal eye is probably important in synchronizing many bodily functions of lizards with photoperiod.

The results of this study are presented in a paper prepared in the style of the Journal of Experimental Zoology.

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TABLE OF CONTENTS

	Page
Introduction	iii
Acknowledgments	iv
List of tables and appendices	vi
List of illustrations	vii
 Parietalectomy and thermal selection in the lizard <u>Sceloporus magister</u>	
Abstract	1
Materials and methods	4
Results	8
Discussion	10
Acknowledgments	18
Literature cited	19
Figure legend	23
Figure	24
Tables	25
Footnote	28
Running page headline	29
Appendices	30

LIST OF TABLES AND APPENDICES

TABLE		PAGE
1	Mean body temperatures selected by parietectomized, control, and sham operated lizards.	25
2	Degree hours accumulated by various treatments of lizards in a thermal gradient	26
3	Mean coefficients of variation of body temperatures of lizards in photophase and scotophase	27

APPENDIX

1	Basic statistics for hourly thermal selection by all treatment groups	30
2	Analysis of variance tables for differences in mean hourly thermal selection	34

LIST OF ILLUSTRATIONS

FIGURE		PAGE
1	Mean hourly body temperature selection by <u>Sceloporus magister</u> in a thermal gradient	24

PARIETALECTOMY AND THERMAL SELECTION
IN THE LIZARD SCELOPCRUS MAGISTER.

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ABSTRACT Lizards were acclimatized to various temperature (15°, 35°C) and photoperiod regimes (LD 08:16, 16:8). Parietalectomized, sham operated, and control animals were placed in thermal gradients and their body temperatures monitored for periods of up to 15 days. Daily rhythms of thermal selection were evident with higher temperatures selected in late photophase and lower temperatures selected in scotophase. Thermal selection was more variable in scotophase than in photophase. Parietalectomized lizards chose significantly higher body temperatures than did shams or controls. Temperature and photoperiod acclimatization had little or no effect on the thermal preferendum. The preferred body temperature of controls was $33.2^{\circ}\text{C} \pm 3.59$. Length of time in the gradient tended to change thermal preference, especially in lizards acclimated to 15°C. Through interactions with the pineal gland the parietal eye is probably important in synchronizing many bodily functions with photoperiod.

The parietal eye (parapineal) of lizards has been ascribed many functions since its initial description by Leydig (1872); however, its true functions remain uncertain. Currently, the most widely accepted

theory of parietal eye function is that proposed by Stebbins and Wilhoft (1966) and summarized by Stebbins and Cohen (1973). Briefly, they suggest that the parietal eye provides sensory information that helps regulate exposure to sunlight and prevents overstimulation of some body functions. Sensory information is believed to be transmitted from the parietal eye via the parietal nerve to the pineal gland (epiphysis) where it affects secretory activity. Engbretson and Lent (in press) have shown in Crotaphytus collaris, that photic information is transduced by the parietal eye and transmitted via the parietal nerve to the central nervous system (CNS), and that norepinephrine and serotonin stimulate the pineal gland which transmits information via the parietal nerve to the parietal eye, in turn, affecting its photosensitivity. Lent and Demian (personal communication) have anatomical evidence of projections of the parietal nerve in the pineal gland. The parietal eye and pineal gland appear to be functionally interdependent.

Evidence from a natural population of Sceloporus occidentalis indicate that parietalectomized (P) lizards spend more time per day exposed to light and P females advance in ovarian development at a faster rate than do sham operated (S) lizards (Stebbins and Cohen, 1973). Stebbins and Wilhoft (1966) found no difference in body temperature (T_b) between P and S Tropidurus albemarlensis in the field but the experimental paradigm prevented precise temperature measurement. Songdahl and Hutchison (1972) found no difference in oxygen consumption in P and S Sceloporus cyanogenys. Hutchison and Kosh (1974) showed P Anolis carolinensis selected higher T_b than did S conspecifics and proposed that the lizard parapineal plays a direct role in thermoregulation in

addition to the indirect function as a "photothermal radiation dosimeter" as suggested by Glaser (1958). Packard and Packard (1972) preferred the term "illuminometer" to photothermal radiation dosimeter and we feel the point is well taken.

Dawson (1975) reviewed the physiological significance of the preferred body temperature (PT) of reptiles. He mentioned that in some species many physiological processes proceed optimally near the PT; these include metabolic capacity for activity, auditory sensitivity, digestion and egestion, immunological response, secretion and action of certain hormones, aspects of renal function, and certain reproductive processes. Licht (1968) examined the influence of thermal acclimation under different photoperiods on the PT of the lizard Anolis carolinensis and concluded that "the thermal preferendum appears to be a relatively stable specific characteristic in lizards." He utilized a photothermal gradient in which light and heat emanated from the same source. Roth (personal communication) showed that P and S lizards behave differently in photothermal gradients in that illumination may be selected in favor of heat; this fact makes it difficult to separate the effects of illumination and heat on thermal preference in photothermal gradients.

Spellerberg (1974) and Regal (1967) noted that lizards select lower T_b at night (voluntary hypothermia) and in addition Spellerberg pointed out that standard deviations of the mean T_b 's during photophase tend to be less than during scotophase hours.

No investigations with more than one combination of temperature and photoperiod have shown the parietal eye to be involved in thermal

selection. This paper reports such an investigation and attempts to explain the effects of parietectomy, photoperiod and thermal acclimatization, and their interactions on saurian thermal selection in a laboratory gradient. It also reports some aspects of behavior in a thigmothermal gradient.

MATERIALS AND METHODS

Sceloporus magister were obtained from commercial suppliers and colleagues. The lizards were maintained in indoor and outdoor pens and in individual covered plastic boxes in environmental chambers or thermostatically controlled rooms. The animals were provided water occasionally and were fed a diet of roaches, crickets, field sweepings, small lizards (Xantusia vigilis and Sceloporus undulatus), immature laboratory mice and all life stages of Tenebrio molitor. When these foods were unavailable, or in short supply, the lizards were force-fed a slurry of Purina Cat Chow and water. Poly-Vi-Sol (Meade Johnson Co.) vitamins were provided occasionally.

