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Activity, microhabitat selection and thermal behavior of the Pyrenean Rock Lizards *Iberolacerta aranica* (ARRIBAS, 1993), *I. aurelioi* (ARRIBAS, 1994) and *I. bonnali* (LANTZ, 1927)
(Squamata: Sauria: Lacertidae)

Aktivität, Mikrohabitatwahl und temperaturabhängiges Verhalten der Pyrenäen-Gebirgseidechsen *Iberolacerta aranica* (ARRIBAS, 1993), *I. aurelioi* (ARRIBAS, 1994) und *I. bonnali* (LANTZ, 1927)
(Squamata: Sauria: Lacertidae)

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KURZFASSUNG

Der Autor legt eine vergleichende Untersuchung über Aktivität, Mikrohabitatwahl (Hangneigung, Flächenanteil von Fels, Steinen, nacktem Boden, Gebüsch und krautiger Vegetation im Lebensraum) und temperaturabhängiges Verhalten von *Iberolacerta aranica* (ARRIBAS, 1993), *I. aurelioi* (ARRIBAS, 1994) und *I. bonnali* (LANTZ, 1927) vor und beschreibt die Unterschiede in den untersuchten Größen im Hinblick auf Art, Geschlecht und Alter der Eidechsen. Im Aktivitätsmuster fanden sich keine Unterschiede zwischen den Arten, doch differierten sie in mehreren Faktoren der Habitatausstattung ihres Aufenthaltsortes signifikant.

Iberolacerta aurelioi wurde in steilerem Gelände als *I. bonnali* besonders aber als *I. aranica* festgestellt, doch waren die Unterschiede in der Hangneigung nicht signifikant. *Iberolacerta aurelioi* und *I. bonnali* bevorzugten felsige Substrate und vermieden steinige Stellen (beide Geschlechter, alle Altersklassen) und nackte Böden (nur *I. aurelioi*). *Iberolacerta aranica* bevorzugte weniger felsigen als eher steinigen und unbewachsenen Bodengrund. Büsche waren im Habitat von *I. bonnali* häufiger als in jenem von *I. aurelioi* und *I. aranica*. Krautige Pflanzen (ganz allgemein alle Formen von Vegetation) fanden sich häufiger im Lebensraum von *I. bonnali* als an Stellen, wo *I. aurelioi* oder *I. aranica* vorkamen.

Die drei Arten unterschieden sich voneinander in der Körpertemperatur (BT) und erwiesen sich als gute aber nicht sehr präzise Thermoregulatoren (besonders gegenüber den Substrattemperaturen) sowie mäßige Thermokonformisten. Die Körpertemperatur war bei *Iberolacerta aurelioi* niedriger als bei *I. bonnali* ($p < 0.05$) und besonders *I. aranica* ($p < 0.01$). Die mittlere Körpertemperatur betrug bei *I. bonnali* 29.20 ± 0.30 ºC (22.8 - 35.2 ºC; $n = 64$), bei *I. aranica* 29.49 ± 0.20 ºC (22 - 36.5 ºC; $n = 143$) und bei *I. aurelioi* 28.13 ± 0.32 ºC (16.6 - 34.4 ºC; $n = 109$). Die Erwärmung schien bei *I. aurelioi* und *I. bonnali* hauptsächlich heliothermisch, bei *I. aranica* tigmothermisch zu erfolgen.

ABSTRACT

The author presents a comparative study about activity, microhabitat selection (slope inclination, proportion of rocks, stones, bare soil, shrubs and herbaceous vegetation) and thermal behavior of *Iberolacerta aranica* (ARRIBAS, 1993), *I. aurelioi* (ARRIBAS, 1994) and *I. bonnali* (LANTZ, 1927). The variation of the studied categories was detailed in terms of species, sex and age of the lizards. No differences were observed in the activity patterns of the species, which, however, differed significantly in many of the habitat factors prevailing at the spotting sites.

Iberolacerta aurelioi were located in steeper areas than *I. bonnali* and especially *I. aranica*, but differences in inclination were not significant. *Iberolacerta aurelioi* and *I. bonnali* positively selected rocky substrates, and avoided stony spots (both sexes and all ages) and bare soiled areas (only *I. aurelioi*) whereas *I. aranica* preferred less rocky and more stony and bare soiled grounds. Shrubs were more frequent in sites of *I. bonnali* than in those of *I. aurelioi* and *I. aranica*. Herbaceous plants (and in general all vegetation types) were more frequently present in *I. bonnali* sites than in places where *I. aurelioi* and *I. aranica* occurred.

The three species differed in their mean body temperatures (BT) and were found to be good but not very precise thermoregulators (especially against substrate temperatures), as well as reasonable thermoconformists. *Iberolacerta aurelioi* had lower BT than *I. bonnali* ($p < 0.05$) and especially *I. aranica* ($p < 0.01$). Mean BT of *I. bonnali* was 29.20 ± 0.30 ºC (22.8 - 35.2 ºC; $n = 64$), of *I. aranica* 29.49 ± 0.20 ºC (22 - 36.5 ºC; $n = 143$) and of *I. aurelioi* 28.13 ± 0.32 ºC (16.6 - 34.4 ºC; $n = 109$). *Iberolacerta aurelioi* and *I. bonnali* were mainly heliothermic lizards, whereas *I. aranica* behaved more tigmothermic.

KEY WORDS

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

INTRODUCTION

The genus *Iberolacerta* ARRIBAS, 1997 is formed by a group of monophyletic lizards from the Iberian Peninsula, Pyrenees, Alps and northern Dinaric Chains, morphologically and osteologically well characterized, and with karyotypes composed of only 36 or less macrochromosomes (ARRIBAS 1997a, 1999b 1999c; ARRIBAS & ODIERNA 2004; ARRIBAS & CARRANZA 2004, 2007; ARRIBAS et al. 2006; ARNOLD et al. 2007; CARRANZA et al. 2004; CROCHET et al. 2004; MAYER & ARRIBAS 2003; ODIERNA et al. 1996).

The Pyrenees are inhabited by three closely related allopatric-parapatric *Iberolacerta* species: *Iberolacerta aranica* (ARRIBAS, 1993), *I. aurelioi* (ARRIBAS, 1994) and *I. bonnali* (LANTZ, 1927), which were almost unknown in terms of their biology until recently (ARRIBAS 1993a, 1993b, 1994, 1997a, 1997b, 1997c, 1999a, 1999c, 2000, 2001, 2008a, 2008b, 2008c; ARRIBAS & MARTINEZ-RICA 1997). Within the genus *Iberolacerta*, these three species constitute a monophyletic group (subgenus *Pyrenesaura* ARRIBAS, 1999) mainly characterized by a dramatic karyotype reduction to 23 - 26 mostly biarmed chromosomes).

Prior to the publication of a monograph of *I. aranica* (ARRIBAS 2007) which included data about other *Iberolacerta* (*Pyrenesaura*) species, only limited information was available about the biology of this genus, namely about alimentation of *I. bonnali* (MARTINEZ-RICA 1977) and *I. aurelioi* (AMAT et al 2008) and thermal ecology of *I. bonnali* (MARTINEZ-RICA 1977). A monograph concerning activity, microhabitat selection and thermoregulation in *I. bonnali* was recently published (ARRIBAS 2009). Concerning reproduction, *I. aurelioi* was analyzed by ARRIBAS (2004) and ARRIBAS & GALAN (2005) compared the three Pyrenean *Iberolacerta* species in this respect.

Iberolacerta bonnali, protected by law both in Spain and France (where it still appears as "*Archaeolacerta monticola*" (sic!) in the 2007 law actualization, classified "EN" [endangered]; POTTIER 2008), is classified "Vulnerable" (VU B1ab+2ab, D2) by Spanish authorities and "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; IUCN 2008). Its distribution spreads from the Ossau Massif in the west to the mountains of San Mauricio-Aigüestortes National Park (Noguera Pallaresa river) in the east. In the last few years it was found in 26 10x10 km^2 UTM (Universal Transverse Mercator) grids, at elevations of 1550-3062 m, but mostly above 2000 m (ARRIBAS 2002c, 2008c).

Iberolacerta aranica is classified "Critically Endangered" (CR B1+2abcd) and protected in Spain and by IUCN (ARRIBAS 2002a; IUCN 2008), but not nominally protected in France (see above), where it is, however, considered "EN" (endangered; POTTIER 2008), and also negligently ignored in European directives. It is endemic in the Mauberme Massif and its spurs. First described in 1993, it is one of the most restricted and threatened European vertebrates. It has been found in six 10x10 km^2 UTM grid squares, in locations between 1940-2800 m (ARRIBAS 2001, 2002a, pers. obs.).

Iberolacerta aurelioi is classified "Endangered" (EN B1+2abcd) in Spain and by IUCN (ARRIBAS 2002b; IUCN 2008) but is absent in European directives (and in French legislation (see above) where it is, however, classified "CR" (Critically Endangered; POTTIER 2008). It is endemic in the easternmost part of the Central Pyrenees, where it only inhabits three mountain massifs: Mont-Roig, Pica d'Estats, and the Coma Pedrosa-Tristaina-Sarrera nucleus. Described in 1994, this species inhabits six 10x10 km^2 UTM grids, in elevations from 2100-2940 m (ARRIBAS 1999a, 2002 b) and is, together with the Aran Rock Lizard, one of the rarest European reptiles.

All three species have insular distribution patterns due to their geographical isolation in supraforestal alpine areas and the presence of unsuitable habitats at lower heights. For a résumé and description of the year-round phenology and characteristics of these Pyrenean high mountain habitats see ARRIBAS (2009).

MATERIALS AND METHODS

Localities were surveyed from 1989 to 2005 in the framework of a comprehensive study of the morphology, bionomy and geographical variation of the Pyrenean high mountain lizards (see ARRIBAS 2000, 2002c, 2008c). *Iberolacerta bonnali* was found on various types of rock substrate in the Central Pyrenees (ARRIBAS 2009), predominantly on siliceous bedrock (slate and schist) where it occurred in common with the other two *Pyrenesaura* species. This is why only records on siliceous bedrock were considered here for comparison with *I. aranica* (predominantly dwelling these kinds of rock but also in Paleozoic limestone) and *I. aurelioi* (only on slate and schist).

