

## FIELD BODY TEMPERATURES, MECHANISMS OF THERMOREGULATION AND EVOLUTION OF THERMAL CHARACTERISTICS IN LACERTID LIZARDS

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We discuss three aspects of the thermal biology of lacertid lizards. First, we provide an overview of the available data on field body temperatures ( $T_b$ ), the thermal sensitivity of various performance functions and selected body temperatures in different species of lacertid lizards. We also briefly summarise information on the mechanisms of thermoregulation. Second, we discuss recent developments to estimate the »precision« of thermoregulation, and the contribution of distinct behavioural mechanisms. Finally, we revise available evidence for the existence of evolutionary adjustments of thermal characteristics in lacertid lizards. Existing studies have mainly dealt with within- and among-species differences in thermoregulatory behaviour (selected temperatures) and thermal physiology of adults (optimal temperatures, heating rates). Available data provide only limited evidence for clear-cut evolutionary shifts in thermal physiology characteristics along climatic gradients.

**Keywords:** body temperatures, thermoregulation, thermal sensitivity, Lacertidae

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Raspravlja se o tri aspekta termalne biologije lacertidnih guštera. Prvo donosimo pregled dostupnih podataka o tjelesnoj temperaturi u prirodi ( $T_b$ ), termalnoj osjetljivosti različitih funkcija i odabranih temperatura tijela kod različitih vrsta lacertidnih guštera. Također se ukratko daju informacije o mehanizmima termoregulacije. Drugo, raspravlja se o nedavnim pokušajima procjene »preciznosti« termoregulacije i koji je doprinos određenih mehanizama ponašanja. Na kraju se daje

pregled dostupnih dokaza o postojanju evolucijskih prilagodbi termalnih osobina lacertidnih gušterica. Postojeće studije su se uglavnom bavile razlikama u termoregulacijskom ponašanju (odabrane temperature) unutar jedne i između više vrsta i termalnom fiziologijom adulta (optimalne temperature, zagrijavanje). Dostupni podaci daju samo ograničene dokaze o jasno određenim evolucijskim pomacima u karakteristikama termalne fiziologije duž klimatskih gradijenata.

**Ključne riječi:** temperatura tijela, termoregulacija, termalna osjetljivost, Lacertidae

## INTRODUCTION

The thermal characteristics of the environment have a pronounced impact on the heat balance and the resulting body temperatures ( $T_b$ ) of ectotherms (PORTER *et al.*, 1973; PORTER & TRACY, 1983). The  $T_b$ s of ectotherms in turn affect the rate at which biochemical and physiological processes proceed and thereby influence whole-animal performance functions and hence fitness (HUEY & STEVENSON, 1979; HUEY, 1982). Consequently, most reptiles attempt to buffer changes in ambient heat loads to keep their  $T_b$ s at a relatively constant level or, perhaps more realistically, between lower and upper threshold temperatures (BERK & HEATH, 1975; BARBER & CRAWFORD, 1977; HUEY, 1982; VAN BERKUM *et al.*, 1986).

When faced with temporal (i.e., short-term) or geographical (i.e. long-term) variation of the thermal environment, lizards and many other ectotherms exhibit two types of responses. The first consists of fast-acting thermoregulatory adjustments. Lizards regulate their  $T_b$  primarily by modifying aspects of their behaviour, although short-term physiological adjustments may also be important (BARTHOLOMEW, 1982). Such regulatory behaviours include changing of activity times, selection of appropriate microhabitats, and postural modifications that alter the rates of heating and cooling (HUEY, 1982; STEVENSON, 1985). These responses are widespread and well-documented (e.g., HUEY *et al.*, 1977; HUEY, 1982; VAN DAMME *et al.*, 1987; ADOLPH, 1990; BAUWENS *et al.*, 1990, 1996). Because thermoregulatory behaviours have an immediate effect on  $T_b$ s, they are especially efficient in coping with short-term (i.e., daily or seasonal) fluctuations of ambient temperatures. Behavioural adjustments are also important, at least in part, to cope with permanent differences in environmental conditions, such as those faced by populations or species that live along a climatic gradient (e.g., HERTZ, 1981; HERTZ & HUEY, 1981; HERTZ & NEVO, 1981; VAN DAMME *et al.*, 1990). However, the effect of behavioural adjustments on  $T_b$  is not unlimited but constrained by environmental conditions. In addition, the time and energy that lizards spend in thermoregulation may curtail those available for other activities. Hence, behavioural adjustments are probably not entirely efficient in compensating for long-term, geographical differences in ambient conditions.

The second type of response consists of evolutionary changes in physiology and behaviour that increase the time that  $T_b$  can be maintained near the level that maximises ecologically important performance capabilities (HUEY & STEVENSON, 1979; HERTZ *et al.*, 1983; HUEY & KINGSOLVER, 1989). These include evolutionary shifts in the thermal sensitivity of performance functions, changes of the preferred temperature levels and modifications in behavioural or physiological attributes that facili-

tate the attainment of the optimal or preferred temperatures. Although such adjustments were once believed to be non-existent (BOGERT, 1949; HERTZ *et al.*, 1983), there is growing evidence that closely-related lizard taxa exhibit evolutionary differences in thermal characteristics in relation to variation in ambient heat loads (e.g., HUEY & WEBSTER, 1976; VAN BERKUM, 1986; HUEY & BENNETT, 1987; SINERVO, 1990; BAUWENS *et al.*, 1995; DÍAZ *et al.*, 1996a).

