Thermal Biology of the Common Garter Snake
Thamnophis sirtalis (L.)

II. The Effects of Melanism

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Summary. The thermoregulatory significance of a striped-melanic colour polymorphism in the common garter snake, *Thamnophis sirtalis*, was assessed through a combination of laboratory experimentation and field study. In experiments with living snakes the melanic morph maintained a higher body temperature than the striped morph, when exposed to natural insolation. Experiments with excised skin showed that this thermal advantage is attributable to some integumental difference between the two morphs. Body temperatures of snakes in the field revealed that, during the colder part of the active season, melanics were able to stay warmer than striped snakes by an amount (1.24 C°) approximating the difference observed in the laboratory. Some evidence and argument is presented to suggest that melanism also may confer protection against overheating in warm periods.

Introduction

The common garter snake, *Thamnophis sirtalis* (L.), a diurnal terrestrial colubrid, is distributed widely in North America. Throughout much of this range, the species is characterized by three light-coloured longitudinal stripes, set against a darker background. However, completely black specimens occur at several localities along the periphery of Lake Erie, as well as on some of the islands in the west basin of that lake (Patch, 1919; Logier, 1929; Conant, 1938; Gibson, 1978). Melanics in these populations are uniformly jet-black above and irridescent blue-black below, with a white "chin" and "throat". Striped and melanic morphs of *T. sirtalis* are distinguished easily, and constitute a clear case of discontinuous polymorphism (Blanchard and Blanchard, 1940).

Variation in the reflectance of squamate integument generally is assumed to affect heat flow (Templeton, 1970; Cloudsley-Thompson, 1971; Heatwole,

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1976) and thus commonly attracts interpretations based on thermoregulation. However, direct demonstrations of such effects are uncommon. This paper presents the results of two laboratory experiments and a field study designed to determine the thermoregulatory significance of the striped-melanic colour polymorphism in the common garter snake. A companion paper (Gibson and Falls, 1979) describes the general thermal biology of this species. Both papers form part of a larger study of the ecological significance of melanism in *T. sirtalis*.

Materials and Methods

A general paired approach to relative morph performance was implemented in two complementary laboratory experiments. The first of these measured body temperatures of striped-melanic pairs of snakes simultaneously exposed to ambient conditions under natural insolation. The second measured heat flow through excised portions of skin from the two morphs while they were exposed, side-by-side, to solar radiation and situated on a common, constant thermal background.

Body temperatures of striped and melanic garter snakes caught in the field were obtained in the course of a mark-recapture study carried out at the eastern tip of Long Point, Norfolk County, Ontario, Canada. The snakes used in the laboratory experiments were obtained at the same location.

Transmitter Experiment

To obtain estimates of the body temperature of living snakes, we used ingestible radio transmitters, the signal from which is a function of temperature. These transmitters (Model X, Mini-Mitter Company) are small (cylindrical; 12 mm diameter and 19 mm length), possess a very short transmission range (about 0.5 m), and have an appropriate temperature span (0–45 °C). The signal is audible on AM radio as a "click", at a rate which varies directly, though not linearly, with temperature. Our calibration procedure is outlined in detail below.

Calibration containers were constructed by soldering inflow and outflow ports of 0.375 in (0.95 cm; O.D.) copper tubing to the lids of 12 fl oz (355 ml) glass jars. A small square of hardware cloth, attached to the floor of the jar with silicone aquarium sealant, served to anchor a layer of beeswax. The transmitter, itself coated with beeswax, could then be secured to this layer. Rubber sealing rings and a liberal application of silicone stopcock grease allowed the lid to be sealed against the fluid pressures realized in these calibrations. A model K2R Electronic Lauda controlled temperature bath, precise to within 0.1 C°, circulated antifreeze through the calibration chamber (containing the transmitter) at a rate well in excess of 300 ml/min. Temperatures were assessed on a mercury thermometer, accurate to 0.1 C°, in the Lauda's main reservoir; possible discrepancies between these readings and those in the calibration chamber, itself separated from the Lauda by nearly 1 metre of rubber hosing, should be minimal due to the high flow rate. Furthermore, because both transmitters received identical treatment, only their absolute accuracy could be affected; the accuracy of a difference would not be altered. At 2 C° increments, from 6 to 38 °C inclusive, output from a transmitter was received on an AM transistor radio and recorded on a Nagra III tape recorder. The two transmitters used in this study were recorded alternately at each increment and so were exposed to precisely the same Lauda setting.

