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Energetic consequences of metabolic depression in tropical and temperate-zone lizards

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Abstract

One response of ectothermic animals to periods of inactivity is inverse acclimation, or metabolic depression, which results in the conservation of energy. Most studies of metabolic depression and acclimation have involved temperate-zone species, and the information from tropical species has been largely restricted to laboratory studies that failed to demonstrate thermal acclimation of metabolism. Recently, metabolic depression has been shown in several species of reptiles from the wet–dry tropics of northern Australia during the dry season. We review existing data on the energy budgets of temperate and tropical species during periods of inactivity and make calculations of energy saved due to metabolic depression across a range of temperatures. Because tropical species experience relatively high temperatures during periods of inactivity, they have a greater potential for energy savings, any enhancement of their metabolic depression is disproportionately advantageous with respect to energy savings, and in some species metabolic depression is probably essential for survival. Thus, we would expect metabolic depression to be well developed in some tropical reptiles. The lack of thermal acclimation in laboratory studies indicates that environmental parameters other than temperature (such as food or water) may initiate metabolic depression in tropical species. Higher temperatures, however, magnify the energy savings accomplished by metabolic depression.

Introduction

Seasonal periods of inactivity are generally associated with changes of environmental temperatures. During inactive seasons, ectothermic animals often undergo physiological adjustments such as metabolic compensation (acclimation response) or metabolic depression (inverse acclimation) (Precht 1958; see Rome *et al.* 1992 for a broader discussion of the definition of acclimation). Under natural conditions such physiological adjustments are termed metabolic acclimatisation, and both metabolic compensation and depression occur in the field (reviewed by Tsuji 1988a; Christian and Conley 1994). Determining why some animals increase metabolism but others decrease metabolism during a season of inactivity is fundamental to our understanding of the metabolic responses of animals to their environment. Metabolic compensation may be advantageous to animals that are occasionally active during their inactive season by enhancing the capacity for activity at sub-optimal temperatures (Tsuji 1988a). Metabolic depression, on the other hand, enhances energy conservation during periods of inactivity, and Tsuji (1988a) has suggested that metabolic depression may be particularly relevant for animals that remain inactive throughout the season.

Most studies of seasonal physiological adjustments involve the responses of temperate-zone species to winter conditions. Some laboratory studies of acclimation responses have involved tropical species, and these have generally concluded that tropical ectotherms do not show an acclimation response to temperature (Feder 1978, 1982, 1987; Tsuji 1988b; Christian *et al.* 1988; Rome *et al.* 1992; Rogowitz 1996a, 1996b).

Until recently, very little information has been available concerning seasonal acclimatisation responses of tropical reptiles, and it has been generally assumed that tropical species undergo little seasonal variation in metabolism in nature (Bennett and Dawson 1976). Recently, metabolic depression has been demonstrated in a tropical African tortoise (Hailey and Loveridge 1997) and several species of reptiles from the wet–dry tropics of Australia during the dry season:

the northern long-neck turtle, *Chelodina rugosa* (Kennett and Christian 1994), the frillneck lizard, *Chlamydosaurus kingii* (Christian *et al.* 1996a), the spotted tree monitor, *Varanus scalaris* (Christian *et al.* 1996b), and the dragon lizard, *Lophognathus temporalis* (Christian *et al.* 1999). Although *C. rugosa* spends its inactive period encased in a mud chamber, and is therefore unambiguously in a state of aestivation, the three species of lizard are occasionally active during their dry-season period of relative inactivity. The metabolic depression exhibited by all of these species is substantial.

Here we summarise the existing data from temperate and tropical reptiles with respect to the degree of metabolic depression during periods of relative inactivity, and we quantify the resulting energy savings for those species for which the appropriate data exist. Contrary to the notion that seasonal variation in metabolism is not found in tropical species of reptiles, we conclude that metabolic depression ought to be at least as well developed in species inactive in hot environments as in ectothermic animals that experience cold winter conditions. We also discuss the implications of the fact that laboratory studies of tropical species consistently fail to demonstrate thermal acclimation of metabolism.

