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Thermal Relations, Metabolism and Winter Dormancy of the Sand Lizard, *Acanthodactylus boskianus*

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Abstract: Field and laboratory studies of thermal relations, metabolism and winter dormancy were conducted on the sand lizard, *Acanthodactylus boskianus*. During daily activity times the lizards were slightly, but significantly warmer than their environment. The standard metabolic rate was exponentially related to temperature. The maximum Q10 (3.86) occurred between 25 and 30°C and minimum one (1.56) between 35 and 40°C. There was no evidence of dormancy or reduced metabolism due to reduced temperature (to 15°C) in summer. Oxygen consumption was essentially the same in the field lizards and in captive ones held either in outdoor cages or at 15°C in summer, when measured at 15°C or 35°C, but consumption was significantly higher in both groups than in field animals when measured at 25°C. Lizards become dormant when exposed continuously to short photoperiods in winter. This lizard could not be maintained in an active condition through winter under laboratory conditions used successfully to keep other local lizards active. Despite the length of photoperiods used (8 h/day or 16 h/day), both groups showed a significantly reduced metabolic rate at 15°C comparable to those measured at 25°C or above. Therefore, dormancy and metabolic rate are controlled independently. The winter dormancy is controlled by reduced photoperiod, but lower metabolic rate is controlled by reduced temperature.

Key words: Thermoregulation- metabolic acclimation- winter dormancy- *Acanthodactylus boskianus*

Introduction

In the half century since Cowles and Bogert (1944) published their pioneering study of desert reptiles, physiological ecologists have worked to evaluate the extent and effectiveness of temperature regulation by field active animals. Temperature regulation, a central paradigm of biophysical and physiological ecology (Bartholomew, 1964, Gates, 1980), is a paramount importance to many aspects of reptilian ecology and behaviour (Huey, 1982). Many species of diurnal reptiles maintain high and constant body temperatures (T_bs) despite wide fluctuations in environmental heat loads (Avery, 1982; Huey, 1982). They achieve these mainly by adjustments of their behaviour, in particular, restriction of activity times, shuttling between hot and cool microhabitats, and postural modifications that alter the rates of heating and cooling (Huey *et al.*, 1977; Hertz and Huey, 1981; Huey, 1982; Stevenson, 1985; Bauwens *et al.*, 1996; Hussein, 2000). However, not all reptiles maintain constant T_bs or spend considerable time and energy in thermoregulatory behaviours. For instance, some lizards that inhabit tropical forests exhibit few regulatory adjustments and their T_bs fluctuate with ambient conditions (Ruibal, 1961; Huey and Webster, 1975; Hertz, 1992). Other species live in habitats where ambient conditions enable them to be active at T_bs near the selected range without thermoregulatory adjustments (Hertz *et al.*, 1993; Shine and Madsen, 1996). Nevertheless, the maintenance of high and stable T_bs during activity and the extensive usage of regulatory behaviours are characteristic of small diurnal lizards that inhabit climates characterized by wide diurnal fluctuations of ambient temperatures.

Thermal and metabolic relations of large number of reptiles have been investigated and extensive summaries of the literature are available (Brattstrom, 1965; Bartholomew, 1968; Templeton, 1970; Gans and Pough, 1982; Avery, 1985; Kayed *et al.*, 1990; Zari, 1990). Previous studies have established that body temperature, mass, phylogeny and ecology are important factors influencing resting metabolism in reptiles (Bennett, 1982; Andrews and Pough, 1985; Al-Sadoon, 1986). Several other factors may affect the metabolic rate of reptiles such as latitude (Davies *et al.*, 1981; Hailey and Davies, 1986), sexual condition and seasonal acclimation (Patterson and Davies, 1984; Zari, 1987), and feeding (Coulson and Hernandez, 1985).

There is considerable information on the effect of temperature on resting metabolic rate in reptiles (Bennett, 1982; Andrews and Pough, 1985). However, additional differentiation along ecological lines (e.g. species adapted to mesic versus xeric, or temperate versus tropical environments) remains unanalyzed and would seen to be a worthwhile and rewarding effort (Bennett, 1982).