Data of *I. bonnali* came from Bigorre Massif (Lac Bleu, Hautes Pyrénées, France; approx. 42°56'25''N, 0°4'33''E; 1928-2238 m a.s.l.), of *I. aranica* from Serra de Pica Palomera (Val d'Aran, Lleida, Spain; approx. 42°46'1.12''N, 0°53'17.14''E, 2000-2360 m a.s.l.) and of *I. aurelioi* from Estany de Sotllo (Lleida, Spain; approx. 42°39' 7.32''N, 1°22'56.19''E, 2200-2450 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 data were taken:

- Date and time of the day (GMT).
- Activity: [inactive, basking, and active]. Temperature data (see below) were taken from active specimens only.
- Sex [coding: 1 - male, 2 - female, and 3 - adult of undetermined sex]. Undetermined specimens were used for global adult comparisons with young individuals only. There were data from 279 specimens of *I. bonnali* (85 males, 98 females, 39 adult and 57 young specimens of undetermined sex), 367 *I. aranica* (102 males, 126 females, 42 adult and 97 young specimens of undetermined sex) and 312 *I. aurelioi* (116 males, 101 females, 55 adult and 40 young specimens of undetermined sex).
- Approximate age [adult (1 - males, 2 - females, 3 - specimens of undetermined sex), subadults (later called also young, juvenile or immature specimens and hatchlings)]. Subadults were classified in calendar-year age classes (coded "40" if of undetermined age). Hatchlings of the year are in their "first calendar year" (1CY; coded "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 young of undetermined age were studied.
- Habitat structures (in percent): In a 2-meter radius around the spot of first localization of the animals, a visual estimate of the percent cover of rocks, stones, bare ground, shrubs and grasses 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 were taken (from active specimens only) with Schultheis-type thermometers (Wesco®, 0 °-50 ° Centigrade, precision: ± 0.1 °C) from the 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 of rocks, stones, bare ground, shrubs and grasses in the different squares. In some instances, especially in dark rock areas, Infrared False Colour 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 grey) (KODAK-PATHÉ 1977; MILSOM 2001).
- Availability and use of resources (Table 4) 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

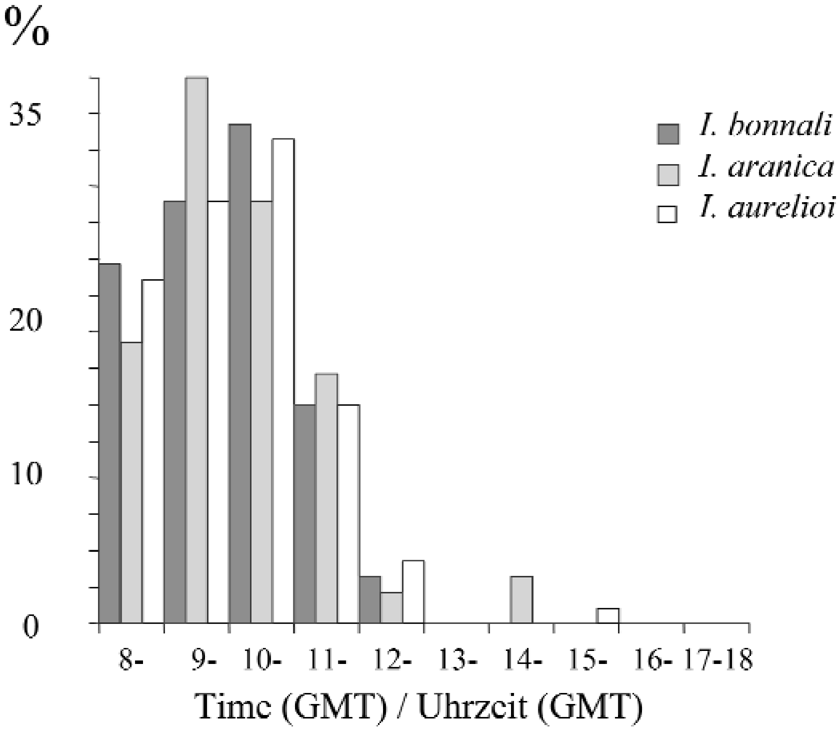

Fig. 1: Bar graph representing the relative frequency (percent of counts) of active specimens of *Iberolacerta bonnali* (dark grey), *I. aranica* (light grey) and *I. aurelioi* (white) during the hours of the day from June through September (n = 588 observations).

Abb. 1: Balkendiagramm zur Darstellung der relativen Häufigkeit (Prozent der Zählwerte) aktiver Exemplare von *Iberolacerta bonnali* (dunkelgrau), *I. aranica* (hellgrau) and *I. aurelioi* (weiß) im Tagesverlauf von Juni bis September (n = 588 Beobachtungen).

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 1/6 = 0.16) indicate presence or absence of preference. Values below this indicate relative avoidance, and above 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 were considered significant, at $p < 0.01$ highly significant. Concrete p values were 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).

Category comparisons were done in terms of:

- Activity months (from June to September).

- Periods ("reproductive" and "post-reproductive"): It was not useful to distinguish natural seasons as all the activity was centred around summer. The lizard's activity was divided 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 instead.

- Sex and ages (see under field data above): Several comparisons, with all categories separated ("sex and ages") (Tables 1-3).

- Both sexes and the juveniles pooled. Three categories: males, females and subadults.

- Adults versus subadults: Adults category included adult individuals of undetermined sex. Only significant differences were referred to in the text.

- Species: Also, the three species were compared globally to detect species-specific differences among them (Table 5).

Characteristics and influence of the different eco-climate and habitat parameters studied in the high mountain biota were explained and discussed in ARRIBAS (2009).

RESULTS AND DISCUSSION

Activity

The circadian activities of the three Pyrenean species were visualized in Fig. 1.

For *I. bonnali* there were differences in the circadian activity among the activity months ($F_{3,237} = 4.21$, $p = 0.00$) with highly significant differences among June and August ($p < 0.01$). In June (summer solstice), when days are longest, activity began slightly sooner than later during the summer [June ($n = 93$; mean = 944.74±11.33; 659-1144), July ($n = 80$; mean = 964.08±14.70; 720-1230), August ($n = 67$; mean = 1006.94 ±13.96; 825-1537), September ($n = 1$; mean = 812)]. These differences were neither observed among the periods (reproductive and postreproductive) ($F_{1,239} = 0.84$, NS) nor in the other categories compared.

For *I. aranica* there were differences in the circadian activity among nearly all the activity months ($F_{3,317} = 25.35$, $p = 0.00$), however difficult to interpret. Highly significant differences resulted from comparisons between June and September, July versus June and September, and August versus June and September ($p < 0.01$), with the September values being not very reliable due to small sample size [June ($n = 81$; mean = 1094.00±30.88; 813-1670), July ($n = 150$; mean = 970.16±7.70; 801-1254), August ($n = 81$; mean = 1009.74 ±13.77; 815 -1334), September ($n = 9$; mean = 1395.44 ± 34.48; 1136-1520)]. As with *I. bonnali*, these differences were not observed among periods (reproductive and postreproductive) or in the other categories compared.

For *I. aurelioi*, contrary to the other two *Pyrenesaura* species, there were no differences in the circadian activity among the activity months, but there were differences among the sexes and different ages (all classes separated) ($F_{5,230} = 5.23$, $p = 0.01$) and among both sexes and all the juveniles collectively (the differences seemed to be focused between males versus females; $p < 0.01$) ($F_{2,233} = 5.20$, $p = 0.01$) [males ($n = 109$; mean = 961.17±12; 727-1415), females ($n = 92$; mean = 1019.47±14.73; 722-1559), juveniles ($n = 35$; mean = 968.6± 21.77; 800-1226)], as there were no differences among all adults versus all juveniles. These differences seemed to parallel a very slight shift towards earlier hours of the male activity as compared to the females.

Globally, there were no significant differences among the activity patterns of the three Pyrenean species (see Table 5). For *I. bonnali* and *I. aranica* the activity peak shifted slightly in the course of the summer in correspondence to the photoperiod. For *I. aurelioi* this shift was not detected. A possible reason for this is that this species lives in the most sunny part of the Pyrenees (FONT TULLOT 1984; ARRIBAS 1998 [2000]) and females are slightly retarded in their activity as compared to males and juveniles.

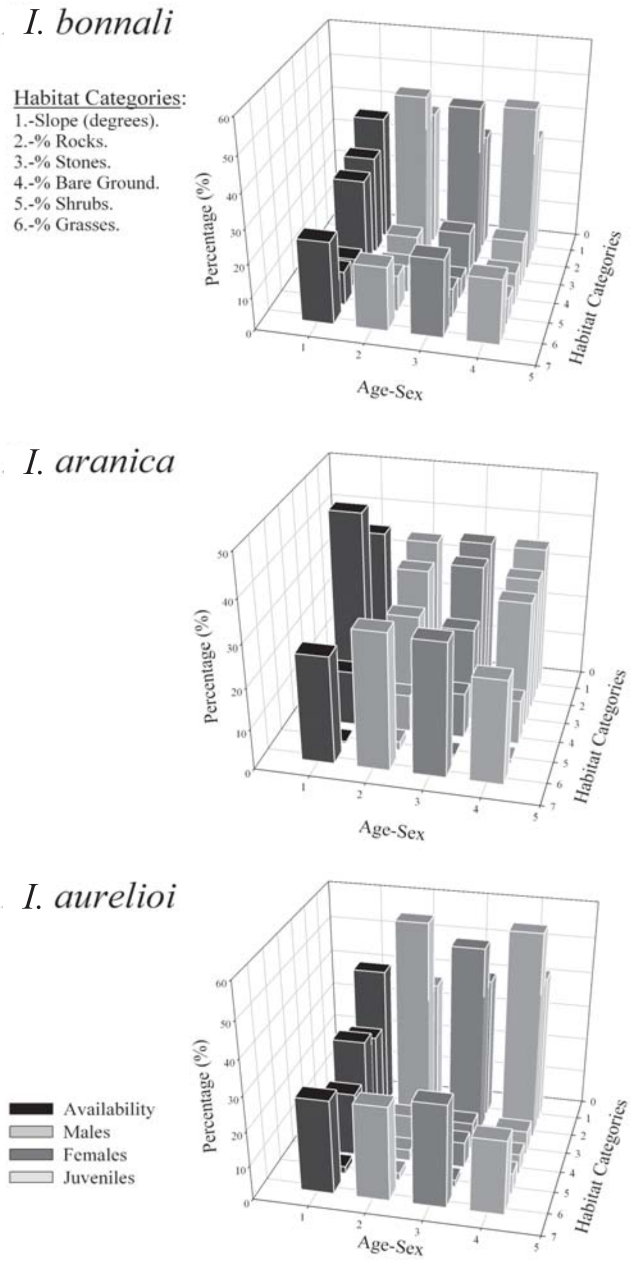

Fig. 2: The utilization (%) of six habitat categories (1 - slope inclination, 2 - rocks, 3 - stones, 4 - bare ground, 5 - shrubs, and 6 - grassy spots) by males (2), females (3) and young (4), and the availability of these structures (1) for the three *Iberolacerta* (*Pyrenesaura*) species studied.

Abb. 2: Die Nutzung (%) von sechs Strukturen der Habitatausstattung (1 – Hangneigung, 2 – Fels, 3 – Steine, 4 – kahler Boden, 5 – Gebüsch, 6 – Grasflächen) durch Männchen (2), Weibchen (3) und Jungtiere (4) sowie die Verfügbarkeit dieser Strukturen (1) bei den drei untersuchten Arten von *Iberolacerta* (*Pyrenesaura*).

Habitat characteristics

Habitat structures specified according to sex and age classes are presented in Tables 1 (*I. bonnali*), 2 (*I. aranica*) and 3 (*I. aurelioi*), a comparison among the three species is made in Table 5. A graphic representation of these values grouped by sex and age for the three species is shown in Fig. 2. Significant acceptance or avoidance of different habitat characteristics occurred in all substrates and sex and age groups (Table 4; all *G*-tests were significant, $p << 0.05$).

Slope inclination (º)

Iberolacerta bonnali did not show significant differences in the inclination of the terrain occupied regarding any of the categories compared (activity month, age, sex).

Contrarily, *I. aranica* showed significant differences in the inclination of slopes occupied in the different activity months ($F_{3,338} = 9.59$, $p = 0.00$), strongest between June versus July and August ($p > 0.01$) [June ($n = 93$; mean = 40.27±0.85; 21-80), July ($n = 151$; mean = 35.49±1; 0-60), August ($n = 96$; mean = 32.39±1.04; 10-60), September ($n = 2$; mean = 22.5±3.53; 20-25)]. This difference was also present when comparing periods (reproductive and postreproductive) ($F_{1,340} = 17.17$, $p = 0.00$) [reproductive ($n = 136$; mean = 37.86±0.78; 0-80), postreproductive ($n = 136$; mean = 32.83±0.89;10-60)], but not in the other comparisons done (by sex and ages).