The lizards were randomly divided into three experimental categories. Control (C) animals received no treatment. Parietectomy (P) was accomplished by severance of the parietal nerve posterior to the parietal eye. The interparietal scale was removed with forceps and an incision was made approximately 1 mm lateral and posterior to the parietal eye and extending through the meninges. The parietal nerve and vein which course posteriorly from the parietal eye through the meninges were severed by the incision. The surgery was made under antiseptic conditions and resulted in the loss of a small drop of cerebrospinal

fluid and slight bleeding. The interparietal scale was then cemented in place with minute quantities of Eastman 910 adhesive (Eastman Chemical Co.). No cement was allowed to contact the fresh incision. A piece of aluminum foil, reflective side uppermost, slightly narrower than the interorbital distance and extending 0.5 cm anterior to and 1.0 cm posterior to the parietal eye, was cemented in place with Eastman 910 adhesive. With the shield in place, the remainder of the dorsal aspect of the head was covered with an opaque mixture of carbon black and rubber cement. All animals surgically treated were allowed one week of recovery prior to experimental use. No anaesthesia was employed and no animals were lost within 1 week of the surgery. Sham (S) animals were treated identically to P animals except that the foil shield directly over the parietal eye was pierced by a hole 1 mm in diameter and the incision about the parietal eye was made lateral to the eye only. This incision also resulted in a slight loss of cerebrospinal fluid and bleeding.

Four identical thermal gradients measuring $2.55 \times 0.17 \times 0.21$ m were constructed from sheet metal. Pairs of gradients were mounted one above the other on wooden platforms and enclosed by a light tight shell of plywood and black plastic film. A heating coil was mounted in one end of each gradient. Each coil was regulated by a rheostat mounted on the outside of the shell. In the opposite end of each pair of gradients was a refrigeration coil connected to compressors. The compressors were slung from ceiling support beams above the gradients to isolate the gradients from the generally high level of vibration generated by the compressors. Screens were placed in the gradients at

both ends to deny the lizards access to the heating and cooling coils; this made the total length of usable gradient 2.1 m. Adjustments to the heating and cooling units were made so that a gradient from approximately 0°C to 50°C was obtained. Wide spectrum fluorescent lamps (Sylvania Gro-Lux) were mounted above each pair of gradients so that uniform illumination was provided over the entire length of each gradient. The lights provided no detectable radiant heat to the gradient substrate. Automatic timer switches (International Register Co.) provided photoperiod control. Light-proof fan assemblies mounted outside the shell removed excess heat generated by the lamp ballast and heating coils. Each gradient was covered with transparent 6.35 mm thick Plexiglas. Fine sand approximately 0.5 cm deep covered the bottom of each gradient. Copper-constantan thermocouples were placed every 35 cm along the gradient 0.5 cm above the substrate to monitor temperature and insure that the proper thermal range existed. Thermocouple output was initially recorded by a Speedomax G 24 channel recorder (L&N Instrument Co.) and, in the latter portions of the study, by a programmable data acquisition system (Kaye Instruments, System 8000).

Animals were acclimatized in individual 32 x 23 x 10 cm covered plastic boxes in environmental chambers to $15 \pm 1^\circ\text{C}$ and $35 \pm 1^\circ\text{C}$ at photoperiods of LD 08:16 (8 hr. photophase alternating with 16 hr. scotophase) and 16:08 for at least one week prior to being placed into the thermal gradients under the same photoperiod employed in acclimatization. The photophase of each photoperiod was centered on 1200 CST. Copper-constantan thermocouples (36 gauge) insulated with Uralane (Furane Plastic Co.) or heat shrink tubing were inserted

approximately 2 cm into the intestine through the cloaca of each animal. Thermocouples were secured by taping the wire exiting the cloaca to the tail of the animal. All connections between the animal or the gradient monitoring thermocouples and the data acquisition systems were with solder free similar metal connectors (Thermo-Electric Co.). Each thermocouple channel was sampled at least once each hour. The animals remained in the gradients for periods from 5 to 15 days. Data were read to the nearest 0.1°C .

Basic statistics and analyses of variance (ANOVA) for significant differences in thermal selection between each hour under each experimental condition were calculated. Differences between acclimatization groups were analyzed by ANOVA. Differences in thermal selection within acclimatization groups were tested with a priori planned comparisons (Sokal and Rohlf, 1969) between the two control types (C & S) and the experimental animals (P).

Degree hours of treatment groups were determined from graphs of mean hourly T_b vs hour of the day. Graphs were cut out and surface area (degree-hours) was measured with an automatic area meter (Hayashi-Denko Co., Ltd. Type AAM-5).

Trends in day to day and hour to hour thermal selection were investigated. Regression coefficients of the mean T_b for each hour or day were calculated with time as the independent variable. Sets of regression coefficients were tested by the simultaneous test procedures (Sokal and Rohlf, 1969). Most calculations were performed on an IBM 370-158 computer at the University of Oklahoma Merrick Computing Center.

RESULTS

No significant difference ($p > 0.05$) existed between mean T_b 's for males and females so all data were grouped. In all treatment groups except for sham animals acclimatized to LD 08:16 and 35°C (S-8:16-35°) there were daily rhythms of thermal selection (Fig. 1). The rhythms were typified by selection of the daily high hourly mean T_b in the latter part of the photophase and the daily low hourly mean T_b in the mid to late scotophase. Significant differences in hourly mean T_b over the 24-hour period were present in all treatments except S-8:16-35°.

Within the four acclimatization groups, significant differences existed between the mean T_b of P animals and S and C animals except for 16:8-35°. In all cases, except 16:8-35°, P's selected higher mean T_b 's than S's and C's for the 24-hour period ($p < 0.001$) (Table 1). When only photophase hours are considered, P's selected higher mean T_b 's in all cases ($p < 0.05$). In scotophase P's again selected higher mean T_b 's except for 16:8-35°.

Time and temperature were integrated for all treatment groups and in all cases P's had a higher total of degree hours accumulated than did C's or S's (Table 2). Note, that although the total number of degree hours is always higher for P's, that parietectomy does not change the percentage of degree hours accumulated in photophase and scotophase.

Day-to-day thermal selection was not constant. Regression analysis showed the animals acclimatized to 15°C chose lower mean T_b 's on successive days in all 6 treatments and that animals acclimatized

to 35°C chose higher mean T_b 's on successive days in 5 of 6 treatments (Table 2), a frequency of occurrence greater than expected by chance alone ($\chi^2=4.33$, $df=1$, $p<0.05$). Despite these trends, regression coefficients were not significantly different from zero except for the 16:8-15° treatment groups and S-8:16-15°. Temperature acclimatization was the main factor affecting daily change in thermal selection ($F_{1,276}=9.54$) but the interaction of photoperiod acclimatization, thermal acclimatization and experimental condition (C,P or S) was also significant in accounting for that change ($F_{2,276}=5.02$).