A great deal has been written about hibernation, particularly about bird and mammal hibernation (Kayser, 1961; Lyman, 1963; Wheeler, 1984). In reading much of literature about hibernation one gets the impression that ectotherms become dormant in winter simply because they are unable to maintain normal metabolic rates at the reduced ambient temperatures occurring at that time of year. This may be true for some ectotherms. There is still considerable disagreement about the causes of hibernation, but there is widespread agreement that definitions of this phenomenon must be clarified. It is generally felt there should be one term for endotherms and another for ectotherms, due to different mechanisms utilized for controlling body temperatures. However, since suitable terms have not been proposed, hibernation will be used in this research to mean winter dormancy of ectothermal vertebrates. There are no published studies on the influence of temperature on resting metabolic rate in *A. boskianus* which is widely distributed in Egyptian deserts. Therefore, the aims of this study are threefold. First, to document the T_bs maintained by lizards at different times of the day. Second, to investigate the metabolic rate – temperature relation in this species and third, to report the field and laboratory study of the thermal ecology, metabolic relations and winter dormancy of *A. boskianus* to demonstrate if the physiological changes in metabolic rate throughout the winter dormancy in this species is temperature-dependent.

Materials and Methods

Species and study site: *A. boskianus* is a desert- dwelling lacertid lizard that occurs in sandy areas of Burg El- Arab region, 50 km west of Alexandria on the north western Mediterranean coastal region of Egypt. The habitat and climatic conditions has been described by Hussein (1992). This lizard was noticed to be active through the months from March to November. The activity in March and November was noticed to be relatively slight if compared to that in other months. The lizard is diurnal and daily activity times extends from 6.00 h to 2000 h and spend their inactive periods under vegetation, among stones and loose soil. The hibernation or winter dormancy takes place throughout the period from December to February. The mean hibernating temperature for this species in the region of study is approximately 15°C (ranged 14.3- 15.6°C).

Field measurements: Body temperature (T_bs) and ambient temperatures (T_as) were collected for a large number of lizards between 8 and 15 June, 2000. Samples of at least five animals were collected each two hours between 600 and 2000 h. Lizard samples were captured by using sticky tape traps. T_bs were recorded for the captured lizards by inserting the bulb of a fast reading thermometer into the individual's cloaca within 10 seconds of capture. In order to determine whether such a daily shift occurs in metabolic rate in *A. boskianus*, oxygen consumption was measured in field animals to establish a base line. Oxygen consumption was measured at 5°C intervals between 15 and 40°C.

To investigate the effect of ambient temperatures on metabolic rate and winter dormancy of the sand lizard, *A. boskianus*, two experiments were conducted:

Summer laboratory experiment: In the late August, 60 lizards were caught and held in outdoor cages under conditions simulating the natural habitat as nearly as possible. Each 20 individual were placed together in a glass cage measuring 70X30X80 cm. The floor of the cages was covered with about 10 cm of sand and a number of rocks and a sheets of thick cardboard provided shelter and shade. The lizards were supplied with nymphs of cockroaches and fly pupae and occasionally allowed excess to water.

We reported that the mean winter hibernating temperature for this species is approximately 15°C. Consequently, twenty *A. boskianus* were held at 15°C during the last two weeks of August in an attempt to make them become dormant (the dormant lizard stayed motionless on or under the sand throughout the normal daily active period and their eyes always remained closed). These animals were held in glass cage 35X15X40 cm. The cage of the experimented was placed on thermal gradient chamber. This chamber had a thermostat at one-end providing various degrees of temperatures and the other end of chamber was provided with 15 Watt GE daylight fluorescent lamp lighted 14 hours daily (normal photoperiod at this time of the year).