For *I. aurelioi* there were differences in the slopes used in the different months of activity ($F_{4,290} = 4.91$, $p = 0.00$), in concrete in August relative to June and September ($p > 0.01$) [June ($n = 135$; mean = 42.30±1.08; 10-90), July ($n = 76$; mean = 39.81±1.95; 10-90), August ($n = 67$; mean = 35.11±1.35; 5-90), September ($n = 16$; mean = 48.75± 1.65; 45-60), October ($n = 1$; mean = 1)], but also by periods (reproductive and postreproductive) ($F_{1,293} = 7.22$, $p = 0.01$) [reproductive (n = 197; mean = 41.85±1.01; 10-90), postreproductive ($n = 98$; mean = 37.33± 1.25; 5-90)]. There were near significant differences by sex and ages (all classes separated) ($F_{5,233} = 2.31$, $p = 0.04$) among males and hatchlings (Table 3). These differences were not found in the other comparisons and thus, are not sound.

Concerning the slope inclination there was no active selection at any age or sex in any of the three Pyrenean species (Table 4).

The three species differed in the mean inclinations of their habitats (Table 5). In summary, *I. aurelioi* were located in steeper areas than *I. bonnali* ($p < 0.05$) and especially than *I. aranica* ($p < 0.01$). In general, all these mountain lizards used stepped sites more frequently during the reproductive period than during the rest of the summer (except *I. bonnali* in which these differences were not detected).

Rocks

Concerning the proportion (%) of rocks in the habitat, no differences were found in any of the comparisons done, both within *I. bonnali* and *I. aurelioi.*

For *I. aranica* this parameter showed significant differences among the activity months ($F_{3,363} = 3.92$, $p = 0.01$), concretely June and August ($p < 0.01$) [June ($n = 107$; mean = 28.73±2.45; 0-100), July ($n = 152$; mean = 33.69±1.95; 0-100), August ($n = 101$; mean = 41.05±2.95; 0-100), September ($n = 7$; mean = 37.14±8.92; 20-70)]. This difference was also found when comparing periods (reproductive and postreproductive) ($F_{1,365} = 11.65$, $p = 0.00$) [reproductive ($n = 221$; mean = 30.56±1.62; 0-100), postreproductive ($n = 146$; mean = 40.05±2.37; 0-100)], but not in the other comparisons. The habitat preference of *I. aranica* shifted progressively to more rocky areas over the summer.

In both of the more obvious rock dwellers, *I. aurelioi* and *I. bonnali* (see ARRIBAS 2007), all sexes and ages positively selected rocks (Table 4).

In summary, the three species differed significantly in the mean proportion of rocks in their habitats ($p < 0.01$). *Iberolacerta aranica* occurred on the least rocky spots, *I. aurelioi* in the most rocky places and *I. bonnali* had intermediate scores. The habitat preference of *I. aranica* shifted progressively to more rocky areas over the summer, whereas *I. aurelioi* and *I. bonnali*

Table 1: *Iberolacerta bonnali.* Habitat structures [slope inclination (°), proportion (%) of rocks, stones, bare soil, shrubs, and grasses in the place where the individual was spotted), activity hours (GMT) and temperatures (°C) of body (BT), air (AT) and substrate (ST) for all the sex and age classes [1CY .... 4CY - first calendar year .... fourth calendar year) of the specimens studied. First line: arithmetic mean ± standard error. Second line: minimum and maximum values. The sample named 'Σ Adults' includes males and females plus adults of undetermined sex. Temperatures refer to active specimens only.

Tab. 1: *Iberolacerta bonnali.* Habitatstrukturen [Hangneigung (°), Anteil (%) von Fels, Steinen, nacktem Boden, Gebüsch und Grasbewuchs am Ort der Beobachtung], Aktivitätszeiten (GMT) und Temperaturen (°C) von Körper (BT), Luft (AT) und Substrat (ST) für alle untersuchten Geschlechter- und Altersklassen [1CY ... 4CY - erstes Kalenderjahr ... viertes Kalenderjahr] bei den untersuchten Individuen. Zeile eins: arithmetisches Mittel ± Standardfehler. Zeile zwei: Minimum und Maximum. Die Stichprobe "Σ Erwachsene" umfaßt Männchen, Weibchen und Adulte unbestimmten Geschlechtes. Temperaturangaben beziehen sich nur auf aktive Individuen.

Iberolacerta bonnali	Males (n = 85) Männchen	Females (n = 98) Weibchen	Hatchlings (1CY) (n = 26) Schlüpfling	Immatures (2CY) (n = 10) Jungtier	Immatures (3CY) (n = 18) Jungtier	Immatures (4CY) (n = 3) Jungtier	Σ Adults (n = 222) Σ Erwachsene	Σ Subadults (n = 57) Σ Subadulte
Activity Hours (GMT) Aktivitätszeit	983±13.57 730-1230	976±15.45 728-1537	922±26.81 659-1133	987±24.35 828-1100	991±21.73 809-1152	988±37.16 914-1026	969±9.09 728-1537	961±14.82 659-1152
Slope Inclination (°) Hangneigung	34.84±1.85 0-90	34.39±1.93 0-80	32.76±2.39 5-60	32.5±3.67 5-45	39.16±2.39 30-60	45±8.66 3-60	37.48±1.20 0-90	35.38±1.57 5-60
% Rocks % Fels	48.88±2.87 0-100	47.02±2.34 0-100	45.53±4.63 0-100	56±6.86 20-90	50±5.81 15-100	33.33±6.66 20-40	49.37±1.66 0-100	48.14±3.08 100
% Stones % Steine	11.67±1.92 0-100	14.65±1.97 0-95	14.57±3.54 0-50	10.5±4.17 0-40	11.22±2.66 0-40	36.66±20.27 0-70	13.18±1.20 0-100	13.96±2.25 0-70
% Bare Soil % nackter Boden	8.21±1.18 0-40	6.22±0.84 0-50	11.03±2.87 0-40	9±2.56 0-25	7.11±1.62 0-25	16.66±9.27 5-35	7.25±0.64 0-50	9.73±1.54 0-40
% Shrubs % Gebüsch	10.88±1.77 0-70	8.88±1.54 0-70	4.03±2.21 0-40	9±4 0-5	13.88±3.6 0-50	6.66±6.66 0-20	9.66±1.03 0-70	8.15±1.76 0-50
% Grasses % Grasbewuchs	11.23±2.23 0-80	23.46±2.12 0-90	24.03±3.74 0-60	15.5±4.17 0-40	17.77±3.75 0-60	6.66±1.66 5-10	19.24±1.36 0-90	19.64±2.25 0-60
BT (°C)	29.18±0.56 24.2-35.2 (n = 27)	29.28±0.39 22.8-33.4 (n = 30)	29.86±1.31 28.4-32.5 (n = 3)	27.8±0 27.8-27.8 (n = 2)	28.7±0.5) 28.2-29.2 (n = 2)	— — (n = 0)	29.3±0.33 22.8-35.5 (n = 57)	28.94±0.62 22.8-32.5 (n = 7)
AT (°C)	18.2±0.66 11.5-25.4	16.98±0.96 9.6-27.4	21.63±2.81 17.7-27.1	18.6±1.4 17.2-20	10.95±1.55 9.4-12.5	— —	17.51±0.51 9.6-27.4	17.71±2.15 9.4-27.1
ST (°C)	26.42±1.05 18.6-41.4	26.07±1.08 15.6-41.8	32.36±1.27 30.5-34.8	23.25±2.05 21.2-25.3	17.6±1 16.6-18.6	— —	26.23±0.75 15.6-41.8	25.54±2.65 16.6-34.8

Table 2: *Iberolacerta aranica.* Habitat structures [slope inclination (°), proportion (%) of rocks, stones, bare soil, shrubs, and grasses in the place where the individual was spotted), activity hours (GMT) and temperatures (°C) of body (BT), air (AT) and substrate (ST) for all the sex and age classes [1CY .... 4CY - first calendar year .... fourth calendar year) of the specimens studied. First line: arithmetic mean ± standard error. Second line: minimum and maximum values. The sample named 'Σ Adults' includes males and females plus adults of undetermined sex. Temperatures refer to active specimens only.

Tab. 2: *Iberolacerta aranica.* Habitatstrukturen [Hangneigung (°), Anteil (%) von Fels, Steinen, nacktem Boden, Gebüsch und Grasbewuchs am Ort der Beobachtung], Aktivitätszeiten (GMT) und Temperaturen (°C) von Körper (BT), Luft (AT) und Substrat (ST) für alle untersuchten Geschlechter- und Altersklassen [1CY ... 4CY - erstes Kalenderjahr ... viertes Kalenderjahr] bei den untersuchten Individuen. Zeile eins: arithmetisches Mittel ± Standardfehler. Zeile zwei: Minimum und Maximum. Die Stichprobe "Σ Erwachsene" umfaßt Männchen, Weibchen und Adulte unbestimmten Geschlechtes. Temperaturangaben beziehen sich nur auf aktive Individuen.

Iberolacerta aranica	Males (*n* = 102) Männchen	Females (*n* = 126) Weibchen	Hatchlings (1CY) (*n* = 37) Schlüpfling	Immatures (2CY) (*n* = 14) Jungtier	Immatures (3CY) (*n* = 43) Jungtier	Immatures (4CY) (*n* = 3) Jungtier	Σ Adults (*n* = 270) Σ Erwachsene	Σ Subadults (*n* = 97) Σ Subadulte
Activity Hours (GMT) Aktivitätszeit	1056±21.87 822-1660	1017±19.44 813-1648	1014±28.70 815-1649	986±59.65 825-1670	992±23.6 831-1605	929±72 801-1050	1033±12.48 813-1660	997±17.30 801-1670
Slope Inclination (°) Hangneigung	34.87±1.06 10-60	35.71±1.06 10-80	32.42±1.41 20-45	38.57±4.14 0-60	36.79±1.57 10-60	33.33±3.33 30-40	36.02±0.72 10-80	35.39±1.09 0-60
% Rocks % Fels	31.42±2.63 0-100	33.55±2.28 0-100	32.70±5.01 0-100	23.92±5.60 0-80	33.72±3.76 10-90	30±10 10-40	35.25±1.61 0-100	31.80±2.67 0-100
% Stones % Steine	24.12±2.78 0-95	22.22±2.31 0-90	32.16±4.97 0-90	31.07±6.18 0-70	27.44±3.35 0-70	38.33±10.92 25-60	21.48±1.58 0-95	30.10±2.57 0-90
% Bare Soil % Nackter Boden	8.99±1.22 0-40	10.97±14.18 0-70	6.35±2.28 0-70	12.85±4.31 0-40	13.60±2.05 0-40	15±2.88 10-20	9.79±0.79 0-70	10.77±1.43 0-70
% Shrubs % Gebüsch	2.10±0.93 0-60	0.47±0.24 0-20	1.21±0.70 0-20	1.42±1.42 0-20	0.93±0.64 0-20	0±0 0-0	1.75±0.49 0-70	1.08±0.44 0-20
%Grasses %Grasbewuchs	32.81±2.42 0-100	32.06±1.98 0-99	25.13±3.27 0-80	29.28±7.89 0-90	24.30±1.97 10-65	16.66±1.66 15-20	30.98±1.37 0-100	25.10±1.88 0-90
BT (ºC)	29.57±0.35 22-34 (*n* = 45)	29.29±0.31 24.4-36.5 (*n* = 57)	29.36±0.86 24.9-36.5 (*n* = 15)	29.02±0.85 26.5-30.1 (*n* = 4)	29.85±0.63 24.7-34.6 (*n* = 17)	31.85±0.25 31.6-32.1 (*n* = 2)	29.42±0.23 22-36.5 (*n* = 105)	29.67±0.45 24.7-36.5 (*n* = 38)
AT (ºC)	17.60±0.55 10.3-24.4	17.56±0.49 9.5-25.5	17.37±1.13 9.5-23.4	20.85±1.32 17-23	18.98±0.87 13.5-23.8	22.35±1.85 20.5-24.2	17.56±0.36 9.5-25.5	8.72±0.64 9.5-24.2
ST (ºC)	29.78±1.16 15.5-47.6	28.91±1.25 11.2-47.4	31.06±2.31 13.5-44.5	33.82±3.33 25.4-41	32.99±1.61 16.5-43	36±3.4 32.6-39.4	29.28±0.84 11.2-47.6	32.47±1.20 13.5-44.5

did not show seasonal differences in the proportion of rocks used. The two latter species positively selected rocky substrates.

