

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

AURORA M. CASTILLA^{1,2}, RAOUL VAN DAMME¹ & DIRK BAUWENS³

¹Department of Biology, University of Antwerp (UIA),
B-2610 Wilrijk, Belgium

²Instituto Mediterráneo de Estudios Avanzados,
E-07071 Palma de Mallorca, Spain

³Institute of Nature Conservation, Kliniekstraat 25,
B-1070 Brussel, Belgium

Castilla, A. M., Van Damme, R. & Bauwens, D: Field body temperatures, mechanisms of thermoregulation and evolution of thermal characteristics in lacertid lizards. *Nat. Croat.*, Vol. 8, No. 3., 253-274, 1999, Zagreb

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

Castilla, A. M., Van Damme, R. & Bauwens, D: Temperatura tijela u prirodi, mehanizmi termoregulacije i evolucija termalnih karakteristika u lacertidnih guštera. *Nat. Croat.*, Vol. 8, No 3., 253-274, 1999, Zagreb.

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 (PORTIER *et al.*, 1973; PORTIER & IRACY, 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 (BARIHOLOMEW, 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 & WEBSIER, 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 (BRATTISROM, 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>Merole 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_b s 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_b s 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, Tropiduridae, Teiidae, Varanidae, Scincidae).

As data accumulated, it became clear that no single T_b characterises a lizard species. Within populations, field T_b s of lacertid lizards have been shown to vary with season (HUEY *et al.*, 1977; ARNOLD, 1987; VAN DAMME *et al.*, 1987; ARGUELLO & SALVADOR, 1988; JI *et al.*, 1996) and time of day (HUEY *et al.*, 1977; ARGUELLO & 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; IOSINI & 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; IOSINI & 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 & HEIDMAIER, 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, IPB). 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

Metabolic rate, respiration, ventilation, heart rate
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;
Foraging efficiency, prey selection, food intake rate, handling time, digestion, growth rate
Avery et al. 1982; Avery 1984; Avery & Mynott 1990; Van Damme et al. 1991; Díaz 1994a; Ji et al. 1996
Locomotion, sprint speed, voluntary speed, gait characteristics, muscle activity
Avery & Bond 1989; Van Damme et al. 1989, 1990a, 1991; Li & Liu 1994; Bauwens et al. 1995; Ji et al. 1996
Chemosensory examination, anti-predatory behaviour
Van Damme et al. 1990b
Gametogenesis, reproductive cycle
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
Incubation time, developmental rate, hatchling phenotype
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), *Psammodromus algirus* (DÍAZ, 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 I_{opt} and IPBs 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 (SIEBBINS *et al.*, 1967; HUEY & WEBSIER, 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; CASILLA & BAUWENS, 1991; MARQUEZ *et al.*, 1997). Nutritional state (BRADSHAW *et al.*, 1980; SIEVERI, 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 spermatocyt- 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 (IOSINI & AVERY 1993, 1996B; BELLIURE *et al.*, 1996). The setpoint temperatures play an important role in the investigation of the proximate cues that influence thermoregulatory behaviour (IOSINI & AVERY 1993, 1996A, 1996B; IOSINI *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 *Psammmodromus 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; BELLIURE *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*, MARTÍNEZ-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 & SLAIKIN, 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_b s within the range that is conducive to optimal performance. Nevertheless, environmental conditions exert physical limits to the T_b s 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 (HERIZ *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 HERIZ *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; HERIZ *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 (PORIER *et al.*, 1973; PORIER & TRACY, 1983; VAN DAMME *et al.*, 1987; DREISIG, 1984; HERIZ *et al.*, 1993).

A comprehensive analysis that considers the different facets of temperature regulation requires at least three kinds of data (HERIZ *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; LICI *et al.*, 1966). Third, one requires the distribution of operative temperatures (T_{es}) at different times and in all available microhabitats. These T_{es} 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; HERIZ, 1992). Hence, the T_{es} 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; HERIZ, 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_{es} , 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_{es} . The differences between the actual T_b s and the T_{es} , 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; HERIZ & 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; CASIILLA & 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.