In this paper we summarise current knowledge of several aspects of the thermal biology of European lacertid lizards. We do not aim to provide a complete overview of all topics that have received attention by researchers. Rather, we will highlight some aspects that we consider of particular interest to students of lizard thermal biology in general and of lacertid lizards in particular. Hence, our own interests and work unashamedly bias this review. Our specific objectives are three-fold. First, we provide an overview of the available data on the activity  $T_b$ s, the thermal sensitivity of various performance functions and selected body temperatures in different species. We indicate that information on these different aspects, and on environmental factors, is needed to gain insight into the causes and consequences of variation in  $T_b$ s. We also briefly summarise information on the mechanisms of thermoregulation. Second, we examine to what extent lacertid lizards regulate their  $T_b$  and evaluate the contribution of distinct types of behavioural adjustments. Specifically, we argue that answering these questions requires the explicit formulation of null hypotheses and a specifically designed research protocol. We also indicate how modifications of this protocol have been used to answer related questions. Third, we revise evidence for the existence of evolutionary shifts of thermal physiology traits (heating rates, thermal sensitivity profiles) and examine whether the observed differences parallel variations in environmental characteristics.

## FIELD, SELECTED AND OPTIMAL TEMPERATURES IN EUROPEAN LACERTIDS

Soon after the disclosure by SERGEYEV (1939) and COWLES & BOGERT (1944) that lizards regulate their  $T_b$ s within a surprisingly narrow range, thermal ecology became a popular topic in herpetology. Ever since, few field herpetologists have departed on their voyages without a quick reading thermometer, and many a lizard cloaca has been uninvitedly probed. At first, studies centered on teiid and iguanid species from the deserts and semi-deserts of the United States (BRATTSTROM, 1965), but soon the fashion of »noosing and goosing« lizards blew over to Europe and data on the thermal biology of lacertid lizards steadily accumulated. A recent (but hasty) scan of the literature revealed nearly 40 studies reporting field body temperatures on more than 50 species of Lacertidae (Tab. 1). Comparison and interpretation of the results is, however, hampered by the inevitable divergence in scope of the different studies. Some have collected data over a complete activity season, others during a single month and some sampled only during the course of a few days. There is also a strong influence of the levels of activity and catchability of the liz-

**Tab. 1.** Studies on field and selected body temperatures of lacertid lizards

Species	Reference
<i>Acanthodactylus boskianus</i>	Duvdevani & Borut 1974; Pérez-Mellado 1992,
<i>Acanthodactylus erythrurus</i>	Busack 1976; Roman 1982; Carretero & Llorente 1991; Bauwens <i>et al.</i> 1995
<i>Acanthodactylus longipes</i>	Pérez-Mellado 1992
<i>Acanthodactylus pardalis</i>	Duvdevani & Borut 1974
<i>Acanthodactylus schreiberi</i>	Duvdevani & Borut 1974
<i>Acanthodactylus scutellatus</i>	Duvdevani & Borut 1974; Pérez-Mellado 1992
<i>Algyroides nigropunctatus</i>	Arnold 1987
<i>Aporosaura anchietae</i>	Brain 1962
<i>Eremias arguta</i>	Böhme 1981
<i>Eremias lineo-ocellata</i>	Huey <i>et al.</i> 1977
<i>Eremias lugubris</i>	Huey <i>et al.</i> 1977
<i>Eremias namaquensis</i>	Huey <i>et al.</i> 1977
<i>Eremias pleskii</i>	Ushakov & Darevsky 1960 in Cloudsley-Thompson 1971
<i>Eremias spekii</i>	Bowker 1984
<i>Eremias strauchii</i>	Ushakov & Darevsky 1960 in Cloudsley-Thompson 1971
<i>Gallotia atlantica</i>	Márquez <i>et al.</i> 1997
<i>Gallotia caesaris</i>	Márquez <i>et al.</i> 1997
<i>Gallotia simonyi</i>	Barbadillo 1987; Márquez <i>et al.</i> 1997
<i>Gallotia stehlini</i>	Márquez <i>et al.</i> 1997
<i>Ichnotropis squamulosa</i>	Huey <i>et al.</i> 1977
<i>Lacerta agilis</i>	Liberman & Pokrovskaja 1943; Tertyshnikov 1976; Bauwens <i>et al.</i> 1995
<i>Lacerta andreanszkyi</i>	Busack 1987
<i>Lacerta bedriagae</i>	Bauwens <i>et al.</i> 1990
<i>Lacerta dugesii</i>	Crisp <i>et al.</i> 1979
<i>Lacerta graeca</i>	Arnold 1987; Maragou <i>et al.</i> 1997
<i>Lacerta horvathi</i>	Arnold 1987; De Luca 1991
<i>Lacerta monticola</i>	Martinez-Rica 1977; Busack 1978; Pérez-Mellado 1982; Arnold 1987; Bauwens <i>et al.</i> 1995
<i>Lacerta mosorensis</i>	Arnold 1987
<i>Lacerta oxycephala</i>	Arnold 1987
<i>Lacerta schreiberi</i>	Salvador & Argüello 1987; Bauwens <i>et al.</i> 1995
<i>Lacerta viridis</i>	Arnold 1987
<i>Lacerta vivipara</i>	Avery 1976; Patterson & Davies 1978; Clerx & Broers 1983; Van Damme <i>et al.</i> 1986, 1987, 1989; Heulin 1987
<i>Latastia longicaudata</i>	Bowker 1984
<i>Meroles cuneirostris</i>	Brain 1962

