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Habitat selection, thermoregulation and activity of the Pyrenean Rock Lizard *Iberolacerta bonnali* (LANTZ, 1927)
(Squamata: Sauria: Lacertidae)

Habitatwahl, Thermoregulation und Aktivität bei der Pyrenäen-Felseidechse
Iberolacerta bonnali (LANTZ, 1927)
(Squamata: Sauria: Lacertidae)

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KURZFASSUNG

Iberolacerta bonnali (LANTZ, 1927) war von 07.00 bis etwa 16.00 Uhr GMT aktiv (gewöhnlich zwischen 09.00 und 11.00 Uhr), unabhängig von Geschlecht oder Alter. Die Orographie und das jeweils herrschende Wetter schränkten die nachmittägliche Aktivität der Eidechse ein. Im Laufe des Sommers und mit abnehmender Tageslänge verschob sich der Aktivitätsgipfel zunehmend in Richtung späterer Tagesstunden. In Kalksteingebieten begann und endete die Tagesaktivität früher als in Schiefergebieten, doch unterstützte in letzteren das tigmothermische Verhalten der Eidechsen wahrscheinlich den Prozeß des Aufwärmens.

Die Hangneigung war nicht mit der Nutzungshäufigkeit durch *I. bonnali* korreliert. Die häufigsten und meist genutzten Mikrohabitate waren felsige oder grasbestandene Stellen. Die Eidechsen glichen Abweichungen von der mittleren Häufigkeit dieser Strukturen in allen drei Substrattypen (Kalk, Schiefer, Grandiorit/Granit) durch Bevorzugung oder Vermeidung der verfügbaren Mikrohabitate aus. In Schiefergebieten war Fels weniger häufig und wurde positiv selektioniert, während lose Gesteinsbrocken relativ häufig waren und weniger angenommen wurden. Im Kalkgestein fehlte die Buschvegetation und die häufigsten Mikrohabitate, Fels und Gras, wurden etwas weniger angenommen, während umherliegende Steine selten auftraten und vermehrt als Aufenthaltsort gewählt wurden. Auf Grandiorit/Granit-Substrat wurden Grasstandorte weniger angenommen als Fels und loses Gestein.

Die Körpertemperaturen aktiver Eidechsen reichten von 20.8ºC bis 35.2ºC (Mittel 28.96°C±0.24ºC) und waren etwas stärker mit der Substrattemperatur ($r = 0.37$) als mit der Temperatur der Umgebungsluft korreliert ($r = 0.33$). Signifikante Unterschiede zwischen den Geschlechtern oder Altersgruppen oder im Hinblick auf unterschiedliche Substrattypen waren nicht feststellbar. *Iberolacerta bonnali* waren effektive Thermoregulatoren (die Anstiege der Regressionsgeraden von 0.14 bzw. 0.21 der Körpertemperatur in bezug zu Substrat- bzw. Lufttemperatur waren stark von 1 verschieden), aber nicht sehr präzise bei der Einstellung ihrer Körpertemperaturen (geringe Korrelationen) und damit eher Thermokonformisten (in einem breiten Temperaturspektrum aktiv), wie auch andere *Iberolacerta*-Arten.

ABSTRACT

Iberolacerta bonnali (LANTZ, 1927) was active from 07:00 a.m. to about 16:00 p. m. GMT (usually between 09:00 and 11:00 a. m.), without differences among sexes or age classes. Orography and daily weather development limited the activity of the lizard during afternoon. Over the summer and in parallel with the shortening of days, the lizards' activity peak shifted progressively towards later hours. In limestone areas activity began and ended sooner than in slates, but in these latter the lizard's tigmothermic behavior probably supported their warming up.

The inclination of slopes was not correlated with the degree of their utilization by *I. bonnali*. The most abundant and widely used microhabitats were rocky and grassy spots. In all three substrate types (limestone, slate/schist, grandiorite/granite), the lizards compensated deviations in the mean relative abundances of these structures by selecting or counterselecting the available microhabitats. On slate/schist, rock was less abundant and positively selected whereas loose stones were relatively abundant and counterselected. On limestone, shrubs were absent and the most abundant microhabitats (rock and grass) slightly counterselected, whereas stones were less abundant and selected. On granodiorite/granite grass was counterselected whereas rock and stones were selected.

Body temperatures of active lizards oscillated from 20.8°C to 35.2°C (average 28.96°C±0.24°C) and were slightly more correlated with substrate ($r = 0.37$) than with ambient air temperatures ($r = 0.33$). There were no significant differences in body temperatures among sexes or ages, nor related to different rock types. *Iberolacerta bonnali* were good thermoregulators (the regression line slopes of 0.14 and 0.21 of the body temperature relative to substrate and ambient air temperatures, respectively, were clearly different from 1), but not very precise in adjusting their body temperatures (low correlations) and rather thermoconformists (active within a wide range of temperatures), as other *Iberolacerta*.

KEY WORDS

Reptilia: Squamata: Lacertidae; *Pyrenesaura*, *Iberolacerta*, *Iberolacerta bonnali*; high mountain environment, microhabitat, body temperatures, habitat selection, thermoregulation, activity, ecology, behavior, physiology, Pyrenees, Spain, France

INTRODUCTION

The Genus *Iberolacerta* ARRIBAS, 1997 is a monophyletic and deeply rooted group of eight species from the Iberian Peninsula, Pyrenees, Alps and northern Dinaric Chains. This group is well characterized by its external morphology, and osteology as well as karyotype, composed of only 36 or less chromosomes, instead of 38 as is usual among Lacertidae (ODIERNA et al. 1996; ARRIBAS 1997a, 1999c; MAYER & ARRIBAS 2003; ARRIBAS & ODIERNA 2004; CARRANZA et al. 2004; CROCHET et al. 2004; ARRIBAS & CARRANZA 2004, 2007; ARRIBAS et al. 2006; ARNOLD et al. 2007).

The Pyrenees are inhabited by three closely related allo- to parapatric *Iberolacerta* species: *Iberolacerta aranica* (ARRIBAS, 1993), *I. aurelioi* (ARRIBAS, 1994) and *I. bonnali* (LANTZ, 1927), which were almost unknown until very recently in terms of their biological aspects (ARRIBAS 1993a, 1993b, 1994, 1997a, 1997b, 1997c; 1999a, 1999c, 2000, 2001, 2008a, 2008b, 2008c; ARRIBAS & MARTÍNEZ-RICA 1997). Prior to the author's monographic publication on *I. aranica* (ARRIBAS 2007), which included information about other *Pyrenesaura* species, only a few alimentation data of *I. bonnali* and *I. aurelioi* (MARTÍNEZ-RICA 1977; AMAT et al. 2008, respectively) and temperatures of *I. bonnali* taken from some distance with an infrared thermometer (MARTÍNEZ-RICA 1977) were known. Reproduction of *I. aurelioi* was analyzed by ARRIBAS (2004) and ARRIBAS & GALAN (2005) compared the three Pyrenean species in this respect.

Iberolacerta bonnali, protected by law both in Spain and France, is classified 'vulnerable' (VU B1ab+2ab, D2) by Spanish authorities and as "Near Threatened" in IUCN lists. The species is also included in Annexes II and III of the Habitats Directive (Berne Convention, European Union) (ARRIBAS 2002c; PEREZ-MELLADO & CHEYLAN 2006c). Its distribution extends from the Ossau Massif in the west to the mountains of San Mauricio-Aigüestortes National Park in the east. It was described in 1927 as *Lacerta* (*Podarcis*) *monticola bonnali* and elevated to species level rank in 1993 (ARRIBAS 1993a; PEREZ-MELLADO et al. 1993). Hardly known for nearly a century, it was reported for the first time in the Spanish territory in 1976 (MARTÍNEZ-RICA 1976). In the last few years *I. bonnali* was found in 26 10×10 UTM (Universal Transverse Mercator) grids, at elevations of 1550 m – 3062 m, but mostly above 2000 m (ARRIBAS 2002c, 2008c).

The distribution pattern of these lizards is insular due to geographical isolation in the supraforestal alpine belt. Harsh and hostile environmental conditions in the high mountain habitat impose strong restrictions and constraints upon the reproduction and life history of these reptiles. They are characterized by a very short annual activity period (from mid-May to mid-October, at most, with two regular temperature falls within this theoretical activity period, one towards mid-June and another in mid-September) conditioned by the duration of the snow cover and the photoperiod. According to MANI (1968) and KÖRNER (2003), Alpine zones in temperate belts of the earth are subjected to strong circadian contrasts in temperature, moisture, wind, insolation, etc., and the ground is snow covered for almost six months. Radiation (including UV light) increases with altitude, but this is only true with clear skies, because daily or altitudinal apparition of clouds imposes strong variations (DIRNIHIR 1964) in this and other parameters. Life in the mountains is mainly constrained by physical components of the environment, but life forms of these areas are specialized rather than limited. In only a few other earth habitats, one can pass over a distance of few meters from snow-bed communities in very cold soil, to very hot desert-like microhabitats in rocky outcrops. South facing slopes are more suitable for lizard life, but are also subjected to more extreme temperature oscillations.

The alpine zone of the Central Pyrenees is covered by different vegetation mosaics, which include meso-xerophilous grasslands of *Festuca airoides* (on acidic substrata) or *Kobresia myosuroides* (on carbonated soils), ericaceous dwarfshrub (formed by, for example, *Rhododendron ferrugineum*, *Arctostaphylos uva-ursi*, *Vaccinium uliginosum*), and sparse vegetation on rocky substrata and scree (BRAUN-BLANQUET 1948; NINOT et al. 2008; ILLA et al. 2006).