Stones

For *I. bonnali*, the proportion (%) of stones in the habitat selected was significantly different among the activity months ($F_{3,275}$ = 6.60, p = 0.00), between July and August in particular ($p < 0.01$), in that significantly less stony areas were used during this latter month [June (n = 119; mean = 12.96±1.48; 0-65), July (n = 92; mean = 18.8±2.36; 0-100), August (n = 67; mean = 6.73±0.93; 0-40), September (n = 1; mean = 0; 0-0)]. This shift was not observed when comparing periods (reproductive and postreproductive) or other categories.

Similarly, *I. aranica* exhibited significant differences among the activity months ($F_{3,363}$ = 3.61, p = 0.01), concretely August (less stony areas) versus June and July ($p <$ 0.01) (more stony sites) [June (n = 107; mean = 27.83±2.65; 0-95), July (n = 152; mean = 25.67±2.06; 0-75), August (n = 101; mean = 17.03±2.45; 0-90), September (n = 7; mean = 17.14±7.54; 0-60)]. This difference was observed also when comparing periods (reproductive and postreproductive) ($F_{1,365}$ = 18.40, p = 0.00), but not within the other categories except adults versus subadults ($F_{1,365}$ = 7.96, p = 0.00) [adults (n = 270; mean = 21.48±1.58; 0-95) subadults (n = 97; mean = 30.10±2.57; 0-90)] as subadults utilized stony areas (probably suboptimal) more frequently than adults.

For *I. aurelioi* there were also differences among the activity months ($F_{4,308}$ = 6.31, p = 0.00) as these lizards appeared in more stony areas in June than in July ($p <$ 0.01) [June (n = 135; mean = 11.66±1.52; 0-80), July (n = 91; mean = 2.60±0.76; 0-40), August (n = 70; mean = 7.22±1.62; 0-50), September (n = 16; mean = 2.5±1.44; 0-20), October (n = 1; mean = 10; 10-10)]. This difference was not present considering periods or age and sex categories.

For *I. bonnali* and *I. aurelioi*, loose stones (grit) were counterselected (Table 4).

The three species differed significantly in the frequency of loose stones present in their spotting sites ($p < 0.01$). *Iberolacerta aranica* was more frequently observed in the most stony areas and *I. aurelioi* in the less stony spots, just contrary to the presence of these species in the parent rocks of their respective localities (Tables 4 and 5).

Summarizing, *I. bonnali* and *I. aranica* used stony areas less frequently in August than in July (and June in the case of *I. aranica*). With this latter species, there was a significant difference among reproductive and postreproductive periods. Conversely, *I. aurelioi* was most frequently observed in stony areas in June rather than in July. Only the juveniles of *I. aranica* (not the other species) were found in stony areas (probably the suboptimal condition) more frequently than adults. Stony areas were counterselected by *I. bonnali* and *I. aurelioi* (all sexes and ages).

Bare soil

For *I. bonnali* there were significant differences in the proportion (%) of bare soil used by lizards during the activity months ($F_{3,275}$ = 3.78, p = 0.02 – without September), with significant differences between June and July ($p < 0.01$). During June, lizards used areas with a greater proportion of bare soil than in July [June (n = 119; mean = 9.69±1.03; 0-50), July (n = 92; mean = 6.38±1.07; 0-40), August (n = 67; mean = 6.32±0.81; 0-25), September (n = 1; mean = 0; 0-0]. There were no differences in the use of bare soil concerning periods (reproductive and postreproductive) or other criteria analyzed.

For *I. aranica* there were no significant differences in any of the comparisons.

For *I. aurelioi* there were significant differences among the activity months ($F_{4,307}$ = 3.01, p = 0.04) which did, however, not persist in the pairwise comparisons of the post-hoc tests [June (n = 135; mean = 6.88±1.0; 0-50), July (n = 90; mean = 4.11± 1.18; 0-75), August (n = 70; mean = 3.2± 1.08; 0-60), September (n = 16; mean = 10± 3.97; 0-40), October (n = 1; mean = 0; 0-0)]. There were differences by both sexes and all juveniles ($F_{2,253}$ = 3.66, p = 0.03) between males and females (females appeared in areas with a slightly higher proportion of bare soil than males) [males (n = 116; mean = 3.27± 0.75; 0-40), females (n = 100; mean

= 7.35± 1.40; 0-75), juveniles ($n = 40$; mean = 5.75± 1.58; 0-30)].

Bare soil was positively selected by females and juveniles of *I. aranica*, and clearly counterselected by males of *I. aurelioi* (Table 4).

All three species differed in the mean percentage of bare soil present at the sites of their first spotting (*I. bonnali*: $p < 0.05$, *I. aranica* and *I. aurelioi*: $p < 0.01$), the former inhabiting areas which were richer in bare soil than the habitats of the latter two species (Table 5).

In summary, the proportion of bare soil at the sites of *I. bonnali* was higher during June than July, due to the *in situ* growth of grass during the vegetative season and probably not actively pursued by the lizards. This tendency was observed also in *I. aurelioi*, but lacked statistical significance. In this latter species, adult females outnumbered the males on places characterized by a slightly increased proportion of bare soil.

Iberolacerta aranica did not reveal significant differences in any of the comparisons done.

Shrubs

For *I. bonnali* significant differences were detected in the proportion (%) of shrubs in the habitat comparing the activity months ($F_{2,276} = 3.85$, $p = 0.02$ – without September), with significant pairwise differences between June and August ($p < 0.05$). The lizards occupied more frequently bushy areas in August than June, possibly in search of shade during the hunting activity [June ($n = 119$; mean = 7.15±1.35; 0-70), July ($n = 92$; mean = 8.85±1.43; 0-50), August ($n = 67$; mean = 13.35±1.93; 0-70), September ($n = 1$; mean = 50; 50-50)]. Differences in the proportion of shrubs in the habitat were neither found comparing periods (reproductive and postreproductive) nor in the other comparisons done.

For *I. aranica* there were no significant differences in any of the comparisons.

For *I. aurelioi*, however, there were significant differences among the months of activity ($F_{4,308} = 2.96$, $p = 0.02$), but these differences did not appear in the post-hoc tests [June ($n = 135$; mean = 0.94±0.43; 0-50), July ($n = 91$; mean = 5.49±1.36; 0-70), August ($n = 70$; mean = 2.5±1.27; 0-60), September ($n = 16$; mean = 3.75±3.75; 0-60), October ($n = 1$; mean = 0; 0-0)]. There were significant differences among sex and ages (all classes separated) ($F_{5,251} = 10.27$, $p = 0.00$) but with unrepresentative (due to small sample sizes) differences between juveniles of the 4th calendar year and the remaining age classes (see values in Table 3). Differences in the proportion of shrubs in the habitat were not found among both sexes and all juveniles pooled ($F_{2,254} = 2.51$, $p = 0.08$), but were present comparing adults versus juveniles ($F_{1,311} = 4.90$, $p = 0.03$) [adults ($n = 273$; mean = 2.28±0.54; 0-60), juveniles ($n = 40$; mean = 6±2.38; 0-70)].

Shrubs in the habitat were avoided by all sexes and ages of *I. aranica* and *I. aurelioi*, but seemed to be of minor relevance to *I. bonnali* (Table 4).

The three lizard species differed in the percentage of shrubs ($p < 0.05$) present in their habitats. Shrubs were more common in sites of *I. bonnali* than *I. aurelioi* and *I. aranica* ($p < 0.01$) (Table 5).

Summarizing, bushy areas were occupied by *I. bonnali* more frequently in August than June, possibly in search of shade during the hunting activity. In this parameter *I. aranica* did not show differences in any of the time and age-class categories studied, whereas there was a weak difference for *I. aurelioi*, in that juveniles appeared in slightly bushier areas than adults. Shrubs were avoided by *I. aranica* and *I. aurelioi*.

Grasses (herbaceous vegetation)

No differences in any of the comparisons were found concerning the percentage of grass (including all kinds of herbaceous vegetation) in the habitat of *I. bonnali*.

Also, for *I. aranica* significant differences were not observed among the activity months ($F_{3,363} = 1.33$, NS), but interestingly, were detected when periods (reproductive and postreproductive) were compared ($F_{1,365} = 5.33$, $p = 0.02$). Lizards were more frequently localized in grassy areas during the second half of the summer [reproductive ($n = 221$; mean = 27.32±1.38; 0-90), postreproductive ($n = 146$; mean = 32.63±1.89; 0-100)]. There were also differences among

Table 3: *Iberolacerta aurelioi*. Habitat structures [slope inclination (°), proportion (%) of rocks, stones, bare soil, shrubs, and grasses in the place where the individual was spotted), activity hours (GMT) and temperatures (°C) of body (BT), air (AT) and substrate (ST) for all the sex and age classes [1CY .... 4CY - first calendar year .... fourth calendar year) of the specimens studied. First line: arithmetic mean ± standard error. Second line: minimum and maximum values. The sample named 'Σ Adults' includes males and females plus adults of undetermined sex. Temperatures refer to active specimens only.

Tab. 3: *Iberolacerta aurelioi*. Habitatstrukturen [Hangneigung (°), Anteil (%) von Fels, Steinen, nacktem Boden, Gebüsch und Grasbewuchs am Ort der Beobachtung], Aktivitätszeiten (GMT) und Temperaturen (°C) von Körper (BT), Luft (AT) und Substrat (ST) für alle untersuchten Geschlechter- und Altersklassen [1CY ... 4CY - erstes Kalenderjahr ... viertes Kalenderjahr] bei den untersuchten Individuen. Zeile eins: arithmetisches Mittel ± Standardfehler. Zeile zwei: Minimum und Maximum. Die Stichprobe "Σ Erwachsene" umfaßt Männchen, Weibchen und Adulte unbestimmten Geschlechtes. Temperaturangaben beziehen sich nur auf aktive Individuen.