Within treatment groups, coefficients of variation of the mean hourly T_b 's were usually smaller in photophase than in scotophase (Engbretson, 1975). The mean coefficient of variation of the mean T_b in photophase and scotophase in both photoperiod acclimatization groups are significantly different (Table 3, t-test, $p<0.05$) and smaller in photophase than scotophase. Coefficients of variation were used to eliminate the effect of magnitude of the means. We thought the above noted difference might be related to temporal changes in thermal selection. Regression coefficients were calculated for hourly mean T_b 's with days as the independent variable. Correlation of these regression coefficients with coefficients of variation of hourly mean T_b 's for the same hours revealed highly significant ($p<0.01$) and positive correlation in the following groups: 1) all animals together ($r=0.53$, $n=288$); 2) controls ($r=0.50$, $n=96$); 3) shams ($r=0.56$, $n=96$); 4) 15° acclimatization ($r=0.50$, $n=144$); 5) 35° acclimatization ($r=0.57$, $n=144$); 6) LD 16:08 acclimatization ($r=0.62$, $n=144$); and 7) LD 08:16 acclimatization ($r=0.51$, $n=144$). This indicates that the variation

about the mean T_b of lizards in a thermal gradient for several days, can be largely explained by daily change in thermal selection and that the greatest daily change in thermal selection takes place in scotophase. The one group which failed to yield a significant positive correlation was all parietectomized animals considered together. This group yielded a nonsignificant ($0.10 > p > 0.05$) negative correlation coefficient ($r = -0.14$, $n = 96$).

DISCUSSION

The term "preferred body temperature" as used by Dawson (1975) refers to "the mean (or in one instance, the modal) body temperature obtained for animals of a particular species while they were in a thermoregulatory state and had access to a full range of biologically relevant thermal conditions, usually in a laboratory thermal gradient." The "thermoregulatory state" referred to by Dawson is probably the same as the photophase for a diurnal animal such as S. magister. Regal (1967) and Hutchison and Kosh (1974) showed that lizards selected a lower T_b in scotophase than in photophase (voluntary hypothermia). Selection of a low T_b at night is a form of thermoregulation as the active selection of a specific temperature implies the active regulation of T_b . Therefore, when normally diurnal lizards voluntarily enter hypothermia at night they are in a thermoregulatory state. "Preferred body temperature" as approved by the International Union of Physiological Sciences refers to a range of T_b 's (Bligh and Johnson, 1973) and that range should be specified (Dawson, 1975). Mean temperatures are much more useful if a measure of dispersion about the

mean is also given (Fraenkel and Gunn, 1940). We have listed both means and standard deviations (the central 68%) in Table 1.

Many factors affect thermal selection by reptiles (Dawson, 1975; DeWitt, 1967; Regal, 1966). To insure our data are useful to other investigators we shall use the term mean PT as the measure of central tendency in the PT range. We define the mean PT as the mean T_b selected by individuals of a species during the period in which they would normally be expected to be active. They must have access to a full range of biologically relevant temperatures and the individual observations must not bias any particular portion of the activity period. Failure to include early morning or afternoon observations would result in different mean PT's (Fig. 1). In addition, animals should not be fed while in the gradient and the gradient used in determining PT must be a thigmothermal gradient to avoid the possibility of the animal selecting a preferred level of illumination (Roth, personal communication) rather than a preferred level of heat.

The PT, as defined above, of S. magister is 33.2°C for C animals ($n=36$ animals, 2531 observations, $s=3.59$). Parker and Pianka (1973) reported a PT of 34.53°C for S. magister, apparently in a photothermal gradient. The animals were tested within two weeks of capture but the exact conditions under which they were held were not reported. The minimum temperature available in their gradient was between 20° and 25°C (room temperature). Such a gradient does not make a wide enough thermal range available to the animal. If lower temperatures are denied to the lizards, a somewhat higher PT should result. Our observations showed S. magister often selects a T_b below 25°C , especially in

scotophase. The animals in the Parker and Pianka study were also fed in the gradient. There appears to be a relation between digestive processes and thermal selection (Dawson, 1975 and Regal, 1966). The possibility also exists that feeding in the gradient might result in the PT of the live food being reflected in the PT of the animal being tested. The differences in experimental paradigms between our study and that of Parker and Pianka may account for the difference in PT reported.

The mean PT in this study (33.2°C) is somewhat below the mean temperatures recorded for S. magister in the field (34.9°C , Bogert, 1949; 34.8°C , Brattstrom, 1965; and 34.8°C , Parker and Pianka, 1973). Such discrepancies between field and laboratory measurements are not unusual, especially in diurnal species (Licht et al, 1966).

Wilhoft and Anderson (1960) showed thermal acclimation to have an effect on PT of S. occidentalis, however, their results were criticized by Licht (1968) on the basis that their acclimation at 35°C may have resulted in a pathological condition. In our study, results obtained from animals which died in the gradient or exhibited poor health were not used. Parker and Pianka (1973) showed that two months of acclimation to "laboratory conditions"(not explained) raised the PT of S. magister from 34.53°C to 36.69°C . The problems inherent in their first figure have been discussed above and they apply to the latter figure also. Although the available evidence is not clear cut, it appears that acclimatization to photoperiod and/or temperature has only a slight or no effect on the PT of lizards (Table 1 and Licht, 1968). Ballinger et al (1969) reported a photoperiod effect on thermal

preference of S. undulatus. However, the photoperiods used (6 and 12 hours of light) could have restricted the activity period enough so that the short photophase group may not have been able to reach and maintain the upper range of T_b 's we see in the late afternoon in our study. The effect would be to bias the observations in favor of the warming up period (Fig. 1) and result in the lower PT reported in their study.

Lizards exhibit daily fluctuations in T_b when measured in thermal gradients (Hutchison and Kosh, 1974; Regal, 1967; and Spellerberg, 1974). The three S. magister Regal (1967) observed showed a fluctuation in mean T_b but the fluctuation had "no evident relation to photoperiod". We believe the failure of S. magister to show a daily T_b fluctuation related to photoperiod was due to the small sample size for it is evident in our study that the species does exhibit such a cycle (Fig. 1).