ACKNOWLEDGEMENTS

During preparation of the manuscript we were illuminated by the harmonious phenotypes of Penélope Cruz, Robert Redford and Inés Sastre. AMC is supported by a contract of the Spanish CSIC; RVD is a senior research assistant of the FWO - Flanders.

Received August 11, 1998

REFERENCES

- ADOLPH, S. C., 1990: Influence of behavioral thermoregulation on microhabitat use by two *Sceloporus* lizards. – *Ecology* 71, 315–327
- AL-SADOON, M. K., 1986: Influence of a broad temperature range on the oxygen consumption rates of three desert lizard species. – *Comp. Biochem. Physiol. A* 84, 339–344
- 1987: The influence of temperature and activity on aerobic and anaerobic metabolism in the viviparous lizard, *Lacerta vivipara* (Jacquin). – *Herpetological J.* 1, 181–185
- AL-SADOON, M. K. & N. M. ABDO, 1991: Temperature and body mass effects on the metabolic rate of *Acanthodactylus schmidti* Weigmann (Reptilia: Lacertidae). – *J. Arid Environm.* 21, 351–361
- AL-SADOON, M. K. & I. F. SPELLERBERG, 1985: Effect of temperature on the oxygen consumption of lizards from different climatic regions. – *Amphibia-Reptilia* 6, 241–258.
- ARGÜELLO, J. A. & A. SALVADOR, 1988: Actividad, selección de hábitat y temperaturas corporales de *Lacerta monticola* en una localidad de la Cordillera Cantábrica (Sauria: Lacertidae). – *Rev. Española Herpetol.* 3, 29–40.
- ARNOLD, E. N., 1987: Resource partition among lacertid lizards in southern Europe. – *J. Zool. (Lond.) (B)* 1, 739–782
- AVERY, R. A., 1976: Thermoregulation, metabolism and social behaviour in Lacertidae. – In: D'A BELLAIRES, A. & C. B. COX: *Morphology and Biology of Reptiles* 245–259. London, Linnean Society Symposium Ser. n° 3
- 1978: Activity patterns, thermoregulation and food consumption in two sympatric lizard species (*Podarcis muralis* and *P. sicula*) from central Italy. – *J. Anim. Ecol.* 47, 143–158
- 1984: Physiological aspects of lizard growth: the role of thermoregulation. – *Symp. Zool. Soc. Lond.* 52, 407–424
- 1993: Diel variation in area of movement of the lizard *Podarcis sicula*. – *Ethology Ecology & Evolution* 5, 511–518.
- AVERY, R. A., J. D. BEDFORD & C. P. NEWCOMBE, 1982: The role of thermoregulation in lizard biology: predatory efficiency in a temperate diurnal basker. – *Behav. Ecol. Sociobiol.* 11, 261–267
- AVERY, R. A. & D. J. BOND, 1989: Movement patterns of lacertid lizards: effects of temperature on speed, pauses and gait in *Lacerta vivipara*. – *Amphibia-Reptilia* 10, 77–84
- AVERY, R. A. & A. MYNOTT, 1990: The effects of temperature on prey handling time in the common lizard, *Lacerta vivipara*. – *Amphibia-Reptilia* 11, 111–122
- BAKKEN, G. S., 1992: Measurement and application of operative and standard operative temperatures in ecology. – *Amer. Zool.* 32, 194–216
- BARBADILLO, I. J., 1987: *La Guía de Incafo de los anfibios y reptiles de la Península Ibérica, Islas Baleares y Canarias*. Madrid, Incafo
- BARBER, B. J. & E. C. CRAWFORD, 1977: A stochastic dual-limit hypothesis for behavioral thermoregulation in lizards. – *Physiol. Zool.* 50, 53–60.
- BARIHOLOMEW, G. A., 1982: Physiological control of body temperature. – In: GANS, C. & F. H. POUGH: *Biology of the Reptilia* Vol. 12. 167–211. London, Academic Press
- BAUWENS, D., A. M. CASILLA, R. VAN DAMME & R. F. VERHEYEN, 1990: Field body temperatures and thermoregulatory behavior of the high altitude lizard *Lacerta bedriagae*. – *J. Herpetol.* 24, 88–91
- BAUWENS, D., T. JR. GARLAND, A. M. CASILLA & R. VAN DAMME, 1995: Evolution of sprint speed in lacertid lizards: morphological, physiological, and behavioral covariation. – *Evolution* 49, 848–863