<i>Meroles suborbitalis</i>	Huey <i>et al.</i> 1977
<i>Mesalina guttulata</i>	Pérez-Mellado 1992
<i>Mesalina olivieri</i>	Pérez-Mellado 1992
<i>Nucras intertexta</i>	Huey <i>et al.</i> 1977
<i>Nucras tessellata</i>	Huey <i>et al.</i> 1977
<i>Ophisops elegans</i>	Pérez-Mellado <i>et al.</i> 1993
<i>Podarcis atrata</i>	Castilla & Bauwens 1991; Bauwens <i>et al.</i> 1995
<i>Podarcis bocagei</i>	Pérez-Mellado 1983; Bauwens <i>et al.</i> 1995
<i>Podarcis erhardii</i>	Kasapidis <i>et al.</i> 1995
<i>Podarcis hispanica</i>	Busack 1978; Pérez-Mellado 1983; Arnold 1987; Carretero & Llorente 1991; Bauwens <i>et al.</i> 1995
<i>Podarcis lilfordi</i>	Bauwens <i>et al.</i> 1995
<i>Podarcis melisellensis</i>	Arnold 1987
<i>Podarcis milensis</i>	Kasapidis <i>et al.</i> 1995
<i>Podarcis milensis</i>	Arnold 1987
<i>Podarcis muralis</i>	Avery 1978; Arnold 1987; Braña 1991; Bauwens <i>et al.</i> 1995
<i>Podarcis peloponnesiaca</i>	Maragou <i>et al.</i> 1997
<i>Podarcis pituyensis</i>	Pérez-Mellado & Salvador 1981
<i>Podarcis sicula</i>	Avery 1978; Arnold 1987; Van Damme <i>et al.</i> 1990
<i>Podarcis taurica</i>	Cruce 1972; Arnold 1987
<i>Podarcis tiliguerta</i>	Van Damme <i>et al.</i> 1989
<i>Psammodromus algirus</i>	Busack 1978; Roman 1982; Pollo-Mateos & Pérez-Mellado 1987; Carrascal & Díaz 1989; Carretero & Llorente 1991; Bauwens <i>et al.</i> 1995; Díaz 1997;
<i>Psammodromus hispanicus</i>	Pollo-Mateos & Pérez-Mellado 1989; Bauwens <i>et al.</i> 1995
<i>Takydromus septentrionalis</i>	Li <i>et al.</i> 1996

ards: many studies are heavily biased towards records taken during the cooler parts of day. Despite these potential pitfalls, we will attempt to highlight some generalities that emerge from the data.

Average field  $T_{bs}$  for lacertids range between 27 and 40°C, with a median of 33.8°C and 50% of all averages falling between 31.9 and 35.5°C (averages for 88 populations of 53 species). Most lacertids thus seem to maintain  $T_{bs}$  that are well above those of nocturnal lizards (Gekkonidae, Eublepharidae) and lizards from (sub)tropical forests (Chamaeleoninae, Polychrotinae) and are comparable to those of (semi-)arid zone lizards (Agaminae, Iguanidae, Tropicuridae, Teiidae, Varanidae, Scincidae).

As data accumulated, it became clear that no single  $T_b$  characterises a lizard species. Within populations, field  $T_{bs}$  of lacertid lizards have been shown to vary with season (HUEY *et al.*, 1977; ARNOLD, 1987; VAN DAMME *et al.*, 1987; ARGÜELLO & SALVADOR, 1988; JI *et al.*, 1996) and time of day (HUEY *et al.*, 1977; ARGÜELLO & SALVA-

DOR, 1988; VAN DAMME *et al.*, 1990; CASTILLA & BAUWENS, 1991). Body temperature fluctuations sometimes, but not always, follow variation in environmental temperatures to some extent. Mean  $T_b$ s in the field may also vary among age classes and sexes (SALVADOR & ARGÜELLO, 1987; CASTILLA & BAUWENS, 1991; CARRASCAL *et al.*, 1992), and, in females, may depend on the reproductive status (VAN DAMME *et al.*, 1987; HEULIN, 1987; TOSINI & AVERY, 1996b). Among populations and species, mean activity  $T_b$ s have been shown to vary with altitude (VAN DAMME *et al.*, 1989, 1990; DÍAZ, 1997) and latitude (ARNOLD, 1987).

Understanding the causes of such variation is not easy and requires additional information on both the animal and its environment. Variation in field  $T_b$ s may reflect both environmental differences and differences in thermal preferences by the lizards. The range of  $T_b$ s that a lizard can possibly attain in the field (operative temperatures, see further) depends on a number of environmental variables and on several morphological and physiological characteristics of the lizard itself. Some of the environmental variables (e.g., air and substrate temperature) are known to be important, and are often reported. Other variables (e.g., wind speed, radiation) are probably as important, but are more difficult to measure and therefore remain unmentioned.

Animal characteristics likely to influence the range of possible  $T_b$ s include the lizard's size, shape, and colour. For instance, juvenile lizards with smaller body mass and high surface-to-volume ratios heat and cool faster than adults (CARRASCAL *et al.*, 1992; MARTIN *et al.*, 1995). Surprisingly, melanic lacertids do not seem to heat measurably faster than non-melanic lizards (CRISP *et al.*, 1979; TOSINI & AVERY 1993). Some of these »characteristics« may be under control of the lizards or may have evolved to meet the needs of the environment. Many species of lacertids alter the shape of their body to capture more solar radiation (flattening, see further). Heating rates may also be under physiological control; *Lacerta viridis* increases its conductance during the sunny parts of the day, and decreases it at the end of the day (RISMILLER & HELDMAIER, 1985, see also further). Some of the interspecific variation in heating rate seems to be adaptive, with fast heating rates in cool-temperate lizards and slower heating rates in Mediterranean species (DÍAZ *et al.*, 1996a)

In theory, both animal and environmental variables could be measured and fed into an energy balance equation (PORTER & TRACY, 1983; VAN DAMME *et al.*, 1987) to obtain predictions on the range of attainable  $T_b$ s. A much more convenient way is the use of hollow copper replicas of lizards (see further).