Various explanations for voluntary hypothermia have been given (Regal, 1967) and it remains to be investigated whether the daily cycle of T_b is a species specific characteristic reflecting certain physiological and ecological relationships. The shape of the curve describing the cycle is affected by photoperiod (Fig. 1). Measuring from the onset of photophase to the hour of maximum mean T_b , one can see that animals acclimatized to LD 08:16 reach that mean T_b faster than those acclimatized to LD 16:08. Conversely, those acclimatized to LD 16:08 cool more rapidly at the onset of scotophase than those acclimatized to LD 08:16. Thermal acclimatization does not appear to affect the configuration of the curve describing the daily cycle of T_b . Thermal acclimatization does, however, affect the day to day change in thermal selection. All 6 15°C treatment groups chose successively

lower mean T_b 's on successive days and 5 of the 6 35°C treatment groups chose successively higher mean T_b 's on successive days (Table 2). Although most of the regression coefficients of mean T_b on successive days were not significantly different from zero, the direction of change could not be explained by chance alone. The nature of thermal conditions under which Anolis carolinensis is kept has little effect on day to day (3 days) change in thermal selection and what little effect is noted is transient (Licht, 1968). The overall precision of thermoregulation in Dipsosaurus dorsalis is constant from day to day for three days (DeWitt, 1967). Perhaps more than three days are necessary for a trend in daily change in PT to be noted in some species or perhaps not all species exhibit such a trend. Further investigation is necessary to resolve the apparent differences noted in the species studied to date.

The reasons for the failure of S-8:16-35° animals to show significant differences in hourly mean T_b 's over a 24-hour period are unknown. A trend for higher hourly mean T_b 's in late photophase is present but no significant differences exist between hourly mean T_b 's in photophase and scotophase. Given the variability of the data, there were no divergent animals that accounted for the difference between this and all other groups. Kosh and Hutchison (1968) found "unnatural" acclimatizations (i.e. long light periods and low temperatures or vice versa) affected the daily rhythmicity of temperature tolerance in Chrysemys picta. Their findings would not explain the S-8:16-35° group in our study as the other 5 treatments receiving "unnatural" acclimatizations responded with a rhythm of T_b similar to those receiving more "natural" acclimatization.

Late afternoon T_b 's are more precisely maintained than are early morning and scotophase T_b 's. The mean coefficient of variation of mean T_b 's in photophase is significantly smaller than that in scotophase (Table 3). Regression analysis of mean hourly T_b 's on successive days in the gradient showed that from day to day the lizards tended to select the same temperature in the late afternoon yet their thermal selection in scotophase changed from day to day. This may reflect acclimatization occurring in the gradient or the lizards could be taking advantage of cooler areas in the gradient as an energy saving measure in response to changing digestive state.

The amplitude of the daily cycle in thermal selection changes from day to day. The highly significant ($p < 0.01$) correlation of the regression coefficients of the mean hourly T_b on successive days in the gradient with the coefficients of variation for each hour indicates that the dispersion about the mean hourly T_b 's can be mostly explained by daily changes in thermal selection. This indicates that the maximum daily temperature is a rather stable characteristic and is not readily affected by acclimatization, but that the minimum daily temperature may be affected to a greater degree. Perhaps S. magister acclimatizes to seasonal conditions throughout its annual activity cycle by widening or narrowing the range of ecritic temperatures.

The primary effect of parietalectomy on thermal selection in S. magister is to increase the PT. It also affects temporal changes in thermal selection and this unexplained phenomenon should be further investigated. Parietalectomy does not affect the timing of the daily cycle of T_b selection. The increase in T_b due to parietalectomy is

more pronounced in photophase than in scotophase (Fig. 1). Further evidence that parietectomy primarily increases PT is found in the fact that the integration of time and T_b failed to indicate any difference in percentage of degree hours accumulated in photophase or scotophase by P animals as opposed to C or S animals.

In previous studies parietectomy has generally resulted in increased locomotor activity (Glaser, 1958), increased exposure to solar radiation (Stebbins and Eakin, 1958; Stebbins, 1970; Stebbins and Cohen, 1973; and Packard and Packard, 1972), and increased thyroid activity (Eakin et al, 1959 and Stebbins and Cohen, 1973).

Parietalectomized lizards also tend to die sooner than S lizards when denied food (Stebbins and Eakin, 1958). Parietalectomized lizards appear to exhibit greater energy usage per day than control animals and so must gain any increased energy by utilizing environmental heat or additional food. It is not known whether parietectomized lizards feed more than controls, but they do appear to utilize a greater amount of environmental heat (this study and Hutchison and Kosh, 1974). Additionally, Stebbins and Eakin (1958) found that lizards with shielded parietal eyes had T_b 's above 37.5°C 7.3% more often than did controls.

Parietalectomized male A. carolinensis were reported to exhibit increased gonadal activity over controls (Clausen and Poris, 1937). Licht and Pearson (1970) in an attempt to duplicate the Clausen and Poris study reported no significant effect on testicular development in the same species although their data show in all 4 experiments that P animals had a slight, nonsignificant, increase in gonad weight over C's. Lizards in the Clausen and Poris study were housed in large cages

with a source providing heat and light during the day. Although the room temperature was approximately 23°C, it is quite likely that the lizards could voluntarily increase their T_b 's by positioning themselves close to the heat source. In the Licht and Pearson experiment the animals were housed in cages in environmental chambers at 25°C or 31°C. Given that parietectomized lizards select increased T_b 's at least during parts of the day, the P lizards in the Clausen and Poris study may have selected higher T_b 's than controls and that increased T_b was responsible for the increased gonadal development noted. Such an effect was not possible in the Licht and Pearson study and hence they correctly noted no direct effect of parietectomy on gonadal development in a thermally controlled situation.

Evidence from field studies support our hypothesis. Parietectomized S. occidentalis females exhibited larger ovaries and higher ova counts the season following parietectomy than did S animals; P and S males showed no difference in gonadal development but the sampling timing was probably not optimal to illustrate differences in testicular development (Stebbins and Cohen, 1973).

The parietal eye functions as a photoreceptor and furnishes photic information to the CNS. The information thus furnished could be used to coordinate bodily functions with photoperiod, possibly via secretions of the pineal gland. Such a mechanism would be highly beneficial to temperate ectotherms whose bodily functions are highly dependent on energy in the form of environmental heat yet live in areas with wide annual and daily fluctuations in thermal conditions. Parietal eyes are more prevalent in families of lizards inhabiting higher latitudes

than those inhabiting the lower latitudes (Gundy, 1974). Information furnished to the CNS by the parietal eye could play an important role in the synchronization of reproduction with photoperiod by affecting the thermal conditions which the animal selects. By influencing thermal selection in the seasons of gonadal development the animal could effectively dampen the effects of environmental heat on gonadal development, which in the case of an early warm spell, would result in reproductive readiness prior to the time of optimal environmental conditions (Stebbins in Eakin, 1973, p. 137).