- BAUWENS, D., P. E. HERTZ & A. M. CASTILLA, 1996: Thermoregulation in a lacertid lizard: the relative contribution of distinct behavioral mechanisms – *Ecology* 77, 1818–1830.
- BELLIURE, J., I. M. CARRASCAL & J. A. DÍAZ, 1996: Covariation of thermal biology and foraging mode in two mediterranean lacertid lizards – *Ecology* 77, 1163–1173.
- BERK, M. I. & J. E. HEATH, 1975: An analysis of behavioral thermoregulation in the lizard *Dipsosaurus dorsalis*. – *J. therm. Biol.* 1, 15–22.
- BOGERT, C. M., 1949: Thermoregulation in reptiles, a factor in evolution – *Evolution* 3, 195–211.
- BÖHME W., 1981: *Handbuch der Reptilien und Amphibien Europas* Vol I Wiesbaden, Aula-Verlag.
- BOWKER, R. G., 1984: Precision of thermoregulation of some African lizards. – *Physiol. Zool.* 57, 401–412.
- BRADSHAW, S. D., C. GANS & H. SAINT-GIRONS, 1980: Behavioral thermoregulation in a Pygopodid lizard, *Lialis burtonis*. – *Copeia* 1980, 738–743.
- BRAIN, C. K., 1962: Observations on the temperature tolerance of lizards in the central Namib desert, South West Africa. – *Cimbebasia* 4, 2–5.
- BRAÑA, F., 1991: Summer activity patterns and thermoregulation in the wall lizard, *Podarcis muralis*. – *Herpetol. J.* 1, 544–549.
- BRATTSIROM, B. H., 1965: Body temperatures of reptiles. – *Am. Midl. Nat.* 73, 377–422.
- BRIZZI, R. & M. GALCANO, 1969: Alcuni dati sull'influenza della luce e della temperatura sul ciclo sessuale annuale maschile di *Lacerta sicula* Raf. – *Boll. Zool.* 36, 367–369.
- BRIZZI, R., O. PICARIELLO, O. & V. BOTTE, 1976: Influence of photoperiod and temperature on the testicular activity of the lizard, *Lacerta s. sicula* Raf. – *Boll. Zool.* 43, 111–124.
- BURY, R. B. & I. G. BALGOOYEN, 1976: Temperature selectivity in the legless lizard, *Anniella pulchra*. – *Copeia* 1976, 152–155.
- BUSACK, S. D., 1976: Activity cycles and body temperatures of *Acanthodactylus erythurus*. – *Copeia* 1976, 826–830.
- 1987: Notes on the biology of *Lacerta andreanszky* (Reptilia: Lacertidae). *Amphibia-Reptilia* 8, 231–236.
- CARRASCAL, I. M. & J. A. DÍAZ, 1989: Thermal ecology and spatio-temporal distribution of the mediterranean lizard *Psammodromus algirus*. – *Holarct. Ecol.* 12, 137–143.
- CARRASCAL, I. M., P. LÓPEZ, J. MARÍN & A. SALVADOR, 1992: Basking and antipredator behaviour in a high altitude lizard: implications of heat-exchange rate. – *Ethology* 92, 143–154.
- CARRETERO M. A. & G. A. LLORENTE, 1991: Thermal ecology of three lacertid lizards in a Mediterranean beach. – Poster presented at the 6th Ord. Gen. Meeting Soc. Eur. Herpetol., Budapest, Hungary.
- CASTILLA, A. M. & D. BAUWENS, 1991: Thermal biology, microhabitat selection, and conservation of the insular lizard *Podarcis hispanica atrata*. – *Oecologia (Berl.)* 85, 366–374.
- CASTILLA, A. M. & J. G. SWALLOW, 1996: Thermal dependence of incubation duration under a cycling temperature regime in the lizard, *Podarcis hispanica atrata*. – *J. Herpetol.* 30, 247–253.
- CLERX, P. M. J. & J. I. V. BROERS, 1982: Oecologisch onderzoek aan *Lacerta vivipara*, de levendbarende hagedis, in het Oostenrijks hooggebergte. – *Lacerta* 41, 78–84.
- CLOUDSLEY-THOMPSON J. I., 1971: *The temperature and water relations of reptiles*. Mellow Publ. Co. Ltd, Watford, UK.
- COWLES, R. B. & C. M. BOGERT, 1944: A preliminary study of the thermal requirements of desert reptiles. – *Bull. Am. Mus. Nat. Hist.* 83, 265–296.
- CRAGG, P. A., 1978: Oxygen consumption in the lizard genus *Lacerta* in relation to diel variation, maximum activity and body weight. – *J. exp. Biol.* 77, 33–56.

