

sexes in the inheritance of phosphorylase *b* kinase by mice in the F_1 generation suggests that the gene for this enzyme resides on the X chromosome. If the locus were on another chromosome, then all of the mice in the F_1 generation should have expressed the enzyme, since our observations indicate that the presence of the enzyme is dominant to its absence.

Accordingly, brother and sister matings within the two groups of the F_1 generation should yield offspring with two predictable patterns. The enzyme should be absent in 50 percent of the males and 50 percent of the females in the offspring, the F_2 generation, which were descended from original matings of I-strain females and C_{57} -strain males. In the F_2 generation from original matings of C_{57} -strain females and I-strain males all of the females should possess the enzyme and 50 percent of the males should lack the enzyme. The data in Table 1 confirm the predictions.

Therefore, the two groups of females in the F_1 generation may be considered to be heterozygous with respect to this kinase. In order to confirm this notion these females were mated with males from their particular paternal strain. The offspring from these matings, the first backcross (B_1), should also yield two predictable patterns. The studies are not yet complete but the initial determinations are as would be expected from the predicted results.

The concentration of glycogen in the resting muscle is 1.2 percent in I-strain mice and 0.5 percent in C_{57} -strain mice (1, 2). No data are presented here (10), but in all offspring the absence of the kinase was associated with the same concentrations of muscle glycogen as found in the parental I strain, and, conversely, the presence of the kinase was associated with the same concentrations of glycogen as found in the parental C_{57} strain. This all-or-none phenomenon suggests a specific relationship, perhaps cause and effect, between phosphorylase *b* kinase and the stores of muscle glycogen in the resting muscle. Although this specific kinase is a key intermediate in a series of reactions which promote glycogen breakdown (11), this tempting conclusion must be considered as only tentative at this time.

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Voluntary Hypothermia in Reptiles

Abstract. Studies on lizards in laboratory thermal gradients which are not shut down at night reveal complex thermoregulatory behavior. Maintenance of the high, characteristic levels of body temperature known for active lizards may be abandoned. Low levels, which incapacitate the lizards, are selected. Evidence of complex responses of the "thermostat" at a reptilian level of organization suggests a reassessment of our theories concerning the evolutionary status of "torpidity" in birds and mammals.

It is commonly assumed that diurnal reptiles become cold and inactive at night because the body cools as the environment cools. In this sense, a lizard's "torpidity" is obligatory and passive. The assumption would seem to follow the fact that few reptiles are able to achieve significant thermal homeostasis with metabolic heat, a python (*1*) being a notable exception. Rather, some reptiles are known to maintain body temperatures within narrow limits by behavioral exploitation of microclimatic thermal mosaics in their environments. It is the basking lizards of the arid areas of North America which have been most carefully (2) studied, and which form the context for generalizations (3, 4).

The following experiments, however, suggest that low body temperatures are the result of a voluntary and actively initiated process in some lizards. The lizards may thus "prefer" and not simply tolerate low nocturnal temperatures. This would be significant to our conceptualization of the evolution of endothermy in birds and mammals (5).

Casual observations upon *Gerrhonotus* (*Anguidae*) and *Klauberina* (*Xantusiidae*) in substrate-heated thermal gradients prompted the experiments. Movement onto the warm surfaces was periodic and usually corresponded to the light periods in the observation room (photoperiod controlled). Inactive individuals would usually become responsive after feeding (6).

For experiments, animals which were judged to be active were placed, two each, in glass terraria (1 by 1 by 2 feet) (0.3 by 0.3 by 0.6 m) maintained

in a constant-temperature room (set at 9° to 17°C in various experiments) with a controlled photoperiod (10 hours light, 14 hours dark). The ambient temperature established the cold end of the gradients, and one end of each terrarium was heated by a 250-watt, red-glassed heat lamp. This was suspended from above and provided each gradient with maximum temperatures which would be lethal to the species. Pieces of cardboard were scattered about so that the lizards could retreat