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LITERATURE CITED

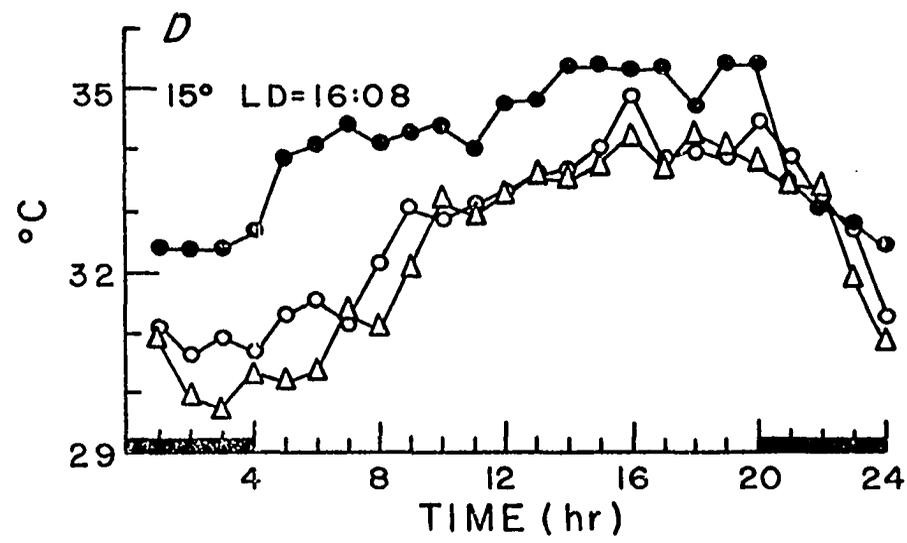
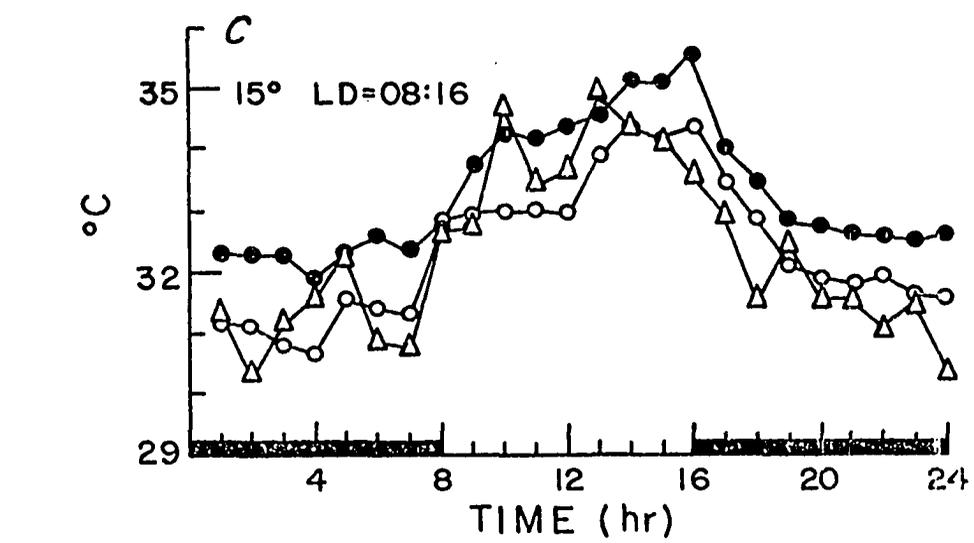
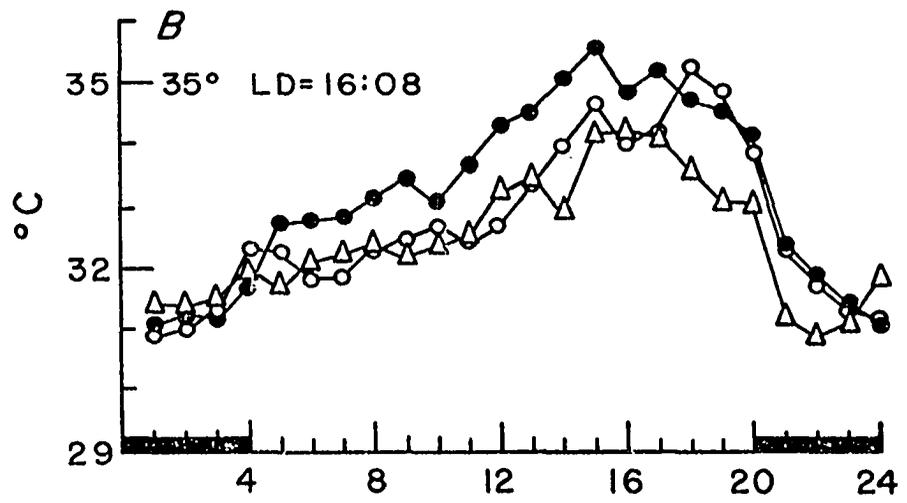
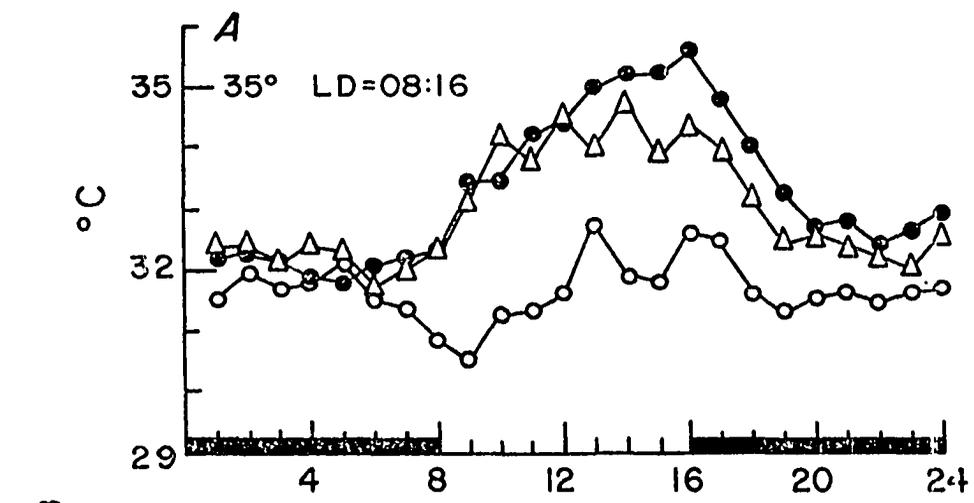
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FIGURE 1. Mean hourly body temperature selection by Sceloporus magister in a thermal gradient after acclimatization to 4 combinations of temperature and photoperiod. Each point consists of 8-12 animals and 45-90 observations. The heavy black line along the abscissa indicates scotophase.