Materials and Methods

For diurnal ectotherms, standard metabolic rate (SMR) is defined as the metabolism of fasted individuals during the night, and resting metabolic rate (RMR) is defined as the metabolism of fasted individuals during daytime (Andrews and Pough 1985). The literature was reviewed for examples of seasonal metabolic depression in lizards. The degree of metabolic depression at a given temperature was expressed as a percentage of the SMR during the active season as follows: $(\text{active season SMR} - \text{inactive season SMR}) \times 100 / \text{active season SMR}$.

To explore the general relationship between temperature and the energy saved by metabolic depression, an empirical equation (Andrews and Pough 1985) was used to relate body size and body temperature to SMR in lizards. The allometric equation calculates metabolic rate in units of $(\text{mL O}_2) \text{h}^{-1}$ as:

$$\text{SMR} = 0.013 \times M^{0.8} \times 10^{0.038T_b}$$

where M = mass (g) and T_b = body temperature of the lizard. The predicted amounts of energy saved at 20, 40, 60 and 80% levels of metabolic depression for a 50-g lizard were calculated across the temperature range of 5–40°C. A factor of $20.08 \text{ J (mL O}_2)^{-1}$, representing a mixed diet of fats, carbohydrates and protein (Schmidt-Nielsen 1987), was used to convert oxygen consumption to units of energy.

A second analysis explored the effect of body size on energy saved by metabolic depression. Again the allometric equation of Andrews and Pough (1985) was used to calculate metabolic rates across a range of body temperatures for lizards with body masses of 10 g, 50 g, 100 g, 500 g, 1 kg, 10 kg and 100 kg. Then, assuming a metabolic depression of 40%, the amount of energy conserved was calculated.

The data needed to calculate energy saved by metabolic depression for specific species under natural field conditions include the body temperatures experienced by inactive lizards during their period of inactivity, their SMR during the active season (at the appropriate temperatures) and their reduced SMR (and RMR) during the inactive season (at the appropriate temperatures). These data were collated for three temperate-zone lizard species and three tropical species of lizards. For *Varanus rosenbergi*, *Varanus scalaris*, *Chlamydosaurus kingii* and *Lophognathus temporalis*, detailed data allowed us to break each day into four periods for which we used a mean body temperature to calculate RMR during the day and SMR at night. The RMR values were approximately 1.4× higher than SMR during both the active and inactive seasons (Christian *et al.* 1996a, 1996b, 1999). Although calculations included a mean temperature during each of the four daily periods, a grand mean daily temperature (a mean of hourly means) was also calculated for each species during the inactive season for the purposes of illustration. The daily energy expenditure was calculated once, assuming the active season SMR at inactive-season body temperatures and again assuming the depressed inactive-season SMR at inactive-season body temperatures. The difference between these daily energy expenditures was taken as the amount of energy saved by metabolic depression.

The energy savings of the other two species, *Dipsosaurus dorsalis* and *Sceloporus occidentalis*, were calculated from published information (Moberly 1963; Tsuji 1988a, 1988b). The energy savings for *Sceloporus occidentalis* assumes an over-wintering temperature of 10°C, and the value was calculated by Tsuji (1988b) using information from Bennett and Nagy (1977).

Results

Table 1 lists the species of lizards known to exhibit metabolic reduction during their season of relative inactivity and the percentage reduction relative to the active season values at the corresponding body temperature. Only species exposed to natural seasonal conditions are included in this table (see Tsuji 1988a for a list of additional species under laboratory conditions). Although the phylogenetic diversity represented in Table 1 could be taken into account using phylogenetically independent contrasts (Felsenstein 1985), the small sample size, particularly with respect to tropical species, and the fact that some measurements do not include ecologically relevant temperatures, preclude any statistical analyses comparing temperate-zone and tropical species. However, inspection of Table 1 shows that *L. temporalis* has the greatest amount of metabolic depression, and the metabolic depression exhibited by *V. scalaris* and *C. kingii* are well within the range of values for temperate-zone species. Thus, it is apparent from Table 1 that metabolic depression can be substantial in both temperate-zone and tropical species of lizards.