The recorded sequences of calibration clicks from the transmitters were replayed, at recording speed, through a model 100B Monsanto counter-timer. The signal was amplified using a Nagra Model DH self-contained speaker-amplifier and the clicks rendered more discrete with an "audio conditioner". The timer yielded a digital display of the duration, in milliseconds, of every second interval between clicks (hereafter "click interval"), the sequences of which were then voice recorded onto a second tape recorder, subsequently transcribed and keypunched.

The relationship between click interval and temperature clearly was well defined but curvilinear, and simple transformations did not yield linearity. For this reason, we used stepwise multiple regression to describe temperature as a polynomial function of click interval. From the first 3 positive and negative integer exponents, the stepwise procedure chose $+1$, $+3$, -1, and -2 (all exponents entering significantly), yielding a highly satisfactory fit: mean absolute deviations of predicted from observed calibration values never reached 0.1 C°.

Each transmitter was calibrated in this manner, both before and after the heating trials to be described below. Presumably due to battery drain, the transmitters "slowed down" slightly; that is, for a given temperature, the click interval was somewhat longer in the final than in the initial calibration. Although this predictable directional change was not great, it was conspicuous against the precision of the individual calibration curves. For this reason, the final prediction equation linearly interpolated between the before and after curves on the basis of time elapsed since the initial calibration.

Six striped-melanic pairs of adult female *T. sirtalis* were chosen so that members of a pair were matched closely in snout-vent length and weight. The within-pair differences in these two parameters were always less than 5% and usually approached measurement error (e.g. 5 mm in a 700 mm snake, 2 g in an individual weighing 130 g). Furthermore, the signs of such differences were variable. All snakes used in these trials had been in captivity for at least 12 months, were rather tame and in excellent condition. Although it was not possible to exactly synchronize the moult cycle of a pair, no runs were made with individuals not obviously in the "resting condition" (stage 1 of Maderson, 1965).

Transmitters were "waterproofed" with two thin layers of beeswax and then placed in a concentrated gelatin solution. After being allowed to set firmly under refrigeration, all but a thin layer of gelatin was trimmed from around the transmitters; the resulting bolus was dipped in a worm-water mixture and fed to the experimental snake. This procedure avoids disturbances associated with force feeding and often renders the animal somewhat quiescent.

During heating trials, the snakes were restrained in specially prepared, individual "Quonset huts". The floors of these chambers measured 10 in (25.4 cm) square and the end walls were semicircular. All were constructed from 0.5 in (1.27 cm) plywood and painted white. A 0.5 in (1.27 cm) sheet of white styrofoam covered the floor. The roof was made from No. 6 mesh Nitex nylon monofilament screen cloth (Tobler, Ernst and Trabler, Inc./Kressilfk Products, Inc.) with a mesh opening of 0.1323 in^2 (0.85 cm^2) and an approximate 40% reduction in open area.

Prior to a set of heating trials, two matched snakes, kept without food for a minimum of five days, were fed transmitters, placed in their Quonset huts and held for an hour or two at room temperature (20–25 °C) to effect removal of the gelatin. The snakes were then moved to a cold room (approximately 10 °C), primarily to reduce battery drain, where they remained when not involved in heating trials.