Iberolacerta aurelioi	Males (*n* = 116) Männchen	Females (*n* = 100) Weibchen	Hatchlings (1CY) (*n* = 23) Schlüpfling	Immatures (2CY) (*n* = 6) Jungtier	Immatures (3CY) (*n* = 7) Jungtier	Immatures (4CY) (*n* = 4) Jungtier	Σ Adults (*n* = 272) Σ Erwachsene	Σ Subadults (*n* = 40) Σ Subadulte
Activity Hours (GMT) Aktivitätszeit	961±12 727-1415	1019±14.7 722-1559	996±31.04 800-1226	982±51.04 858-1200	964±41.49 813-1106	829±5.63 819-845	977±8.20 722-1559	968±21.27 800-1226
Slope Inclination (º) Hangneigung	37.81±1.3 5-85	40.40±1.30 20-90	47.95±5.08 10-90	35±2.23 30-45	38.57±3.73 20-45	31.25±2.39 25-??	40.05±0.8 5-90	42.42±3.07 10-90
% Rocks % Fels	59.12±2.83 0-100	53.5±2.94 0-100	64.56±6.73 10-100	25±2.23 20-30	65.75±10.20 20-100	65±14.28 30-100	58.30±1.88 0-100	58.87±4.93 10-100
% Stones % Steine	7.80±1.42 0-60	7.64±1.32 0-50	6.08±2.72 0-50	18.33±5.27 5-40	4.28±4.28 0-30	0±0 0-0	7.64±0.88 0-80	7±2.02 0-50
% Bare Soil % Nackter Boden	3.27±0.75 0-40	7.35±1.40 0-75	4.78±2.07 0-30	13.33±4.01 0-25	5.71±4.28 0-30	0±0 0-0	5.34±0.70 0-75	5.75±1.58 0-30
% Shrubs % Gebüsch	2.41±0.85 0-60	2±0.78 0-45	3.04±1.93 0-40	0±0 0-0	4.28±4.28 0-30	35±14.28 0-70	2.28±0.54 0-60	6±2.38 0-70
% Grasses % Grasbewuchs	27.17±2.27 0-100	29.62±2.08 0-80	20±4.53 0-60	43.33±6.14 30-60	20±7.86 0-60	0±0 0-0	26.38±1.36 0-100	21.5±3.48 0-60
BT (ºC)	28.87±0.44 21.7-34.4 (*n* = 48)	27.62±0.45 21.4-33.8 (*n* = 42)	21.8±2.35 16.6-28.9 (*n* = 5)	30.55±1.75 28.8-32.3 (*n* = 2)	— — (*n* = 0)	28.06±1.56 26.4-31.2 (*n* = 3)	28.40±0.30 21.4-34.4 (*n* = 99)	25.43±1.73 16.6-32.3 (*n* = 10)
AT (ºC)	15.95±0.63 8-26.8	14.78±0.65 6.6-22.4	9.46±2.59 3.2-15.7	19.05±3.45 15.6-22.5	— —	16.4±0.25 16.1-16.9	15.56±0.44 6.6-26.8	13.46±1.9 3.2-22.5
ST (ºC)	29.29±1.35 10.6-60	26.99±1.47 10.4-51.7	14.58±2.32 8.9-21.1	41.65±7.95 33.7-49.6	— —	23.46±1.72 20.8-26.7	29.25±0.98 10.4-60	22.6±3.80 8.9-49.6

Table 4: Habitat structures at the sites of first spotting of *Iberolacerta* (*Pyrenesaura*) *bonnali*, *I. aranica* and *I. aurelioi* 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 0.0 in each column for all habitat categories) given in %. Positive or negative signs indicate selection or avoidance. Only deviations exceeding 5 % ($p < 0.05$; highlighted in bold) are considered and discussed in the text. In the lower part of the table, *G*-test values and their probabilities are indicated.

Tab. 4: Die Habitatstrukturen am Ort der Erstbeobachtung bei *Iberolacerta* (*Pyrenesaura*) *bonnali*, *I. aranica* and *I. aurelioi* und die Annahme der Strukturen im Vergleich zu ihrer Verfügbarkeit (AV). Zeile eins: arithmetisches Mittel ± Standardfehler. Zeile zwei: in Klammern, Minimum und Maximum. Zeile drei: Selektionsindex, (*w*, siehe Material und Methoden). Zeile vier: standardisierte Anteile (in %; die Spaltensummen über alle Habitatkategorien ergeben jeweils 0). Positive bzw. negative Vorzeichen bezeichnen Annahme bzw. Vermeidung. Nur Abweichungen von über 5 % ($p < 0.05$; in Fettdruck markiert) werden beachtet und im Text behandelt. Im unteren Tabellenteil sind *G*-test Werte und ihre Wahrscheinlichkeiten angegeben.

	Iberolacerta bonnali				*Iberolacerta aranica*				*Iberolacerta aurelioi*			
Sex /Age	Male	Female	Subadult	AV	Male	Female	Subadult	AV	Male	Female	Subadult	AV
	n = 85	*n* = 98	*n* = 57	%	*n* = 102	*n* = 126	*n* = 97	%	*n* = 116	*n* = 101	*n* = 40	%
Habitat	Männchen	Weibchen	Subadulte		Männchen	Weibchen	Subadulte		Männchen	Weibchen	Subadulte	
Slope Inclination (degrees)	39.84±1.8	34.4±1.9	35.38±1.5	37.0	34.87±1.1	35.71±1.1	35.39±1.1	35.8	37.81±1.3	40.40±1.3	42.42±3.1	40.3
Hangneigung-	(0-90)	(0-80)	(5-60)		(10-60)	(10-80)	(0-60)		(5-85)	(20-90)	(10-90)	
(Grad)	0.1794	0.1649	0.1630		0.1712	0.1732	0.1744		0.2025	0.1998	0.2064	
	+1.3 %	-0.2 %	-0.4 %		+0.5 %	+0.6 %	+0.8 %		+3.6 %	+3.3 %	+4.0 %	
% Rocks	48.88±2.8	47.02±2.3	48.14±3.1	29.4	31.42±2.6	33.55±2.3	31.8±2.6	12.9	59.12±2.8	53.5±2.9	58.87±4.9	25.2
Fels	(0-100)	(0-100)	(0-100)		(0-100)	(0-100)	(0-100)		(0-100)	(0-100)	(10-100)	
	0.2770	0.2837	0.2791		0.1942	0.2047	0.1944		0.3984	0.3330	0.3604	
	+11.0 %	**+11.7 %**	**+11.3 %**		+2.8 %	+3.8 %	+2.8 %		**+23.2 %**	**+16.6 %**	**+19.4 %**	
% Stones	11.67±1.9	14.65±1.9	13.96±2.2	27.2	24.12±2.7	22.22±2.3	30.10±0.9	47.2	7.80±1.4	7.64±1.3	7.00±2.0	28.6
Steine	(0-100)	(0-95)	(0-70)		(0-95)	(0-90)	(0-90)		(0-60)	(0-50)	(0-50)	
	0.0715	0.0956	0.0875		0.1611	0.1466	0.1989		0.0568	0.0514	0.0463	
	-9.5 %	**-7.1 %**	**-7.9 %**		- 0.6 %	-2.0 %	+3.2 %		**-11.0 %**	**-11.5 %**	**-12.0 %**	
% Bare Soil	8.21±1.2	6.22±0.8	9.73±1.5	8.4	8.99±1.2	10.97±1.2	10.77±1.4	13.3	3.27±0.7	7.35±1.4	5.75±1.5	18.2
Nackter Boden	(0-40)	(0-50)	(0-40)		(0-40)	(0-70)	(0-70)		(0-40)	(0-75)	(0-30)	
	0.1629	0.1314	0.1974		0.1944	0.2343	0.2304		0.0771	0.1601	0.1232	
	-0.4 %	-3.5 %	+3.1 %		+2.8 %	**+6.8 %**	**+6.4 %**		**-9.0 %**	-0.7 %	-4.3 %	
% Shrubs	10.88±1.7	8.88±1.5	8.15±1.7	10.1	2.10±0.9	0.47±0.2	1.08±0.4	0.5	2.14±0.8	2.00±0.7	6.00±2.4	2.0
Gebüsch	(0-70)	(0-70)	(0-50)		(0-60)	(0-20)	(0-20)		(0-60)	(0-45)	(0-70)	
	0.1795	0.1560	0.1375		0.0378	0.0083	0.0192		0.0473	0.0362	0.1069	
	+1.3 %	-1.1 %	-2.9 %		**-12.9 %**	**-15.8 %**	**-14.7 %**		**-11.9 %**	**-13.0 %**	**-6.0 %**	
% Grasses	19.23±2.2	23.46±2.1	19.64±2.2	24.7	32.81±2.4	32.06±1.9	25.10±1.9	26.0	27.17±2.2	29.62±2.1	21.50±3.5	27.1
Grasbewuchs	(0-80)	(0-90)	(0-60)		(0-100)	(0-99)	(0-90)		(0-100)	(0-80)	(0-60)	
	0.1297	0.1685	0.1355		0.2413	0.2329	0.1826		0.2179	0.2194	0.1567	
	-3.7	+0.2	-3.1		**+7.4 %**	**+6.6 %**	+1.6 %		**+5.1 %**	**+5.3 %**	-1.0 %	
G-test (5 d.f.)	23.61	16.88	19.62		12.43	20.65	14.32		55.28	46.56	48.13	
p	0.0003	0.0049	0.0016		0.0291	0.0010	0.0138		0.0000	0.0000	0.0000	

both sexes and all juveniles pooled ($F_{2,322}$ = 3.78, p = 0.02) [males (n = 102; mean = 32.81±2.41; 0-100), females (n = 126; mean = 32.06± 1.98; 0-99), juveniles (n = 97; mean = 25.10±1.88; 0-90)] and between adults versus juveniles ($F_{1,365}$ = 5.32, p = 0.02) [adults (n = 270; mean = 30.98± 1.37; 0-100), juveniles (n = 97; mean = 25.10± 1.88; 0-90)]. These differences could be explained by the fact that adults selected grassy areas for successful hunting during the summer, whereas juveniles were more frequently found restricted to suboptimal sites.

Comparisons of the percentage of grass in the habitat of *I. aurelioi* revealed no differences in any of the categories considered. Differences among sex and ages (2nd and 4th calendar year juveniles) visualized in Table 3 are not representative due to small sample size of the age-classes concerned.

Adults (but not juveniles) of both *I. aranica* and *I. aurelioi* positively selected grassy areas.

The three species differed significantly (p < 0.05) in the mean percentage of grass present at their localities. As with shrubs, herbaceous vegetation was significantly more common in the habitat of *I. bonnali* than *I. aurelioi* and *I. aranica* (p < 0.01) (Table 5).

Summarizing, in *I. bonnali* and *I. aurelioi* there were no differences in the percentage of grass of the lizard localisation spots. *Iberolacerta aranica* specimens were more frequently located in grassy areas during the second half of summer, which, to a certain degree, probably paralleled the effect of the grass growth as the vegetative season progressed. Also, *I. aranica* adults were more common in grassy areas (best hunting areas during summer) than juveniles (suboptimal habitat).

Thermoregulation

Body temperatures

Mean body temperature (BT, °C) was 29.20±0.30 (range: 22.8-35.2; n = 64) for *I. bonnali* and 29.49±0.20 (range: 22.0-36.5; n = 143) for *I. aranica*, without differences among the categories studied. This constancy in BT is remarkable and is maintained also on different parent rock substrates, as was demonstrated for *I. bonnali* (ARRIBAS 2009).

For *I. aurelioi* BT was 28.13±0.32 (range: 16.6-34.4; n = 109), but there were differences between both sexes and all juveniles pooled ($F_{2,97}$ = 4.86, p = 0.01) with lower temperatures in juveniles (significant only between juveniles and adult males; p < 0.05) [males (n = 48; mean = 28.87±0.44; 21.7-34.4), females (n = 42; mean = 27.62± 0.45; 21.4-33.8), juveniles (n = 10; mean = 25.43±1.73; 16.6-32.3)]. These differences persisted in the comparison between adults versus juveniles ($F_{1,107}$ = 7.43, p = 0.01) with lower temperatures in juveniles [adults (n = 99; mean = 28.40± 0.30; 21.4-34.4) juveniles (n = 10; mean = 25.43±1.73; 16.6-32.3)].

