Behavioral Thermoregulation in Lizards: Importance of Associated Costs

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parent movement caused by the wind.

It thus appears that sudden cessation of a strong odor stimulus resets the moth's anemotactic angle, causing the moth's course to deviate from the upwind direction until the zigzags of its track become perpendicular to the wind. In addition, the intervals between the successive track reversals to right and left of the wind line increase as time passes. In practice, flight paths remain more or less upwind only when the wind is uniformly permeated with the odor (6, 7). With an odor plume from a small source the stimulation is discontinuous within the plume as well as between it and the surrounding air (2, 6, 7), and the typical flight track consists of irregular zigzags obliquely upwind along the plume (Fig. 1A) (2, 7). These left-right reversals, also, could be anemotactic reversals if we postulate that the anemotactic angle is variable, being some function of the odor stimulation. Such a system would give a strong impression of chemotaxis.

This anemotactic hypothesis does not exclude some role for chemoklinokinetic or even chemotactic responses, although evidence for the latter is scant (9). An experiment reported by Farkas and Shorey (2) suggested that *Pectinophora gossypiella* males can follow a pheromone trail in stationary air, but it seems to us inconclusive since the males had in every case taken off into the odor plume while the wind was still blowing. The possibility is therefore not excluded that their flight direction had been set anemotactically before the wind stopped. When they entered clean stationary air, after being exposed to odor-bearing wind and then to clean wind [condition 3 of Farkas and Shorey (2)], they diverged from the central axis of the tunnel, instead of staying close to it as they did when a stationary odor plume was there. This does not necessarily mean that the odor trail guided them chemotactically, for they would be expected to deviate when they entered the clean wind if *P. gossypiella*, like the other moths above, starts casting when the odor disappears from the wind.

Quoting unpublished experiments by Meyer on males of *Plodia interpunctella* with crossed-over antennae, Shorey (10) suggests a chemotropotactic mechanism of guidance along an odor plume. Since removing one antenna would likewise be expected to prevent tropotactic orientation, we have performed this operation on 14 male *P. interpunctella* and released them downwind of a calling female. Ten took off and flew

in zigzags upwind to the female in a manner indistinguishable from that of intact males; the other four failed to respond at all.

We are led to conclude that, although the mechanism of odor-regulated optomotor anemotaxis remains largely unanalyzed, it is still the most plausible guidance mechanism for the male moths studied so far.

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4. Males that crossed the upwind line were brought back to the midline for the next test by moving the stripes in that direction. Those that crossed the downwind line returned upwind spontaneously when the stripes were stationary.
5. On the few occasions when a male continued to fly for many seconds in the tunnel with no wind or odor plume, it was observed to orient itself with stripe movement and fly at about the same speed and to turn around accordingly through 180° whenever the stripe movement was reversed. Visually, this is equivalent to orienting into wind.
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11. We thank A. A. G. Thomas, J. G. Ions, A. R. Ludlow, and K. E. Marsh for their help, and J. N. Brady and J. E. Moorhouse for criticism.

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Behavioral Thermoregulation in Lizards: Importance of Associated Costs

Abstract. *The Puerto Rican lizard* Anolis cristatellus *behaviorally regulates body temperature in an open habitat but passively tolerates lower and more variable temperatures in an adjacent forest where basking sites are few and distant. Thermoregulation may be adaptive only when costs resulting from associated losses of time and energy are low.*

Many lizards behaviorally regulate body temperatures within a narrow range by shuttling between sun and shade or hot and cold microenvironments to alter heat flux (1), by modifying posture to alter surface areas exposed to heat sources or sinks (2), and by regulating activity times (3). When costs resulting from associated losses

Fig. 1. Percentage of *A. cristatellus* perched in full sun during a day. Anoles in partial sun were counted as being half in sun, half in shade. Open circles indicate lizards in the open park and closed circles indicate lizards in the forest; $N =$ 10 for all samples unless noted.

of time and energy (4) are substantial, thermoregulation to optimal levels is impractical (5, 6); indeed, some lizards rarely thermoregulate (7, 8). In theory one could predict the amount of thermoregulation that would maximize net benefits within a habitat by measuring the costs and benefits of achieving specific body temperatures. In practice I estimate a correlate of certain costs and demonstrate that a tropical Puerto Rican lizard, *Anolis cristatellus* (9), thermoregulates less carefully in habitats where this cost is great.