- CRISP, M., I. M. COOK & F. V. HERWARD, 1979: Color and heat balance in the lizard *Lacerta dugesii* – *Copeia* 1979, 250–258.
- CROWLEY, S. R., 1985: Thermal sensitivity of sprint-running in the lizard *Sceloporus undulatus*: support for a conservative view of thermal physiology – *Oecologia (Berl)* 66, 219–225
- CRUCE, M., 1972: L'influence de la température sur le comportement du lézard *Lacerta taurica taurica* Pall., 1831. – *Rev Roum Biol Zoologie* 17, 361–369
- DE LUCA, N., 1991: Notes on the biology and ecology of the Horvath's rock lizard (*Lacerta horvathi* Méhely, 1904, Reptilia: Lacertidae) – In KORSÓS Z. & I. KISS: Proceedings of the 6th Ordinary General Meeting of the Societas Europaea Herpetologica, 129–136 Budapest, Hungary.
- DE VERA PORCELL, I. & J. G. GONZALEZ, 1986a: Cardiac responses to temperature in the lizard *Gallotia galloti* – *Comp. Biochem. Physiol.* 85, 389–394
– 1986b: Effect of body temperature on the ventilatory responses in the lizard *Gallotia galloti* – *Resp. Physiol.* 65, 29–37
- DÍAZ, J. A., 1991: Temporal patterns of basking behaviour in a mediterranean lacertid lizard. – *Behaviour* 118, 1–14.
– 1992: Choice of compass directions around shrub patches by the heliothermic lizard *Psammodromus algirus*. – *Herpetologica* 48, 293–300
– 1994a: Effects of body temperature on the predatory behaviour of the lizard *Psammodromus algirus* hunting winged and wingless prey – *Herpetol J* 4, 145–150.
– 1994b: Field thermoregulatory behavior in the western canarian lizard *Gallotia galloti*. – *J. Herpetol.* 28, 325–333
– 1997: Ecological correlates of the thermal quality of an ectotherm's habitat: a comparison between two temperate lizard populations – *Funct. Ecol.* 11, 79–89.
- DÍAZ, J. A., D. BAUWENS & B. ASENSIO, 1996a: A comparative study of the relation between heating rates and ambient temperatures in lacertid lizards – *Physiol. Zool.* 69, 1359–1383
- DÍAZ, J. A., R. DÍAZ-URIARTE & A. RODRÍGUEZ, 1996b: Influence of behavioral thermoregulation on the use of vertical surfaces by Iberian wall lizards *Podarcis hispanica* – *J. Herpetol.* 30, 548–552
- DREISIG, H., 1984: Control of body temperature in shuttling ectotherms – *J. therm. Biol.* 9, 229–233
- D'UVA, V., G. CIARCIA, F. ANGELINI & A. CIARLETTA, 1982: Effects of photoperiod and temperature on the subcommissural organ of *Lacerta s. sicula* Raf. – *Monit. Zool. Ital.* 16, 313–323
- DUVDEVANI, I. & A. BORUT, 1974: Mean body temperature and heat absorption in four species of *Acanthodactylus* lizards (Lacertidae) – *Herpetologica* 30, 176–181
- FISCHER, K., 1969: Einflüsse von Licht und Temperatur auf die Jahresperiodik der Fortpflanzung bei männlichen Ruineidechsen – *Zool. Anz.* 32, 278–283
- GARLAND, T. J. & J. B. LOSOS, 1994: Ecological morphology of locomotor performance in squamate reptiles. – In: WAINWRIGHT, P. C. & S. M. REILLY: *Ecological Morphology: Integrative Organismal Biology* 240–302 Chicago, Univ. Chicago Press
- GAVAUD, J., 1991: Role of cryophase temperature and thermophase duration in thermoperiodic regulation of the testicular cycle in the lizard *Lacerta vivipara* – *J. exp. Zool.* 260, 239–246.
- GELINEO, S., 1964: Temperaturadaption und Sauerstoffverbrauch bei Eidechsen. – *Helgoländer wiss. Meeresuntersuch.* 9, 428–432
- GELINEO, S. & A. GELINEO, 1955: La consommation d'oxygène chez différentes espèces de lézards à habitats différents – *C. R. Sci. Soc. Biol.* 149, 565–568
- GONZALEZ, J. & P. L. VERA, 1986: Physiological thermoregulation of the Canary lizard *Gallotia galloti* – *Comp. Biochem. Physiol. A* 83, 709–713.