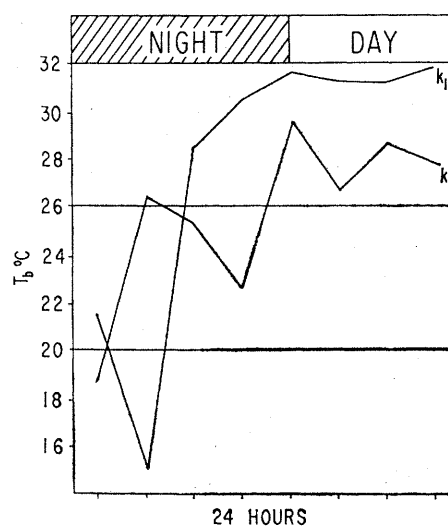


Fig. 1. Each point represents average cloacal temperatures for 3-hour sampling periods (two or three records each period) over 24 hours. K_1 is the larger of two male *Klauberina riversiana* lizards in the same terrarium. K_2 is a male in a terrarium with a female. The available temperatures in the gradient were constant through time, so that the nocturnal lows are achieved by voluntary movements of the lizards.

to shelters over a wide range of temperatures. The room was isolated from all activity and I entered as quietly and briefly as possible. The lizards were not fed, and were not disturbed for 3 days. The cloacal temperatures were then taken with a small-bulb mercury thermometer at intervals no more frequent than 1 hour.

The data revealed that for some period during the night the lizards selected low temperatures at which they became torpid. Orientation to high temperatures is not, therefore, constant. Figure 1 illustrates the results for 24 hours of sampling two *Klauberina*. Both show the drop in cloacal temperatures during the night and the orientation to higher temperatures during the light phase of the photoperiod.

The lizards are torpid at the lower temperatures. They move only with difficulty; they are poorly coordinated and relatively helpless. When replaced, after their temperature is taken, they typically retire rather than bask and move about. The capacity for directed movement is retained, that is, rewarming requires directed activity, and therefore the apparent incapacitation can be only in part due to low body temperatures per se.

The voluntary orientation to low temperatures was unexpected, but on reflection the survival value of such a phenomenon becomes apparent. If these lizards were to "prefer" high temperatures as an invariable aspect of their orientation to the environment, they might face a dilemma at the end of

each day. Since at sunset, different parts of the habitat cool at different rates, orientation to isolated warmer areas could lead the lizards away from shelter and make them perhaps more vulnerable to predation. It would seem advantageous for the lizards to possess a mechanism insuring a reversal of high-temperature orientation following appropriate stimuli (exogenous or endogenous), so that they will not direct themselves toward maintenance of warm body temperatures when the environment is cooling and becoming suboptimal for behavioral thermoregulation. It is known that many reptiles take shelter before the natural environment actually becomes unfavorable. It is, however, difficult to distinguish preferences for low temperatures from shelter-seeking from some sort of threat, for example, fright overriding thermal preference. It is also difficult to establish that the shelters are cool at the time the reptiles locate them. In cases where reptiles are found in cool ground on warm days, it is difficult to establish that the animal can sense the more optimal conditions elsewhere. In short, natural history observations suggest that the phenomenon seen in the laboratory may be effective in nature, but field data to support the suggestion that thermal "preferences" change are not yet available.

Little is known of the thermoregulatory responses of "low-temperature" lizards such as *Gerrhonotus* and *Klauberina*, and so the experiments were continued with more familiar heliothermic (basking) lizards: *Phrynosoma cornutum*, *Sceloporus magister*, and *Uma notata*. These forms, in contrast to *Gerrhonotus* and *Klauberina*, burrow in the sand when sleeping at night; *Phrynosoma* and especially *Uma* burrow for considerable lengths of time during the day. Large terraria (6 by 2 by 2 feet) were covered with 3 to 6 cm of fine sand, and two heat lamps established the hot end of the gradients. Lizards would burrow deeper than 1 cm, and since 1 cm of this sand will block all light, lizards buried in different parts of the terrarium presumably experienced only temperature differences. Only buried individuals were measured. Temperatures were taken once during the night and once during the day over several cycles of the photoperiod (10 hours light, 14 hours dark). Food (mealworms) was continually available.