Oxygen consumption was measured in outdoor captive group, 15°C captive group and freshly captured field animals at the end of the two weeks period. Only adults were used (snout-vent length ranges from 74- 86 mm and body mass ranges from 33.22 to 38.19 g), so the slight differences in weight had little effect on oxygen consumption. No food or water was offered the 15°C lizards during the two weeks, since they are unable to metabolize food successfully at this temperature. Lizards from outdoor cages was fed as before, but received no food for 48 h preceding oxygen consumption measurements. Metabolic rates of the field lizards were measured within 48 h of capture, also without feeding. Oxygen consumption was measured at 15, 25 and 35°C respectively.

Oxygen consumption was measured with constant pressure respirometer (Kayed *et al.*, 1990). The average oxygen consumption (cc O_2/ g.h) of at least five individuals from each group studied at the selected ambient temperature was measured from 800 to 1400 h in a temperature- controlled room (± 1°C). For acclimation, the animals were kept at the selected experimental temperature for at least 30 min before measurements were taken. These lizards are very docile, and few of them moved about during the experiments. Nevertheless, data obtained from moving lizards were eliminated.

Winter laboratory experiment: In late November (immediately prior to hibernation), twenty lizards were placed in each of three environmental chambers. Additional animals remained in outdoor cages. The indoor cages in the chambers were as described previously, but the temperature regime was changed. These chambers were maintained at 15, 25 and 35°C. Oxygen consumption was measured at the same manner and at the same conditions of food and photoperiods, as described before in the summer experiment, for at least five individuals from each group (field active, 15°C indoor, 25°C indoor, 35°C indoor and outdoor group).

The effect of light on metabolic rate and dormancy was indicated by subjecting another groups of captive animals (each of twelve individuals) to two different photoperiods throughout the first two weeks of December. The photoperiods are 8 and 16 hours of light [L] alternating with 16 and 8 hours of dark [D], i.e. LD 8:16 and 16:8 respectively under the control of three thermal conditions (15, 25 and 35°C respectively). Light was obtained from one 100 W incandescent light in each cage. The cages had sandy substrates and no object that might provide the animals with a shelter from light. Oxygen consumption was measured at the end of two week period, as described before, for one- half the animals in each cage and the animal activities were observed for the other half.

Significance of differences among groups of different treatments were analyzed statistically by ANOVA and t-tests (Bailey, 1981) to test if any significant differences were likely. If significant changes were indicated, levels of significance were inferred at $P < 0.01$.

Results

The mean ambient air temperatures (T_a) and body temperatures (T_b) of the sand lizard, *A boskianus* and the differences between them were computed (Fig. 1). Mean body temperature throughout the day was 29.6°C ranging from 25.2 to 34.0°C. In the field, the sand lizard held internal temperature consistently higher than ambient (Fig. 1a). Of sixty- four lizards measured fifty- five (85.9 %) had body temperatures higher than those of ambient air. However, the magnitude of the differentials was slightly difference and appeared to vary throughout the day. T_b -T_a differences from 600 to 2000 h were significantly different ($P < 0.05$) throughout the day based on t- test, averaging only 0.77°C (range 0.20 to 1.30°C). Maximum differences occurred between 1600 and 1800 h (average, 1.30°C) as ambient temperatures fell more rapidly than body temperatures.

Results of the oxygen consumption tests are presented in Fig. 2. As expected, oxygen consumption was exponentially related to temperature and Q_{10} approximated two over the range of temperatures tested. The sharpest increase in metabolic rate occurred between 25 and 30°C (Q_{10} 3.86) , but the oxygen consumption leveled off between 35 and 40°C (Q_{10} 1.56). Lizards held in the respirometer at 35 and 40°C obviously were under stress. This may be reflected by the sharp depression of

Table 1: Estimates of the Q_{10} of metabolic rates in *A. boskianus* between ambient temperatures 15- 40°C.