Individual trials took the following form. The snakes, still in their Quonset huts, were transferred from the cold room to the roof of the Zoology building in individual styrofoam coolers. On the roof, they were removed from the coolers (striped first, then melanic) and placed on a table about 1.2 m apart, fully exposed to the sun. Output from the transmitters was recorded onto a Nagra III tape recorder (tape speed: 9.5 cm/s), alternating between striped and melanic in sequential 30 s bouts, beginning with the striped and eventually ending with the melanic. After the trial, the pair was returned to the cold room. Notes were made concerning weather conditions and behaviour of the snakes during the trials. Trial length varied from 27 to 86 min. Overheating of the snakes forced termination of several trials.

Each pair of snakes underwent four such trials within a period ranging from one to four days between 23 August and 4 October, 1976. Most runs took place under clear skies; although none was carried out under overcast or even conspicuously cloudy days, varying degrees of light haze occasionally exerted an effect. At the completion of a set of four such trials, the transmitters were gently palped from the snakes. Before being fed to another pair of snakes, the transmitters were cleaned of their beeswax coating (often rather "scratched", presumably during ingestion, but not obviously digested in any way) and re-coated.

The magnetic tapes containing the sequences of transmitter "clicks" from these trials were processed in the same manner as described above for the calibration data. The resulting click intervals were converted to temperature readings (°C) using the prediction equation, and an average body temperature, T, calculated for each snake for each 30 s recording bout. Body temperatures

for a pair of snakes then were compared over the course of a trial by defining the difference, D, over a 60 s interval, t, between the striped and melanic as follows:

$$D(t) = Tmel(t) - \{Tstp(t+1) + Tstp(t)\}/2.0.$$

This procedure was made necessary by the pattern of alternate recording. There exists a slight bias favouring the striped member of a pair for the removal of this morph from the styrofoam coolers and subsequent exposure to the sun's radiation invariably preceded that of the melanic.

The sequence of differences for a given trial was analyzed as a paired t-test. The signs of the differences were also used to determine one-tailed binomial probabilities under the null hypothesis of equal probability of thermal superiority. A somewhat more conservative version of this latter test evaluated the sign only of those differences the absolute magnitude of which exceeded 0.20 C°.

Similarly, the sign of the outcome (most frequent sign) of each individual trial was assessed for all 24 trials, as well as for that subset of trials in which one morph was clearly superior, and associated binomial probabilities determined. Finally, the sign of the outcome for the set of trials of each pair was assessed and the binomial probability calculated.

Heat-Flow Experiment

The heat-flow sensors used in this experiment (1 in^2 {6.45 cm^2} sensables Heat Flux Sensors, Hy-Cal Engineering) produce a voltage output proportional to the heat flux. This output was measured on a model 425 A Hewlett Packard DC micro volt-ammeter.

To provide a stable thermal background against which to assess the relative heat-flow properties of striped and melanic integument, a brass "heat sink" flow chamber was constructed. Shallow wells in the 0.5 in (1.27 cm) thick upper surface of the chamber house the two heat-flow sensors; a thin layer of lanolin improved contact between the box and the sensor. Brass walls (1 in {2.54 cm} high, 0.125 in {0.32 cm} thick), when roofed with Saran wrap, serve to bring air temperature over the sensors toward box temperature. Antifreeze circulated from a model K2R Electronic Lauda controlled-temperature bath through the box via inflow and outflow ports. The inflow stream was directed against the inside upper surface of the box between the two wells housing the heat-flow sensors.

Pairs of striped and melanic snakes used in these trials were matched on snout-vent length, although with less concern for precision than in the transmitter experiments; particular attention was given here to ensuring there were no obvious differences in moult cycle status. Snakes were dispatched by freezing, a method not only likely the most merciful for at least temperate-zone ophidians, but also one that provided the necessary degree of tissue death.