All these characteristics make the supraforestal areas very harsh, extreme environments for ectotherms, such as these lizards. The Pyrenean lizards constitute an excellent model to study the mechanisms of speciation in continental areas, as well as the survival in climatically extreme localities for ectothermic animals (ARRIBAS 1997a, 1997b, 1997c, 1999c, 2007; ARRIBAS & MARTÍNEZ-RICA 1997; ARRIBAS & GALAN 2005). The ectothermic character of lizards endows a metabolic economy that allows them to survive in places where a mammal or a bird could not live or maintain stable and dense populations (PIANKA 1986). On the other side, they are constrained to have a small body size, extremely slow maturation, limited growth period, and the necessity to heat when initiating the activity phase and also to cool quickly and escape overheating during the greater part of the sunny hours.

Central and West European mountain habitats, despite some modification since the Mesolithic (ca. 11000 – 6000 y BP), remained well conserved until very recently. Apart from the presence of grazing animal herds in summer pastures or the sporadic presence of hunters, there was very little human impact until the last century (FIELDING & HAWORTH 1999). Today there is a renewed interest in the fragile alpine biota, with an international year of the mountains – in 2002 – and numerous international programs and initiatives (KÖRNER 2003). Mountain areas are places of outstanding biodiversity richness and frequenty constitute hotspots sorrounded by more impoverished and humanized lowland areas. Not only large scale alpinism and winter sport leisure industry but also the current progressive climatic change could profoundly affect the mountain biota, leading to fragmentation and promoting speciation, but also if very rapid, to the disappearance of a number of species or communities, as has occurred during mild periods in the past, especially during the Pleistocene and Holocene (ARRIBAS 2004).

MATERIALS AND METHODS

Localities were surveyed from 1989 to 2002 in the framework of a complete study on the morphology, bionomy and geographical variation of this species (ARRIBAS 2000, 2002c, 2008c). *Iberolacerta bonnali* was found on various substrates in the Central Pyrenees. The main data from granodioritic (cristalline) substrate localities came from the Maladeta Massif (Estany de Llauset, Huesca, Spain; 42°35'09"N / 0°41'05"E; 2180-2300 m a.s.l.), limestone substrate data from Monte Perdido Massif (Ordesa, Huesca, Spain; 42°39'47"N / 0°0'50"E, 2000-2400 m a.s.l.) and data from siliceous localities (slates and schists) from Bigorre Massif (Lac Bleu, Hautes Pyrénées, France; 42°56'25"N / 0°4'33"E; 1928-2238 m a.s.l.). Data from isolated records were eliminated so that comparisons between the main types of localities could be accomplished.

Field data

From each specimen found active or under stones, the following information was taken:

* Date and hour (GMT).

* Activity [inactive, basking, and active]. Temperature data (see below) were taken from active specimens only.

* Sex [1 – males, 2 – females, and 3 – undetermined]. Undetermined specimens were used for global adult comparisons with young individuals only. There are data from 138 males, 143 females and 41 adults of uncertain sex.

* Aproximate age [adults (1, 2 and 3 – males, females, undetermined), subadults (young specimens), and hatchlings]. Subadults were classified in calendar-year age-classes ("40" if of undetermined age). Hatchlings of the year are in their "first calendar year" (1CY; "41"). After their first hibernation they are in their "second calendar year" (2CY; "42"). After their second hibernation they are in their "third calendar year" (3CY; "43"), etc. In total, 40 specimens from 1st CY, 11 from 2nd CY, 20 from 3rd CY, 4 from 4th CY and 1 of undetermined age were studied.

* Habitat structures (in percent): In a 2-meter radius around the first localization

spot of the animals, a visual estimate of percent cover of rocks, stones, bare ground, grass and shrubs was assessed. These percent covers (%) were calculated by means of visual estimation scales (PRODON & LEBRETON 1981; EMBERGER 1983).

* Slope (inclination in discrete categories: 0°-10°, 10°-20°, 20°-40°, 40°-50°, 50°-70°, 70°-80°, 80°-90°) was measured with a clinometer.

* Temperatures: Temperatures were taken (from active specimens only) with Schultheis-type thermometers (Wesco®, 0°-50° Centigrade, precision: ±0.1°C) from cloaca (body temperature, BT) within 20 seconds of their first localization, substrate (ST), and ambient air (AT) in the shadow 20 cm above the ground.

* Habitat availability was calculated by photointerpretation, overlaying a grid and calculating the percent covers in the different squares. In some instances, especially in dark rock areas, Infrared False Color Photography (Kodak Infrared EIR Film®) was used for sharp discrimination of vegetation (diverse tones of red, the more vivid the color the more photosynthetically active were the plants) from rock (diverse tones of gray) (KODAK-PATHÉ 1977; MILSON 2001).

* Availability and use of resources were compared by testing the null hypothesis of random selectivity, a Chi-square log-likelihood statistics (also known as *G*-test) ($p < 0.05$), and selection or avoidance of a habitat quantified by means of an electivity index (a normalized version of the forage ratio), the forage ratio or selection index: $w_i = o_i / p_i$; where w_i = forage ratio for the habitat category i; o_i = proportion or percent of the habitat category i used; p_i = proportion or percent of the habitat category i available in the environment (KREBS 1989, 1999).

These indexes are presented as standardized ratios, which sum up to 1.0 for all habitat categories. Standardized ratios of 1/(number of resources) (in our case, in the schist and granitoid localities: 1/6 = 0.16; and in the limestone localities where the shrubs category was eliminated because of its absence: 1/5 = 0.20) indicate no preference. Values below this indicate relative avoidance, and values above indicate relative preference (calculations are after KREBS 1989, 1999). Only deviations of more than 5% ($p < 0.05$) were considered and discussed in the text.

Statistical study

General statistical calculations were made with NCSS-2002® software (HINTZE 2001). Univariate comparisons among categories were done by ANOVA with Tukey-Kramer post-hoc multiple comparison tests. At $p < 0.05$, results are considered significant, at $p < 0.01$ highly significant. Concrete p values are given only in case of significance or near significance, otherwise only NS (not significant) is stated. Diversity measurements and selection indexes were calculated with Ecological Methodology® 6.1.1 software (KREBS 1999).

Comparisons were done in terms of:

a) Activity months: June (142 observations), July (133 observations), August (92 observations), September (15 observations).

b) Period of the year: Reproductive period (189 observations) and Post-reproductive period (193 observations). It was not useful to distinguish natural seasons as all the activity was centered around summer, but to divide the lizard's activity in "reproductive" (from the start of the activity until the clutch deposition) and "post-reproductive" (from clutch deposition until the end of the activity season) periods.

c) Sex and age: See above. Several comparisons were done, with all categories separated ("sex and age") as in Table 1 or grouped by classes of immatures and adults ("grouped sex and age": males, females and immatures), or simply by "age" (adults versus immatures).

d) Slope orientation: General orientation of the slope within the Pyrenean Range (i. e. south or north facing at the study site). There are 220 observations from north facing and 174 from south facing slopes.

e) Geological substrate: Lizards observed on granodiorite/granite (crystalline rocks, 68 observations), limestone (sedimentary rocks, 67 observations) and slate/schist (metamorphic rocks, 263 observations). For differences in habitat structures related to the diverse substrates see Table 2.

RESULTS AND DISCUSSION

Activity

There were no differences in the circadian activity schedule among sexes and ages (all classes separated) ($F_{6,322}$ = 1.23, NS). Overall daily activity of adults and juveniles is represented in Fig. 1. There were, however, differences in the activity among the different months ($F_{3,327}$ = 6.81, p = 0.00), especially when comparing August with June ($p < 0.05$) and September ($p < 0.01$) [June (n = 98; mean = 945.91±10.78; 659-1144), July (n = 124; mean = 955.13± 10.48; 716-1230), August (n = 93; mean = 996.81±11.8; 756-1537), September (n = 15; mean = 875.6± 22.43; 745-1045)]. In August, activity began slightly later than in June and September, but the small sample from this last month could have distorted the results. Differences between June and September can be explained by the shortening of the days as the summer advances; this progressively shifts the activity peak towards the late morning hours.

These differences were not significant when months were grouped and only reproductive and post-reproductive periods were compared (T = 0.21; NS). The same, no differences concerning the activity were found depending on the general slope orientation.

There were, however, differences in the activity between lizards on different substrates ($F_{2,328}$ = 3.54, p = 0.03), in concrete among slate/schist and limestone localities ($p < 0.05$) [granite (n = 56; mean = 966.48±12.05; 756-1200), limestone (n = 49; mean = 920.59±13.45; 716-1100), slate/schist (n = 225; mean = 967.76±8.17; 659-1537)]. On limestone, activity began and ended sooner than on slates. White limestone reflected the sunlight intensely and perhaps favored the early thermoregulation (by heliothermy) in these areas, whereas dark slates absorbed the heat and favored a slightly later heliothermy, but also the heating by tigmothermy in the meantime, out of sight, under flat stones, as was frequently seen in this and other *Pyrenesaura* species

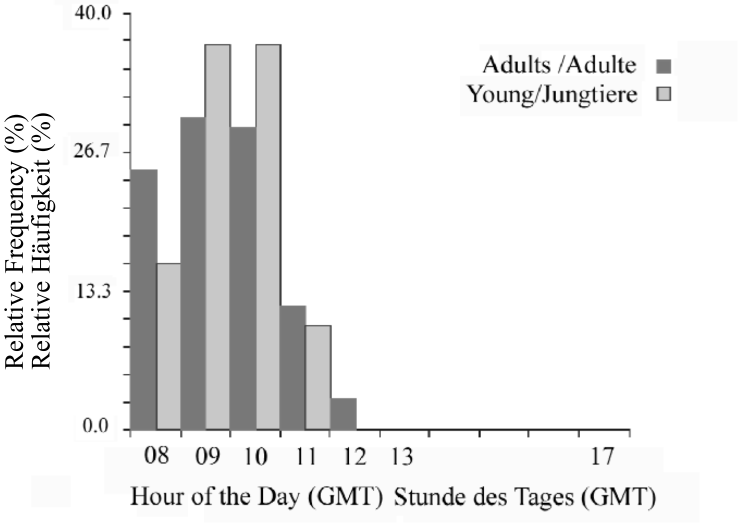


Fig. 1: Bar graph representing the relative frequency (percent of counts) of active adult (dark bars) and young (light bars) individuals of *Iberolacerta bonnali* over the hours of the day from June through September (n = 330). Activity was zero to low in the morning hours and during the afternoon

Abb. 1: Balkendiagramm zur Veranschaulichung der relativen Häufigkeit (Prozent Anzahl Individuen, percent of counts) aktiver adulter (dunkle Balken) und juveniler (helle Balken) *Iberolacerta bonnali* im Tagesverlauf. Die Aktivität war in den Morgenstunden und am Nachmittag sehr schwach ausgeprägt oder gleich null.