- GRANI, B. W. & A. E. DUNHAM, 1988: Thermally imposed time constraints on the activity of the desert lizard *Sceloporus merriami* – *Ecology* 69, 167–176
- HEATH, J. E., 1964: Reptilian thermoregulation: evaluation of field studies – *Science* 146, 784–785.
— 1965: Temperature regulation and diurnal activity in horned lizards. – *Univ Calif Publ Zool* 64, 97–136.
- HERTZ, P. E., 1981: Adaptation to altitude in two West Indian anoles (Reptilia: Iguanidae): field thermal biology and physiological ecology – *J Zool (Lond)* 195, 25–37
— 1992: Temperature regulation in Puerto Rican *Anolis* lizards: a field test using null hypotheses – *Ecology* 73, 1405–1417
- HERTZ, P. E. & R. B. HUEY, 1981: Compensation for altitudinal changes in the thermal environment by some *Anolis* lizards on Hispaniola. – *Ecology* 62, 515–521
- HERTZ, P. E., R. B. HUEY & E. NEVO, 1983: Homage to Santa Anita: thermal sensitivity of sprint speed in agamid lizards – *Evolution* 37, 1075–1084
- HERTZ, P. E., R. B. HUEY & R. D. STEVENSON, 1993: Evaluating temperature regulation by field-active ectotherms: the fallacy of the inappropriate question – *Am Nat* 142, 796–818
- HEULIN, B., 1987: Temperature diurne d'activité des mâles et des femelles de *Lacerta vivipara* – *Amphibia-Reptilia* 8, 393–400
- HOUSE, S. M., P. J. TAYLOR & I. F. SPELLERBERG, 1980: Patterns of daily behaviour in two lizard species *Lacerta agilis* L. and *Lacerta vivipara* Jacquin – *Oecologia (Berl)* 44, 396–402
- HUEY, R. B., 1982: Temperature, physiology, and the ecology of reptiles. – In: GANS, C. & F. H. POUGH: *Biology of the Reptilia*. Vol. 12, 25–91. London, Academic Press
- HUEY, R. B. & A. F. BENNETT, 1987: Phylogenetic studies of coadaptation: preferred temperatures versus optimal performance temperatures of lizards – *Evolution* 41, 1098–1115.
- HUEY, R. B. & J. G. KINGSOLVER, 1989: Evolution of thermal sensitivity of ectotherm performance – *Trends Evol Ecol* 4, 131–135.
- HUEY, R. B., E. R. PIANKA & J. A. HOFFMAN, 1977: Seasonal variation in thermoregulatory behavior and body temperature of diurnal Kalahari lizards – *Ecology* 58, 1066–1075
- HUEY, R. B. & M. SLATKIN, 1976: Cost and benefits of lizard thermoregulation – *Quart Rev Biol* 51, 363–384
- HUEY, R. B. & R. D. STEVENSON, 1979: Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. – *Am Zool* 19, 357–366.
- HUEY, R. B. & I. P. WEBSTER, 1976: Thermal biology of *Anolis* lizards in a complex fauna: the *crisatellus* group on Puerto Rico – *Ecology* 57, 985–994.
- JENSEN, J. K., 1982: Relations between temperature and incubation time for eggs of the sand lizard (*Lacerta agilis* L.) – *Amphibia-Reptilia* 2, 385–386
- Ji, X., W. G. DU & P. Y. SUN, 1996: Body temperature, thermal tolerance and influence of temperature on sprint speed and food assimilation in adult grass lizards, *Takydromus septentrionalis* – *J. therm Biol* 21, 155–161
- JOLY, J. & H. SAINT-GIRONS, 1981: Influence de la température sur la vitesse de la spermatogénèse de *Lacerta vivipara* et comparaison avec *Lacerta muralis* (Reptilia: Lacertidae) – *Bull. Soc. Zool France* 106, 337–340.
- KASAPIDIS, P., C. ADAMOPOULOU, P. MARAGOU & E. D. VALAKOS, 1995: Preferred body temperatures of the species *Podarcis erhardii* and *Podarcis milensis* – In: *Proceedings of the 2nd International Symposium of Lacertids of the Mediterranean Basin* 19 Algarve, Portugal.
- LI, R. D. & N. F. LIU, 1994: Temperature effects on ATP-ase activity of gastrocnemius in lizards – *Acta Zool. Sinica* 40, 45–50
- LIBERMANN, S. S. & N. V. POKROVSKAJA, 1943: Ecology of *Lacerta agilis*. – *Zool Zh* 22, 247–256