Fig. 1 shows the calculated energy savings as a function of body temperature experienced during the inactive season for a 50-g lizard, assuming metabolic depressions of 20, 40, 60 and 80% relative to metabolic rates during the active season. The energy savings increase with increasing temperature during the inactive season, and the curves representing different levels of metabolic depression diverge at higher temperatures.

Table 1. Metabolic depression in lizards

The extent of metabolic depression in lizards during their inactive seasons is expressed as a percentage of metabolic rate during their active season (see text)

Species	T _b (°C)	Mass (g)	Metabolic depression (%)	Zone	Source
<i>Dipsosaurus dorsalis</i>	30–35	50	50	Temperate	Moberly (1963)
<i>Dipsosaurus dorsalis</i>	40	50	31	Temperate	John-Alder (1984)
<i>Lacerta viridis</i>	25	38	47	Temperate	Rismiller and Heldmaier (1991)
"	30	38	35	"	"
<i>Lacerta vivipara</i>	10	3	55	Temperate	Patterson and Davies (1978)
<i>Phrynosoma m'calli</i>	35	16	32	Temperate	Mayhew (1965)
<i>Sceloporus occidentalis</i>	25	9	26	Temperate	Heusner and Jameson (1981)
<i>Sceloporus occidentalis</i>	10	10	34	Temperate	Tsuji (1988a)
"	16	"	37	"	"
"	35	"	37	"	"
<i>Tiliqua rugosa</i>	35	504	29	Temperate	Christian and Conley (1994)
<i>Varanus rosenbergi</i>	35	1204	45	Temperate	Christian and Conley (1994)
<i>Xantusia henshawi</i>	27	–	42	Temperate	Mautz and Case (1974)
<i>Chlamydosaurus kingii</i>	18	533	29	Tropical	Christian <i>et al.</i> (1996a)
"	24	"	36	"	"
"	30	"	31	"	"
"	36	"	25	"	"
<i>Lophognathus temporalis</i>	18	43	54	Tropical	Christian <i>et al.</i> (unpublished)
"	24	"	67	"	"
"	30	"	69	"	"
"	36	"	54	"	"
<i>Varanus scalaris</i>	18	103	50	Tropical	Christian <i>et al.</i> (1996b)
"	24	"	53	"	"
"	30	"	42	"	"
"	36	"	45	"	"

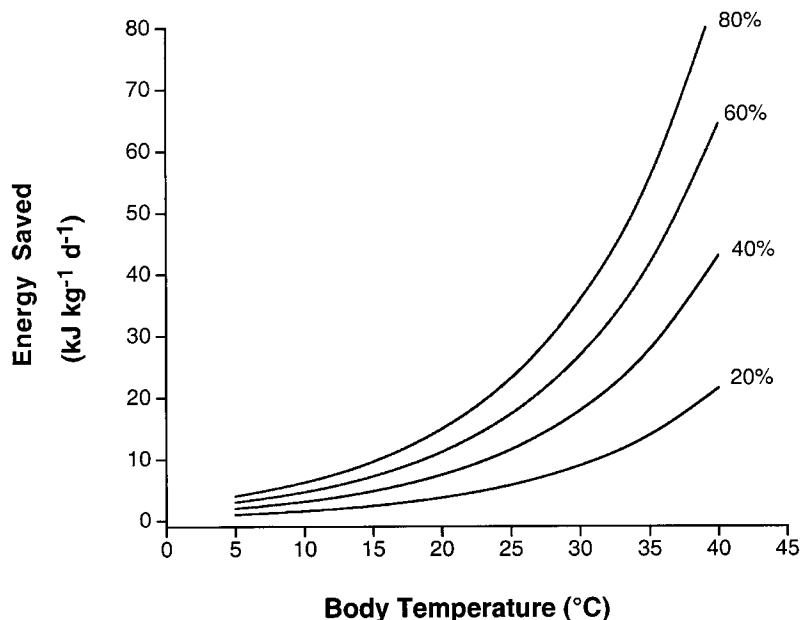


Fig. 1. Energy saved by lizards, as a function of temperature experienced during the inactive season, due to metabolic depression during that season. The curves represent the calculated energy savings for a 50-g lizard at any temperature between 5 and 40°C assuming metabolic depressions of 20, 40, 60 and 80% relative to standard metabolic rates during the active season, as calculated from the generalised lizard equation of Andrews and Pough (1985).