(ARRIBAS 2007). The intense heating of these dark slates possibly also permitted the lizards to continue their activity when the sky turned cloudy and air cooled rapidly at midday or during afternoon. The interaction between months and substrate was not significant ($F_{6,318} = 0.39$, NS).

In summer MARTÍNEZ RICA (1977) observed activity from 8:30 a.m. on, with a clear reduction from 13:00 to 18:00 p. m. and total retreat after this time. Hunting occurred from 8:30 until 10:30 a.m. In the present study there was very little or no activity in the later hours of the afternoon, when the rocks became excessively hot. In the Pyrenees, high mountain crests frequently shade lizard habitats already early in the afternoon. Thus, they remained protected from the sun and cooled rapidly during the second part of the day.

Like other members of the alpine biota, Pyrenean lizards were opportunistic with respect to the moment of their emergence from hibernation, in that they emerged when the snow melted, usually in the second half of May. However, they were very conservative as to the moment of their retreat to hibernate (photoperiod controlled), usually during the second half of September in adults, and the first half of October in juveniles (ARRIBAS 2004; ARRIBAS & GALAN 2005). When lizards began their activity, days were long, near to their maximum duration, and the sun rays reached the ground with high intensity and perpendicularly, leading to rapid retreat of the snow. During the activity season, day length shortens, which explains the progressive shift in the lizard's circadian activity schedule between June and September, when the length of the day declines to equal the length of the night. The temperature progressively cooled down from the sencond half of August, and frequently the first snow storms marked the time when the adult lizards disappeared followed by the young ones some days after (ARRIBAS 2004; ARRIBAS & GALAN 2005).

Daily lizard activity began not before the sun shined sufficiently to develop heliothermic behavior. It was observed that at times when the rocks were very cold, lizards flattened their bodies and raised them from the cold rock substrate in a very particular behavior (ARRIBAS 2007). Activity occurred from 7:00 to about 16:00 GMT, with its maximum in the morning. On clear and sunny days, the rocks became too hot to the lizards around midday; this made the lizards disappear and they only reappeared when clouds hid the sun or late in the afternoon. Orographic (storm) clouds frequently grew in the morning and progressively covered the sun towards midday, extending the daily activity of the lizards. In the Pyrenees, storms usually develop during midday (in the Alps later, during the afternoon), which is due to the contribution of moist air from the ocean that favors the early maturation of storms (THILLET 1997). In the study localities, there was very little lizard activity in the afternoon, due to clouds or the particular disposition of the orography that made the sun disappear behind mountain crests.

Lizard prey species (e.g., Orthoptera, Hemiptera, Coleoptera, Lepidoptera and Diptera) absorbed warmth in the morning well before they became active, but most species disappeared from the surface during the hours of the most intensive sunshine. The predator lizards paralleled the insects' activity pattern and would not forage at the hottest times of the day unless they were involved in more important activities such as reproduction. In the upper layers of the soil, the terricolous insect life is richest during the morning hours (about 9:00-10:00 a.m.) (MANI 1968), which coincided with the time of maximum lizard activity (see Fig. 1). Later in the morning, the insects move deeper into the ground and return in reduced number (or not at all as in many Diptera and some Hymenoptera) to the surface towards 16:00-17:00 p. m. (MANI 1968). Wind ceased insect activity and also that of the lizards (especially feeding), except in cases in which thermoregulation continued in the wind-sheltered side of the rocks (i.e. males at the beginning of the activity season or females during vitellogenesis).

Habitat characteristics

Habitat structures specified according to sex and age classes are presented in Table 1. A graphic representation of these values grouped by sex and age is available in Fig.

2. Significant acceptance or avoidance of different habitat characteristics occurred in all substrates and sex and age groups (Table 2; *G*-tests were all higly significant, $p << 0.01$), except for juveniles in limestone localities (small sample size).

Slope inclination

There were significant differences in the slope inclination (°) of the areas inhabited by lizards among the various months of the activity period ($F_{3,360} = 3.63$, $p = 0.01$). Differences were observed between July and August ($p < 0.05$) [June ($n = 124$; mean = 37.08±1.34; 0-80), July ($n = 133$; mean = 32.72±1.22; 0-90), August ($n = 92$; mean = 38.72±2; 5-80), September ($n = 15$; mean = 41.2±1.82; 30-50)]. However, inclination did not differ significantly by periods (reproductive versus post-reproductive) ($T_{362} = 0.29$, NS), sex and ages ($F_{6,356} = 2.14$, $p = 0.05$, and also not in post-hoc tests) (see Table 1), grouped by sex and ages ($F_{2,320} = 2.35$, NS) (Fig. 2), ages ($T = 0.78$, NS), or substrate types ($F_{2,361} = 1.63$, NS). Thus, lizards seemed to inhabit slightly steeper slopes during August than in July, but differences were not very consistent as they were not maintained over longer periods (i.e. reproductive and post-reproductive).

Consistent differences were found concerning the general orientation of the slopes ($T = 2.83$; $p = 0.00$) [north facing slopes ($n = 217$; mean = 37.98±1.23; 0-90), south facing slopes ($n = 147$, mean = 33.25±0.88; 0-70)]. It was obvious that lizards from north facing localities inhabited steeper areas than those of the south facing slopes, but this difference was not based on the lizards' different preferences but an imposition of the physiognomy of the habitats available and the particular localities studied. The interaction between the differences in the months and the general orientation of the slopes was not significant. There was no active selection concerning the slope inclination at any age, sex or substrate type (Table 2).

As a rule, the richest mountain animal and plant communities appear in plane and moderately sloped areas that do better in retaining water and snow (Mani 1968).

Proportion of rocks

Proportion of rocks forming the surface of places where lizards were first-sighted did not vary by month ($F_{3,378} = 2.34$, NS) nor by period (reproductive versus post-reproductive) ($T_{380} = 0.06$, NS), sex and ages ($F_{6,374} = 0.80$, NS) (Table 1), grouped by sex and ages ($F_{2,338} = 0.28$, NS) (Fig. 2) or simply by ages ($T = 0.89$, NS).

However, the proportion (%) of rocky surfaces on lizard sites was correlated with the general orientation of the slopes ($T = 3.10$; $p = 0.00$) [north facing slopes ($n = 217$; mean = 48.77± 1.54; 0-100), south facing slopes ($n = 165$, mean = 56.41±2.01; 0-100)]. Lizards from south facing slopes inhabited areas where more parent rock (bedrock) was present than in lizard sites from north facing slopes ($p < 0.01$), which was a locality imposition rather than the lizards' selection. There were also differences in the proportion (%) of rock cover among different substrate types ($F_{2,379} = 12,38$, $p = 0.00$) [granodiorite ($n = 65$; mean = 64.46±3.06; 0-100), limestone ($n = 64$; mean = 54.53± 2.8; 10-100), slate/schist ($n = 253$; mean = 48.33± 1.49; 0-100)]. In the lizard localities, the proportion (%) of rocky surfaces was notably greater on granodiorite than on limestone ($P < 0.05$) and slate/schist ($p < 0.01$). There was no interaction between differences in the general orientation of the slopes and the substrate type.

Regarding the selection of rocks by lizards there were obvious differences among the substrate types (Table 2). On slates and schists, rocks were clearly positively selected by all sexes and ages. In limestone areas there was a slight (NS) avoidance of bare rocks, whereas on granodiorite females (NS) and juveniles positively selected the rocks for their activity (for significances see Table 2).

This paragraph on rocks as an extreme habitat in high mountains largely reflects the considerations of Mani (1968). The rock surface is exposed to full force of sunlight and it is baked hot and dry during the hours of intense insolation. Evaporation is strong and the diurnal and seasonal temperature changes are the highest when compared to other habitats. If directly exposed to sunlight, rock surface heats rapidly, but remains as cool as the air if in the shadow. A cloudy halfhour can bring down the rock surface temperature even below that of the air minimum in the shade. Differences between air and surface rock temperature are near 20°C at a distance of 10 cm or 30°C at 15 cm. However, if retreated under stones, lizards can cool rapidly. Under stones, lizards become sheltered from wind and intensive insolation, the evaporation being very low (10°C-22°C temperature and 80-95% sometimes even 100% relative humidity). Relative humidity is lowest in the air layer inmediately above the rock surface and the rate of evaporation is, therefore, extremely high. Microclimate stability in the lapidicolous environment is directly correlated with the size of the stones, but the hypolithion (communities of the interstice between and under the stones) is the most important community in high mountain areas and practically reaches its climax here.

Rocks offered protection against cold winds. The temperatures of wind-sheltered specimens were much higher than of specimens in the open air (up to 22°C of difference measured in *I. bonnali*, 32°C BT vs. 10°C AT in June 1996 in Estany de Cavallers, on a granodiorite rock substrate). Cooling is fairly more intensive in horizontal than in vertical surfaces (KÖRNER 2003).

There were also differences among populations living on different kinds of substrates: white limstones reflected the sunlight intensely and perhaps favored the early thermoregulation, whereas dark slates absorbed the heat intensely by its dark tone and favored a slightly later appearance of the specimens, however, yet with partially heated bodies by tigmothermy under these flat and thin slabs.