There were differences in mean BT among the three Pyrenean species. *Iberolacerta aurelioi* had a slightly lower BT than *I. bonnali* (p < 0.05) and especially *I. aranica* (p < 0.01) (Table 5).

Summarizing, the mean body temperature was 29.20±0.30 (range: 22.8-35.2; n = 64) in *I. bonnali* and 29.49±0.20 (range: 22.0-36.5; n = 143), for *I. aranica*, without differences among the categories studied. For *I. aurelioi* BT was 28.13±0.32 (range: 16.6-34.4; n = 109) with lower temperatures in juveniles than adults (especially adult males). By species, mean BT was lowest for *I. aurelioi* and highest for *I. aranica*.

Air temperatures

Mean air temperatures (AT, °C) at observation points of *I. bonnali* differed among the activity months ($F_{2,60}$ = 5.25, p = 0.01), with significant differences between June and August (p < 0.01) [June (n = 26; mean = 16.09±0.73; 9.4-21.9), July (n = 20; mean = 17.38±0.78; 13.6-27.4), August (n = 17; mean = 19.82±1.02; 14.1-27.1)]. These differences were maintained in comparisons

Table 5: Comparison of the habitat structures utilized by three *Iberolacerta* (*Pyrenesaura*) species studied. Temperatures of body (BT), air (AT), and substrate (ST). First line: arithmetic mean ± standard error. Second line: in parentheses, minimum and maximum values. ANOVA results (*F* value, *p* - probability) and significant pairwise comparisons among species are given. Temperature data came from active specimens only, values for the other habitat characteristics were based on all specimens available.

Tab. 5: Die Nutzung von Habitatstrukturen bei den drei untersuchten Arten von *Iberolacerta* (*Pyrenesaura*) im Vergleich. Körper- (BT), Luft- (AT) und Substrattemperaturen (ST). Zeile eins: arithmetisches Mittel ± Standardfehler. Zeile zwei: in Klammern, Minimum und Maximum. ANOVA Ergebnisse (*F* Werte, *p* - Wahrscheinlichkeiten) und signifikante Paarvergleiche sind angegeben. Temperaturangaben beziehen sich nur auf aktive Individuen, den übrigen Daten liegt die Gesamtheit der untersuchten Stichprobe zugrunde. ALL - Alle.

	I. bonnali (BO) (n = 279)	*I. aranica* (AR) (n = 367)	*I. aurelioi* (AU) (n = 313)	ANOVA F-test p value / p Wert	Comparisons Vergleiche
Activity Hours (GMT)	967±7.78	1000±9.31	980±8.91	$F_{2,913} = 2.63$	---
Aktivitätszeit	659-1537	801-1455	722-1559	0.072842	---
Slope Inclination (°)	37.05±1.01	35.85±0.60	40.35±0.80	$F_{2,913} = 8.66$	AU-BO ($p < 0.05$)
Hangneigung	5-90	0-80	5-90	0.000189	AU-AR ($p < 0.01$)
% Rocks	49.10±1.46	34.34±1.38	58.37±1.75	$F_{2,955} = 66.31$	ALL ($p < 0.01$)
Fels	0-100	0-100	0-100	0.000000	
% Stones	13.34±1.06	23.76±1.35	7.56±0.81	$F_{2,956} = 54.93$	ALL ($p < 0.01$)
Steine	10-100	0-95	0-80	0.000000	
% Bare Soil	7.75±0.60	10.05±0.69	5.39±0.64	$F_{2,955} = 13.11$	ALL ($p < 0.05$)
Nackter Boden	0-50	0-70	0-75	0.000002	AR-AU ($p < 0.01$)
% Shrubs	9.35±0.9	1.58±0.37	2.75±0.56	$F_{2,956} = 44.65$	BO-AR ($p < 0.01$)
Gebüsch	0-70	0-70	0-70	0.000000	BO-AU ($p < 0.01$)
%Grasses	19.32±1.17	29.43±1.13	25.76±1.27	$F_{2,956} = 17.80$	BO-AR ($p < 0.01$)
Grasbewuchs	0-90	0-100	0-100	0.000000	BO-AU ($p < 0.01$)
BT (°C)	29.20±0.30	29.49±0.20	28.13±0.32	$F_{2,313} = 7.43$	AU-BO ($p < 0.05$)
	22.8-35.2	22-36.5	16.6-34.4	0.000704	AU-AR ($p < 0.01$)
	(n = 64)	(n = 143)	(n = 109)		
AT (°C)	17.53±0.57	17.86±0.31	15.37±0.44	$F_{2,312} = 11.99$	AU-BO ($p < 0.01$)
	9.4-27.4	9.5-25.5	3.2-26.8	0.000010	AU-AR ($p < 0.01$)
ST (°C)	26.15±0.72	30.14±0.70	28.64±0.96	$F_{2,310} = 4.73$	BO-AR ($p < 0.01$)
	15.6-41.8	11.2-47.6	8.9-60	0.009500	

of the periods (reproductive and postreproductive) ($F_{1,61} = 4.65$, $p = 0.03$) [reproductive ($n = 41$; mean = 16.75±0.59; 9.4-27.4), postreproductive ($n = 22$; mean = 19±0.89; 13.6-27.1)], and corresponded to the increase of air temperatures during the summer. There were no differences in terms of the other groups or categories compared.

Iberolacerta aranica did not reveal significant differences in any of the categories studied, except in the global comparison by periods (reproductive and postreproductive) ($F_{1,141} = 6.06$, $p = 0.01$) [reproductive ($n = 74$; mean = 17.12±0.43; 9.5-24.6), postreproductive ($n = 69$; mean = 18.66± 0.45; 10.4-25.5)], probably indicating a tendency towards conditions as found with *I. bonnali* and *I. aurelioi*, but the monthly differences less pronounced.

In *I. aurelioi* there were significant differences in AT between the activity months ($F_{3,105} = 7.78$, $p = 0.00$), with differences between June and July as well as June and August (both at $p < 0.01$) [June ($n = 51$; mean = 13.35±0.64; 3.2-26.3), July ($n = 28$; mean = 17.68±0.58; 12.4-26.8), August ($n = 25$; mean = 16.42±0.95; 8.2-25.2), September ($n = 5$; mean = 17.8±0.64; 15.5-19.4)]. These differences did not persist in comparisons by periods or the other categories, but vaguely pointed to a tendency toward AT increase over the summer as observed in the other two species.

Air temperatures at the lizard's localization spots differed among the three species. For *I. aurelioi* sites, AT was slightly lower than in places where *I. bonnali* and *I. aranica* were observed ($p < 0.01$).

Summarizing, air temperatures increased in parallel to the advance of the summer. *Iberolacerta bonnali* and *I. aranica* inhabited oceanic-influenced areas with

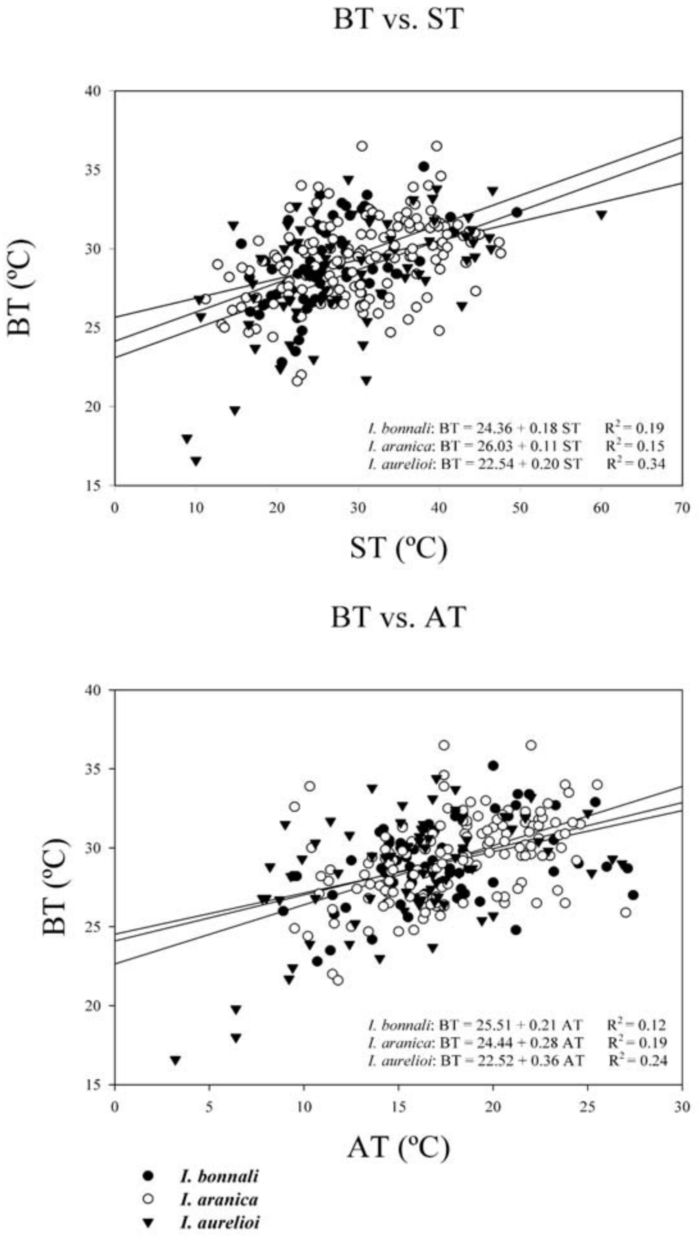

Fig. 3: Scatter plots and regression lines of body temperatures (BT, °C) versus substrate temperatures (ST, °C - above), and air temperatures (AT, °C - below) for the three *Iberolacerta* (*Pyrenesaura*) species studied. Regression line equations and determination coefficients (R^2) are given.

Abb. 3: Streudiagramme und Regressionsgeraden der Körpertemperaturen (BT, °C) in Abhängigkeit von denen des Substrats (ST, °C, oben), und der Luft (AT, °C, unten) bei den drei untersuchten Arten von *Iberolacerta* (*Pyrenesaura*). Die Gleichungen der Regressionsgeraden und die Bestimmtheitsmaße (R^2) sind angegeben.

less contrasting more even temperatures, whereas climate conditions in the range area of *I. aurelioi* were rather continental and more oscillating (Arribas (1998)[2000]) that may explain the differences observed among months.

Substrate temperatures

For *I. bonnali* ($n = 63$) no differences in the substrate temperatures (ST, °C) were measured in any of the categories compared.

For *I. aranica* significant differences in ST resulted only from comparisons between adults versus juveniles ($F_{1,139} = 4.13$, $p = 0.04$) [adults ($n = 103$; mean $= 29.28 \pm 0.84$; 11.2-47.6), juveniles ($n = 38$; mean $= 32.47 \pm 1.20$; 13.5-44.5)], with the juveniles localized in warmer places than adults. For *I. aurelioi* the situation was just contrary to that of *I. aranica*, with differences of low significance between adults versus juveniles ($F_{1,107} = 3.98$, $p = 0.05$) [adults ($n = 99$; mean $= 29.25 \pm 0.98$; 10.4-60), juveniles ($n = 10$; mean $= 22.66 \pm 3.80$; 8.9-49.6)]; but here, average temperatures of the lizard's spotting sites were lower in the juvenile than in the adult sample. In both cases these observations could be related to the juvenile lizard's activity forced to extend into suboptimal places (temperatures above or below optimum), whereas adults could choose thermally more stable and presumably favorable sites during activity.

Substrate temperatures differed statistically ($p < 0.01$) only between *I. bonnali* (lower) and *I. aranica* (higher).