△—△CONTROL ○—○SHAM ●—●PARIETALECTOMIZED

TABLE 1. Mean (\bar{X}) body temperatures selected by parietectomized, control, and sham operated Sceloporus magister in a thermal gradient after acclimatization to various photoperiod and temperature regimes. Significance (p) tested using planned a priori comparisons of parietectomized versus both sham operated and control animals. s=1 standard deviation. C=control, S=sham operated, P=parietectomized. Thus control animals acclimatized to a photoperiod of LD=08:16 and 15°C = C-8:16-15°.

Treatment	Sample Size		Body Temperature Selected								
	Animals	Observations	24-hours			Photophase			Scotophase		
			\bar{X}	s	p	\bar{X}	s	p	\bar{X}	s	p
C-8:16-15°	8	1094	32.33	5.01		33.95	3.39		31.52	5.61	
S-8:16-15°	10	1412	32.42	4.79		33.63	4.54		31.81	4.82	
P-8:16-15°	11	1400	33.29	3.75	.001	34.58	3.41	.05	32.64	3.77	.001
C-8:16-35°	9	1098	32.97	3.42		34.05	3.10		34.45	3.46	
S-8:16-35°	10	1134	31.65	6.94		31.70	7.54		31.62	6.63	
P-8:16-35°	9	1058	33.28	2.84	.001	34.57	2.30	.001	32.63	2.87	.001
C-16:8-15°	9	1483	32.31	4.40		32.81	4.00		31.30	4.99	
S-16:8-15°	8	1270	32.69	2.96		33.13	2.65		31.85	3.38	
P-16:8-15°	10	1359	34.01	2.83	.001	34.69	2.30	.001	32.68	3.32	.05
C-16:8-35°	10	1250	32.44	3.57		32.97	3.42		31.41	3.68	
S-16:8-35°	11	1285	32.72	3.19		33.33	3.20		31.50	2.85	
P-16:8-35°	13	1516	33.18	3.68	ns	34.05	3.54	.01	31.49	3.42	ns

TABLE 2. Degree hours accumulated by various treatments of Sceloporus magister in a thermal gradient. Treatment abbreviations as in Table 1. m=regression coefficient of mean body temperature per day on successive days. Regression coefficients followed by significance from zero.

<u>TREATMENT</u>	<u>DEGREE HOURS</u>				<u>TOTAL</u>	<u>m</u>	
	<u>PHOTOPHASE</u>	<u>%</u>	<u>SCOTOPHASE</u>	<u>%</u>			
C-8:16-15 ⁰	271.1	34.9	504.7	65.1	775.8	-0.06	ns
S-8:16-15 ⁰	268.3	34.5	510.0	65.5	778.3	-0.41	0.05
P-8:16-15 ⁰	275.1	34.4	523.7	65.6	798.8	-0.07	ns
C-8:16-35 ⁰	271.4	34.3	520.3	65.7	791.7	0.03	ns
S-8:16-35 ⁰	252.8	33.3	507.0	66.7	759.8	0.34	ns
P-8:16-35 ⁰	274.9	34.4	523.9	65.6	798.8	-0.24	ns
C-16:8-15 ⁰	523.0	67.5	252.1	32.5	775.1	-0.39	0.05
S-16:8-15 ⁰	528.8	67.3	256.8	32.7	785.6	-0.33	0.01
P-16:8-15 ⁰	553.1	67.8	262.7	32.2	815.8	-0.18	0.01
C-16:8-35 ⁰	527.2	67.7	251.9	32.3	779.1	0.14	ns
S-16:8-35 ⁰	531.8	67.8	253.2	32.2	785.0	0.12	ns
P-16:8-35 ⁰	543.2	68.2	253.4	31.8	796.5	0.06	ns

TABLE 3. Mean (\bar{X}) coefficients of variation (C.V.) of mean body temperatures of Sceloporus magister in a thermal gradient at photoperiods of LD 08:16 and 16:08. N=number of C.V.'s, s=1 standard deviation, t=student's t value, p=level of significance.

	\bar{X}	N	s	t	p
LD=08:16					
Photophase	0.120	48	0.00364	-2.237	.05
Scotophase	0.140	96	0.00235		
LD=16:08					
Photophase	0.090	96	0.00088	-4.69798	.001
Scotophase	0.111	48	0.00090		

FOOTNOTE

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RUNNING PAGE HEADLINE

PARIETALECTOMY AND THERMAL SELECTION IN A LIZARD

APPENDIX 1

Basic statistics for hourly thermal selection by Sceloporus magister.
 \bar{X} =arithmetic mean, n=number of observations, s=one standard deviation, and
 C.V.= coefficient of variation. Treatment abbreviations as in Table 1, p.25.

HOUR	C-8:16-15 ^o				S-8:16-15 ^o				P-8:16-15 ^o			
	n	\bar{X}	s	C.V.	n	\bar{X}	s	C.V.	n	\bar{X}	s	C.V.
0100	45	31.33	6.64	0.212	58	31.24	4.77	0.153	58	32.34	4.26	0.132
0200	47	30.34	6.00	0.198	58	31.17	4.67	0.150	58	32.26	4.23	0.131
0300	43	31.15	6.21	0.199	58	30.79	4.70	0.153	58	32.24	3.92	0.122
0400	43	31.57	5.35	0.169	57	30.64	5.13	0.168	57	31.87	4.10	0.129
0500	46	32.26	5.09	0.158	57	31.67	4.93	0.156	58	32.32	3.98	0.123
0600	46	30.83	5.51	0.179	57	31.39	4.14	0.132	57	32.57	3.48	0.107
0700	46	30.78	5.39	0.175	58	31.36	5.26	0.168	57	32.40	3.18	0.098
0800	44	32.69	4.23	0.129	58	32.95	4.16	0.126	57	32.75	3.26	0.100
0900	46	32.76	4.00	0.122	58	33.02	4.45	0.135	56	33.65	3.54	0.105
1000	45	34.63	2.94	0.085	60	33.00	4.74	0.144	56	34.24	3.58	0.105
1100	47	33.49	3.70	0.110	59	33.02	5.37	0.163	57	34.13	3.09	0.090
1200	46	33.69	3.44	0.102	57	32.96	4.71	0.143	55	34.33	3.17	0.092
1300	46	34.93	2.64	0.076	57	33.94	4.15	0.122	61	34.50	4.14	0.120
1400	46	34.38	3.53	0.103	60	34.41	3.63	0.106	61	35.07	3.52	0.100
1500	46	34.13	2.77	0.081	61	34.20	4.42	0.129	62	35.03	3.03	0.086
1600	44	33.56	3.50	0.104	60	34.40	4.52	0.131	60	35.53	2.77	0.078
1700	48	32.94	4.69	0.142	62	33.53	4.79	0.143	60	33.96	2.61	0.077
1800	46	31.55	4.61	0.146	59	32.90	4.78	0.145	59	33.50	2.76	0.082
1900	46	32.51	5.05	0.155	60	32.14	5.07	0.158	59	32.82	3.78	0.115
2000	48	31.62	5.44	0.172	60	31.94	4.87	0.152	59	32.72	3.99	0.122
2100	46	31.60	5.62	0.178	60	31.85	4.88	0.153	59	32.68	3.75	0.115
2200	45	31.12	6.29	0.202	60	31.96	4.68	0.146	59	32.59	3.85	0.118
2300	44	31.56	6.58	0.208	59	31.66	4.65	0.147	59	32.54	4.29	0.132
2400	45	30.38	6.48	0.213	59	31.63	5.00	0.158	58	32.62	4.20	0.129