Heat retention by the dark slates also enabled lizards, to a greater extent than limestone or granodiorite, to continue activity if the sky turned cloudy and the air cooled rapidly. There was very little or no activity in the first hours of the afternoon, when the rocks became too hot by continuous insolation or too cool if the weather turned bad.

The proportion of the substrate categories present (stones, bare soil, shrubs, grass) was determined by the kind of bedrock prevailing (i.e. in general, slates have less parent rock with more stones and bare earth than other geologic substrates).

Proportion of stones

Proportion of stones in spots where lizards were observed differed among months ($F_{3,378}$ = 8.30, p = 0.00)[June (n = 142; mean = 15.26±1.51; 0-80), July (n = 133; mean = 14.75±1.76; 0-100), August (n = 92; mean = 6.58±1.14; 0-60), September (n = 15; mean = 0)]. Differences were observed between June and July relative to August ($p < 0.01$) and September ($p < 0.05$). The proportion of loose stones was higher in the lizards' habitats occupied during the first half of the summer, which was paralleled by differences by periods (T_{380} = 4.26, p = 0.00) [reproductive (n = 189; mean = 16.20±1.35; 0-80), post-reproductive (n = 193; mean = 8.67±1.14, 0-100)]. In conclusion, lizards preferred stony areas during the reproductive period ($p < 0.01$) compared to the later activity season.

There were differences in the proportion of loose stones depending on the kind of geologic substrate ($F_{2,379}$ = 3.58, p = 0.03) [granodiorite (n = 65; mean = 7.15±2.3; 0-100), limestone (n = 64; mean = 12.78±2.29; 0-80), slate/schist (n = 253; mean = 13.65± 1.07; 0-95)]. Differences in the proportion of loose stones covering the surface were found between localities on granodiorite (low) and slate/schist ($p < 0.05$). This agrees well with the meteorization process of these rock types. Granodiorite rocks disgregate directly into sands, and limestones (even with intermediate sized stones coming from karstic processes) to clay, without leaving stones of intermediate size, whereas slate/schist parent rock meteorizes into a lot of small-sized stones that are very abundant in the ground. This could explain the positive selection of parent rock, which produces an overabundance of loose stones (platelets and minute schist fragments) in the latter geological substrates.

The interaction between months and geologic substrates was highly significant ($F_{6,370}$ = 8.42, p = 0.00) and these differences seemed to be sustained especially by the temporal factor ($F_{3,370}$ = 2.75, p = 0.04), confirming that lizards utilized stones of different size during the different months of the activity period.

There were no differences by sex and ages ($F_{6,374}$ = 0.68, NS) (Table 1) nor grouped by sex and ages ($F_{2,338}$ = 0.8, NS) (Fig. 2), or simply by ages (T = 0.21, NS). Also, there were no differences depending on the general orientation of the slopes (T = 1.13; NS).

In slate/schist localities loose stones (grit) were counterselected by all sexes and ages, on limestone grit was positively selectioned by adults, and on granodiorite loose stones were but slightly preferred by males and juveniles (Table 2).

In general all the Pyrenean lizard species are inhabitants of rocky areas (mirrored by their common name "Rock Lizards"). Within these rocky areas, they utilize various kinds of microhabitats for hunting and sheltering, not only parent bedrock. *Iberolacerta bonnali* was observed in stony areas (parent rock meteorized) more frequently in June and July, during the reproductive period, than in August and September (postreproductive). Possibly this is due to the increased range covered by the specimens, especially males, during the reproductive period.

In conclusion stones are more abundant than parent rock in slate/schist localities but not in granodiorite sites, due to particularities of the meteorization process. In the slate/schist localities stones were so abundant that they were comparatively counterselected by all sexes and ages. Stones were positively sought out by adults on limestone localities (instead of parent rock, they selected more loose rock areas), and only slightly preferred by males and juveniles (but not by females) in granodiorite areas. Size of the stones utilized by the lizards during the months of the activity period differed among the different geologic substrates.

In fact, there was a correlation between the abundance (density) of *I. bonnali* and the kind of substrate prevailing. Granodiorite rocks were poorer in lizards (and fissures) than the slab-covered slopes of slate/schist localities or the deeply carved "lapiaz" areas in limestone regions, where *I. bonnali* was more abundant (ARRIBAS 2002c, 2007).

Proportion of bare soil

The proportion of bare soil in areas where lizards were first spotted differed among months ($F_{3,378}$ = 4.43, p = 0.00) [June (n = 142; mean = 8.26±1.51; 0-50), July (n = 133; mean = 5.93±0.95; 0-75), August (n = 92; mean = 5.09±0.69; 0-25), September (n = 15; mean = 0)]. Differences were found between the two extremes of the activity period, June and September ($p < 0.05$), suggesting that lizards frequented areas with a higher proportion of bare soil at the beginning of the active season.

There were also differences in the proportion of bare soil regarding the general orientation of the slopes (T = 5.94; p = 0.00) [north facing slopes (n = 217; mean = 8.91± 0.69; 0-50), south facing slopes (n = 165, mean = 3.02±0.68; 0-75)]. In localities of the north facing slopes, lizards were more frequenly found on bare soil. Differences were also found in terms of the kind of substrate ($F_{2,379}$ = 9.43, p = 0.00) [granodiorite (n = 65; mean = 3.10± 0.91; 0-40), limestone (n = 64; mean = 3.54± 1.41; 0-75), slate/schist (n = 253; mean = 7.91±0.62; 0-50)]. The proportion of bare soil was higher in slate/schist areas than in places where other substrates were present. Significant differences in the proportion of bare soil were observed between granodiorite localities (low) and slate/schist ($p < 0.05$). This result is well in accordance with the characteristics of the meteorization process of these rock types. The interactions of the differences in these factors (general slope orientation, geologic substrate and months) are not significant in all cases.

Differences in the proportion of bare soil utilized were insignificant (however close to significance) in comparisons by periods (T_{380} = 1.90, p = 0.06) [reproductive (n = 189; mean = 7.35±0.75; 0-50), postreproductive (n = 193; mean = 5.4 ±0.68, 0-75)] and by ages (T = 1.93, p = 0.05) [adults (n = 310; mean = 5.9±0.55; 0-75) and juveniles (n = 71; mean = 8.45±1.29; 0-40)] whereas differences by sex and ages ($F_{6,374}$ = 1.09, NS) (Table 1), and grouped by sex and ages ($F_{2,338}$ = 2.34, NS) were clearly not significant (Fig. 2). Young specimens were more frequently spotted on bare ground than adults.

Table 1: Habitat structures, activity hours and temperatures of body (BT), air (AT) and substrate (ST) for all the sex and age classes of *Iberolacerta bonnali* studied. First line: arithmetic mean ± standard error. Second line: minimum and maximum values. The sample named adults includes the males and females plus 41 specimens of undetermined sex. Temperatures refer to active specimens.

Tab. 1: Habitatstrukturen, Aktivitätszeiten, Körper (BT), Luft- (AT) und Substrattemperaturen (ST) für Individuen aller Geschlechter- und Altersklassen von *Iberolacerta bonnali*. Zeile eins: arithmetischer Mittelwert ± Standardfehler; Zeile zwei: Minimum und Maximum. Die Stichprobe der Adulten beinhaltet die Männchen und Weibchen sowie 41 Exemplare unbestimmten Geschlechtes. Temperaturangaben beziehen sich auf aktive Individuen.

Sex / Age Geschl. / Alter	Males Männchen (n = 133)	Females Weibchen (n = 136)	Hatchlings (1CY) Schlüpflinge (1LJ) (n = 36)	Inmatures (2CY) Jungtiere (2LJ) (n = 11)	Inmatures (3CY) Jungtiere (3LJ) (n = 20)	Inmatures (4CY) Jungtiere (4LJ) (n=4)	Adults Adulte (n = 310)	Young Jungtiere (n = 71)
Hour GTM	969±10.54	960±12.31	941±19.29	984±22.29	996±21.29	972±30.68	959±7.33	965±12.3
Uhrzeit GTM	730-1230	716-1537	659-1200	828-1100	809-1152	914-1026	716-1537	659-1200
Slope (º)	37.49±1.41	33.84±1.54	31.58±2.02	32.27±3.32	39.25±2.27	?5±6.12	36.45±0.97	34.60±1.42
Hangneigung (°)	0-90	0-80	5-60	5-45	30-60	30-60	0-90	5-60
% Rocks	52.70±2.16	50.86±2.08	48.86±3.79	52.72±7.01	51.5±5.62	42.5±10.3	52.71±1.40	49.84±2.73
% Fels	0-100	0-100	0-100	20-90	15-100	20-70	0-100	0-100
% Stones	11.35±1.54	13.24±1.63	13.16±3.02	10.45±3.78	10.6±2.45	27.5±17.01	12.34±1.01	12.83±2
% Steine	0-100	0-95	0-60	0-40	0-40	0-70	0-100	0-70
% Bare Soil	6.09±0.97	5.25±0.69	8.66±2.19	9.09±2.31	6.9±1.51	12.5±7.77	5.9±0.55	8.45±1.29
% Kahlboden	0-75	0-50	0-40	0-25	0-25	0-35	0-75	0-40
% Bushes	7.59±1.22	7.47±1.20	3.19±1.63	8.18±3.71	13±3.31	5±5	7.53±0.79	6.83±1.46
% Buschwerk	0-70	0-70	0-40	0-35	0-50	0-20	0-70	0-50
%Grasses	21.50±1.96	23.56±1.87	25.55±3.17	19.54±5.53	18±3.67	12.5±5.95	20.75±1.23	21.76±2.14
% Grasfläche	0-90	0-90	0-60	0-60	0-60	5-30	0-90	0-60
TB (ºC)	28.78±0.38	28.73±0.41	28.96±1.12	27.8±0	27.31±0.74	-	28.76±0.28	28.02±0.56
Körper-	23.2-35.2	20.8-33.4	25.5-32.5	27.8-27.8	24.0-29.3	-	20.8-35.2	24.5-32.5
temperatur	(n = 54)	(n = 49)	(n = 5)	(n = 2)	(n = 6)	-	(n = 103)	(n = 13)
TA (ºC)	16.51±0.53	16.23±0.6	20.46±2.14	18.6±1.4	13.02±1.53	-	16.38±0.4	17.05±1.47
Lufttemperatur	9.4-25.4	8.9-27.4	14.6-27.1	17.2-20	9.4-18.7	-	8.9-27.4	9.4-27.1
TS (ºC)	24.55±0.93	24.54±.94	22.26±4.9	23.25±2.05	20.9±1.65	-	24.54±0.66	21.89±2.25
Substrattemp.	9.9-41.4	10.1-41.8	5.6-34.8	21.2-25.3	16.6-25.6	-	9.9-41.8	5.6-34.8