One sensor on the brass heat sink was covered with a skin segment from the striped member of a pair while the other sensor received that of the melanic member. Segments were aligned such that the first scale row above the ventral scutes on the left side was parallel to one edge of the sensor. The skin then was gently spread, but only to the point where its natural elasticity became evident. This procedure was necessary to ensure consistent treatment. The segments were carefully "rolled" with a short length of rubber hosing to remove air bubbles between the skin and sensor, and to effect a good contact between the two surfaces. The top of the brass box then was covered with a single layer of Saran wrap.

In the case of the striped segment, the sensor thus was covered by the left lateral stripe, left interstripe region, the dorsal stripe and a variable proportion of the right interstripe region. This procedure presumably overestimated the absorption capacity of striped integument for the interstripe region invariably is much darker than the dorsal and lateral stripes.

Individual trials took the following form. The brass box, with 25 °C antifreeze being circulated through it, was situated on the inside ledge of a south-facing window and oriented such that the top surface was nearly perpendicular to the sun's radiation. After allowing two to three minutes for equilibration, readings of the voltage output from the heat-flow sensors began, alternating between the two morphs as quickly as possible. When 12 such readings had been accumulated from each morph, the window blinds were drawn and a short pause taken. Five to 10 min later the procedure was repeated; six such runs were made on each pair of skin segments.

Two sets of skin segments from each of three pairs of snakes and one set from each of

another three pairs were processed in this way. The voltage readings were converted to comparable heat-flow values using the calibration figures provided with the sensors.

The sensor on which the striped skin was placed had a lower calibration constant and thus yielded a lower voltage reading at a given heat flow than did that under the melanic skin. When switching from a striped reading to a melanic reading therefore, the voltmeter needle perforce would move up the scale, and vice versa when switching back. Any tendency for an asymptotic approach to true values by the voltmeter thus would result in an overestimate of striped values and an underestimate of melanic values. However, in trial runs using either the uncovered sensors or skin segments from a single striped snake, the two sensors yielded essentially identical heat-flow readings.

The sign of the difference, between striped and melanic integument, in average heat flow was assessed for each of the individual runs and the one-tailed binomial probability determined, again with the null hypothesis of equal probability of heat-flow superiority. Similarly, the sign of this difference was assessed for each set of skin segments and for each pair of snakes and corresponding one-tailed binomial probabilities calculated.

Field Study

The Long Point study area and our field procedures there are described in a companion paper (Gibson and Falls, 1979) and will not be detailed here. Basically, we carried out an intensive comparison of the field ecology of striped and melanic garter snakes on Long Point. As part of this work we obtained body temperatures of the two morphs under natural conditions. Snakes were located by searching on foot and captured by hand. Body temperature was estimated with a flexible small-animal probe mounted on a Yellow Springs Instruments Telethermometer (model 43TD).

Our analyses of the general thermal ecology of this species (Gibson and Falls, 1979) revealed several sources of body temperature variability. Therefore we have restricted the striped-melanic comparison to captures made on sunny days between the hours 0800 and 1600. Similarly, the data are classified by month of capture, and sex. Within each sex and month, the body temperature of the two morphs was compared using the Wilcoxon two-sample test.

Results

Transmitter Experiment

The temperatures of striped and melanic snakes over the course of four trials are displayed in Fig. 1. Similar plots for the remaining 20 trials, and additional summary material, can be found in Gibson (1978). Three of the 24 trials resulted in significantly higher temperatures for the striped member. In every one of the remaining 21 trials, the melanic member had either a significant (19 trials) or borderline (2 trials) temperature advantage. The one-tailed binomial probability associated with such an outcome is 0.000017. The mean D, averaged over all 24 trials, is 0.86 C°. Of the 14 trials having one or the other morph clearly and consistently superior (e.g. Fig. 1a), all resulted in melanic thermal dominance ($P=0.000061$). The mean D for this subset of trials is 1.34 C°.