The range of operative temperatures delineates the physically feasible. At the other extreme lies the physiologically ideal. Body temperatures are known to affect many important whole-animal processes of lacertids (Tab. 2). Physiological performance is typically zero below a critical minimum, poor at low body temperatures, rises to an optimum ( $T_{opt}$ ) and then rapidly falls to become zero again at an upper critical temperature. Ideally, a lizard would like to keep its  $T_b$  near  $T_{opt}$ , or at least within a range of temperature at which performance is at 80 or 95% of its maximum (the 80 and 95 thermal performance breadth, TPB). Several studies have compared field  $T_b$ s of lacertid lizards to thermal sensitivity curves determined in

**Tab. 2.** Studies of the thermal dependence of various functions in lacertid lizards

<b>Metabolic rate, respiration, ventilation, heart rate</b>
Gelineo & Gelineo 1955; Nielsen 1961; Gelineo 1964; Tromp & Avery 1977; Cragg 1978; Al-Sadoon & Spellerberg 1985; Al-Sadoon 1986, 1987; Al-Sadoon & Abdo 1991; de Vera Porcell & Gonzalez 1986ab;
<b>Foraging efficiency, prey selection, food intake rate, handling time, digestion, growth rate</b>
Avery et al. 1982; Avery 1984; Avery & Mynott 1990; Van Damme et al. 1991; Díaz 1994a; Ji et al. 1996
<b>Locomotion, sprint speed, voluntary speed, gait characteristics, muscle activity</b>
Avery & Bond 1989; Van Damme et al. 1989, 1990a, 1991; Li & Liu 1994; Bauwens et al. 1995; Ji et al. 1996
<b>Chemosensory examination, anti-predatory behaviour</b>
Van Damme et al. 1990b
<b>Gametogenesis, reproductive cycle</b>
Brizzi & Galcano 1969; Fisher 1969; Licht et al. 1969; Brizzi et al. 1976ab; Joly & Saint-Girons 1981; d'Uva et al. 1982, 1983; Gavaud 1991
<b>Incubation time, developmental rate, hatchling phenotype</b>
Maderson & Bellairs 1962; Raynaud & Chandola 1969; Oka 1981, Zakharov et al. 1982; Jensen 1982; Strijbosch 1988; Rykena 1988; Van Damme et al. 1992; Castilla & Swallow 1996

the field. In most cases, individuals of *Podarcis tiliguerta* (VAN DAMME et al., 1989), *Podarcis atrata* (CASTILLA & BAUWENS, 1991), *Psammotromus algirus* (DIAZ, 1997), *Takydromus septentrionalis* (JI et al., 1996) and *Lacerta vivipara* in the field were able to run at more than 80% of their maximal performance, although in the latter species, performance levels were greatly reduced under cloudy and variable weather conditions (VAN DAMME et al., 1991).

The use of  $T_{opt}$  and TPBs as a yardstick for the »physiologically« ideal is somewhat thwarted by both practical and theoretical problems. Practically, determining thermal sensitivities of whole-animal functions is often laborious. This prevents the measurement of large numbers of individuals and, as a consequence, little is known about factors that may cause variation in thermal sensitivity curves. Theoretically, choosing a relevant function may be difficult. Because of its apparent importance for survival, and because of the relative ease with which it can be measured, sprint speed is by far the favourite performance measure taken. But for different animals, and at different times, other functions (e.g. gametogenesis, embryonic development, food intake, digestion, growth) may be more important. Choosing the right function becomes especially tricky when different physiological functions tend to have different thermal sensitivity curves, as has been suggested in lacertids (VAN DAMME et al., 1991; Ji et al., 1996).

One way around these practical and theoretical problems is to use body temperatures selected ( $T_{sel}$ ) in a thermal gradient as a yardstick. The body temperatures that lizards adopt in an artificial environment with extremely low costs of thermoregulation are thought to reflect a behavioural choice that maximises the

physiological needs. If different physiological functions have different thermal sensitivities, then the median  $T_{sel}$  may at any time represent a compromise that optimises all functions jointly, or optimises those functions that are most important at the given time. The latter possibility seems more likely, since many studies have demonstrated that  $T_{sel}$  is not the invariant, static, evolutionarily-conservative character it was once believed to be (STEBBINS *et al.*, 1967; HUEY & WEBSTER, 1976; RUBAL & PHILIBOSIAN, 1970; BRADSHAW *et al.*, 1980). In lacertids,  $T_{sel}$  has been shown to vary with season (PATTERSON & DAVIES, 1978; VAN DAMME *et al.*, 1986; RISMILLER & HELDMAIER, 1988), photoperiod (RISMILLER & HELDMAIER, 1982, 1988), time of day (RISMILLER & HELDMAIER, 1982), and may differ between age classes and sexes (PATTERSON & DAVIES 1978; VAN DAMME *et al.*, 1986; CASTILLA & BAUWENS, 1991; MARQUEZ *et al.*, 1997). Nutritional state (BRADSHAW *et al.*, 1980; SIEVERT, 1989), environmental moisture (BURY & BALGOOYEN, 1976), and disease (WARWICK, 1991) have been reported to affect  $T_{sel}$  in other lizard families.

In some cases, the variation in  $T_{sel}$  can be related to specific physiological functions. For instance, the relative high  $T_{sel}$  of adult male *Lacerta vivipara* in late summer and early spring has been linked tentatively to spermatocyto- and spermiogenesis during these periods; adoption of a low  $T_{sel}$  by females of this species may be related to the low thermal optimum of the *in vitro* development of embryos (VAN DAMME *et al.*, 1986). In many other cases, the physiological reasons for the observed variation in  $T_{sel}$  remain unclear.