- LICHT, P., H. E. HOYER & P. G. W. J. VAN OORDT, 1969: Influence of photoperiod and temperature on testicular recrudescence and body growth in the lizards, *Lacerta sicula* and *Lacerta muralis* - J Zool (Lond.) 157, 469-501
- LICHT, P., W. R. DAWSON, V. H. SHOEMAKER & A. R. MAIN, 1966: Observations on the thermal relations of western Australian lizards. - Copeia 1966, 97-111
- MADERSON, P. F. A. & A. D'A BELLAIRS, 1962: Effects of temperature variation and tail removal on lizard embryos in culture - J. Anat., Lond 96, 416
- MARAGOU, P., E. VALAKOS, B. CHONDROPOULOS, 1997: Comparative thermal ecology of two endemic lacertid species of Greece, *Lacerta graeca* and *Podarcis peloponnesiaca*. - In: ROCEK, Z. & S. HART: Abstracts of the 3rd World Congress of Herpetology. 135. Prague, Czech Republic
- MÁRQUEZ, R., D. CEJUDO & V. PÉREZ-MELLADO, 1997: Selected body temperatures of four lacertid lizards from the Canary Islands - Herpetological Journal 7, 122-124
- MARTÍN, J., P. LÓPEZ, I. M. CARRASCAL & A. SALVADOR, 1995: Adjustment of basking postures in the high-altitude Iberian rock lizard (*Lacerta monticola*) - Can. J. Zool 73, 1065-1068
- MARTÍNEZ-RICA, J. P., 1977: Observaciones ecológicas *Lacerta monticola bonnali*, Lantz en el Pirineo Español - Publ. Cent. pir. Biol. exp 8, 103-122
- NIELSEN, B., 1961: On the regulation of the respiration in reptiles. I. The effect of temperature and CO₂ on the respiration of lizards (*Lacerta*). - J. exp. Biol 38, 301-314
- OKA, I., 1981: Developmental processes in the lizard *Takydromus tachydromoides*. 2. Effects of incubation temperatures on a series of developmental stages - Jap. J. Herpetol 9, 67.
- PATTERSON, J. W. & P. M. C. DAVIES, 1978: Preferred body temperature: seasonal and sexual differences in the lizard *Lacerta vivipara*. - J. therm. Biol. 3, 39-41
- PÉREZ-MELLADO, V., 1983: Activity and thermoregulation patterns in two species of Lacertidae: *Podarcis hispanica* (Steindachner, 1870) and *Podarcis bocagei* (Seoane, 1884). - Cienc. Biol. Ecol. Syst. (Portugal) 5, 5-12.
- 1992: Ecology of lacertid lizards in a desert area of eastern Morocco - J. Zool (Lond.) 226, 369-386
- PÉREZ-MELLADO, V. & A. SALVADOR, 1981: Actividad y termorregulación estival de *Podarcis pityuensis* Bosca, 1883 (Sauria: Lacertidae) en Ibiza y Formentera - Amphibia-Reptilia 2, 181-186.
- PÉREZ-MELLADO, V., E. D. VALAKOS, F. GUERRERO, M. J. GIL-COSIA, 1993: Ecological similarity of lacertid lizards in the Mediterranean region. The case of *Ophisops elegans* and *Psammotromus hispanicus*. - In: VALAKOS E. D., W. BÖHME, V. PÉREZ-MELLADO & P. MARAGOU: Lacertids of the Mediterranean Region. 231-242. Athens, Hellenic Zoological Society.
- POLLO MAIEOS, C. & V. PÉREZ-MELLADO, 1989: Activity and thermoregulation in three Mediterranean species of Lacertidae - Herpetol. J. 1, 343-350
- PORIER, W. P., J. W. MITCHELL, W. A. BECKMAN & C. B. DEWITT, 1973: Behavioral implications of mechanistic ecology. Thermal and behavioral modeling of desert ectotherms and their microenvironment - Oecologia (Berl.) 13, 1-54
- PORIER, W. P. & C. R. TRACY, 1983: Biophysical analyses of energetics, time-space utilization, and distributional limits - In: HUEY, R. B., E. R. PIANKA & T. W. SCHOENER: Lizard ecology. Studies on a model organism. 55-83. Cambridge, Harvard Univ. Press.
- RAYNAUD, A. & A. CHANDOLA, 1969: Effets du refroidissement sur le développement de l'embryon du lézard vert (*Lacerta viridis* Laur.). - C. R. Hebd. Séanc. Acad. Sci., Paris 269, 1863-1865
- RISMILLER, P. D. & G. HEIDMAIER, 1982: The effect of photoperiod on temperature selection in the European green lizard, *Lacerta viridis* - Oecologia (Berl.) 53, 222-226
- 1985: Thermal behavior as a function of the time of day: heat exchange rates and oxygen consumption in the lacertid lizard *Lacerta viridis* - Physiol. Zool 58, 71-79