In determining the thermal "winner" for each pair of snakes, only pair 2 offers any challenge to melanic superiority. Three of the four trials for this pair returned statistically significant striped wins (the only such outcomes obtained in the entire experiment); trial four was a significant melanic win. A decision based on frequency would assign a striped win for this pair. However, more refined, albeit a posteriori, considerations indicate otherwise. During the
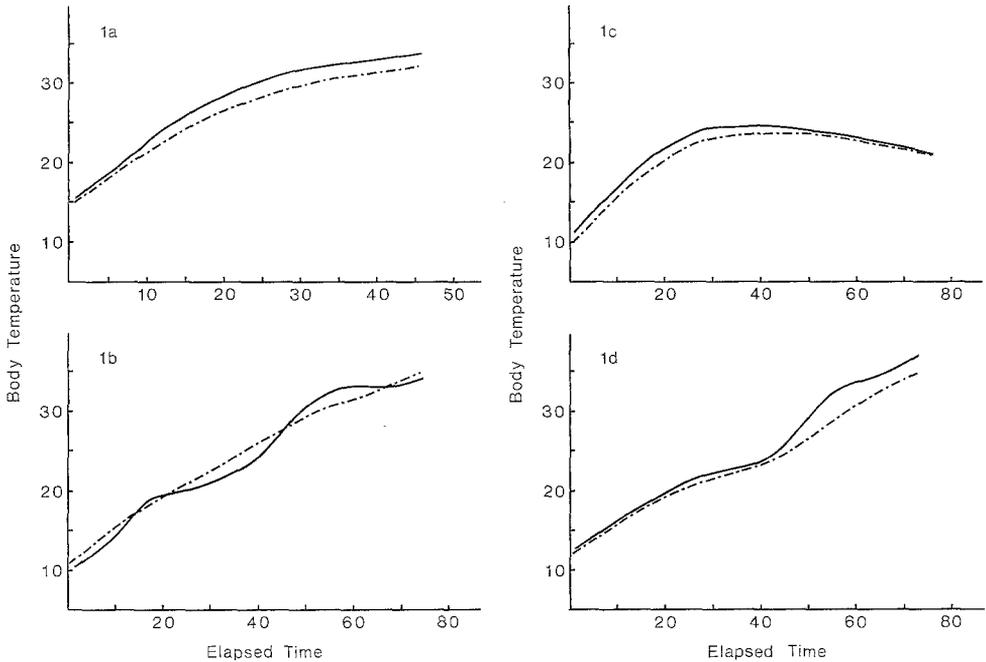
A.R. Gibson and J.B. Falls

Fig. 1a–d. Body temperature (°C) over time (min) for striped and melanic garter snakes. The broken line represents the striped morph, and the solid line represents the melanic morph. One plot for each of two pairs (**a** and **b**) are shown together with two plots (**c** and **d**) for a third pair. Body temperatures were recorded while the snakes were situated side by side, out of doors, exposed to natural insolation. See text for details

three trials at issue (e.g. Fig. 1b), the body temperature of the striped varied in a rather even manner, whereas that of the melanic changed in a roughly stepwise fashion, rising above that of the striped at the end of periods of rapid increase. This suggests that the melanic snake somehow was resisting an inevitable rise in body temperature; bouts of vasoconstriction followed, perhaps of necessity, by short intervals of vasodilation could explain the stepwise pattern of increase. These different periods of heat gain, which were obvious during the trials, were not in any way associated with particular behaviours or locations within the Quonset hut. Indeed the melanic snake usually was loosely coiled and quiet as the rate of temperature increase varied.

In the final trial for pair 2, the body temperature of both snakes changed in an even manner and the outcome was a clear melanic win. We submit that it is not unreasonable to assume that this fourth trial is most representative of the relative thermal properties of this pair. Hence, for all six pairs, the melanic member can be assigned the win; the biomial probability associated with such an outcome is 0.015625.

Two trials require individual mention here. The third run of pair 1 took place in the early evening, sunset occurring about eight minutes prior to the end of the run. The gradual drop in absolute temperature of the pair over

the last half of this trial, as well as the steady reduction in the difference between their body temperatures, reflect these conditions (Fig. 1c). The fourth run of this pair began on a morning in which the sun was reduced in intensity by a layer of light haze. About 40 min into the trial, the haze rather suddenly disappeared and the snakes were exposed abruptly to more intense insolation. As can be seen in Fig. 1d their body temperatures responded accordingly.