Careful observation of lizards in thermogradients revealed that thermoregulation does not revolve around a single body temperature, but rather involves two »set-point« temperatures; an upper setpoint ( $T_{move}$ , Shade Seeking  $T_b$ ) at which the lizard ceases basking and starts a foraging bout, and a lower setpoint ( $T_{bask}$ , Basking  $T_b$ ), at which basking is resumed. Either or both setpoints may show intra- and interspecific variation (TOSINI & AVERY 1993, 1996B; BELLIORE *et al.*, 1996). The setpoint temperatures play an important role in the investigation of the proximate cues that influence thermoregulatory behaviour (TOSINI & AVERY 1993, 1996A, 1996B; TOSINI *et al.*, 1995).

Most lacertid lizards will try to move their  $T_b$ s into a subset of all possible temperatures that is close to the »physiological ideal«. Although some species may be capable of limited physiological adjustments of body temperatures (RISMILLER & HELDMAIER, 1985, GONZALEZ & VERA, 1986), thermoregulation is largely behavioural. Lacertids regulate  $T_b$  by adjusting activity times, by selecting thermally favourable microhabitats, and by using postural adjustments that alter heat exchange with the environment (BAUWENS *et al.*, 1996). Restriction of activity times to periods with suitable weather conditions occurs on a seasonal base (hibernation), as well as on a diel base. Cool temperate species such as *Lacerta vivipara* and *L. agilis* (HOUSE *et al.*, 1980) and montane species such as *Lacerta monticola* (ARGÜELLO & SALVADOR, 1988) and *Lacerta bedriagae* (BAUWENS *et al.*, 1990) seem to be active throughout the day as long as the conditions are favourable. Bimodal circadian rhythms of activity, with peaks after sunrise and in the afternoon, and a low at noon, have been described in Mediterranean species such as *Psammotromus algirus* (CARRASCAL & DÍAZ, 1989) and *Podarcis atrata* (BAUWENS *et al.*, 1996), and in species from desert ar-

eas such as *Acanthodactylus scutellatus*, *A. boskianus*, *A. longipes*, *Meroles olivieri* (PÉREZ-MELLADO, 1992) and *Eremias lineocellata* (HUEY *et al.*, 1977). However, the fact that fewer individuals are seen during the hottest hours of the day may not mean that lizards are not active; they may be confined to more shady and sheltered places, but still remain fully alert and foraging (AVERY, 1993).

The selection of favourable microhabitats usually involves shuttling between hot (usually sunlit) areas and cool (shaded) areas. The frequency and duration of both these movements and the interspersed periods of stationary basking have been shown to vary (DÍAZ, 1991; CARRASCAL *et al.*, 1992; BELLIORE *et al.*, 1996). Basking (heliothermy) seems to be the predominant way to increase heat loads in lacertid lizards, although species inhabiting subalpine environments may occasionally absorb some heat from rocks (thigmothermy; e.g., *Lacerta monticola*, MARTINEZ-RICA, 1977; MARTÍN *et al.*, 1995).

Many lacertid lizards employ postural adjustments to optimise heating rates while basking. They position themselves on surfaces that face the sun and flatten the body dorso-ventrally to maximise the incidence of solar radiation on the dorsal part of the body (AVERY, 1976; VAN DAMME *et al.*, 1987; BAUWENS *et al.*, 1990; CARRASCAL *et al.*, 1992; MARTÍN *et al.*, 1995). Basking postures are most pronounced in cool-climate lacertids and less common or even unknown from Mediterranean species (DÍAZ *et al.*, 1996a).

Although bringing the  $T_b$  close to the physiological ideal may seem beneficial, thermoregulation may also be costly, in terms of energy (needed for shuttling) and time (for shuttling, basking). In addition, thermoregulating lizards may be more conspicuous to predators. The precision with which lizards will thermoregulate is thought to be a function of both the costs and the benefits of thermoregulation (HUEY & SLATKIN, 1976). As both costs and benefits may vary considerably in time and space (see above), it is not surprising to see that the degree of thermoregulation may do the same (HEULIN, 1987; VAN DAMME *et al.*, 1987; 1989; SALVADOR & ARGÜELLO, 1987; CARRASCAL *et al.*, 1992; JI *et al.*, 1996; DÍAZ, 1997). However, the measurement of the accuracy and precision of thermoregulation has long been clouded by some methodological shortcomings.

## THE ACCURACY AND MECHANISMS OF BEHAVIOURAL THERMOREGULATION

Behavioural adjustments are the primary means by which lizards buffer fluctuations in ambient heat loads to maintain their  $T_{bs}$  within the range that is conducive to optimal performance. Nevertheless, environmental conditions exert physical limits to the  $T_{bs}$  that can be achieved and biotic considerations, such as the diversion of available time and energy to distinct demands, may curtail the time devoted to behavioural thermoregulation. Hence, a question that has for a long time directed field studies of thermal biology is: How carefully do lizards thermoregulate? Although this question seems simple and straightforward, only recently have the con-

ceptual and methodological advances been made that make it possible to provide an adequate answer (HERTZ *et al.*, 1993).

The notion of »thermoregulation« implies that organisms actively use behavioural or physiological adjustments to (i) divert their  $T_b$ s from those that would result from the passive exchange of heat with the environment (i.e., in the absence of regulatory processes), and (ii) maintain  $T_b$ s within a preference zone (i.e., the »set-point« range). Indices that have traditionally been used as measures of temperature regulation do not, or do only partially, capture this concept of thermoregulation (see HERTZ *et al.*, 1993 for a detailed account). For instance, the variance in  $T_b$  does not account for variation in ambient conditions, nor does it make any reference to the set-point range (VAN DAMME *et al.*, 1987, 1989; HERTZ *et al.*, 1993). The slope of the regression of  $T_b$  on air temperature (HUEY & SLATKIN, 1976) is also inappropriate because it ignores the set-point range, and because air temperature provides a very incomplete picture of the thermal heat loads that a lizard experiences (PORTER *et al.*, 1973; PORTER & TRACY, 1983; VAN DAMME *et al.*, 1987; DREISIG, 1984; HERTZ *et al.*, 1993).