APPENDIX 1 cont.

HOUR	C-8:16-35 ^o				S-8:16-35 ^o				P-8:16-35 ^o			
	n	\bar{X}	s	C.V.	n	\bar{X}	s	C.V.	n	\bar{X}	s	C.V.
0100	47	32.40	3.23	0.100	47	31.53	6.73	0.213	43	32.19	3.76	0.117
0200	47	32.45	3.26	0.100	47	31.98	6.82	0.213	43	32.30	3.65	0.113
0300	47	32.17	3.09	0.096	48	31.69	6.71	0.212	44	32.15	3.89	0.121
0400	46	32.43	2.89	0.089	48	31.76	6.77	0.213	45	31.86	4.37	0.137
0500	46	32.35	2.92	0.090	48	32.09	6.78	0.211	45	31.77	3.12	0.098
0600	46	31.75	4.79	0.151	48	31.52	6.55	0.208	45	32.07	2.60	0.081
7000	45	32.02	4.59	0.143	48	31.42	6.46	0.206	44	32.20	2.19	0.068
8000	44	32.34	2.66	0.082	47	30.90	6.71	0.217	42	32.34	2.80	0.087
0900	44	33.18	2.78	0.084	47	30.49	8.21	0.269	42	33.45	2.62	0.078
1000	45	34.16	2.46	0.072	51	31.24	7.87	0.252	42	33.47	2.79	0.083
1100	42	33.74	2.37	0.070	49	31.35	7.24	0.231	42	34.16	2.40	0.070
1200	42	34.52	2.45	0.071	50	31.63	7.67	0.243	46	34.52	2.31	0.067
1300	43	33.94	2.65	0.078	46	32.81	7.21	0.220	47	34.94	2.16	0.062
1400	43	34.76	3.17	0.091	45	31.88	7.65	0.240	45	35.17	1.81	0.051
1500	49	33.81	4.80	0.142	45	31.72	7.89	0.249	44	35.18	1.70	0.048
1600	47	34.35	2.99	0.087	47	32.61	6.77	0.208	45	35.52	1.44	0.040
1700	47	33.94	3.01	0.089	46	32.48	6.62	0.204	44	34.73	1.69	0.049
1800	46	33.18	3.98	0.120	46	31.58	6.56	0.208	44	33.98	1.94	0.057
1900	46	32.45	3.34	0.103	46	31.29	6.78	0.217	45	33.22	2.48	0.075
2000	47	32.53	3.32	0.102	46	31.50	6.72	0.213	45	32.71	2.71	0.083
2100	48	32.41	3.36	0.104	47	31.58	6.71	0.213	44	32.74	1.88	0.057
2200	47	32.21	3.39	0.105	47	31.47	6.70	0.213	45	32.42	1.73	0.053
2300	48	32.01	3.43	0.107	47	31.57	6.62	0.210	44	32.59	1.92	0.059
2400	46	32.55	3.17	0.097	48	31.63	6.62	0.209	43	32.88	1.69	0.051

APPENDIX 1 cont.

HOUR	C-16:8-15 ^o				S-16:8-15 ^o				P-16:8-15 ^o			
	n	\bar{X}	s	C.V.	n	\bar{X}	s	C.V.	n	\bar{X}	s	C.V.
0100	61	30.92	4.96	0.160	54	31.17	3.65	0.117	57	32.34	3.41	0.105
0200	62	29.86	5.41	0.181	54	30.60	3.16	0.103	57	32.35	3.41	0.105
0300	62	29.75	6.07	0.204	54	30.90	2.91	0.094	57	32.37	3.54	0.109
0400	63	30.32	5.76	0.190	55	30.65	3.01	0.098	57	32.66	3.43	0.105
0500	60	30.15	6.10	0.202	53	31.26	2.49	0.080	57	33.90	2.40	0.071
0600	60	30.35	5.85	0.193	54	31.54	2.48	0.079	57	34.05	1.89	0.055
0700	60	31.37	5.66	0.181	53	31.18	2.75	0.088	56	34.43	2.32	0.067
0800	60	31.04	6.22	0.201	52	32.11	2.10	0.065	56	34.07	2.54	0.075
0900	64	32.02	5.05	0.158	50	33.11	1.99	0.060	55	34.23	2.26	0.066
1000	62	33.19	2.01	0.061	50	32.84	2.58	0.079	53	34.32	2.12	0.062
1100	62	32.98	3.27	0.099	52	33.13	2.43	0.073	54	33.99	2.16	0.063
1200	62	33.24	1.76	0.053	52	33.33	2.12	0.064	55	34.69	2.15	0.062
1300	62	33.59	2.15	0.064	52	33.55	2.55	0.076	56	34.72	2.36	0.068
1400	65	33.47	3.32	0.099	54	33.58	2.57	0.076	60	35.32	2.00	0.057
1500	62	33.73	3.26	0.097	51	33.97	2.43	0.072	58	35.33	2.23	0.063
1600	61	34.20	2.10	0.061	50	34.83	2.62	0.075	58	35.26	2.52	0.071
1700	62	33.58	2.14	0.064	53	33.65	2.29	0.068	58	35.28	2.54	0.072
1800	62	34.19	2.07	0.061	54	33.92	2.68	0.079	57	34.63	2.17	0.063
1900	62	34.00	2.16	0.064	53	33.80	2.40	0.071	57	35.33	2.00	0.057
2000	62	33.73	1.91	0.057	54	34.46	2.19	0.064	56	35.31	2.11	0.060
2100	61	33.45	1.71	0.051	54	33.81	2.60	0.077	57	33.49	3.26	0.097
2200	62	33.44	2.35	0.070	54	33.17	3.30	0.099	57	33.03	2.94	0.089
2300	62	31.88	4.50	0.141	54	32.64	3.53	0.108	57	32.72	3.02	0.092
2400	63	30.78	5.73	0.186	54	31.87	3.27	0.103	57	32.45	3.44	0.106

APPENDIX 1 cont.