Heat-Flow Experiment

Mean heat-flow (HF) values of striped skin for each run were used to calculate the relative advantage, A, of melanic integument, expressed as follows:

$$A = (HFmel - HFstp)/HFstp.$$

In a paired design of this sort, some measure of relative performance is necessary for across-trial summary. The sign of the difference in HF values would have sufficed for nonparametric testing but the index A carries more information. We stress here that A, although largely influenced by, is not equivalent to, the ratio of absorbances. Because air temperature over the skin segments is expected to equilibrate above box temperature, part of the heat flow monitored derives from this source. For this reason, A is an underestimate of the ratio of absorbances.

All 53 runs on nine sets of skin segments from six pairs of snakes returned values of A greater than zero. The associated binomial probability is 1.110×10^{-16}. In progressively more conservative fashion, the probabilities associated with 9 sets of skin segments and 6 pairs of snakes are 0.00195 and 0.0156 respectively. The overall mean relative advantage of melanic integument is 0.063.

Field Study

Body temperatures of snakes obtained in the field on sunny days between 0800 and 1600 h were classified by month of capture, sex, and of course morph (Table 1). In no one of the 12 comparisons does the difference between striped and melanic snakes approach significance. Nevertheless, a most interesting pattern emerges from a consideration of the sign of these differences. During the summer months of June, July and August, melanics are slightly but consistently cooler than are their striped counterparts. In contrast, melanics are appreciably warmer during May, September and October. This arrangement occurs in both males and females. Considering one or the other sex separately, the pattern observed is the only one of the 20 $(6!/(3! \times 3!))$ distinguishable permutations (Remington and Schork, 1970) consistent with a thermoregulatory interpretation. Consequently, the resulting probability of 0.05 (1/20) commands attention. More importantly, the same pattern occurred in both sexes; the associated probability, 0.0025 (0.05^2), robustly forces rejection of the hypothesis of random occurrence of morph differences.

Table 1. A comparison of the body temperature of striped and melanic garter snakes, classified by month of capture and sex. All captures are from sunny days during the hours 0800 through 1600 h. $\bar{x}$ = mean body temperature; s^2 = sample variance; n = sample size; Sign = sign of difference in body temperature of the two morphs, melanic-striped. The morphs are compared using the Wilcoxon two-sample test; an approximation of U to the t distribution (infinite degrees of freedom) was used when the larger of the two sample sizes exceeded 20

	Striped			Melanic				
	$\bar{x}$	s^2	n	$\bar{x}$	s^2	n	Sign	t, U
Males								
May	25.7	26.11	12	26.3	20.79	12	+	73.5
June	29.3	4.41	13	28.9	8.35	16	−	104.0
July	29.8	3.61	13	29.8	2.92	15	−	103.5
Aug	29.2	4.88	12	28.3	3.65	17	−	123.0
Sept	27.3	8.47	9	30.2	1.32	3	+	−
Oct	24.9	9.12	3	25.3	21.44	3	+	−
Females								
May	26.9	12.82	27	28.0	8.70	28	+	1.11
June	30.3	4.28	32	30.2	3.69	45	−	0.65
July	30.5	2.86	23	30.3	2.76	44	−	0.47
Aug	30.3	4.45	16	29.9	8.07	31	−	0.21
Sept	28.1	16.48	7	29.3	20.43	13	+	59.0
Oct	22.0	15.05	7	23.4	17.64	13	+	56.5

Note: all comparisons fall far short of significance.