Figure 2 (top) shows that nearly all the buried *Phrynosoma* at night selected temperatures below the so-

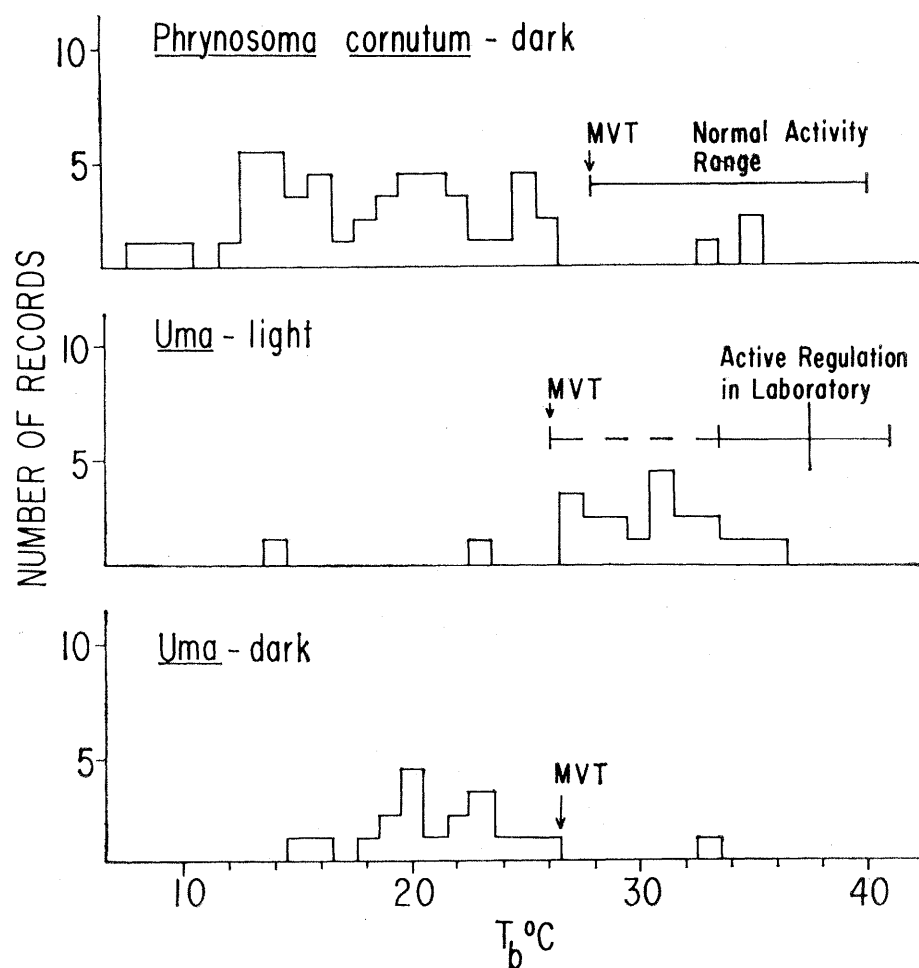


Fig. 2. (Top) Cloacal temperatures of *Phrynosoma cornutum* in sand at night (dark phase of photoperiod). Measurements were made twice a day (once each dark phase) on five individuals over a period of days. Those not in sand at a given time were ignored. *MVT* represents the "minimum voluntary temperature" (3), which is the lower end of the activity range and the imposed temperature at which a diurnally active animal can be forced to retreat from activity. At night, then, the lizards nearly always voluntarily select temperatures below the *MVT*. (Middle and bottom) Cloacal temperatures of buried *Uma notata* determined in the same way as for *Phrynosoma*. Like *Phrynosoma*, *Uma* would usually (see text) select temperatures below the *MVT* at night voluntarily, but not in the daytime. Cowles and Bogert's (3) value for the *MVT* is used and Licht's (12) mean and range for active *Uma* (no sand) are illustrated. The lower end of that range bears no essential relationship to the *MVT* which is a temperature eliciting particular types of behavior.

called "minimum voluntary temperature" (3), which is the lower limit for activity as conventionally determined (3, 4). *Phrynosoma* spent much of the day active, above the surface of the sand, so relatively few data are available. Those that I have indicate day burials above the minimum voluntary temperature and within the basking and activity ranges.

