Ontogenetic and sexual variation in the coloration of the lacertid lizards *Iberolacerta monticola* and *Podarcis bocagei.* Do the females prefer the greener males?

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Abstract

Changes in the coloration of the lacertid lizards *Iberolacerta monticola* and *Podarcis bocagei* with age in populations from NW Spain are described. The onset of sexual maturity in *P. bocagei* males involves a change in the ventral (yellow) and dorsal (green) colorations, which is different from immature males (dorsally brownish in color). In *I. monticola* males, the ventral coloration also changes to a deep green when they reach maturity, while the dorsal coloration remains brownish as in the immature specimens. In this species, the green dorsal coloration is acquired gradually after maturity. Only the oldest individuals have a predominantly green dorsal coloration. The differences between the two species in the time males take to acquire the green dorsal coloration could be related to their different longevity. The coloring is acquired gradually in the most long-lived species (*I. monticola*). A field study was carried out on the behaviour of adult males of *I. monticola* during the reproductive period. The males with green dorsal coloration were seen to pair with females significantly more frequently than those with the brownish dorsal color. The increase in the green dorsal coloration (conspicuous) with the size and age of the males of this species would appear to have a clear function as an intersexual or intrasexual signal.

Keywords

Coloration; Lacertidae; ontogenetic color changes; reptiles; sexual dichromatism; sexual selection

Introduction

The coloration of the body has a wide social significance in vertebrates (Andersson, 1994; Espmark et al., 2000). Many species use body color as a form of communication, for example as a means of sexual recognition and a way to send out information on their capacity to fight or their sexual stage (Cooper and Greenberg, 1992; Houde, 1997; Cuadrado, 2000; LeBas and Marshall, 2000). In the case of reptiles, many species of Squamata, especially from the Scleroglossa clade (including some scincids, cordilids and lacertids), sexual recognition is often based on color signals, particularly in species that

present marked sexual dichromatism, where the males usually display more conspicuous colors than the females (Vitt and Cooper, 1985; Cooper and Greenberg, 1992; Olsson, 1994). These Scleroglossa lizards use visual displays in interactions, which are an indication of aggressiveness or the intention to mate (Díaz, 1993; López et al., 2004; Pough et al., 2004).

The intensity of the conspicuous coloration of the males of some lizard species would seem to be important in terms of the aggressive interactions between individuals of this sex, providing us with information on their fighting capacity (Olsson, 1994). However, there is little evidence that these bright colorations in males are important to the females when choosing a partner (Olsson and Madsen, 1995; Tokarz, 1998). There is also little evidence that the females of many lizard species make an active choice of a partner based on visual characters (Olsson and Madsen, 1995, 2001; LeBas and Marshall, 2001; Olsson, 2001).

The marked sexual dichromatism of many lizard species, especially in those where the males develop a bright coloration during reproduction, might be related to signals regarding the sexual recognition of males who are searching for a partner. However, experiments carried out with the lacertid *Podarcis hispanica* show that chemical signals have preference over visual signals in sexual recognition (López and Martín, 2001). In spite of this, coloration can play an important role in communication in certain saurian species, co-existing along with chemical signals, at least in those exhibiting marked changes of both an ontogenetic and seasonal nature, in the pigmentation of one of the sexes (Galán, 2000). Both types of signals are important depending on the context. Therefore, visual signals could be important for long-distance communication whereas chemical signals are useful at shorter distances (López and Martin, 2001; López et al., 2004).

Two species of small-sized lacertid lizards live in the north-west corner of Spain (northern Galicia). They are endemic to the north-western area of the Iberian peninsula: Bocage's wall lizard (*Podarcis bocagei*), which lives primarily on slopes and in areas of scrub, and the Iberian rock lizard (*Iberolacerta monticola*; previously *Lacerta monticola*), which lives in rocky and stony areas. Both species can live in the same areas and coexist in certain habitats, such as stone walls or clearings in woods (Galán and Fernández, 1993).

Iberolacerta monticola is a species with a high variability in dorsal coloration and design, especially the adult males, whose dorsal color can vary from brown to bright green, with a complex pattern of black spots arranged irregularly over the coloration (Arribas, 1996; Martín, 2005). This dorsal coloration is particularly developed in males from low-altitude populations in Galicia (north-western Iberian peninsula), displaying a marked contrast between the brown, green and black colors, especially during the reproductive period (Galán and Fernández, 1993; Galán, unpublished).