HOUR	C-16:8-35°				S-16:8-35°				P-16:8-35°			
	n	\bar{X}	s	C.V.	n	\bar{X}	s	C.V.	n	\bar{X}	s	C.V.
0100	53	31.39	3.62	0.115	54	30.84	3.08	0.100	64	31.02	3.35	0.108
0200	53	31.40	4.20	0.134	54	30.98	2.56	0.083	65	31.24	3.33	0.107
0300	53	31.49	3.56	0.113	53	31.39	2.92	0.093	65	31.13	4.00	0.129
0400	53	32.03	3.62	0.113	53	32.28	2.89	0.090	65	31.67	3.70	0.117
0500	53	31.57	3.98	0.126	53	32.22	3.72	0.115	63	32.72	3.29	0.101
0600	52	32.09	3.85	0.120	52	31.82	3.31	0.104	63	32.80	3.37	0.103
0700	51	32.16	3.74	0.116	52	31.80	3.39	0.107	64	32.83	3.62	0.110
0800	51	32.42	3.37	0.104	52	32.46	2.95	0.091	61	33.16	3.64	0.110
0900	51	32.20	3.58	0.111	53	32.49	3.23	0.099	59	33.48	3.58	0.107
1000	51	32.41	3.17	0.098	53	32.70	3.03	0.093	60	33.09	3.72	0.112
1100	47	32.52	3.16	0.097	53	32.48	2.89	0.089	58	33.65	4.12	0.122
1200	49	33.22	3.89	0.117	53	32.65	3.08	0.094	58	34.29	3.72	0.109
1300	49	33.49	3.04	0.091	59	33.44	3.32	0.099	58	34.53	3.62	0.105
1400	47	32.94	3.53	0.107	59	33.99	3.06	0.090	58	35.08	3.09	0.088
1500	51	34.18	2.85	0.083	50	34.69	2.98	0.086	61	35.57	2.92	0.082
1600	56	34.25	2.92	0.085	48	34.00	2.81	0.083	70	34.82	2.98	0.086
1700	54	34.16	2.89	0.085	55	34.30	3.51	0.102	70	35.24	3.33	0.095
1800	53	33.61	2.93	0.087	55	35.30	2.01	0.057	70	34.68	3.36	0.097
1900	54	33.10	3.02	0.091	54	34.88	2.05	0.059	64	34.54	3.36	0.097
2000	54	33.09	3.30	0.100	54	33.90	2.53	0.075	65	34.15	3.20	0.094
2100	54	31.21	3.73	0.120	54	32.22	2.67	0.083	63	32.39	2.98	0.092
2200	54	30.84	3.68	0.119	54	31.72	2.70	0.085	63	31.91	3.02	0.095
2300	54	31.14	3.58	0.115	54	31.33	2.74	0.088	64	31.43	3.23	0.103
2400	53	31.84	3.43	0.108	54	31.27	2.95	0.094	65	31.14	3.49	0.112

APPENDIX 2

Analysis of variance tables for significant differences in mean hourly temperature selection by Sceloporus magister in a thermal gradient. Significance of F_s value indicated as follows: $p \leq 0.001 = ***$, $0.001 > p \leq 0.01 = **^s$, $0.01 > p \leq 0.05 = *$, $p > 0.05 = ns$.

c-8:16-15°

<u>Source of variation</u>	<u>df</u>	<u>MS</u>	<u>F_s</u>
between samples	23	87.486	3.546 ***
within samples	<u>1071</u>	24.669	
total	<u>1094</u>		

s-8:16-15°

<u>Source of variation</u>	<u>df</u>	<u>MS</u>	<u>F_s</u>
between samples	23	76.899	3.482 ***
within samples	<u>1389</u>	22.084	
total	<u>1412</u>		

P-8:16-15°

<u>Source of variation</u>	<u>df</u>	<u>MS</u>	<u>F_s</u>
between samples	23	67.037	5.070 ***
within samples	<u>1377</u>	13.221	
total	<u>1400</u>		

c-8:16-35°

<u>Source of variation</u>	<u>df</u>	<u>MS</u>	<u>F_s</u>
between samples	23	37.946	3.417 ***
within samples	<u>1075</u>	11.105	
total	<u>1098</u>		

s-8:16-35°

<u>Source of variation</u>	<u>df</u>	<u>MS</u>	<u>F_s</u>
between samples	23	11.735	0.240 ns
within samples	<u>1111</u>	48.858	
total	<u>1134</u>		

APPENDIX 2 cont.

P-8:16-35^o

<u>Source of variation</u>	<u>df</u>	<u>MS</u>	<u>F_s</u>
between samples	23	64.469	9.540 ***
within samples	<u>1035</u>	6.758	
total	1058		

C-16:8-15^u

<u>Source of variation</u>	<u>df</u>	<u>MS</u>	<u>F_s</u>
between samples	23	148.230	8.530 ***
within samples	<u>1460</u>	17.377	
total	1483		

S-16:8-15^u

<u>Source of variation</u>	<u>df</u>	<u>MS</u>	<u>F_s</u>
between samples	23	87.264	11.868 ***
within samples	<u>1247</u>	7.353	
total	1270		

P-16:8-15^o

<u>Source of variation</u>	<u>df</u>	<u>MS</u>	<u>F_s</u>
between samples	23	67.404	9.593 ***
within samples	<u>1336</u>	7.026	
total	1359		

C-16:8-35^o

<u>Source of variation</u>	<u>df</u>	<u>MS</u>	<u>F_s</u>
between samples	23	55.106	4.599 ***
within samples	<u>1227</u>	11.981	
total	1250		

S-16:8-35^o

<u>Source of variation</u>	<u>df</u>	<u>MS</u>	<u>F_s</u>
between samples	23	90.441	10.339 ***
within samples	<u>1262</u>	8.748	
total	1285		

APPENDIX 2 cont.

P-16:8-35⁰

<u>Source of variation</u>	<u>df</u>	<u>MS</u>	<u>F_s</u>
between samples	23	137.738	11.745
within samples	<u>1493</u>	11.731	
total	<u>1516</u>		