To study the effect of habitat on thermoregulation and body temperature, I monitored *A. cristatellus* in two adjacent lowland habitats (shaded forest and open park) during a full day (10). To index the cost to lizards of raising body temperature by shuttling between sun and shade, I measured the shortest transit distance from an anole perched in partial sun or in shade to a patch of full sun on a contiguous perch (11) and included a category "no way" (NW), indicating
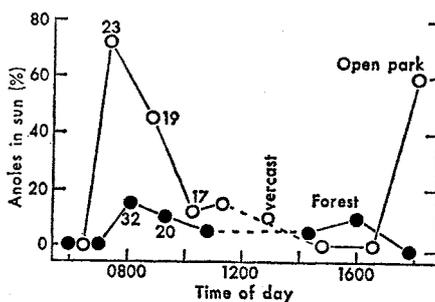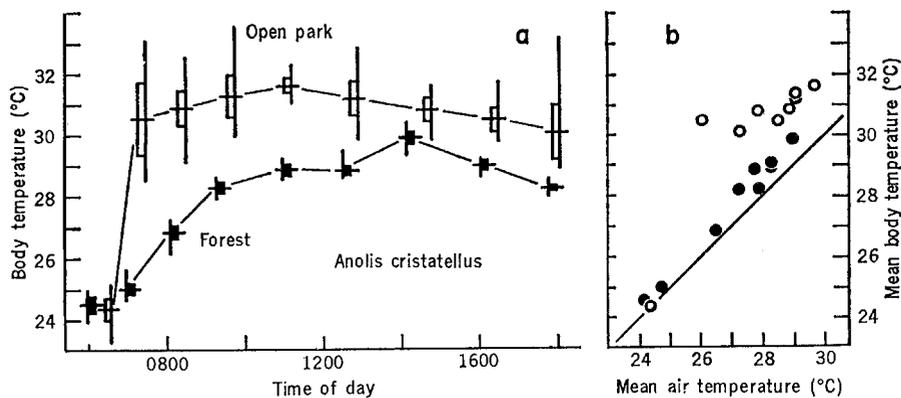
Fig. 2. Body temperatures of *A. cristatellus* in two adjacent habitats as a function of (a) time of day and (b) mean air temperature. Vertical lines indicate range, horizontal lines indicate mean, and bars equal ± 2 standard errors. Open circles or bars indicate lizards in open park and closed symbols indicate lizards in shaded forest; $N = 10$ for all samples.

that the tree or shrub was completely shaded. Also, I recorded whether each anole was perched in full sun, partial sun, or shade; body temperature (cloacal, Schultheis thermometer); air temperature (shaded bulb, 1 cm above perch); and perch height.

Significantly more anoles in the forest (*G*-test, $P < .001$) were unable to reach full sun without changing trees (NW = 76.3 percent, $N = 80$) than were those in the open park (NW = 12.5 percent, $N = 80$). Also, the average distance to full sun for the remainder was significantly greater (*t*-test, $P < .001$) for forest lizards (7.9 ± 0.8 m) as compared to those in the open (1.2 ± 0.2 m). Therefore, the cost to raise the body temperature is considerably greater for forest anoles.

Few forest lizards were in full sun and presumably basking during the day (Fig. 1). In contrast, anoles in the open were significantly more heliothermal (*G*-test, $P < .001$), basking in full sun both early and late in the day but avoiding sunny perches at midday.

Perch heights of lizards in the forest were similar (Kolmogorov-Smirnov test, $P > .5$) in censuses taken during warm periods (0915 to 1705 hours) ($\bar{X} = 1.2 \pm 0.1$ m) and cool periods ($\bar{X} = 1.1 \pm 0.1$ m). However, lizards in the open perched significantly higher ($P < .01$) during the warm censuses (1.6 ± 0.1 m) than during cool censuses ($1.1 = 0.1$ m), which suggests avoidance of warm midday microclimates near the ground (*12*). Thus, anoles in the open behaviorally regulate body temperature by "sun-shuttling" and microhabitat selection while lizards in the forest do not.