Podarcis bocagei is less variable in color and design. The adult males have a green dorsal band, whereas the flanks are brown. The black pattern usually forms longitudinal lines and irregular spots (Galán, 1986; Galán and Fernández, 1993). In the two species the bright dorsal colorations (greens) of the adult males develop during the reproductive period, from April to July, becoming less intense or going back to brown the rest of the year (Galán and Fernández, 1993; Galán, 1995).

These two lizard species are considered "small-sized lacertids", however, *I. monticola* is, on average, 16% larger than *P. bocagei*. Correlated with this, the differences in their life histories are important. *I. monticola* males reach sexual maturity on average a year later (2-3 years as opposed to 1-2 for *P. bocagei*; Galán, 1996, 1999a; Rúa and Galán, 2003) and the maximum longevity of *I. monticola* males (8 years of age) is twice as high as that of the *P. bocagei* males (4 years of age). These two characteristics (age at maturity and longevity) are closely related (Bauwens and Díaz-Uriarte, 1997). Therefore, of the varying degrees in the life history patterns of lacertids, ranging from species having short life spans and early sexual maturity at one end, to species that are long-lived and attain sexual maturity later, at the other (Bauwens and Díaz-Uriarte, 1997), *P. bocagei* would come closer to the former, while *I. monticola* would be more similar to the latter (Galán, 1999a; Rúa and Galán, 2003). With regard to other life history pattern characteristics, such as multiple clutches in the same year (up to 2 in *I. monticola* and 3 in *P. bocagei*) and clutch size (an average of 6 eggs in *I. monticola* and 4 in *P. bocagei*) (Galán, 1991, 1997, 1999a; Rúa and Galán, 2003), their positions are somewhat different in this multivariant covariation axis of the life history patterns reported by Bauwens and Díaz-Uriarte (1997).

Ontogenetic changes in color are very common in reptiles, but they continue to be a poorly understood phenomenon in many species (e.i., Hawlena et al., 2006; Germano and Williams, 2007). For this reason, the following aspects will be studied in this article: (1) The ontogenetic changes in the coloration of the different parts of the body of *Iberolacerta monticola* and *Podarcis bocagei*, from birth to sexual maturity. (2) Changes in the dorsal coloration of the males of these two species after reaching sexual maturity. In the event they do occur, the extent to which such changes are related to the size and age of the individuals. (3) Finally, an attempt will be made to contrast the hypothesis that the change in dorsal coloration from brown to green in males is related to sexual recognition. Also if the green dorsal pigmentation in males is found to increase over the course of the adult life in either of the two species, this could be related to sexual recognition cues taken by the females. Hence, the study will focus on the behaviour adopted by the differently-colored adult males with respect to the females (courting and mate guarding) in the field.

Material and methods

Two populations of *Iberolacerta monticola* located in the fluvial valleys of the rivers Eume (UTM: 29T NJ70) and Mandeo (UTM: 29T NH79), in the province of A Coruña, Galicia, north-western Spain, were studied. These populations occur in the same geographical (Artabrian Gulf) and climatic (Wet Oceanic climate type) area, at a similar altitude (50-200 m above sea level, Galán, 1982) and type of habitat (rocky outcrops, slopes and walls in Atlantic *Quercus robur* forests with *Alnus glutinosa*, *Betula alba* and *Castanea sativa* mixed with reforestation of *Pinus pinaster* and *Eucalyptus globulus*). The annual and reproductive cycle of both populations is very similar (Galán, 1991; Rúa and Galán, 2003). Three populations of *Podarcis bocagei* have also been studied; two in the same locations as *I. monticola* (valleys of the rivers Eume and Mandeo), where they live in sympatry, and a third in Carral (UTM: 29T

NH58), situated at a distance of 12 and 24 km respectively from the others, in the same geographical and climatic area, at a similar altitude (90 m above sea level) and habitat. The annual and reproductive cycle of these three populations is also similar (Galán, 1997, 1999a).