Temperature interval (°C)	Q_{10}
15 – 20	2.54
20 – 25	2.71
25 –30	3.86
30 – 35	3.77
35 – 40	1.56
Overall	
15-40	2.89

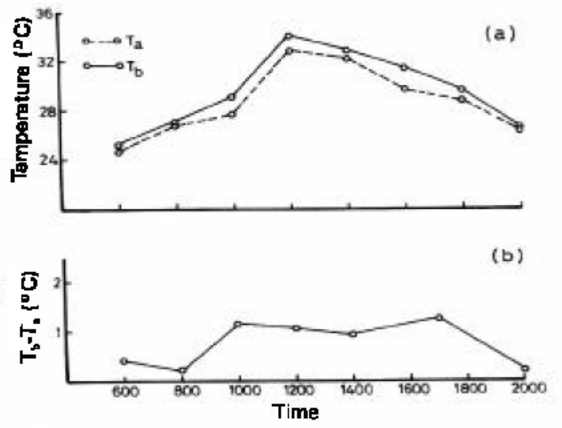

Fig. 1: (a) Ambient air temperatures (Ta) and lizard body temperatures (Tb) measured throughout the day. Points are the mean of five measurements for each hour. (b) The difference between Tb and Ta

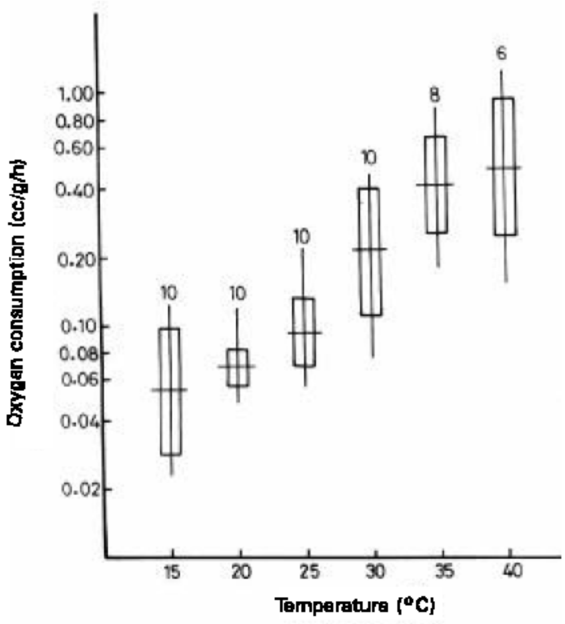

Fig. 2: Oxygen consumption of the field active *A. boskianus* at different ambient temperatures. Bars denote means, vertical lines the ranges and rectangles twice the standard error above and below the means. Numbers indicate sample size. The points are plotted on a logarithmic grid.

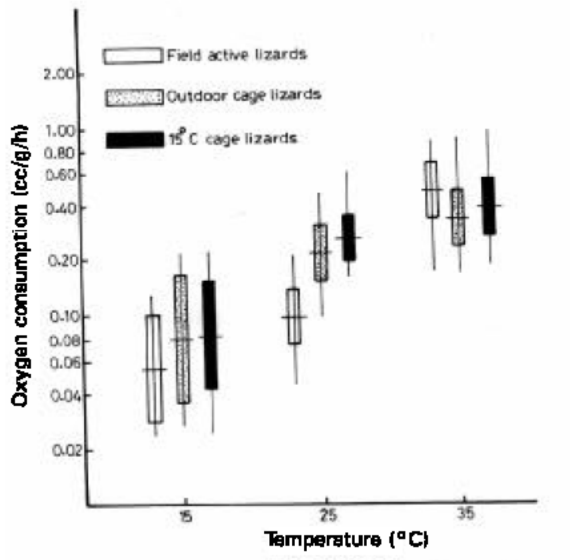

Fig. 3: Comparison of oxygen consumption at three temperatures in field, outdoor cage, and 15°C cage *A. boskianus* in summer (data for field lizards from Fig. 2). Figure is based on ten lizards at all temperature regimes. See Fig. 1 for explanation of symbols. The points are plotted on a logarithmic grid