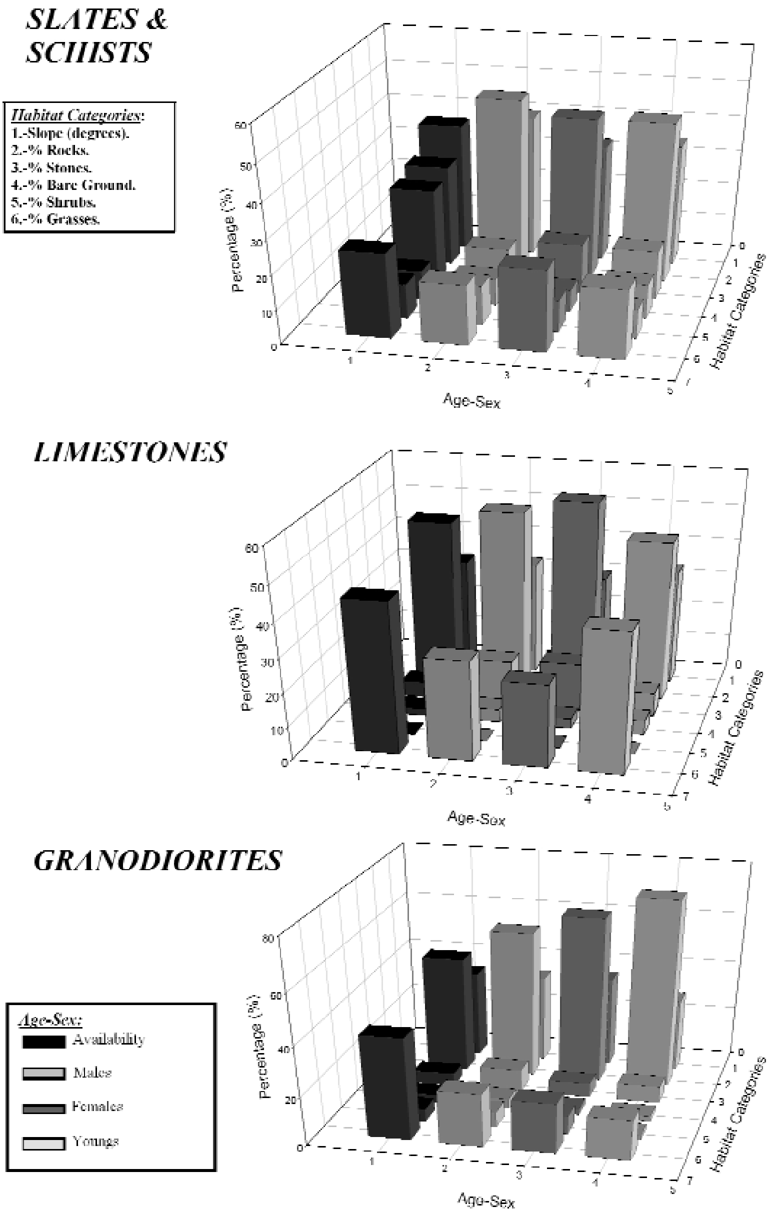


Fig. 2: The utilization (%) of six habitat categories (1-slope inclination, 2-rocks, 3-stones, 4-bare ground, 5-shrubs, and 6-grassy spots) by males (2), females (3) and young (4) *Iberolacerta bonnali*, and the availability of these structures (1) in the substrate types slate/schist, limestone and granodiorite/granite.

Abb. 2: Die Nutzung (%) von sechs Habitatkategorien (1-Hangneigung, 2-Fels, 3-Steine, 4-nackter Boden, 5-Gebüsch, 6-Grasflächen) durch Männchen (2), Weibchen (3) und Junge (4) von *Iberolacerta bonnali* und die Verfügbarkeit dieser Strukturen (1) auf Schiefer (slate/schist), Kalkstein (limestones) und Granodiorit/Granit.

There was a weak preference of bare soil in the different sexes, ages or substrates (very low in males and more pronounced in juveniles on limestone) (Table 2).

As with the stony areas, the proportion of bare soil occupied by lizards was highest at the beginning of the active season (June), i.e. during the breeding period when lizards moved most intensively. Young specimens representing the most mobile age class in lizards, were more frequently spotted on bare ground than adults. This was to be expected in the most dispersive phase of the species.

In the Alps dark humic grounds exposed to full sunlight, were registered to heat up to temperatures of 80°C (TURNER 1958), and even more dry mosses or grounds lacking evaporative cooling effects. Temperatures lethal to lizards were easily reached there.

Proportion of shrubs

Although small shrubs (usually *Erica*, *Calluna* or *Rhododendron*) were not rare in the lizard localities, they were usually absent in the lizards' microhabitats proper. There were differences among months ($F_{3,378}$ = 5.99, p = 0.00) [June (n = 142; mean = 5.99±1.15; 0-70), July (n = 133; mean = 6.2±1.05; 0-50), August (n = 92; mean = 12.33±1.55; 0-70), September (n = 15; mean = 3.3±3.3; 0-50)], in particular between August with respect to June (p < 0.01) and July (p < 0.05). Lizards increasingly utilized shrub-covered areas in the hottests parts of the summer (probably searching for shade). These differences were not observed when analyzed by periods (T_{380} =1.90, p = 0.06) suggesting that they were not linked to the phenology of the species but to its thermal biology. However, there were differences regarding the general slope orientation (T = 5.58; p = 0.00) [north facing slopes (n = 217; mean = 10.6± 1.05; 0-70), south facing slopes (n = 165, mean = 3.39± 0.75; 0-50)]. In the south facing slopes there were less shrubs in the areas inhabited by lizards than in localities of the north facing slopes. Differences in the proportion of shrubs did also depend on the kind of substrate ($F_{2,379}$ = 12.87, p = 0.00) [granodiorite (n = 65; mean = 7.27±1.61; 0-50), limestone (n = 64; mean = 0±0; 0-0), slate/schist (n = 253; mean = 9.45±0.94; 0-70)]. Shrubs did not exist in limestone localities, whereas they were present on the other substrates (p < 0.01 in both comparisons). The interactions of differences in the factors general slope orientation, geologic substrate and months were not significant. There were no differences by sex and ages ($F_{6,374}$ = 1.17, NS) (Table 1), grouped by sex and ages ($F_{2,338}$ = 0.10, NS) (Fig. 2) or simply by ages (T = 0.39, NS).

On granodiorite substrate a slight preference of shrub areas was observed in females and a slight avoidance in juveniles. No significant trend was seen on slate/schist, whereas in the limestone areas shrubs were not utilized because they were absent (Table 2).

In places where shrubs were present, lizards increasingly frequented shrub-covered areas in the hottests parts of the summer (searching for shade) *Rhododendron ferrugineum* thickets were more frequent in north facing slopes. These *Rhododendron* formations ecologically function like miniaturized dense forests for small animals and are usually not used by mountain lizards.

Proportion of grass (herbaceous vegetation)

Herbaceous vegetation (diverse species of the genera *Festuca*, *Kobresia*, *Nardus* that constitute the alpine pastures and their accompanying mono- and dicotyledonean species) was fairly abundant in areas inhabited by lizards and frequently constituted their hunting grounds. There were differences in the proportion of the herb cover among months ($F_{3,378}$ = 3.45, p = 0.00) [June (n = 142; mean = 15.63±1.51; 0-80), July (n = 133; mean = 25.54±1.8; 0-90), August (n = 92; mean = 18.58±2.3; 0-80), September (n = 15; mean = 45.33±4.74; 10-70)], in particular between June with respect to July (p < 0.01) and September (p < 0.01), between August and September (p < 0.01) and between July and September (p < 0.01). In June (reproductive period) lizards occupied grassy areas to a minor degree than during the rest of the activity period. The proportion of grassy habitats utilized increased during July (maximum vegetation growth), decreased slightly in August (drought period) and increased strongly again in September relative to the other months. The proportion of grass in the habitats utilized by the lizards differed by periods ($T_{380} = 3.69$, $p = 0.00$) [reproductive ($n = 189$; mean = 17.01±1.26; 0-80), post-reproductive ($n = 193$; mean = 24.83±1.69, 0-90)] with a clear increase in the post-reproductive period, linked to the growth of the vegetation over the summer and to the shift of the lizards' activities towards alimentation in these more grassy areas.

In addition, differences in the proportion of the herbaceous vegetation depended on the general slope orientation ($T = 4.31$; $p = 0.00$) [north facing slopes ($n = 217$; mean = 17±1.22; 0-80), south facing slopes ($n = 165$, mean = 26.16± 1.82; 0-90)]. In the north facing slopes there was less grass in the lizards' areas than in south facing slope localities ($p < 0.01$). There were also differences depending on the kind of substrate ($F_{2,379} = 5.39$, $p = 0.00$)[granodiorite ($n = 65$; mean = 19.27±2.66; 0-80), limestone ($n = 64$; mean = 28.75±3.14; 0-90), slate/schist ($n = 253$; mean = 19.42±1.21; 0-90)]. Limestone localities showed a considerable greater surface proportion of grasses than siliceous grounds (granite and slate/schist) ($p < 0.05$ relative to granodiorite, and $p < 0.01$ with respect to slate/schist). The interactions of differences in the factors general slope orientation, geologic substrate and months were not significant. There were no significant differences by sex and ages ($F_{6,374} = 3.15$, $p = 0.01$) (Table 1), grouped by sex and ages ($F_{2,338} = 0.34$, NS) (Fig. 2) or simply by ages ($T = 0.36$, NS).