The initial results for *Uma* were variable. While many voluntarily selected low temperatures at night, others were active at night and torpid in the day! Some lizards did not show any indication of the voluntary selection of temperatures below "normothermic" levels on any regular basis. A simple photoperiod appeared to be inadequate to simulate dusk and dawn for this group of individuals under conditions of ad libitum heat.

The procedure was then changed in an effort to reduce the individual variability. One of the two red-glass heat lamps was replaced by a clear-glass lamp and placed in the circuit with the room lights so that when the room lights would go off, the total area comprising the hot end of the gradient would become reduced. Thus, while the temperatures at the extremes of the gradient did not alter, dusk was simulated in that a sharp reduction in light intensity was associated with substrate cooling in some areas and with a reduction in the radiant environment in a part of the gradient.

Under the new conditions nearly all *Uma* selected low temperatures when burrowing at night (Fig. 2) but levels above the minimum voluntary temperature when buried during the day. Parts of the gradient shifted their boundaries at "dusk," but most lizards were found covered where the gradient was stable. A trap effect cannot, then, explain the results.

Only three *Sceloporus* were observed. They would remain active for days at a time, burrowing in cool sand (cloacal temperatures were 14.5° to 18.8°C) and becoming torpid only about once a week. This hypothermia was, of course, voluntary, even though it had no evident relation to photoperiod.

To summarize, the tendency to orient voluntarily to low temperatures has been demonstrated in several species of lizards under conditions that would permit the animals to maintain body temperatures constantly at activity levels. This generally occurs at night, but regular, periodic behavior

may require simulation of dusk for certain species. Physiological benefits may well underlie the phenomenon, but the ecological advantage is more obvious at present.

It seems reasonable that the endothermic birds and mammals evolved from behaviorally thermoregulating ectotherms, and that the initial role of metabolic heat production was as an adjunct to an already sophisticated thermoregulatory system (7). These ancestral ectotherms might be assumed to have faced problems similar to those faced by modern behavioral regulators. With daily exposure to suboptimal temperatures, one would expect (using these modern lizards as a model) that they would develop mechanisms to protect them from inopportune thermally directed behavior and consequent exposure to hazards. Given a trend toward endothermy, voluntary hypothermia would gain the added protective function of energy and water conservation. It follows that active, periodic changes in the thermoregulatory system, or "thermostat," were probably part of the heritage of the birds and mammals from ectothermic ancestries and through the transitions to endothermy.

From this point of view it would appear that a hypothermic state such as daily torpidity is primitive, having been modified and retained wherever adaptive. Cade (8) has observed that torpidity appears in the phylogenetically conservative lines of rodents, and on this basis has come to the same conclusion.

The more orthodox view at present is that hypothermic states represent adaptive specializations and are advanced conditions in vertebrate endotherms (9). It is of course possible that thermostatic control became continuous and nonperiodic in the founders of the marsupial and placental lines of mammals, and that the hypothermic states of today represent secondary phenomena. This might have happened if ancestral forms were large at some stage well along toward endothermy. The energy expense of warming a large body every day could have resulted in continuous regulation becoming more practical (10). It is very difficult, of course, to determine if any particular fossil is directly ancestral or, indeed, endothermic.

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Avena ventricosa: Possible Diploid Contributor to Hexaploid Oats

Avena ventricosa Balansa, with a diploid number (2n) of 14, is the least-known diploid oat species. Only two collections of this species have been reported (1), one from Algeria (subsp. *ventricosa*) and one from Baku (subsp. *bruhsiana*). We have examined samples from both locations (2) and have found that *A. ventricosa* is distinct from other diploid *Avena* in that it lacks awns on the tips of its lemmas and has an extremely asymmetrical karyotype. It has six pairs of chromosomes with subterminal centromeres and only one pair of satellited chromosomes (Fig. 1). All other diploid oats