Fig. 2 illustrates the allometric relationship between body mass and the amount of energy saved as a function of temperature experienced during the inactive season, assuming 40% metabolic depression. Smaller lizards, because of their higher mass-specific metabolic rates, conserve more energy than larger species (on a mass-specific basis) at a given temperature. Superimposed on this information are six points representing three tropical species of lizards and three temperate-zone lizards for which data exist to allow the calculation of energy saving due to metabolic depression. The value of energy savings for *Dipsosaurus dorsalis* is set to 0, despite the fact that metabolic depression has been found in this species at body temperatures greater than 30°C (Moberly 1963; John-Alder 1984; Table 1) because estimates of the temperature experienced by these lizards during winter do not exceed 20°C (Moberly 1963). Although the masses of the six species are similar to some of the masses assumed for the curves in Fig. 2, only the point for *C. kingii* falls on the appropriate curve. Deviations from the curves are the result of metabolic depression levels other than 40% and species-specific deviations from the generalised equation for lizards (Andrews and Pough 1985).

Discussion

Early studies of the physiology of over-wintering lizards demonstrated metabolic depression in *Dipsosaurus dorsalis* (Moberly 1963) and *Phrynosoma m'calli* (Mayhew 1965) at high temperatures (30–40°C in the former and 35°C in the latter), but metabolism was not depressed at lower temperatures in these species. Both authors concluded that metabolic depression at high temperatures would result in substantial energy savings. The field data of soil temperatures at sites likely to reflect the environments of hibernating *D. dorsalis*, however, did not indicate that these lizards would experience temperatures this high during winter, and no field data were