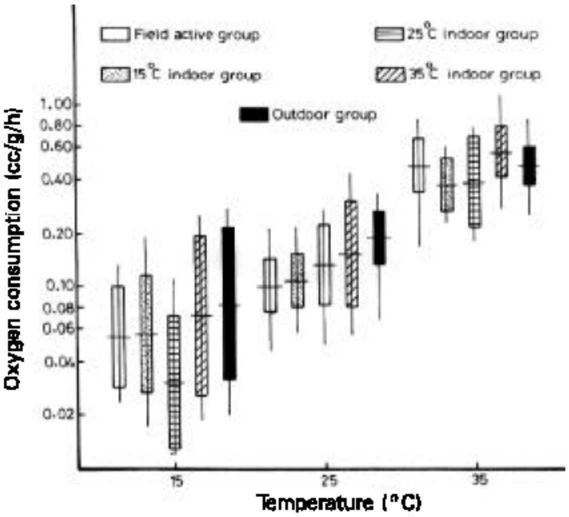

Fig. 4: The relation of oxygen consumption of *A. boskianus* to different temperature regimes in winter plotted logarithmically. Figure is based on at least ten lizards at all groups

Q_{10} between 35 and 40°C (Table 1). They were more restless than when held at lower temperatures. The lizards tested at 40°C were noticeably sluggish and barely able to move when returned to aquarium and required 10- 15 min at room temperature before they behaved normally. Lizards tested at lower temperatures (15°C) were very active when removed from the respirometer than those run at higher temperature. In summer laboratory experiment there is a gradual increase in

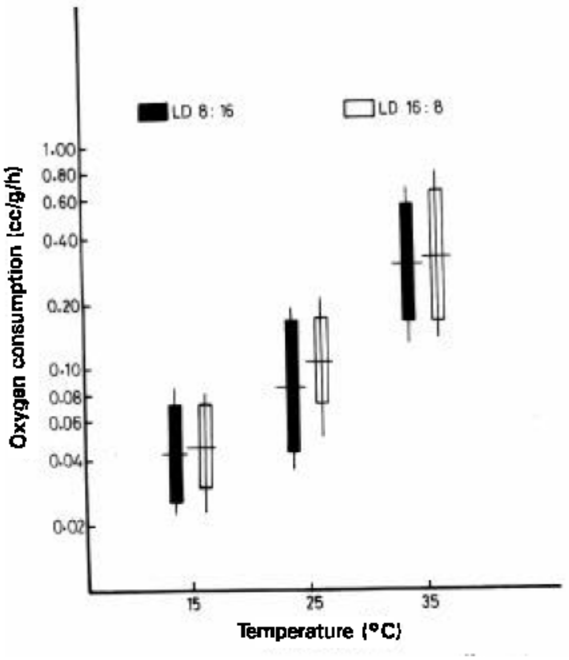

Fig. 5: Comparison of oxygen consumption at three different temperatures and two photoperiods. The points are plotted on a logarithmic grid

the rate of oxygen consumption with the increase in temperature to 25 and 35°C respectively as shown in Fig. 3. Lizards that held at low temperatures (15°C) were remained active when returned to room temperature. No reduced metabolism was observed in these animals compared to outdoor cage or field lizards. Outdoor cage and 15°C cage groups used significantly much oxygen than the field lizards at 25°C but no significant difference was observed when any groups at 15 or 35°C. Thus, there is no evidence of dormancy or reduced metabolism due to reduced temperatures in summer.

On the other hand, oxygen consumption was measured throughout winter in lizards exposed to several temperature regimes at the same three experimental temperatures used in the summer but the animals were maintained at 15, 25 and 35°C in additional indoor cages. The results are shown in fig. 4. There is no significant difference in oxygen consumption between any of the groups at 15 or 25°C. However, only lizards previously held at 35°C had a similar metabolic rate comparable to summer field lizards when measured at 35°C. The mean metabolic rate for all other groups was significantly less at 35°C. The observations throughout this experiment also showed that winter dormancy is no temperature dependent. The span of time in which lizards become dormant was approximately the same at all temperatures. This was true for lizards held under different conditions.