Mean body temperatures of lizards in the forest increased slowly during the morning (Fig. 2a) and were strongly correlated with mean air temperatures during the day (Fig. 2b) ($r_S = .997$, $P < .01$). Mean body temperatures of anoles in the open rose quickly in the morning (Fig. 2a) as a result of basking (Fig. 1), and were less strongly correlated with mean air temperatures ($r_S = .883$, $P < .01$). Except for the first census, anoles in the open always had significantly higher body temperatures than did lizards in the forest (Kolmogorov-Smirnov tests, all $P < .01$).

Mean body temperatures of lizards in the forest varied by 4.9°C between 0704 and 1750 hours, whereas those of lizards in the open varied by only 1.6°C between 0738 and 1819 hours (Fig. 2a). Body temperatures of anoles in the open were significantly less variable (*F*-test, $P < .025$) within these time intervals.

Anolis cristatellus behaviorally regulate body temperature in habitats where costs of raising temperature are low (*13*). However, in habitats where these costs are apparently prohibitive, anoles are passive to ambient conditions and thus active at lower and more variable temperatures. Thermoregulation to avoid the hazards of extreme temperatures (*1, 14*) is always adaptive: Within these limits, however, thermoregulation may yield greater net benefits than passivity only when associated costs are low. Behavioral versatility and the implicit ability of *A. cristatellus* to be active over broad ranges of temperature [eurythermy (*15*)] may partially account for the success of this species as a colonist in the Caribbean (*8; 16*, p. 369).

Anolis cristatellus contrasts strikingly with most previously examined species, chiefly desert and open-habitat lizards (*1–3, 17*). The careful thermoregulation generally characteristic of these species is related both to the low cost of raising body temperature (basking sites are readily available) and to the necessity of avoiding heat stress at midday during summer (*1*). Stenothermy in such areas may be adaptive because of the relative ease of temperature control (*18*). In temperate zone forests, however, thermoregulation is difficult, and passivity may yield insufficient benefits because of more variable thermal regimes (*19*): This may help to explain the relative absence of lizard species from temperate forests.

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11. The greater the distance, the more energy and time expended in shuttling. Restriction of measurements to within shrubs or trees is arbitrary, since individual *A. cristatellus* may use several trees [A. S. Rand, thesis, Harvard University (1961)].
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haves similarly (R. B. Huey and T. P. Webster, in preparation). B. Lister (in preparation) has found comparable situations in *A. sagrei* on Great Abaco Island, Bahamas, and *A. monensis* on Mona Island, Puerto Rico.
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Temporal Summation of Light by a Vertebrate Visual Receptor

Abstract. *Using aspartate to isolate mass receptor activity, we have investigated the reciprocity of flash intensity and flash duration in determining the response of the frog's cone receptor. The durations over which reciprocity holds decrease with increases in either flash energy or ambient light intensity. These findings parallel those of human psychophysical experiments.*

In 1885 Bloch suggested that the visual effect of brief flashes of light is determined by the total quantity (flash intensity × flash duration) of light (*1*). There followed an unusually large number of psychophysical studies confirming what became known as Bloch's law (*2*). It states that for flash durations up to some critical duration, the visual system responds equally to flashes of equal energy. As flash duration is further increased this reciprocity of intensity and duration decreases until the visual response is determined solely by flash intensity. It has also been shown that critical duration is dependent upon a number of factors including ambient light intensity and response measure (*3*, *4*). Data from electrophysiological studies (*5*) with a variety of different animals and response measures also exhibit these relations.