The magnitude of morph differences during the two periods of opposed sign (summer = June, July, August; spring-fall = May, September, October) was explored further. Each difference was weighted by its appropriate sample size and averaged, combining results from both sexes. In summer, when melanics possessed lower body temperatures, the mean difference was 0.28 C°. During spring-fall, however, melanics on average were 1.24 C° warmer than their striped counterparts. The swing in temperature differences, then, spans about 1.5 C°. The magnitude of the spring-fall melanic advantage corresponds very closely with the difference obtained in laboratory experiments described above.

Discussion

Results of the laboratory experiments reported herein indicate firmly that melanic *T. sirtalis* are able to maintain a higher body temperature than striped individuals, when exposed to natural insolation. Moreover, this thermal advantage is attributable to some integumental difference between the two morphs, and reflectance is the obvious and reasonable candidate. Body temperatures of snakes in the field reveal that during the colder part of the active season, melanics are able to stay warmer than striped snakes by an amount which approximates closely the difference observed in the laboratory. Thus melanics have an improved ability to convert the sun's radiation to body heat, and

appear to express this ability at that time of the year when maintaining an elevated body temperature presumably is most challenging.

During the summer months, melanics of both sexes average slightly cooler than their striped counterparts. This suggests an additional thermoregulatory property of melanism. It is safe to assume that, during much of the summer, the avoidance of overheating is a more pervasive problem than is the attainment of a preferred range. In *T. sirtalis*, the voluntary maximum is about 35 °C and the lethal maximum is about 39 °C (Stewart, 1965). On sunny days in the summer, it is easy to obtain substrate temperatures well in excess of these limits. The relative inactivity of snakes during the hottest part of the day (St. Girons and St. Girons, 1956; Gibson and Falls, MS in preparation) no doubt reflects this elemental feature of their microenvironment. In the squamate integument, most of the melanin occurs at the dermis-epidermis junction (Bagnara and Hadley, 1973), and the epidermis is much thinner than the dermis. In melanics most insolation presumably is absorbed in the melanin layer (Monteith, 1973). Through judicious control of its peripheral circulation, a melanic snake may better be able to minimize the vascular transport of heat to its core, leaving more at the periphery to be lost be convection and radiation. The reduced melanin content (or extent) in the skin of a striped snake may allow deeper radient penetration of the dermis and concomitant reduction in vascular control of heat flow. The significance of this hypothetical function of melanin is limited. Under those conditions which generate the danger of overheating, a large portion of the total radiant load on an organism consists of long-wave infrared (Gates, 1962). Absorption of radiation at this wavelength by living organisms is high (Monteith, 1973) and presumably not much affected by pigment.

Some lizards undergo diurnal changes in colour, being darkest in early morning and lightest at mid-day. Frequently it is assumed that these colour changes affect the rate of heat gain, but there are very few direct measurements. In an across-species comparison, Cole (1943) found that the rate of heating increased with skin darkness. We are not aware of another study in which direct measures of heat gain or body temperature in squamate reptiles have been related to reflectivity. Norris (1967) quantified diurnal colour changes in desert lizards using reflectance spectrophotometry, and from this calculated the increase in heat gain thought to be accruing to the darker phase. The results of the present study, together with those of Cole (1943), suggest that an increase in heat gain does accompany a decrease in albedo, at least for squamate integument. For those organisms with external insulation, the relationship is more complex; black may result in better heat gain than white in some cases (Hamilton and Heppner, 1967; Lustick, 1969; Heppner, 1970) but the opposite also prevails (Krog, 1955; Oritsland, 1974, and references therein; Cena and Monteith, 1975). Thus, the external "coats" of some organisms show a positive association between heat gain and reflectance. It is not inconceivable that this phenomenon could find some analogue in the squamate integument, given the remarkable micro-ornamentation found in some species (e.g. Ruibal, 1968; Stewart and Daniel, 1972, 1973). Thus, it may be unwise to extrapolate casually from reflectivity to heat gain in snakes and lizards.

Ecological and evolutionary implications of morph differences in thermoregulatory ability will be discussed elsewhere (Gibson and Falls, MS in preparation).

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