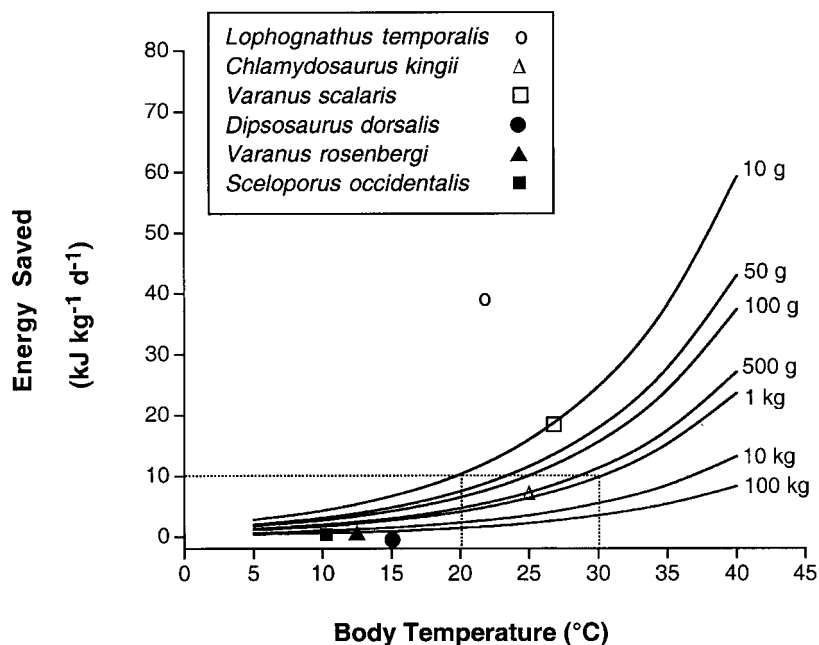


Fig. 2. Energy saved by lizards ranging in mass from 10 g to 100 kg as a function of temperature experienced during the inactive season, assuming metabolic depression of 40% relative to standard metabolic rates during the active season. As in Fig. 1, the curves were calculated using the generalised lizard equation of Andrews and Pough (1985). Superimposed on this information are six points representing three tropical species of lizards (open symbols) and three temperate-zone lizards (closed symbols) for which mean body temperatures during the inactive season are known, allowing the calculation of energy saved due to metabolic depression under field conditions. The mean masses for the species were: 43 g for *Lophognathus temporalis*, 533 g for *Chlamydosaurus kingii*, 103 g for *Varanus scalaris*, 1204 g for *Varanus rosenbergi*, 50 g for *Dipsosaurus dorsalis* and 10 g for *Sceloporus occidentalis*. The dotted lines indicate that mass-specific energy conservation is less for a 10-g lizard at any temperature less than 20°C than for a 1-kg lizard at 30°C.

presented for *P. m'calli*. Whether or not these two species of lizards ever experience winter temperatures high enough to take advantage of their observed physiological abilities awaits further study. However, the logic of these investigators, which allowed them to conclude that substantial energy savings are possible at higher temperatures, can be applied to inactive tropical species.

Tropical environments provide greater opportunities for energy savings, as is illustrated by the low energy savings at low temperatures even at high levels of metabolic depression (Fig. 1). A given increase in metabolic depression results in disproportionately greater energy savings at higher temperatures, as illustrated by the divergence of the curves (Fig. 1) at higher temperatures.

In addition to the effects of temperature, the amount of energy saved by metabolic depression is also related to body size. This allometric relationship is shown in Fig. 2, which illustrates that, at a given level of metabolic depression and body temperature, smaller animals conserve more energy on a mass-specific basis than larger animals. However, over an ecologically relevant range of temperatures and body sizes, the effect of body size is less important than the temperature effect. To illustrate this point we will consider the extreme case of large tropical lizards inactive at a mean temperature of 30°C compared with small temperate lizards inactive at

lower temperatures. The dotted lines in Fig. 2 illustrate that energy conservation is similar for a 1-kg lizard in the tropics (at 30°C) and a 10-g lizard with a mean body temperature of 20°C. If, as would almost certainly be the case in temperate environments, the 10-g lizard had a mean body temperature of <20°C during winter, then the larger tropical lizard would conserve more energy on a mass-specific basis than the small temperate-zone lizard. Similarly, the energy savings of a 10-kg tropical lizard would be greater than the energy savings of a 10-g temperate-zone species if the temperate-zone lizard experienced a body temperature less than 12°C. Thus, for the range of realistic body masses and temperatures, species inactive in warm climates benefit more from metabolic depression than those in cold climates. This conclusion is supported by the available field data, as illustrated by the six points on Fig. 2: the three temperate-zone species all save less energy with metabolic depression than the three tropical species, regardless of body mass.

Results from isotopic analyses and stomach flushing indicate that the three tropical species of lizards discussed here continue to eat small amounts during the dry season, and all three species also actively thermoregulate to lower levels during the dry season (Christian and Green 1994; Christian and Bedford 1995, 1996; Christian *et al.* 1996a, 1996b, 1999). Calculations indicate that, given the low levels of food availability, frillneck lizards could not survive the dry season without employing energy-conserving measures such as metabolic depression, lower body temperatures and reduced activity (Christian *et al.* 1996a). These points lead to the conclusion that we could expect tropical species to have high levels of metabolic depression during periods of relative inactivity because at high environmental temperatures substantial energy savings are possible, and, at least in some cases, essential.

The amount of energy saved by having a depressed metabolic rate at low temperatures may be very small (Fig. 1). However, it could also be argued that any amount of energy conserved is energy that does not need to be gathered at a later date. Tsuji (1988b) cogently argued that the amount of energy saved by metabolic depression in northern populations of *Sceloporus occidentalis* is ecologically relevant. The amount of energy conserved by this species due to metabolic depression is 3.2 kJ over 7.5 months and represents the energy gained in 9 days of foraging (Tsuji 1988b). The estimated amount of energy conserved by *L. temporalis* due to metabolic depression is 192 kJ over the five-month dry season and represents the energy gained in 24 days of foraging, assuming that the animal is in energy balance (Christian *et al.* 1999). Although the mass of *L. temporalis* used in these calculations (32 g) was only about 3× the mass of *S. occidentalis*, the estimated energy saved during the period of metabolic depression was 60× greater. Thus, after body mass has been taken into account, and comparing animals at ecologically relevant temperatures, tropical species conserve more energy for a given level of metabolic depression.