The aim of the study was to monitor, over a period of several years, individuals marked by a code which combines toe clipping with the arrangement of the cephalic plates and other scalation characteristics, able to be determined thanks to the high interindividual variability in scalation in these lacertid lizards species. Seven highly variable scalation characteristics were considered: contact pattern (separated plates, contact at one point, broad contact) between: (i) rostral-frontonasal, (ii) frontonasal-frontal and (iii) interparietal-occipital plates, (iv) presence and location of supernumerary scales, the number of (v) maseteric and (vi) supratemporal plates on the left and right sides of the head, and (vii) number of perianal scales (and any other anomalies of the plates). This combination of toe clipping with these seven individual scalation characteristics allowed us to identify the individual when recaptured, including those marked as juveniles several years later (see below). A photograph of the dorsal pattern of the adult individuals accompanied the code. The marking and recapture period lasted from 1989 until 1996 in the Eume and Carral areas and from 1993 until 2004 in the Mandeo.

Several gravid females (with oviductal eggs) of both species from these areas were taken to the laboratory where clutches were obtained and incubated until eclosion took place. The hatchlings were marked individually as described and set free in the place where their mothers had been captured, together with their mothers (*I. monticola*: Galán, 1991; Rúa and Galán, 2003; *P. bocagei*: Galán, 1997, 1999a). The recapture records of these juveniles over the following years enabled us to obtain information on their growth, age and size at which they reach sexual maturity, longevity and the changes that occur in their coloration, during both the subadult and adult phases.

After monitoring the marked individuals of both species throughout the annual cycle (from February to October) it was observed that the dorsal coloration in adult males undergoes significant seasonal variations, in the same way that the green dorsal pigmentation shown by some individuals during the reproductive period (from April to June) becomes brown or grey-green the rest of the year (from August to March; Galán, 1995, unpublished). Therefore, and for the purposes of this study, only the individuals captured during the reproductive period of both species, between the months of April and July (Galán, 1991, 1997, 1999a; Rúa and Galán, 2003), when this coloration is at its highest level of development (Galán, 1995 and unpublished data), were taken into consideration. Individuals were captured by noosing or by hand.

The mark of each individual was recorded (in the case of recaptures, for identification), according to age class (*juveniles,* during their first calendar year; *subadults,* from the beginning of the second calendar year up until the onset of sexual maturity, and *adults: I. monticola*, males SVL>52 mm, females SVL>56 mm; *P. bocagei*, males SVL>50 mm, females SVL>45 mm), sex, snout-vent length (with a precision of 0.1 mm with a digital calliper), weight (with a precision of 0.1 g with a Pesola spring balance) and dorsal

coloration (back and flanks), ventral coloration (ventral and gular areas) and tail coloration. For tail coloration, animals with broken, injured or regenerated tails were not considered.

In the case of the dorsal coloration (granular dorsal and flank scales), the number of dorsal scales of each color in a ring in the center of the body was also counted (see below).

The coloration used as a reference was based on the standard color keys according to the *Pantone* code and the *Color Atlas* (Küppers, 1994), which has been used in the past to define the coloration of other Lacertidae (Galán, 1995, 2000). Since the angle at which the light hits the scales affects color perception, coloration was determined in all cases under good lighting conditions (natural, outside light). The lizard was hand-held, perpendicular to the observer, who proceeded to compare the coloration of each area of the body with the standard color layers (Küppers, 1994). The most similar color code was recorded. Once the coloration of the different parts of the body had been determined, the coloration of the dorsal scales in a ring in the center of the body was recorded using a hand-held 10x magnifying glass. All the observations were carried out by the same person.

Differentiations were made between the following colors (color coordinates according to Küppers, 1994): (1) *Green:* color coordinates: N_{00} and N_{10} and $> C_{50}$, $>A_{50}$ and from A_{40} to A_{99} and $>C_{50}$, $<M_{30}$. (2) *Brown*: N_{40} to N_{80} and $>A_{50}$, $<C_{60}$. (3) *Black*: N_{90} and N_{99}. (4) *White or whitish*: N_{00} and $<C_{30}$, $<A_{50}$. (5) *Yellow or pale yellow. Yellow*: N_{00} and $<C_{10}$, $>A_{70}$. *Pale yellow*: N_{00} and $<C_{10}$, and from A_{50} to A_{70}. (6) *Pale green*: N_{10} and $<C_{50}$, $>A_{50}$. (7) *Blue or blue-green. Blue*: N_{00} and $>C_{50}$, $<A_{50}$. *Blue-green*: N_{20} and $>C_{50}$, $>A_{50}$. These color categories were clearly differentiated, and colors were identified within the central range of each category, to avoid any overlapping categories.