A comprehensive analysis that considers the different facets of temperature regulation requires at least three kinds of data (HERTZ *et al.*, 1993). First, one must document the  $T_b$ s of a representative sample of field active animals. Second, one must independently identify the »set point« range or, alternatively, the range of selected temperatures, as an estimate of the target  $T_b$ s that ectotherms maintain in the absence of environmental constraints on temperature regulation (HEATH, 1965; LICHT *et al.*, 1966). Third, one requires the distribution of operative temperatures ( $T_{e,s}$ ) at different times and in all available microhabitats. These  $T_{e,s}$  can be measured with hollow-bodied copper models that mimic the size, shape and radiative properties of lizards and integrate the effect of various biophysical factors (e.g., air temperature, solar radiation, wind) that affect a lizard's heat balance (BAKKEN, 1992; HERTZ, 1992). Hence, the  $T_{e,s}$  estimate the equilibrium  $T_b$ s of non-thermoregulating animals. When models are randomly placed in the distinct available microhabitats, appropriate null hypotheses of »no thermoregulation« can be formulated. This is a prerequisite to demonstrate unequivocally that organisms do regulate their  $T_b$  (HEATH, 1964; HUEY *et al.*, 1977; GRANT & DUNHAM, 1988; ADOLPH, 1990; HERTZ, 1992; DÍAZ, 1994b).

We used this protocol to study temperature regulation by the lizard *Podarcis atrata* during sunny days in early autumn (BAUWENS *et al.*, 1996). Throughout its daily activity period, this lizard maintains remarkably constant  $T_b$ s within, or very close to, the range of selected temperatures. This indicates that this population thermoregulates with high accuracy. In addition, the activity  $T_b$ s deviated clearly from the  $T_{e,s}$ , especially during early morning and late afternoon, when  $T_b$ s were generally higher, and during the middle portion of the day, when  $T_b$ s were often lower than the  $T_{e,s}$ . The differences between the actual  $T_b$ s and the  $T_{e,s}$ , which estimate the body temperatures of non-thermoregulating lizards, must be attributed to the effects of thermoregulatory behaviour, and show that *P. atrata* thermoregulates very effectively.

We used similar methods to study seasonal variation in temperature regulation in *Lacerta vivipara* (VAN DAMME *et al.*, 1987). The  $T_b$ s of free-ranging lizards varied seasonally, being noticeably lower at the onset of the activity period (March-April).

In early spring,  $T_{b,s}$  were considerably below the range of selected temperatures, whereas during other months of the year lizards maintained  $T_{b,s}$  close to the selected range. Estimates of »maximal operative temperatures« demonstrate that environmental conditions during the cooler months actually prevent the lizards attaining  $T_{b,s}$  within the selected range. Thus, the reduced accuracy of thermoregulation in early spring is an inevitable consequence of restrictions imposed by the thermal environment. Moreover, lizards maintained their  $T_{b,s}$  close to the maximal  $T_{e,s}$ , in other words, as high as was physically possible. Hence, lizards regulated their  $T_{b,s}$  at the maximal possible level.

Although similar studies for other species would be highly welcome, these examples reinforce our general impression that European lacertid lizards can be considered as »accurate« and »efficient« thermoregulators. They maintain their  $T_{b,s}$  close to the selected range, at least when ambient conditions allow them to do so, and their  $T_{b,s}$  differ clearly from those that would be attained in the absence of regulatory adjustments. However, the research protocol outlined above does not identify the behaviours by which lizards thermoregulate.

It is generally acknowledged that the primary mechanisms of behavioural temperature regulation include the restriction of activity times, the selection of thermally appropriate microhabitats, and postural adjustments that alter rates of heat exchange (e.g., AVERY, 1976; HUEY *et al.*, 1977; HERTZ & HUEY, 1981; HUEY, 1982). AVERY (1993) advocated the performance of more detailed behavioural observations to elucidate the contribution of distinct behaviours to a regulated  $T_b$ . A large number of studies on European lacertids use this approach, at least to some extent (e.g., AVERY 1976, 1978, 1993; VAN DAMME *et al.*, 1987, 1989; BAUWENS *et al.*, 1990; CASTILLA & BAUWENS, 1991; DÍAZ, 1991, 1992, 1994; DÍAZ *et al.*, 1996b). However, observations of behaviours can only provide indirect evidence on their pertinence for thermoregulation. For instance, the mere observation that lizards do not use microhabitats randomly may suggest that microhabitat selection is a mechanism of thermoregulation, although it may equally well reflect non-random distribution of food, predators or conspecifics.

We recently used a different approach to evaluate the relative contributions of several behavioural mechanisms (activity times, use of microhabitats and sun-shade patches, basking, and shuttling) to thermoregulation in a population of *Podarcis atrata* (BAUWENS *et al.*, 1996). To assess the contribution of selection of microsites (combinations of structural microhabitats and sun/shade patches), we combined results from direct behavioural observations with information on the  $T_{e,s}$  in different microsites at different times of day. Observations indicated that, at different times of day, lizards did not use microsites in proportion to their availability. To what extent is this nonrandom pattern induced by thermoregulatory considerations?

One extreme strategy would be that lizards restrict activity to thermally favourable microsites, that is, to sites where  $T_e$  is within the selected temperature range. We can formalise this »only thermoregulation« hypothesis by identifying, using the  $T_e$  data obtained with copper models, those microsites that are thermally favourable at different times of day. Comparison of the actual use of microsites by the lizards with the predicted pattern indicates that *P. atrata* does not adopt this extreme strategy. Thus, lizards did not restrict their activities to thermally favourable sites,

such that thermoregulatory considerations are not the sole determinants of microsite selection by the lizards.