Preference or avoidance of grassy areas was not clearly expressed in slate/shist localities, but grassy places seemed to be counterselected in limestone and granodiorite areas by all sexes and ages (Table 2). The proportion of grass present in the lizard localities increased along the vegetative season; it was lower at the beginning of the summer than during the post-reproductive period, and increased in parallel to the growth of the vegetation and the shift of the lizards' activities towards alimentation grounds in the more productive grassy areas. These differences in the proportion of the grass cover may be due to both the permanence of snow on the ground and the moment of the lizards' first emergence in relation to the vegetative period (grass is still to grow). On the other hand lizards might simply prefer rocky areas where visibility is better among conspecifics displaying their territorial behavior or where thermoregulatory conditions are more favorable to start reproductive activities. In September there was a considerable increase in utilizing spots covered by herbaceous vegetation, which seemed to be due to the presence of dispersive juveniles that ventured out in more open areas (ARRIBAS unpublished). It is known that any kind of vegetation (even mosses or lichens) retards wind speed and thus evaporation.

Thermoregulation

In high mountain regions sun rays penetrate an atmosphere, which is extremely clear and transparent before they heat material particles (gas molecules in the air, or solid structures like lizards or rocks). Heat is a measure of the vibration of the atoms, with the heat capacity being higher in dense objects like solids (heliothermic lizards or rocks), than in loosely packed objects like gases (air layer around dense objects).

Based on the author's observations, the process of heating in these lizards is first by heliothermy (along with the heating of the substrate), and later by tigmothermy (by contact with the increasingly warming substrate) up to their preferred temperatures. In the mountains, low air temperature is a problem for a basking lizard, which wants to increase its temperature, but on the other hand helps to dissipate the excess of heat when the substrate becomes too hot (usually very fast in summer), especially in dark colored rocks, such as slates or schists.

Thermoregulation happens in lizards that actively use behavioral or physiological adjustements to: a) control and finetune their body temperature in addition to what would result from passive heating through the environment (passive heating with lack of thermoregulatory behavior) and b) maintain the body temperature within a preferred interval (CASTILLA et al. 1999).

Body temperatures (BT)

The mean cloacal body temperature (BT) in active *I. bonnali* was 28.96±0.24°C (from 20.8°C to 35.2°C). Body temperatures did neither differ significantly among the activity months (close to significance; September temperatures were lower, but the sample was small) ($F_{3,112} = 2.64$, $p = 0.05$) [June ($n = 53$; mean = 28.22±0.43; 20.8-35.2), July ($n = 32$; mean = 29.15±0.42; 24.2-33.3), August ($n = 24$; mean = 29.56±0.41; 26.8-33.2), September ($n = 7$; mean = 26.91 ±0.93; 24.4-32)], nor by periods ($F_{1,114}$ = 2.79, NS) with a very slight but not significant increase in the post-reproductive period. Also there were no differences by sex and ages ($F_{4,111}$ = 0.44, NS) (Table 1) or grouped by sex and ages ($F_{2,113}$ = 0.41, NS), simply by ages ($F_{1,114}$ = 0.81, NS), by the general slope orientation ($F_{1,114}$ = 0.10; NS), nor the kind of substrate ($F_{2,113}$ = 0.74, NS).

Contrary to the author's previous view, there were no differences in body temperatures among lizards dwelling in different types of substrates, nor in different moments of the activity season nor by sexes or ages. This reveals that these lizards are fairly good thermoregulators that maintain their optimum temperatures independently of the moment, habitat thermal constraints and other circumstances. This fact also goes with the phenomenon of the so-called thermal rigidity (VAN DAMME et al. 1989), in that lizard species, if free from other constraints, frequently show fairly constant intraspecific mean temperatures.

Air temperatures (AT)

Air temperatures at which lizards were found active differed among the activity months and corresponded to the rise of temperatures over the summer ($F_{3,107}$ = 8.33, $p = 0.00$). Significant differences were reached between August and June ($p < 0.01$) and August and September ($p < 0.05$) [June ($n = 50$; mean = 14.98±0.50; 8.9-21.9), July ($n = 31$; mean = 17±0.68; 11.1-27.4), August ($n = 23$; mean = 19.46±0.77; 14.1-27.1), September ($n = 7$; mean = 14.62± 1.79; 9.4-22.8)]. Correspondingly, air temperatures near by active lizards differed by periods ($F_{1,109}$ = 6.26, $p = 0.01$) with lower temperatures during the reproductive than post-reproductive period ($p < 0.05$)[reproductive ($n = 65$; mean = 15.65±0.47; 8.9-27.4), post-reproductive ($n = 46$; mean = 17.54± 0.63, 9.4-27.1)]. There were no differences by sex and ages ($F_{4,106}$ = 0.28, p = 0.06) or grouped by sex and ages ($F_{2,103}$ = 0.20, NS), simply by ages ($F_{1,109}$ = 0.28, NS) or by the general slope orientation $F_{1,109}$ = 2.67; NS). There were differences, however, depending on the type of substrate ($F_{2,108}$ = 3.22, $p = 0.04$), with differences between limestone and slate localities ($p < 0.05$) [granodiorite ($n = 14$; mean = 15.91± 0.81; 10-20.4), limestone ($n = 35$; mean = 15.18± 0.63; 9.4-22.8), slate/schist ($n = 62$; mean = 17.29±0.54; 8.9-27.4)]. Some few centimeters above ground slate/schist localities (with dark rocks) became hotter than limestone sites (with brighter or even white rocks). The interactions of differences in these factors (geologic substrate and months) were not significant. Differences in AT were compensated by active thermoregulation and did not influence the lizards' BT.

Substrate temperatures (ST)

Substrate temperatures at which lizards were found active did not differ significantly among months ($F_{3,108}$ = 1.72, NS), or periods ($F_{1,110}$ = 3.89, $p = 0.05$), with lower temperatures during the reproductive than post-reproductive period [reproductive ($n = 66$; mean = 23.9±0.87; 5.6-41.8), post-reproductive ($n = 46$; mean = 25.73±0.90, 11.3-40.3)]. There were also no differences by sex and ages ($F_{4,107}$ = 0.48, NS), grouped by sex and ages ($F_{2,109}$ = 0.87, NS), simply by ages ($F_{1,110}$ = 1.76, NS), by the general slope orientation ($F_{1,110}$ = 1.37; NS), or the type of substrate ($F_{2,109}$ = 3.42, $p = 0.04$). Despite the higher mean and extreme temperatures of the dark slates and schists, the substrates' temperatures did not differ significantly [granodiorite ($n = 14$; mean = 22.32± 0.91; 17.4-28.5), limestone ($n = 35$; mean = 22.38±1.34; 9.9-40.3), slate/schist ($n = 63$; mean = 25.69± 0.8; 5.6-41.8)]. When exposed to the sun, dark rocks absorb heat more rapidly than pale rocks, but otherwise loose it more quickly, e.g. when shaded. The heat radiation emitted by cooling dark rock warms the air layer next to the rocks and could be responsible for the phenomenon that in spite of similar rock temperatures, the air temperatures were clearly different between localities on dark and pale rock.

Thermoregulatory behavior

Body temperatures (BT) and their relationships with both air (AT) and substrate temperatures (ST) are shown in Fig. 3.

In the present study, *I. bonnali* was found to have a mean BT of 28.67°C (20.8°C-35.2°C). Body temperature was better correlated with the temperature of the substrate ($r = 0.37$; $p = 0.00$) than of the ambient air ($r = 0.33$; $p = 0.00$). This difference was still present when the effect of the third variable was extracted (partial correlation, TB-TS extracting TA effect: $r = 0.27$; TB-TA extracting TS effect: $r = 0.21$).

Slopes were significantly different from 1 (if there was no thermoregulatory behavior, the lizards' rhythm of heating up would exactly have paralleled the heating rhythm of the substrate, with slope = 1). In the relationship of BT and ST, the slope was 0.14 (BT = 25.2154 + 0.1478 ST; $R^2 = 0.1388$), whereas it was 0.21 in the relationship of BT and AT (BT = 25.3176 + 0.2130 AT; $R^2 = 0.1110$). Thus, *I. bonnali* thermoregulated more distinctly relative to the substrate than to the air temperatures.

Low slopes tell us that the lizards are good thermoregulators, but low correlations suggest that they are not very precise in adjusting their body temperatures. With respect to ST (slope = 0.14), *I. bonnali* was very similar to *I. aranica* (slope = 0.11) and both high-mountain lizards were clearly better thermoregulators than the mid-mountain species *I. monticola* (slope = 0.30) and *I. horvathi* (MÉHELY, 1904) (slope = 0.55). As to AT, *I. bonnali* (slope = 0.21) was the best thermoregulator, very similar to *I. aranica* (0.28) and clearly better than *I. monticola* (0.52) and *I. horvathi* (0.76).

In its accuracy to adjust the BT, *I. bonnali* was not very precise as correlations with ST and AT were not very high (BT-ST: $r = 0.37$; BT-AT: $r = 0.33$), and very similar to *I. aranica* (0.37 and 0.42, respectively - ARRIBAS 2007), whereas *I. monticola* (0.55 and 0.56 - ARGÜELLO & SALVADOR 1988) and especially *I. horvathi* (0.64 and 0.77 - DE LUCA 1992) were obviously more precise in adjusting their temperatures.