As a résumé, substrates on which *I. aranica* and *I. aurelioi* adults were spotted exhibited fairly stable and equivalent temperatures. Juveniles of these species were found in places with significantly higher or lower temperatures than adults, perhaps related to the juveniles' activity in suboptimal conditions (more extreme temperatures) or habitats. *Iberolacerta bonnali* did not show differences in the ST selected in any of the categories analyzed.

Thermal behavior

The lizard's body temperatures (BT, °C) and their relationships with both air (AT, °C) and substrate temperatures (ST, °C) are represented in Figure 3.

In the present study only slate-schist substrates were considered to make all three species fully comparable. *Iberolacerta bonnali* was found to have a mean BT of 29.20 (22.8-35.2) [28.67 (20.8-35.2) if all kinds of substrate utilized by this species were considered, see Arribas 2009]. Body temperature was closer correlated with the temperature of the substrate ($r = 0.44$; $p = 0.00$) than with the ambient air ($r = 0.35$; $p = 0.00$). This difference was still present when the effect of the third variable was extracted (partial correlation, TB-TS extracting TA effect: $r = 0.37$; TB-TA extracting TS effect: $r = 0.24$).

The same was true for *I. aurelioi* which exhibited a mean BT of 28.13 (16.6-34.4). Its body temperature was closer correlated with the temperature of the substrate ($r = 0.58$; $p = 0.00$) than of the ambient air ($r = 0.49$; $p = 0.00$). This difference was maintained even if the effect of the third variable was extracted (partial correlation, TB-TS extracting TA effect: $r = 0.47$; TB-TA extracting TS effect: $r = 0.31$).

Finally, *I. aranica* revealed a mean BT of 29.49 (22.0-36.5). Contrary to *I. bonnali* and *I. aurelioi*, the body temperature of this species was better correlated with the temperature of the air ($r = 0.44$; $p = 0.00$) than the substrate ($r = 0.39$; $p = 0.00$). This difference was maintained even if the effect of the third variable was extracted (partial correlation, TB-TA extracting TS effect: $r = 0.29$; TB-TS extracting TA effect: $r = 0.21$).

Infrared solar radiation warms the substrate and simultaneously the heliothermic lizards. Later, the warmed substrate itself emits infrared radiation and thereby warms the adjacent air layer and tigmothermic lizards, if present. Since in heliothermic lizards both body and substrate temperatures depend directly on the intensity of the solar radiation, they are expected to be well correlated with each other and to increase in parallel. The lizards' daily warming process can gain thermal energy from both sources, from the sun by irradiation and from the substrate by conduction. However, in the case of *I. bonnali* and *I. aurelioi* the body temperatures parallel more closely the substrate temperatures, qualifying these two species clearly as heliothermic lizards. In the case of *I. aranica* the congruence between BT and AT is stronger than between BT and ST. This seems to indicate that *I. aranica* lizards absorb warmth predominantly by tigmothermy among the tiny slate slabs, as was pointed out by ARRIBAS (2007).

The correlation between ST and AT mirrors an unintentional physical (not biological) process and, if purposeful thermoregulatory behavior existed, should be lower than the correlations between BT and AT as well as BT and ST. In fact this hypothetical interconnection was observed. The ST-AT correlation coefficients (r) were 0.32 for *I. bonnali*, 0.41 for *I. aurelioi* and 0.50 for *I. aranica*. The last value, however, was abnormally high and surpassed the biologically influenced BT-AT and BT-ST correlations of this species, posing an interesting problem in connection with the black, mainly Silurian slates that constitute the habitat of *I. aranica* in the study area. As AT (microclimate within a few centimetres above ground) as well as BT in (at least in part) tigmothermic lizards were strongly dependent on ST, this latter seemed to impose a strong constraint on the thermoregulatory capacity and behavior of *I. aranica*. Tigmothermy of *I. aranica* could largely be due to the high thermal capacity (temperature inertia) of the black slate rock, which had a strong effect on the simultaneous warming of the lizard's body and the ambient air. This might explain the high parallelism of BT and AT in *I. aranica* (not present in the other two species), and the very high "non-biological, but inertia-caused" ST-AT correlation.

The thermoregulatory capacity of the *Iberolacerta* species studied is higher relative to the substrate (slopes much different from 1) than to the ambient air temperatures. The relatively low correlations, however, suggest that these lizards are not very precise in adjusting their body temperatures. All regression line slopes were significantly different from 1 (if there was no thermoregulatory behavior, the lizards' rhythm of warming up would exactly have paralleled the heating rhythm of the substrate or the air, resulting in a slope of 1).

In the BT-ST relationship of *I. bonnali*, the slope was 0.18 (BT = 24.36 + 0.18 ST; $R^2 = 0.19$), whereas it was 0.21 in the BT-AT relationship (BT = 25.52 + 0.21 AT; $R^2 = 0.12$). In the BT-ST relationship of *I. aranica*, the slope was 0.11 (BT = 26.04 + 0.11 ST; $R^2 = 0.15$), whereas it was 0.28 in the BT-AT relationship (BT = 24.44 + 0.28 AT; $R^2 = 0.19$). In the BT-ST relationship of *I. aurelioi* the slope was 0.20 (BT = 22.54 + 0.20 ST; $R^2 = 0.34$), whereas it was 0.36 in the BT-AT relationship (BT = 22.53 + 0.36 AT; $R^2 = 0.24$). The low slopes show that these three lizard species are good thermoregulators.

In their thermoregulatory capacity relative to the substrate temperature, the heliothermic species *I. bonnali* (slope 0.18) and *I. aurelioi* (slope 0.20) were very similar, the more tigmothermic and even better thermoregulator *I. aranica* (slope 0.11) included. All these *Pyrenesaura* (true high mountain dwellers) were clearly better thermoregulators than the mid-mountain species *I. monticola* (BOULENGER, 1905) (slope 0.30) and *I. horvathi* (MÉHELY, 1904) (slope 0.55) These and the following comparative data on *I. monticola*, *I. horvathi* and *I. cyreni* were taken from ARGÜELLO & SALVADOR (1988), DE LUCA (1992) and MARTIN & SALVADOR (1993).

As to their thermoregulatory capacity relative to the ambient air temperature, *I. bonnali* (slope 0.21) was the best thermoregulator, very similar to *I. aranica* (slope 0.28), and both were slightly better than *I. aurelioi* (slope 0.36). Relative to AT, all three *Pyrenesaura* were clearly better thermoregulators than *I. monticola* (slope 0.52) and *I. horvathi* (slope 0.76).

In their accuracy of adjusting the body temperature (BT), the three species were not very precise, as the correlations of BT with ST and AT were not very high (*I. bonnali*: BT-ST, $r = 0.44$; BT-AT: $r = 0.35$; *I. aranica*: 0.39 and 0.44; and for *I. aurelioi*: 0.58 and 0.49, respectively). Comparative data of *I. monticola* (0.55 and 0.56) and *I. horvathi* in particular (0.64 and 0.77) show that these mid-mountain species are more precise in adjusting their body temperatures.

The thermal behavior of *I. bonnali* and *I. aurelioi* is very special. In related lizards (as in saurians in general) BT is usually closer (cor)related to AT than to ST, contrary to what was observed in these two species that live in areas with fairly low AT. For *I. aranica*, BT values were better correlated with AT than ST, as is usual in low altitude lizard species. However, in the case of *I. aranica*, this result was produced by a strong effect of ST (becoming very high when exposed to direct sun) simultaneously influencing both BT and AT. In the high altitude areas studied, AT usually did not rise so much during the day, whereas rocks (ST) heated up easily, especially if of dark color. Thus, one could hypothesize that high mountain environment should lead to the selection of lizards which are good thermoregulators and well able to adjust their body temperatures relative to the two thermal extremes represented by cold air and frequently excessively hot substrate.

The total ranges of body temperatures of active lizards (i. e. thermoconformism) were the following: *I. bonnali* – 12.4 °C (14.4 ºC for all kinds of substrate, ARRIBAS 2009), *I. aranica* – 14.5 ºC (17.9 ºC for all kinds of substrate, ARRIBAS 2007, 2009) and *I. aurelioi* – 17.8 ºC. *Iberolacerta aurelioi* BT covered the widest range and, thus, characterized the most versatile thermoconformist although living in a single type of substrate only. All above ranges were fairly similar to those of *I. monticola* and *I. horvathi* (both 15.0 °C) as well as *I. cyreni* (MÜLLER & HELLMICH, 1937) (16.8 ºC). According to all data known about *Iberolacerta*, *I. aurelioi*, which is bound to a unique substrate, and *I. aranica*, that lives in a variety of substrates, are the most pronounced thermoconformists, and *I. bonnali* is the least.

Other *Iberolacerta* species, such as *I. horvathi*, with a mean BT of 28.69 °C (20-35 °C), were also thermoregulating more effectively relative to ST (slope 0.55; r = 0.64) than to AT (slope 0.76; r = 0.77) (DE LUCA 1992). The same applies to *I. monticola* with a mean BT of 29.3 °C (20.4-35.4 °C), being also a good thermoregulator that is more effective in relation to ST (slope 0.30; r = 0.56) than to AT (slope 0.52; r = 0.56) (ARGÜELLO & SALVADOR 1988). *Iberolacerta cyreni* field BT averaged 29.4 °C (18.4-35.2 °C) for tailed specimens, and 29.5 °C (17.5-34.4 °C) for tail-autotomized individuals (MARTIN & SALVADOR 1993). The mean body temperatures of the *Iberolacerta* species studied are below the median temperature calculated from 53 lacertid lizard species (33.8 °C) (CASTILLA et al. 1999). All three *Pyrenesaura* species are very similar in their thermal requirements and very constant independent of sex, time or environmental conditions, as postulated by the so called "thermal rigidity" principle (VAN DAMME et al. 1989).

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REFERENCES

AMAT, F. & PÉREZ-MELLADO, V. & HERNANDEZ ESTEVEZ, J. & GARCÍA-DIEZ, T. (2008): Dietary strategy of a Pyrenean lizard, *Iberolacerta aurelioi*, living in a poor resources alpine environment.- Amphibia-Reptilia, Leiden; 29: 329-336.

ARGÜELLO, J. A. & SALVADOR, A. (1988): Actividad, selección de habitat y temperaturas corporales de *Lacerta monticola* en una localidad de la Cordillera Cantábrica (Sauria: Lacertidae).- Revista Española de Herpetología, Salamanca; 3(1): 29-40.

ARNOLD, E. N. & ARRIBAS, O. & CARRANZA, S. (2007): Systematics of the Palaearctic and Oriental lizard tribe Lacertini (Squamata: Lacertidae: Lacertinae), with descriptions of eight new genera.- Zootaxa, Auckland; 1430:1–86.

ARRIBAS, O. J. (1993a): Estatus específico para *Lacerta* (*Archaeolacerta*) *monticola bonnali* LANTZ, 1927 (Reptilia, Lacertidae).- Boletín Real Sociedad Española Historia Natural (Sec. Biol.), Madrid; 90: 101-112.

ARRIBAS, O. J. (1993b): Intraspecific variability of *Lacerta* (*Archaeolacerta*) *bonnali* LANTZ, 1927 (Squamata: Sauria: Lacertidae).- Herpetozoa, Wien; 6: 129-140.

ARRIBAS, O. J. (1994): Una nueva especie de lagartija de los Pirineos Orientales: *Lacerta* (*Archaeo-*

lacerta) *aurelioi* sp. nov. (Reptilia: Lacertidae).- Bolletino, Museo Regionale di Scienze Naturali, Torino; 412: 327-351.