In order to study the effect of light on dormancy, lizards were placed in indoor cages under different temperature conditions (15, 25 and 35°C), and exposed to different photoperiods (LD 8:16 and LD 16:8) for two weeks. Lizards exposed to short photoperiod (8 h/day) become dormant in all temperature conditions (dormant lizards stayed motionless on or under the sand). Dormancy in this species was found to be controlled by reducing the length of photoperiod, since no dormancy occurred in lizards maintained continuously on long photoperiod (16 h of light/ day) in all temperature conditions. On the other hand, there was no significant difference between oxygen consumption of the lizards exposed to 8 or 16 h of light/ day in the same temperature condition (Fig. 5) but showed a reduced metabolic rate in the two photoperiods when measured at 15°C comparable to animals measured at 25°C or above.

Discussion

During the period of normal activity, *A. boskianus* is consistently if only slightly warmer than the air surrounding it. However, the temperature differentials involved makes this hypothermia of questionable ecological significance. Many species of reptiles that inhabit rigorous habitats where they are subjected to wide fluctuations in ambient temperatures often show sophisticated thermoregulatory behaviours (Templeton, 1970; Huey *et al.*, 1977; Hertz and Huey, 1981; Huey, 1982; Van Damme *et al.*, 1989; Castilla and Bauwens, 1991; Bauwens *et al.*, 1996; Hussein, 2000), or make various cardiovascular and metabolic adjustment (Bartholomew, 1966; Weathers, 1971; Dmi'el and Borut, 1972; Congdon *et al.*, 1982; Dunham *et al.*, 1989) to keep body temperature within much narrow limits. In tropical lizards inhabiting areas where thermal conditions are more stable, however, selective pressures to develop elaborate thermoregulatory behaviours may not be strong and the lizards would achieve thermal equilibrium at the microsites they occupied. Although small lizards have low thermal inertia (Stevenson, 1985), this assumption is unlikely to be met when lizards move frequently among microsites (Tracy and Christian, 1986; Hertz *et al.*, 1993).Thus, in our data, lizards may have achieved thermal equilibrium with the environment in the early morning and late afternoon when mean residence time in microsites was high, but they were probably not in thermal equilibrium and the lizards were slightly warmer than their environment during midday activity hours when mean residence time was short due to increasing temperature during midday hours.

Rates of oxygen consumption for *A. boskianus* are normal in comparison to those of other species of lizards (Bartholomew and Tucker, 1964; Templeton, 1970; Gans and Pough, 1982; Kayed *et al.*, 1990). The overall Q_{10} of 2.89 is similar to that usually found in other species. The Q_{10} for lizards typically ranges from 2.5-3.3 (Templeton, 1970; Avery, 1985; Kayed *et al.*, 1990). The variation in Q_{10} at selected temperature in *A. boskianus* is considerable. The maximum Q_{10} (3.86) occurs between 25- 30°C and minimum (1.56) between 35- 40°C. Interestingly, 20- 40°C is probably the broadest range of temperature to which *A. boskianus* would ever be exposed its natural habitat. The Q_{10} between 20- 25°C represent the pattern of metabolic increase in this species of lizards at lower limit of its temperature range and Q_{10} between 35- 40°C is the pattern at upper range of temperatures. This type of metabolic response where Q_{10} diminishes with temperature increasing from 30- 40 is analogous to that of some desert species, which have similar patterns, but over much broader temperature ranges (Bennett and Dawson, 1976; Davies and Bennett, 1981; Zari, 1987; Kayed *et al.*, 1990).

The metabolic rates of *A. boskianus* are lower than those previously reported for cool- temperate lizards. In fact, desert lizards generally have lower metabolic rates than cool-temperate lizards (Dawson and Templeton, 1963; Wheeler, 1984). The resting metabolic rates of three desert species (*Chalcides ocellatus*, *Acanthodactylus schmiti* and *A. opheodurus)* are lower than those of comparable cool-temperate species such as *Lacerta vivipara*, *L. agilis*, and *Anguis fragilis* (Al- Sadoon, 1983).