The thermal behavior of *I. bonnali* is unique and interesting, as in related lizards (and in general) BT is usually closer (cor)related to AT than to ST. However, in these high mountain lizards, AT usually did not rise so much during the day but was very oscillant and could change dramatically within minutes, whereas rocks (ST) heated up easily, especially if dark colored. The high mountain environment, obviously led to the development of lizards which are good thermoregulators and adjust their body temperatures especially relative the cold air and the extremely hot substrate.

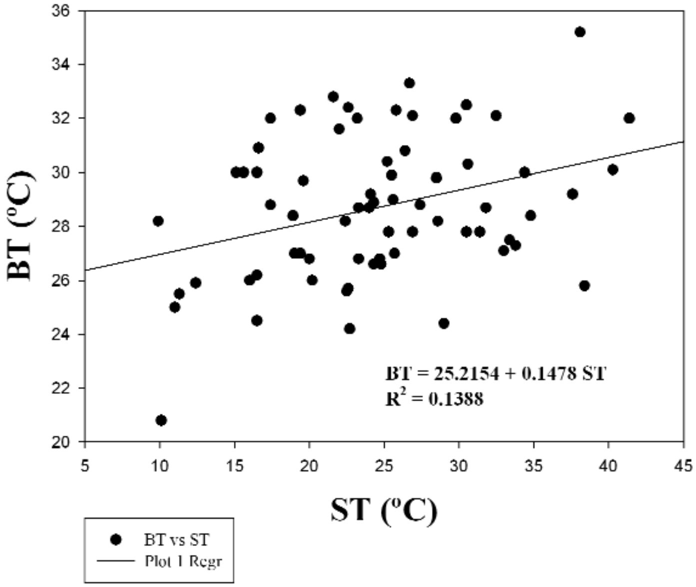
Regarding to its thermoconformism (i. e. the range of temperatures of activity, BT total range), *I. bonnali* (total range of activity temperatures 14.4°C) is very similar to *I. monticola* and *I. horvathi* (15°C - ARGÜELLO & SALVADOR 1988; DE LUCA 1992), all of them being slightly less tolerant than in *I. aranica* (17.9°C - ARRIBAS 2007).

When studying *I. bonnali*, MARTINEZ-RICA (1977) found the slope of the correlation BT-ST to be steeper (0.55 – which would mean much less thermoregulatory capacity than observed in the present study), the correlation among both variables very strong ($r = 0.78$), and the body temperature to average 33.6°C, which is rather high for *Iberolacerta* (see above). This author reported abnormally high BTs for the species (several measurements of 37, 38 and 39°C) close to accidentally observed lethal temperatures for the species (40.6°C, preceded by trembling and uncoordinated movements at 39.2 to 39.6°C; ARRIBAS 2007), whereas in the present study the temperature of active specimens was never higher than 35.2°C. MARTINEZ-RICA (1977) interpreted his data in the way that *I. bonnali* would lack an ecological mechanism of stabilization of its temperatures due to the fact that the variability (variance) of its body temperature was greater than of the substrate, and intermediate between the AT and ST. MARTINEZ-RICA (1977) also found that BT did not differ significantly from ST during summer, and that this species would not regulate its body temperature during the hottest hours of the day. All these surprising results may be due to an error-prone meas-

Table 2 (following page): Habitat structures at the spotting sites of active *Iberolacerta bonnali* (males, females and young specimens) on three types of substrate (slate/schist, limestone and granodiorite) and selection of these with respect to their availability (AV). First line: arithmetic mean ± standard error. Second line: in parentheses, minimum and maximum values. Third line: selection index, (*w*, see Materials and Methods). Fourth line: standardized proportions (which sum up to 1.0 in each column for all habitat categories) given as %. Positive or negative signs indicate selection or counterselection. Only deviations above 5% ($p < 0.05$) are considered and discussed in the text. In the lower part of the table, *G*-test values and their probability are indicated. Significant selection or counterselection of different habitat characteristics was found for all substrates, sex and age groups except for juveniles in limestone localities.

Tab. 2: Habitatstrukturen im Fundbereich aktiver *Iberolacerta bonnali* (Männchen, Weibchen, Jugtiere) auf den drei Substrattypen (Schiefer, Kalkgestein, Granodiorit) und deren Nutzung in bezug zu ihrer Verfügbarkeit (AV). Zeile eins: arithmetischer Mittelwert ± Standardfehler; Zeile zwei: in Klammern, Minimum und Maximum; Zeile drei: Auswahlindex (*w*; siehe Material und Methoden); Zeile vier: standardisierte Anteile in % (ihre Summen betragen innerhalb der Spalten 1,0). Positive und negative Vorzeichen weisen auf Nutzung bzw. Vermeidung hin. Nur Abweichungen über 5% ($p < 0.05$) werden betrachtet und im Text diskutiert. Im unteren Tabellenbereich sind *G*-Test Werte und ihre Wahrscheinlichkeiten angegeben. Signifikanz in Zuspruch bzw. Vermeidung bestimmter Habitatmerkmale fand sich bei allen Geschlechter- und Altersklassen auf allen Substrattypen außer bei Jungtieren auf Kalkgestein.

	Slates and Schists / Schiefer				Limestones / Kalke				Granodiorite (Granites) / Granite			
Sex /Age Geschl. / Alter	Males Männchen (n = 70)	Females Weibchen (n = 93)	Young Jungtier (n = 55)	AV	Males Männchen (n = 32)	Females Weibchen (n = 23)	Young Jungtier (n = 7)	AV	Males Männchen (n = 31)	Females Weibchen (n = 20)	Young Jungtier (n = 10)	AV
Slope (°) Hangneigung	40.82±2.2	33.82±2	35.48±1.6	37.0%	33.47±2.	30.93±2.	34.28±3.5	32.9%	34.84±2	36.25±3.2	29.44±2.3	34.7%
	(0-90)	(0-80)	(5-60)		(0-50)	(5-45)	(20-45)		(5-60)	(10-70)	(10-50)	
	w=0.1827	w=0.1610	w=0.1618		w=0.1340	w=0.1300	w=0.1579		w=0.1395	w=0.1653	w=0.1591	
	+ 1.6%	+0.5%	+0.5%		-6.6%	-7%	-4.2%		-2.7%	-0.1%	-0.7%	
% Rocks % Fels	49.85±3.2	45.94±2.3	46.25±2.8	29.4%	52.81±3.7	56.95±5.3	47.14±6.4	48.8%	59.03±4.5	66.75±5.8	75.5±7.5	46.7%
	(0-100)	(0-90)	(0-90)		(10-90)	(10-100)	(20-70)		(0-100)	(20-100)	(40-100)	
	w=0.2808	w=0.2753	w=0.2655		w=0.1427	w=0.1614	w=0.1465		w=0.1758	w=0.2263	w=0.3035	
	+11.4%	+10.8%	+9.8%		-5.7%	-3.8%	-5.3%		+0.9%	+5.9%	+13.7%	
% Stones % Steine	11.45±1.8	14.58±2	14.47±2.3	27.2%	13.37±3.4	14.34±4.2	7.14±2.8	4.7%	9.03±3.9	5.75±3.3	7±5.9 (0-60)	5.0%
	(0-60)	(0-95)	(0-70)		(0-80	(0-80)	(0-20)		(0-100)	(0-60)	(0-60)	
	w=0.0697	w=0.0944	w=0.0898		w=0.3747	w=0.4216	w=0.2302		w=0.2508	w=0.1819	w=0.2625	
	-9.7%	-7.2%	-7.7%		+17.5%	+22.2%	+3%		+8.4%	+1.5%	+9.6%	
% Bare Soil % Kahlboden	7.97±1.2	6.45±0.8	10.09±1.6	8.4%	3.96±.6	3.04±1.4	4.28±2	2.0%	4.03±1.6	2.25±1.4	2±1.1	3.0%
	(0-40)	(0-50)	(0-40)		(0-75)	(0-20)	(0-10)		(0-40)	(0-25)	(0-10)	
	w=0.1571	w=0.1353	w=0.2027		w=0.2608	w=0.2100	w=0.3243		w=0.1866	w=0.1186	w=0.1250	
	-0.9	-3.1%	+3.6%		+6.1%	+1.0%	+12.4%		+2%	-4.8%	-4.2%	
% Bushes % Buschwerk	11.64±1.9	9.36±1.6	8.45±1.81	10.1%	0	0	0	absent fehlend	6.29±2.4	7.25±2.8	2±1.3	5.0%
	(0-70)	(0-70)	(0-50)		(0-0)	(0-0)	(0-0)		(0-50)	(0-40)	(0-10)	
	w=0.1909	w=0.1633	w=0.1412		-	-	-		w=0.1747	w=0.2294	w=0.0750	
	+2.4%	+0.3%	+2.5%		-	-	-		+0.8%	+6.3%	-9.2%	
% Grasses % Grasfläche	17.71±2.4	23.92±2.2	20.36±2.3	24.7%	29.68±4.8	24.78±5.1	41.42±5.5	44.5%	21.6±3.8	20.5±5.5	16.5±5.8	41.4%
	(0-80)	(0-90)	(0-60)		(0-90)	(0-60)	(20-60)		(0-60)	(0-80)	(0-50)	
	w=0.1187	w=0.1706	w=0.1391		w=0.0878	w=0.0770	w=0.1410		w=0.0726	w=0.0784	w=0.0748	
	-4.8%	+0.4%	-2.7%		-11.2%	-12.3%	-5.9%		-9.4%	-8.8%	-9.2%	
G-test (5 d.f.)	26.204	15.786	16.862		18.042	24.971	3.359		17.699	21.764	38.566	
p	0.0001	0.0076	0.0049		0.0013	0.0001	0.5018		0.0035	0.0007	0.0000	



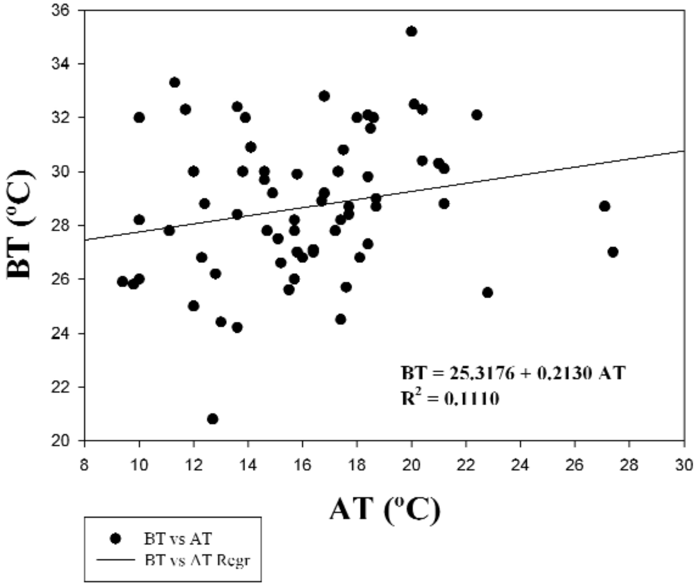


Fig. 3: Scatter plot and regression line of body temperatures (BT, °C) versus substrate temperatures (ST, °C) above, and air temperatures (AT, °C) below in *Iberolacerta bonnali*. Regression line equation and determination coefficient are given. See text for details.