- 1988: How photoperiod influences body temperature selection in *Lacerta viridis* - *Oecologia* (Berl) 75, 125-131
- ROMAN, E. S., 1982: Taxocenosis de lacertidos en un arenal costero alicantino. - Universidad de Alicante, Spain
- RUIBAL, R. & R. PHILIBOSIAN, 1970: Eurythermy and niche expansion in lizards. - *Copeia* 1970, 645-653.
- RYKENA, S., 1988: Innerartlichen Differenzen bei der Eizeitigungsdauer von *Lacerta agilis* - *Mertensiella* 1, 41-53.
- SALVADOR, A. & J. A. ARGÜELLO, 1987: Temperaturas corporales del lagarto verdinegro (*Lacerta schreiberi*) (Sauria: Lacertidae) - *Rev Española Herpetol* 2, 71-82
- SERGEYEV, A. M., 1939: The body temperatures of reptiles in natural surroundings - *C. r. Acad. Sci. URSS* 22, 247-256
- SEVERT, L. M., 1989: Postprandial temperature selection in *Crotaphytus collaris*. - *Copeia* 1989, 987-993
- SINERVO, B., 1990: Evolution of thermal physiology and growth rate between populations of the western fence lizard (*Sceloporus occidentalis*). - *Oecologia* (Berl) 83, 228-237.
- STEBBINS, R. C., J. M. LOWENSTEIN & N. W. COHEN, 1967: A field study of the lava lizard (*Tropidurus albemarlensis*) in the Galapagos Islands - *Ecology* 48, 839-851
- STEVENSON, R. D., 1985b: The relative importance of behavioral and physiological adjustments controlling body temperature in terrestrial ectotherms - *Am. Nat.* 126, 362-386.
- STRIJBOSCH, H., 1988: Reproductive biology and conservation of the Sand lizard. - *Mertensiella* 1, 132-145
- TERIYSHNIKOV, M. F., 1976: Influence of weather and climate on activity of sand and varicolored lizards. - *Ekologiya* 3, 57-61.
- IOSINI, G. & R. A. AVERY, 1993: Intraspecific variation in lizard thermoregulatory set points: a thermographic study in *Podarcis muralis*. - *J. therm. Biol.* 18, 19-23
- 1996a: Dermal photoreceptors regulate basking behavior in the lizard *Podarcis muralis* - *Physiol. & Behav.* 59, 195-198
- 1996b: Pregnancy decreases set point temperatures for behavioural thermoregulation in the wall lizard *Podarcis muralis* - *Herpetol. J.* 6, 94-96
- IOSINI, G., S. JONES & R. A. AVERY, 1995: Infra-red irradiance and set point temperatures in behaviourally thermoregulating lacertid lizards - *J. therm. Biol.* 20, 497-503.
- TROMP, W. I. & R. A. AVERY, 1977: A temperature-dependent shift in the metabolism of the lizard *Lacerta vivipara*. - *J. therm. Biol.* 2, 53-54
- USHAKOV, B. P. & I. S. DAREVSKIY, 1959: Comparison of the heat tolerance of muscle fibers and behaviour towards temperature in two sympatric species of semidesert lizards. - *Dokl. Akad. Nauk SSSR* 128, 833-835
- VAN BERKUM, F. H., 1986: Evolutionary patterns of the thermal sensitivity of sprint speed in *Anolis* lizards. - *Evolution* 40, 594-604
- VAN BERKUM, F. H., R. B. HUEY & B. A. ADAMS, 1986: Physiological consequences of thermoregulation in a tropical lizard (*Ameiva festiva*). - *Physiol. Zool.* 59, 464-472
- VAN DAMME, R., D. BAUWENS, F. BRAÑA & R. F. VERHEYEN, 1992: Incubation temperature differentially affects hatching time, egg survival, and hatchling performance in the lizard *Podarcis muralis*. - *Herpetologica* 48, 220-228
- VAN DAMME, R., D. BAUWENS, A. M. CASTILLA & R. F. VERHEYEN, 1989: Altitudinal variation of the thermal biology and running performance in the lizard *Podarcis tiliguerta* - *Oecologia* (Berl) 80, 516-524.