What are the thermal consequences of the observed pattern of microsite selection? We can estimate this by calculating a weighted  $T_e$ -distribution, with the weighing factors proportional to the actual microsite by the lizards. This distribution in fact estimates the expected  $T_b$ s of hypothetical lizards that use microsites in the same way as real lizards do, but that do not exhibit any other form of thermoregulatory behaviour. The  $T_e$ s associated with the lizards' use of specific microsites were on average ca 2 °C closer to the selected temperature range than were the randomly available  $T_e$ s. In other words, microsite selection alters the heat loads to which lizards are exposed. They select relatively warm sites when it is cool, and prefer cooler sites during the warmer hours. The thermal consequences of microsite selection were most apparent during the early morning and late afternoon hours (BAUWENS *et al.*, 1996).

In the former paragraphs we described how measurements of  $T_e$ s were used explicitly to test hypotheses about thermoregulation and the thermal consequences of particular aspects of behaviour. The conclusions that lizards thermoregulate effectively and that microhabitat selection does contribute to temperature regulation are not surprising, and coincide with common expectations. Hence, some may find these findings »obvious« and the research procedures unnecessarily cumbersome. It should, however, be recognized that progress in science is too often hampered by the acceptance of seemingly long established »facts« that have never, or only very rarely, been tested.

We also note that  $T_e$  measurements can be used to estimate and compare the thermal quality of different macrohabitats. This forms a basis to formulate testable hypotheses on the putative relation between the thermal suitability of habitats and demographic parameters. DÍAZ (1997) gives an excellent example of this application.

## EVOLUTION OF THERMAL PHYSIOLOGY CHARACTERISTICS

Thermoregulatory behaviour is the primary means by which lizards buffer fluctuations of the thermal environment. However, abiotic conditions may temporarily impede lizards from achieving  $T_b$ s within the selected range and this may be associated with a reduction of their performance capacities. When such restrictions acquire a permanent character, for instance when climatic conditions change, natural selection should favour a shift in physiological characteristics, to restore performance to its maximal levels (HERTZ *et al.*, 1983; HUEY & BENNETT, 1987; HUEY & KING-SOLVER, 1989). Here we summarise results of comparative studies that examined whether physiological adjustments to climatic conditions have evolved in European lacertid lizards.

### Interspecific variation in heating rates

Many species of lacertid lizards spend much time increasing their  $T_b$  by »basking« (e.g., AVERY, 1976; VAN DAMME *et al.*, 1987, 1989; BAUWENS *et al.*, 1996). This re-

duces the time available for other activities. It seems reasonable to assume that lizards will attempt to minimise the time spent heating, to prolong the time that  $T_b$  can be maintained within the selected range. Because lizards that inhabit cool climate zones require more time to warm to their selected temperature, we expect that they exhibit compensatory physiological (and behavioural) adjustments that increase the rate of heat gain. Hence, the hypothesis of evolutionary adjustments of thermal physiology in relation to climatic conditions predicts that heating rates will be fastest in species that inhabit the coolest environments. This idea was recently examined by DÍAZ *et al.* (1996a).

These authors compared heating rates, measured under standardised laboratory conditions, of eight species of lacertids that live in diverging climate zones. Phylogenetically based analyses of covariance show that species with a northern/montane distribution warm at a faster mass-specific rate than lizards that inhabit a southern (Mediterranean) climate area. Correlational analyses, using phylogenetically independent contrasts, confirm that continuous among-species variation in mass-specific heating rates is negatively related to clinal differences in ambient temperatures in the lizards' habitats. In other words, species that inhabit relatively cool areas heat faster than similarly sized lizards from warmer areas. This is exactly the pattern that is predicted by the hypothesis of evolutionary adjustments of thermal physiology in relation to climatic conditions. Hence, these results are considered strong evidence for the existence of adaptive adjustments of heating rates to climatic conditions within this clade of lacertid lizards (DÍAZ *et al.*, 1996a).

### **Intra- and interspecific variation in the thermal optimum of sprint speed**

Sprint speed, which is considered an ecologically important whole-animal performance trait (GARLAND & LOSOS, 1994), is highly dependent on the lizards'  $T_b$ . To achieve maximal sprinting speed, lizards should maintain their  $T_b$  close to the physiological optimum temperature for sprinting. Species or populations that live in diverging climates, and that maintain different activity  $T_b$ s, are therefore expected to exhibit parallel differences in the optimal temperature for sprint speed. This hypothesis was examined at both the intra- and interspecific level.

VAN DAMME *et al.* (1989, 1990) compared two populations of both *Lacerta vivipara* and *Podarcis tiliguerta* living at different altitudes (sea level and mountain). In both cases the ambient temperatures and the  $T_b$ s maintained during activity were significantly lower at the mountain sites. However, in neither of the two species did the populations differ in the optimal temperature for sprinting. Thus, populations of these species that live in diverging climate conditions have not evolved parallel differences in the thermal sensitivity of sprinting speed. Similar findings have been reported in an agamid (HERTZ *et al.*, 1983) and a phrynosomatid lizard (CROWLEY, 1985). In both cases, differences in ambient conditions were associated with parallel variation in activity  $T_b$ s, but not with among-population differences in the optimal temperature for sprint speed.

BAUWENS *et al.* (1995) studied the thermal sensitivity of sprinting speed in 13 species of European lacertid lizards that live along a climatic gradient. There were clear-cut among-species differences in the optimal temperature for sprinting. Thus, different species have evolved different optimal temperatures for running speed.

However, the critical question is whether the variation in optimal temperatures is related to differences in the thermal environment (i.e., ambient temperatures). The data do not provide evidence for the existence of a tight, positive relation. Hence, these results do not support the hypothesis of adaptation of the thermal sensitivity of sprinting to ambient conditions. At the same time, however, they do not falsify this hypothesis.