The dormancy and metabolism of the sand lizard, *A. boskianus* are controlled independently. However, this is noticed under normal circumstances because the controlling factors for both phenomena probably operate in the field simultaneously. The most obvious environmental changes that occur at the time of normal hibernation (in winter season) are reduced temperature and a shorter day- length. The beginning of dormancy in *A. boskianus* appears to be temperature independent, because lowered temperature did not produce dormancy in summer. In contrast, lizards become dormant at approximately the same time at all temperatures in winter. This situation would not be especially unusual, since other lizards possess additional types of temperature independent activity rhythms (Hoffman, 1960; Porter and James, 1979; Wheeler, 1986).

On the other hand, dormancy in this species is controlled by reducing the length of the photoperiod. Therefore dormancy occurred in lizards maintained continuously on 8 h of light/day. The response of lizards to the changes in the duration of light would be similar to the refractory period that found in some birds. Farner's (1964) research on white- crowned sparrows (*Zonotrichia leucophrys*) have produced the first evidence of light period in a photoperiodic response. These animals respond to light stimulation only during specific intervals following a dark period. McNamara *et al.*, 1994 and Rogers *et al.*, 1994 pointed out that in migratory birds an endogenous clock with an annual periodicity seems implicated. Many other animals use day- length measurements to orient themselves to changes of seasons (Pittendrigh and Mimis, 1964; Price *et al.*, 1988; Norberg, 1996). Consequently, such a mechanism in *A. boskianus* would not be unique among animals. The dormancy rhythm is driven by the lizard's biological clock. The fact that the rhythm shows a dormancy period at the same time every year precludes the possibility that the rhythm is exogenously driven by some unsuspected geophysical cue. Any such cue would be expected to have a periodicity associated with the period of the earth's rotation around the sun, that is, exactly a year (Aschoff, 1965). Thus, it is possible the stimulus for the next dormant period is produced by reduced photoperiod every winter.

The effective photoperiod in lizards presumably is controlled by animal behaviour (Mayhew, 1964; Porter and James, 1979). *A. boskianus* like many diurnal desert lizards, has an inactive period in the middle of summer days during which it goes under the sand. The time spent beneath the surface varies with he environmental temperature. Consequently, these lizards are not exposed to light from sunrise to sunset, as are most diurnal desert animals, but experience a photoperiod that is determined by environmental temperature. It is conceivable *A. boskianus* may have a comparable ability so that it can respond only to the ends of daily photoperiod, and be unaffected by the dark period in the middle of the day. Thus, the present evidence suggests winter dormancy is controlled by reduced photoperiod.

On the other hand, the lowered metabolic rate in the hibernating A. boskianus apparently controlled by reduced temperature. The reduced metabolic rate at the relatively high experimental temperature in winter is independent of photoperiod. However, this metabolic shift possibly is initiated by reduced temperature, since 35°C winter indoor animals did not show metabolic reduction (Fig. 4). However, temperature reduction would be effective only at the right time of the year (winter season), because a reduced temperature (to 15°C in 15°C indoor lizards) in summer did not produce a reduction in oxygen consumption (Fig. 3).

The reduced metabolic rate that is observed in *A boskianus* in winter is similar to the result obtained by Patterson and Davies 1984) with another desert lizard *Psammodromus hispanicus*. In fact, reduced oxygen consumption at such temperature during winter could be adaptive, since relatively warm soil temperatures which may occur in late fall and sometimes in winter in the desert. The ability of animals to metabolize at a relatively low rate while environmental temperatures are relatively high could prevent the total depletion of stored energy before the termination of the normal dormant period (Avery, 1976; Huey, 1982). Thus, this mechanism could serve as an additional safety factor in ensuring the animal's survival through a warm winter days.

We concluded that the dormancy and metabolic rate of hibernating *A. boskianus* apparently are controlled independently. Winter dormancy is controlled by reduced photoperiod but lower metabolic rate is controlled by reduced temperature. In both cases, however, such changes in environmental conditions produce these physiological modifications associated with hibernation only during the proper season (winter season) which is characterized by reduced photoperiod and temperature.

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