ARRIBAS, O. J. (1997a): Morfología, filogenia y biogeografía de las lagartijas de alta montaña de los Pirineos. PhD thesis, Universidad Autónoma de Barcelona, Bellaterra; pp. 353.

ARRIBAS, O. J. (1997b): *Lacerta aranica* ARRIBAS, 1993; pp. 213-215. In: PLEGUEZUELOS, T. J. (ed.): Distribución y biogeografía de los anfibios y reptiles de España y Portugal. Monografías de la AHE, vol. 3, Univ. Granada, Granada.

ARRIBAS, O. J. (1997c): *Lacerta aurelioi* ARRIBAS, 1994; pp. 216-218. In: PLEGUEZUELOS, T. J. (ed.): Distribución y biogeografía de los anfibios y reptiles de España y Portugal. Monografías de la AHE, vol. 3, Univ. Granada, Granada.

ARRIBAS, O. J. (1998) [2000]: Caracterización de los factores fisiográficos, geológicos y climáticos del área de distribución de las lagartijas de alta montaña de los Pirineos (*Iberolacerta* ARRIBAS, 1997; subgen. *Pyrenesaura* ARRIBAS, 1999) y otros lacértidos del piso alpino de los Pirineos.- Lucas Mallada, Huesca; 10: 67-85.

ARRIBAS, O. J. (1999a): Taxonomic revision of the Iberian "Archaeolacertae" II: Diagnosis, morphology and geographic variation of '*Lacerta*' *aurelioi* ARRIBAS, 1994.- Herpetozoa, Wien; 11: 155-180.

ARRIBAS, O. J. (1999b): Phylogeny and relationships of the mountain lizards of Europe and Near East (*Archaeolacerta* MERTENS, 1921, Sensu Lato) and their relationships among the Eurasian Lacertid Radiation.- Russian Journal of Herpetology, Moskva; 6: 1-22.

ARRIBAS, O. J. (1999c): Biogeografía del Piso Alpino y su congruencia con la distribución y diferenciación geográfica de las lagartijas de alta montaña de los Pirineos (*Archaeolacerta* s. l.).- Lucas Mallada, Huesca; 9: 9-33.

ARRIBAS, O. J. (2000): Taxonomic revision of the Iberian 'Archaeolacertae' III: Diagnosis, morphology, and geographic variation of *Iberolacerta bonnali* (LANTZ, 1927).- Herpetozoa, Wien; 13: 99-131.

ARRIBAS, O. J. (2001): Taxonomic revision of the Iberian 'Archaeolacertae' IV. Diagnosis, morphology and geographic variation of *Iberolacerta aranica* (ARRIBAS, 1993).- Herpetozoa, Wien; 14: 31-54.

ARRIBAS, O. J. (2002a): *Lacerta aranica*; pp. 215-217. In: PLEGUEZUELOS, J. M. & MÁRQUEZ, R. & LIZANA, M. (eds.): Atlas y Libro Rojo de los anfibios y reptiles de España. Dirección General de Conservación de la Naturaleza-A.H.E., Madrid.

ARRIBAS, O. J. (2002b): *Lacerta aurelioi*; pp. 218-219. In: PLEGUEZUELOS, J. M. & MÁRQUEZ, R. & LIZANA, M. (eds.): Atlas y Libro Rojo de los anfibios y reptiles de España. Dirección General de Conservación de la Naturaleza-A.H.E., Madrid.

ARRIBAS, O. J. (2002c): *Lacerta bonnali*; pp. 223-224. In: PLEGUEZUELOS, J. M. & MÁRQUEZ, R. & LIZANA, M. (eds.): Atlas y Libro Rojo de los anfibios y reptiles de España. Dirección General de Conservación de la Naturaleza-A.H.E., Madrid.

ARRIBAS, O. J. (2004): Characteristics of the reproductive biology of *Iberolacerta aurelioi* (ARRIBAS, 1994) (Squamata: Sauria:Lacertidae).- Herpetozoa, Wien; 17(1/2): 3-18.

ARRIBAS, O. J. (2007): Istòria naturau e evolucion dera Cernalha Aranesa, *Iberolacerta aranica*. Huesca (Graficas Alós-Conselh Generau d'Aran), 446 pp.

ARRIBAS, O. (2008a): Lagartija aranesa – *Iberolacerta aranica*. In: CARRASCAL, L. M. & SALVADOR, A. (eds.): Enciclopedia virtual de los vertebrados Españoles. Museo Nacional de Ciencias Naturales, Madrid. < http://www.vertebradosibericos.org/ >

ARRIBAS, O. (2008b): Lagartija pallaresa – *Iberolacerta aurelioi*. In: CARRASCAL, L. M. & SALVADOR, A. (eds.): Enciclopedia virtual de los vertebrados Españoles. Museo Nacional de Ciencias Naturales, Madrid. < http://www.vertebradosibericos.org/ >

ARRIBAS, O. (2008c): Lagartija pirenaica – *Iberolacerta bonnali*. In: CARRASCAL, L. M. & SALVADOR, A. (eds.): Enciclopedia virtual de los vertebrados Españoles. Museo Nacional de Ciencias Naturales, Madrid. < http://www.vertebradosibericos.org/ >

ARRIBAS, O. J. (2009): Habitat selection, thermoregulation and activity of the Pyrenean Rock Lizard *Iberolacerta bonnali* (LANTZ, 1927) (Squamata: Sauria: Lacertidae).- Herpetozoa, Wien; 22 (3/4): 145-166.

ARRIBAS, O. J. & CARRANZA, S. (2004): Morphological and genetic evidence of the full species status of *Iberolacerta cyreni martinezricai* (ARRIBAS, 1996).- Zootaxa, Auckland; 634: 1-24.

ARRIBAS, O. & CARRANZA, S. (2007): Lagartija leonesa – *Iberolacerta galani*. In: CARRASCAL, L. M. & SALVADOR, A. (eds.): Enciclopedia virtual de los vertebrados Españoles. Museo Nacional de Ciencias Naturales, Madrid. < http://www.vertebradosibericos.org/ >

ARRIBAS, O. & CARRANZA, S. & ODIERNA, G. (2006): Description of a new endemic species of mountain lizard from Northwestern Spain: *Iberolacerta galani* sp. nov. (Squamata: Lacertidae).- Zootaxa, Auckland; 1240: 1-55.

ARRIBAS, O. J. & GALÁN, P. (2005): Reproductive characteristics of the Pyrenean High-Mountain Lizards: *Iberolacerta aranica* (ARRIBAS, 1993), *Ib. aurelioi* (ARRIBAS, 1994) and *Ib. bonnali* (LANTZ, 1927).- Animal Biology, Leiden; 55(2): 163-190.

ARRIBAS, O. J. & MARTINEZ-RICA, J. P. (1997): *Lacerta bonnali*; pp. 219-221. In: PLEGUEZUELOS, T. J. (ed.): Distribución y biogeografía de los anfibios y reptiles de España y Portugal, Monografías de la AHE, vol. 3, Univ. Granada, Granada.

ARRIBAS, O. J. & ODIERNA, G. (2004): Karyological and osteological data supporting the specific status of *Iberolacerta* (*cyreni*) *martinezricai* (ARRIBAS, 1996).- Amphibia-Reptilia, Leiden; 25: 359-367.

CARRAZA, S. & ARNOLD, E. N. & AMAT, F. (2004): DNA phylogeny of *Lacerta* (*Iberolacerta*) and other lacertine lizards (Reptilia: Lacertidae): did competition cause long-term mountain restriction?- Systematics and Biodiversity, London; 2: 57-77.

CASTILLA, A. M. & VAN DAMME, R. & BAUWENS, D. (1999): Field body temperatures, mechanisms of thermoregulation and evolution of thermal characteristics in lacertid lizards.- Natura Croatica, Zagreb; 8 (3): 253-274.

CROCHET, P. A. & CHALINE, O. & SURGET-GROBA, Y. & DEBAIN, C. & CHEYLAN, M. (2004): Speciation in mountains: phylogeography and phylogeny of the rock lizards genus *Iberolacerta* (Reptilia: Lacertidae).- Molecular Phylogenetics and Evolution, Orlando; 30: 860-866.

DE LUCA, N. (1992): Notes on the biology and ecology of the Horvat's rock lizard (*Lacerta horvathi* MÉHELY, 1904, Reptilia: Lacertidae); pp. 129-135. In:

KORSÓS, Z. & KISS, I. (eds.): Proceedings of the sixth Ord. General Meeting of the Societas Europaea Herpetologica, Budapest, 19-23 August 1991.

EMBERGER, L. [Rev. by GODRON, M.] (1983): Vademecum pour le relevé méthodique de la vegetation et du milieu: extrait du "Code pour le relevé méthodique de la végétation et du milieu". Paris (CNRS - Centre National de la Recherche Scientifique); 169 pp.

FONT TULLOT, I. (1984): Atlas de la radiación solar en España. Madrid (Instituto Nac. de Meteorología). 14 pp., 30 plates.

HINTZE, J. (2001): NCSS and PASS. Kaysville, Utah (NCSS - Number Cruncher Statistical Systems, PASS - Power Analysis and Sample Size) [Software and manuals available at < http://www.ncss.com >].

IUCN 2008. 2008 IUCN Red List of Threatened Species. < www.iucnredlist.org > [downloaded on 23 December 2008].

KODAK-PATHÉ (1987): La photographie infrarouge et ses applications. Paris (Editions V.M.); 85 pp.

KREBS, C. J. (1989): Ecological methodology. New York (Harper Collins Publ.); 654 pp.

KREBS, C. J. (1999): Ecological methodology (second edition). Menlo Park CA (Benjamin/Cummings); XII, 620 pp.

MARTÍN, J. & SALVADOR, A. (1993): Thermoregulatory behaviour of rock-lizards in response to tail loss.- Behaviour, Leiden [Brill]; 124: 123-136.

MARTÍNEZ-RICA, J. P. (1977): Observaciones ecológicas de *Lacerta monticola bonnali*, LANTZ en el Pirineo español.- Publicaciones del Centro Pirenaico de Biología Experimental, Jaca; 8: 103-122.

MAYER, W. & ARRIBAS, O. J. (2003): Phylogenetic relationships of the European lacertid genera *Archaeolacerta* and *Iberolacerta* and their relationships to some other 'Archaeolacertae' (sensu lato) from Near East, derived from mitochondrial DNA sequences.- Journal of Zoological Systematics & Evolutionary Research, Berlin; 41: 157-161.

MILSOM, H. (2001): Infra-red photography. A complete workshop guide. Faringdon (Fountain Press); 176 pp.

ODIERNA C. & APREA, G. & ARRIBAS, O. J. & CAPRIGLIONE, T. & CAPUTO, V. & OLMO, E. (1996): The karyology of the Iberian Rock Lizards.- Herpetologica, Lawrence; 52 (4): 542-550.

POTTIER, G. (coord.) (2008): Atlas de répartition des reptiles et amphibiens de Midi-Pyrenées. Collection Atlas naturalistes de Nature Midi Pyrénées. Toulouse (Ed. Nature Midi-Pyrenees), 126 pp.

PRODON, R.& LEBRETON, J. D. (1981): Breeding avifauna of a mediterranean succession: the holm oak and the cork oak series in the eastern Pyrénées. I. Analysis and modelling of the structure gradient.- Oikos, Lund; 37: 21-38.

VAN DAMME, R. & BAUWENS, D. & CASTILLA, A. M. & VERHEYEN, R. F. (1989): Altitudinal variation of thermal biology and running performance in the lizard *Podarcis tiliguerta*.- Oecologia, Berlin; 80: 516–524.

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