The hypothesis of adaptation adjustments of the thermal physiology predicts a relationship with ambient temperatures only when variation in environmental conditions translates directly into differences in activity  $T_{bs}$ . Indeed, it is the  $T_{bs}$  maintained during activity that affect performance capacities, not the ambient temperatures alone. Through the extensive use of short-term behavioural adjustments, the  $T_{bs}$  of lacertid lizards deviate notably from the ambient temperatures. Hence, species that live in different climates may maintain identical activity  $T_{bs}$ , because they display different thermoregulatory behaviours or because they invest different amounts of time in behavioural temperature regulation. Thus, a more stringent test of the hypothesis would be to search for a putative relationship between the optimal temperature and the  $T_{bs}$  maintained by active animals. Regrettably, the low level of standardisation among published data of field  $T_{bs}$  in the lacertids impedes a thorough test of this prediction.

VAN BERKUM (1986) provided support for this hypothesis in a group of *Anolis* lizards that live along an altitudinal gradient. She found, as predicted, a clear positive relationship between the optimal temperature of sprint speed and the activity  $T_{bs}$  experienced by different species in nature. It is worth noting that the *Anolis* species studied have far more restricted thermoregulatory abilities, and hence exhibit much larger among-species differences in  $T_{bs}$  than the European lacertid lizards.

In addition, BAUWENS *et al.* (1995) report, within a clade of lacertids, a positive evolutionary correlation between the optimal temperature for sprinting and the median selected temperature. This result gives evidence that the evolution of the thermal sensitivity of sprint speed has proceeded in concert with the evolution of the set-point range of  $T_{bs}$  that lizards attempt to achieve during activity. This result supports the hypothesis of adaptive adjustments of the thermal sensitivity to the activity  $T_{bs}$ , but only if we assume that the field  $T_{bs}$  match the selected temperatures in all species. Available data do not allow us to test this assumption. Some studies have shown that, during some periods of the day or year, ambient conditions prevent lizards achieving the selected temperatures in the field (VAN DAMME *et al.*, 1987, 1989, 1990). However, it is at present unclear whether this occurs in only some populations or species, or is a more general phenomenon.

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## SUMMARY

### Field body temperatures, mechanisms of thermoregulation and evolution of thermal characteristics in lacertid lizards

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We discuss three aspects of the thermal biology of lacertid lizards. First, we provide an overview of the available data on field body temperatures ( $T_b$ ), the thermal sensitivity of various performance functions and selected body temperatures in different species of lacertid lizards. We also briefly summarise information on the mechanisms of thermoregulation. Second, we discuss recent developments to estimate the »precision« of thermoregulation, and the contribution of distinct behavioural mechanisms. This requires predictions of the  $T_b$ s of non-thermoregulating lizards. Such null hypotheses are provided by measurements of operative temperatures using copper models of lizards. Studies that used this protocol indicate that lacertids thermoregulate with high »precision«, »accuracy« and »effectiveness«. The main behavioural mechanisms are the restriction of activity times, microhabitat choice, shuttling between microhabitats and overt basking. We show that the contributions of each of these adjustments to temperature regulation can be evaluated by the formulation of specific null-hypotheses, comparison with distributions of  $T_b$  and direct behavioural observations. Finally, we revise available evidence for the existence of evolutionary adjustments of thermal characteristics in lacertid lizards. Existing studies have mainly dealt with within- and among-species differences in thermoregulatory behaviour (selected temperatures) and thermal physiology of adults (optimal temperatures, heating rates). Available data provide only limited evidence for clear-cut evolutionary shifts in thermal physiology characteristics along climatic gradients.

## SAŽETAK

### Temperatura tijela u prirodi, mehanizmi termoregulacije i evolucija termalnih karakteristika u lacertidnih guštera

A. M. Castilla, R. Van Damme & D. Bauwens

Raspravlja se o tri aspekta termalne biologije lacertidnih guštera. Prvo donosimo pregled dostupnih podataka o tjelesnoj temperaturi u prirodi ( $T_b$ ), termalnoj osjetljivosti različitih funkcija i odabranih temperatura tijela kod različitih vrsta lacertidnih guštera. Također se ukratko daju informacije o mehanizmima termoregulacije. Drugo, raspravlja se o nedavnim pokušajima procjene »preciznosti« termoregulacije i doprinosu određenih mehanizama ponašanja. To zahtijeva predviđanja  $T_b$ -a ne-termoregulirajućih guštera. Takve nul-hipoteze omogućavaju mjerenja operativnih temperatura korištenjem bakrenih modela guštera. Studije u kojima su korišteni takvi protokoli ukazuju na to da lacertidni gušteri termoreguliraju s visokom »preciznošću«, »točnošću« i »efektivnošću«. Glavni mehanizmi ponašanja su ograničenje vremena aktivnosti, izbor mikrostaništa, izmjene između mikrostaništa i očitog »sunčanja«. Pokazali smo da se doprinosi svake od ovih prilagodbi na regulaciju temperature mogu procijeniti formuliranjem specifičnih nul-hipoteza, usporedbom s raspodjelom  $T_b$  i izravnim opažanjem ponašanja. Na kraju se daje pregled dostupnih dokaza o postojanju evolucijskih prilagodbi termalnih osobina lacertidnih gušterica. Postojeće studije su se uglavnom bavile razlikama u termoregulacijskom ponašanju (odabrane temperature) unutar jedne i između više vrsta i termalnom fiziologijom adulta (optimalne temperature, zagrijavanje). Dostupni podaci daju samo ograničene dokaze o jasno određenim evolucijskim pomacima u karakteristikama termalne fiziologije duž klimatskih gradijenata.