While the extent of the reciprocity of intensity and duration, sometimes called temporal summation, has been measured at various levels in the visual system, a direct measure of temporal summation has not been made for any vertebrate photoreceptor. Using aspartate to isolate mass receptor activity, we have measured the extent of this reciprocity for the frog's 580-nm cones. The magnitude of the critical duration and how it is affected by light adaptation and response measure are comparable to the results from human psychophysics and animal electrophysiological recordings. This suggests that perhaps some of the temporal phenomena observed in human psychophysical studies are determined by receptor characteristics.

Gross extracellular receptor potentials, isolated with aspartate, were recorded from isolated frog (*Rana pipiens*) retinas. The details of the preparation, the optical system, and the recording apparatus have been presented previously (*6*). Aspartate isolates the receptor response of the electroretinogram (ERG) by blocking postsynaptic activity and thus eliminating the other components of the ERG (*7*). This allows the recording of receptor potentials with conventional gross electrodes.

To record cone responses, a 5-minute adapting light was used to bleach about 90 percent of the rod pigment, rhodopsin (*8*). The retina was then dark-adapted for 50 minutes. The rod pigment does not regenerate in the isolated retina (*9*), but 90 percent of the cone pigment does (*10*), and the cone

receptor threshold returns to within 0.16 log unit of its prebleach sensitivity (*6*). In this state, the cones containing a visual pigment absorbing maximally at 580 nm (580 cones) have been shown to control the response to 630-nm light. In fact, they are over 1.5 log units more sensitive to a 50-msec, 630-nm flash than any of the other frog receptors, including the rhodopsin-containing rods (*8*). All the responses recorded in this study were from the 580 cones.

Figure 1 shows polygraph records of cone responses. All stimulus presentations for each column were of equal energy (that is, as duration was increased the intensity was decreased such that energy was held constant). The stimulus energy for columns 2 and 3 was 0.6 log unit higher than for column 1. For column 3, a background was added which decreased the peak amplitude to the 20-msec stimulus of column 2 to the amplitude of column 1. The X's under the responses give the peak amplitude and latency for the response to the 20-msec flash for that column. In all three columns, the peak response amplitude is approximately the same for equal-energy 20- and 40-msec flashes. However, for successive stimulus durations within each column, the peak response amplitude decreases while the latency increases. This implies that as the duration is increased, the light energy is not as effective, as measured by the peak amplitude. Compare the responses to the 20- and 80-msec flashes across columns. In column 1, the peak for the 80-msec flash is the same as that for the 20-msec flash. In column 2, it is 90 percent, and in column 3 it is 76 percent. Thus,
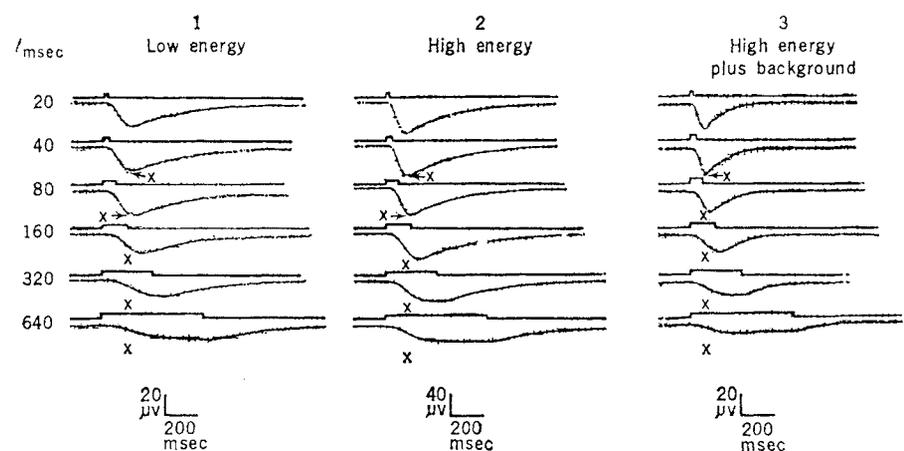

Fig. 1. Polygraph records of cone responses to equal-energy, 630-nm flashes. The stimulus energy for columns 2 and 3 was 0.6 log unit higher than for column 1 (*19*). The flashes of column 3 were presented as increments upon a steady, 501-nm background. The bandpass was d-c to 100 hertz.