Despite relatively stable environmental temperatures, many tropical environments are nevertheless seasonal. Other parameters such as the availability of food and water may be the primary factors that determine seasonal physiological changes. One species in the wet-dry tropics of Australia which does not exhibit seasonal metabolic depression is the water monitor, *Varanus mertensi* (Christian *et al.* 1996c). This species lives in the same region as *V. scalaris*, *C. kingii* and *L. temporalis*, but it lives in and around permanent water, providing circumstantial evidence that the environmental parameter(s) responsible for metabolic depression in some species in the wet-dry tropics are food, water or both. Further evidence for the importance of food and water in determining seasonal energetics of lizards of the wet-dry tropics is provided by *Varanus panoptes*. Woodland populations of this lizard aestivate in the dry season, but lizards living in adjacent habitats that contain water remain active as long as the water is available despite similar thermal conditions in the two habitats (Christian *et al.* 1995).

Laboratory experiments that have examined thermal acclimation of metabolism of tropical species have consistently shown no response. This, however, does not necessarily imply that seasonal metabolic changes in response to factors other than temperature do not occur in natural environments. It would be interesting, although possibly technically difficult, to perform

laboratory experiments examining acclimation with respect to water or food levels.

Although we do not disagree with the interpretations of data from previous studies, we disagree with extrapolations of those studies to broader generalisations, particularly about tropical ectotherms. For example, although tropical environments may be relatively stable with respect to the thermal environment, it can not be generally stated that metabolism does not change seasonally in tropical reptiles (Bennett and Dawson 1976). Similarly, it can not be generally stated that 'inverse acclimation, in particular, appears to be an adaptation to conserve energy in cool seasons' (Tsuiji 1988*b*). To be fair to this author, the topic under discussion was thermal acclimation, and the statement may be correct in that limited context. However, we wish to emphasise that, because environmental parameters other than temperature may elicit acclimation/acclimatisation responses, metabolic depression is not restricted to cold seasons. The final over-generalisation we wish to dispel is related to the relationship between metabolic depression and activity during periods of relative inactivity. Although metabolic depression may be found in species that do not exhibit winter activity in temperate regions (Tsuiji 1988*a*) (although see Christian and Conley 1994 for apparent exceptions), the tropical species we have discussed above are not completely inactive during their periods of relative inactivity, yet they have strikingly depressed metabolic rates. This decoupling of metabolic depression and activity follows from the notion that there is some degree of independence between SMR and activity metabolism (Else and Hulbert 1985; Taylor *et al.* 1987). All of the points discussed above serve to illustrate that metabolic depression is a versatile mechanism that can operate in systems other than in animals sequestered underground during winter.

The arguments and conclusions given above for tropical reptiles during the dry season also could be made for aestivating reptiles in hot temperate-zone environments (Heatwole 1983; Hochachka and Guppy 1987), but very little is known about the microenvironmental conditions experienced by aestivating reptiles in temperate regions. All aestivating species of amphibians studied to date exhibit metabolic depression (Pinder *et al.* 1992), but in a review of aestivation and hibernation by amphibians, Pinder *et al.* (1992) noted that microenvironments experienced by aestivating amphibians are almost entirely unknown. Thus, as is the case with temperate-zone reptiles, the energetic consequences of metabolic depression cannot be quantified for most aestivating amphibians from hot temperate regions (but see Seymour 1973).

Only when more data are available from mesic temperate zones, deserts, seasonal tropical areas and wet tropical habitats will we be in a position to determine whether meaningful generalisations can be drawn with respect to acclimation, acclimatisation and metabolic depression. We nevertheless propose the following generalisation based on the current level of knowledge: although metabolic depression can be effective for conserving energy and other resources under many environmental conditions, it may be most effective in tropical environments, despite the fact that it generally has not been recognised as being a part of the physiological repertoire of tropical reptiles.

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