Abb 3: Streudiagramm und Regressionsgerade der Körpertemperaturen (BT, °C) in bezug zu den Substrattemperaturen (ST, °C) (oben) und den Lufttemperaturen (AT, °C) (unten) von *Iberolacerta bonnali*. Die Gleichung der Regressionsgeraden und das Bestimmtheitsmaß sind angegeben. Details im Text.

urement method of the temperature. Data were taken from a distance by means of an infrared detector with a detection angle of 2.8°, resulting in a measuring field of 1 cm in diameter at 20 cm distance. Measuring the temperature of a basking lizard from this and a greater distance (which is more probable) would have caused considerable inaccuracy in that the temperature of the sorrounding substrate was measured or included in the measurement rather than the lizard body temperature alone. This could explain the high values of BT, their similarity to ST, the steep regression line slope and apparent lack of thermoregulatory processes during the hottest hours of the day.

The closely related *I. aranica* showed a mean body temperature of 29.21°C (18.6°C-36.5°C). As in *I. bonnali*, thermoregulation in *I. aranica* was more effective with regard to ST (slope 0.11; $r = 0.37$) than AT (slope 0.28; $r = 0.42$). The two species' very similar behavior parallels the close relationship of these ecologically equivalent geographical vicariants (ARRIBAS 2007).

In *I. horvathi*, DE LUCA (1992) found a mean BT of 28.69°C (20°C-35°C). This species also thermoregulated more effectively relative to ST (slope 0.55; $r = 0.64$) than to AT (slope 0.76; $r = 0.77$).

According to ARGÜELLO & SALVADOR (1988), *I. monticola* was a good thermoregulator, also more effective in relation to ST (slope 0.30; $r = 0.559$) than to AT (slope 0.52; $r = 0.561$). Their mean BT was 29.3°C (20.4°C-35.4°C), without significant differences regarding sex and ages.

For *Iberolacerta cyreni* field BTs averaged 29.4°C (18.4°C-35.2°C) for tailed specimens and 29.5°C (17.5°C- 34.4°C) for tail-autotomized individuals. Under laboratory conditions, temperatures selected in a thermic gradient were 32.2°C (29.8°C-33.9°C) in tailed, and 31.9°C (28.5°C-33.4°C) in tail-autotomized *I. cyreni* (MARTIN & SALVADOR 1993), whereas the tests of BAUWENS et al. (1995) resulted in a mean of 34.53°C. Maximum velocity was observed at 34.5°C, and the lethal body temperature averaged 43,6°C (MARTÍN & SALVADOR 1993; BAUWENS et al. 1995 – as "*I. monticola*" BAUWENS pers. comm.).

The above results cannot be compared with the data given by PEREZ MELLADO (1982) which – based on our present knowledge – represent a blend of measurements from three species of the Western Sistema Central [*I. monticola*, *I. cyreni* and *Iberolacerta martinezricai* (ARRIBAS, 1996)]. Probably the greatest part of his data came from *I. monticola* from Estrella and showed that the thermoregulatory capacity was better relative to AT (slope –0.02; $r = 0.34$) than to ST (slope 0.31; $r = 0.37$). The mean BT was 33.47°C (29°C-37.7°C). In the study by PEREZ MELLADO (1982) some of the air temperatures measured were even higher than the corresponding BTs (which caused the negative slope). This would represent an extremely unlikely situation in the Pyrenees (but theorically possible in populations living in a Mediterranean climate like *I. martinezricai* or in the Iberian Sistema Central mountains under special summer conditions; ARRIBAS & CARRANZA 2004; ARRIBAS & ODIERNA 2004; ARRIBAS 2007) and prevents further comparisons.

Detailed studies about thermoregulation in *Iberolacerta galani* ARRIBAS, CARRANZA & ODIERNA, 2006 and *I. martinezricai* are lacking; regarding *I. aurelioi*, they are in preparation.

The mean body temperatures of all the *Iberolacerta* species studied are lower than the median temperature calculated from 53 lacertid lizard species (33.8°C) (CASTILLA et al. 1999). Lizards, if free from other constraints, frequently show fairly constant intraspecific mean temperatures, the so-called thermal rigidity (sensu VAN DAMME et al. 1989), but even among closely related species, body temperatures tend to vary and are related to their biogeographical origins rather than to current environmental conditions (BAUWENS et al. 1995). In the case of *I. bonnali*, no intraspecific differences were found among different ages, periods or substrates. The mean body temperature in *I. bonnali* (28.67°C) was very similar to that of the other Pyrenean *Iberolacerta* species (29.21°C in *I. aranica* and 28.13°C in *I. aurelioi*; ARRIBAS 2007, and unpublished data), the Alpine *I. horvathi* (28.69°C), and only slightly below the temperatures observed in the "*monticola* group" species so far studied (29.3°C in *I. monticola* and 29.4°C in *I. cyreni*), which all apear very similar in their thermal requirements.

On the whole, body temperatures (BT) were correlated with the temperatures of the substrate (ST) rather than the ambient air (AT), i.e. *I. bonnali* thermoregulated more effectively relative to the substrate than the air. The low slope of the regression line of BT in respect to ST or AT showed that the lizards were very good thermoregulators, but the moderate correlations indicated that the lizards were not very precise in adjusting their body temperatures (*I. monticola* and *I. horvathi* are more precise thermoregulators). In this feature *I. bonnali* closely resembled *I. aranica*, the two being better thermoregulators (but more imprecise) both regarding AT and ST than *I. monticola* and *I. horvathi*. With respect to their thermoconformism, *I. bonnali* is very similar to *I. monticola* and *I. horvathi*, and only slightly less thermoconformist than *I. aranica*.

These results are interesting, as in related lizards (and lizards in general) BT is usually correlated with AT rather than ST. However, in the high mountain habitats where air temperatures usually do not rise very much during the day, whereas rocks heat up readily, especially if dark colored, *Iberolacerta* species were forced to develop towards successful thermoregulators regarding high substrate temperatures more than the lizard species of lower elevations. In fact, during their activity period, montane lizards are exposed to a climate, which is more similar to desert than to polar conditions.

The climate of the alpine environment of lizards depends largely on three components: (a) solar radiation, (b) slope orientation and exposure of the habitat, and (c) position of the lizards above the ground. Additional components which modulate the interplay of these three main factors, are wind velocity, ambient air temperature between or above the vegetation and properties of the ground such as surface structure, moisture and thermal conductivity. Moreover, it is difficult to study the role of the lizards' movements on the soil or rocks in this context. For exemple, in a certain place, 50 cm above the ground the temperature of the air may be 4°C, its moisture 40%, with a wind velocity of 5 m/s, whereas 1-2 cm above the ground among grass temperature may be 27°C, moisture 98% and the wind speed 0 m/s (KÖRNER 2003). Small animals living close the ground are submitted to microclimate conditions that may differ considerably from the macroclimate considered relevant by investigators (MANI 1968). In reality the climate in the immediate sorrounding of lizards is a microclimate or, in other words, the climate of a few square or cubic centimeters, or of the soil under stones, on rock surfaces or inside rock crevices, in underground cavities, under or close to the snow cover, under plant cushions, etc. Factors affecting microclimate characters are, for instance, irregularities of the ground, percentage of rock, snow and bare ground, distance to crestlines, orientation of valleys, distance to snow edges, predominant winds, etc. Trying to consider and register all above parameters is almost impossible. Only simplified models of well defined problems studied under highly controlled laboratory conditions will render future advancements possible in all these aspects.

In high altitudes the climate's spatial variability (hardly measurable) is more important than its temporal variability (the focus of meteorological measurements). In other words, even data from high altitude meteorological stations are of very limited usefulness in drawing conclusions about the thermal conditions of life of the alpine biota (KÖRNER 2003). Discoupled conditions are typically found in cushion-like plants, prostrate dwarf shrubs of herbaceous rosettes habitats, whereas the climate is more similar to the meteorological measurements in tall herbs, "Krummholz" (stunted arborescent) vegetation and trees (KÖRNER 2003).

Another interesting field could be the study of the ratio between the extensions of scale covered and exposed scaleless (naked) skin portions, as there is probably a compromise between thermoregulation and water loss in these lizards (evaporation doubles as the air pressure decreases by one third, as stated by BARRY 1978). Also evaporation increases in warmed bodies such as a warm and active lizard (KÖRNER 2003). The thermoregulatory function of the grainy, liquid-filled stratum below the scales of these mountain lizards (especially *Pyrenesaura*) is currently under study. These scales, very granular and even nearly hemispheric and liquid filled, seem to increase the surface for heat dissipation during activity hours. Other montain dwellers e.g. Caraboidea like *Peryphus* spp. leave spaces under their elytra to enclose air for insulation (MANI 1968).

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