- VAN DAMME, R., D. BAUWENS, D. VANDERSIIGHELEN & R. F. VERHEYEN, 1990: Responses of the lizard *Lacerta vivipara* to predator chemical cues: the effect of temperature. – Anim. Behav. 40, 298–305.
- VAN DAMME, R., D. BAUWENS & R. F. VERHEYEN, 1986: Selected body temperatures in the lizard *Lacerta vivipara*: variation within and between populations – J. therm. Biol. 11, 219–222
- 1987: Thermoregulatory responses to environmental seasonality by the lizard *Lacerta vivipara*. – Herpetologica 43, 405–415.
- 1990: Evolutionary rigidity of thermal physiology: the case of the cool temperate lizard *Lacerta vivipara*. – Oikos 57, 61–67
- 1991: The thermal dependence of foraging behaviour, gut passage rate and food consumption in the lizard *Lacerta vivipara*. – Funct. Ecol. 5, 507–517.
- WARWICK, C., 1991: Observations on disease-associated preferred body temperatures in reptiles. – Appl. Anim. Behav. Sci. 28, 375–380
- ZAKHAROV, V. M., A. S. BARANOV & A. V. VALEIZKY, 1982: Influence of incubation temperature on duration of development in the sand lizard, *Lacerta agilis* (Lacertidae, Squamata). – Zool. Zh. 61, 883–889.

SUMMARY

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

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

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 netermoregulirajućih 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.