Given the difficulties entailed in comparing the color tones of the dorsal coloration (granular dorsal scales, which cover the animal's back and flanks) with a magnifying glass, only three colors were differentiated: (1) green, (2) brown and (3) black. Scales of each color were counted in a ring in the center of the body. This enabled us to quantify the expanse of each of the three colors. This method of quantifying dorsal coloration was used in all age categories, in both males and females, although in the latter, dorsal coloration generally remained brown throughout their lives.

In the case of ventral coloration (including the gorge), four colors were distinguished: (1) green, (6) pale green, (5) yellow or pale yellow and (4) white or whitish.

Finally, as regards tail coloration (dorsal area of the upper half) three categories were able to be distinguished: (1) green, (2) brown and (7) blue or blue-green.

Since the colors were found to show a continuous variation between different tones, well-defined color categories were chosen, thus enabling us to clearly assign a color to each scale. In the event of possible confusion (between blue and blue-green, for example), a single color category was chosen.

It must also be taken into account that in addition to the colors discernible within the visible spectrum of the human eye, other species can detect the near UV, including some lizard species (Fleishman et al., 1993; Thorpe and Richard, 2001). Preliminary studies carried out on *Iberolacerta monticola* would indicate that certain areas of the

body whose coloration is already bright (for example, the blue axillary ocelli and blue or white dots on the lower lateral part) could also be UV-reflecting and may be used in intraspecific communication (Arribas, 2002). All of these structures already present bright colorations in the visible spectrum, thus the UV reflectance would make them even brighter to animals able to see this part of the spectrum (Arribas, 2002). In this study, however, only the colorations in the visible spectrum will be considered.

Ontogenetic variation of coloration

For this part of the study, the coloration of individuals of all age classes was studied (*I. monticola*, n = 376; *P. bocagei*, n = 362). The coloration of the different parts of the body was also recorded: dorsal coloration (considering the back and flanks separately, not counting, in this case, the number of scales of each color, and comparing the general color of each area using the Küppers system), ventral coloration (ventral area and gorge) and tail coloration. Here, only the green or brown colors and not the pattern of black marks found over the coloration of these individuals was considered (despite the fact that the expanse of this black pattern was sometimes greater than the green or brown background coloration). Although the variation in color and design is continuous, in this case, individuals were divided into different dorsal coloration categories according to the presence and extent of the green and brown dorsal and flank pigmentations. In *Podarcis bocagei*, the color of the flanks stays brown in all the individuals throughout their lifetime. Therefore only two categories of dorsal coloration were differentiated: (a) individuals with brown flanks and back (B – B), and (b) individuals with green back and brown flanks (G – B).

In *Iberolacerta monticola* four categories were able to be discerned:(a) brown back and flanks (B – B), (b) brown back and brown and green flanks (B – BG), (c) brown and green back and green flanks (BG – G), and (d) green back and flanks (G – G). These four dorsal *I. monticola* coloration categories are not random. Rather, they correspond to a gradient of sizes and ages, (a) pertaining to the youngest and smallest adult males and (d) pertaining to the oldest and largest adult males, bearing in mind that the green dorsal pigmentation first appears on the scales of the flanks, later spreading to the dorsal scales (see Results).

Changes in the dorsal coloration of the adult males

For this part of the study, only sexually mature adult specimens were considered. The sexual maturity of the males was estimated by the presence of well-developed hemipenes (a visible bulge at the base of the tail) and the relative size of the femoral pores. However, since the only way to prove for certain whether or not an individual is sexually mature is by examining its internal reproductive organs, in previous studies carried out on these populations, a number of specimens of both species were dissected to determine the degree of testicle and epididymis development in relation to their body size (*I. monticola*, Galán, 1991; *P. bocagei*, Galán, 1996). This shed light on the size (SVL) at which the males of each species reach sexual maturity (males, *I. monticola*, SVL > 53 mm; Galán, 1991; Rúa and Galán, 2003; *P. bocagei*, SVL > 46 mm; Galán, 1996) and allowed us to

relate it to certain external characteristics, such as ventral coloration. In this way, it was possible to determine whether or not a given individual was mature.

Quantitative data on the degree of development of each coloration were obtained by counting the number of green, brown and black dorsal scales in a ring in the center of the body (a methodology similar to the one used to obtain an estimation of the number of dorsal scales in studies on lacertid taxonomy; see, for example, Darevsky, 1967; Galán, 1986; Arribas, 1996). In these lacertid lizard species, body coloration is arranged in somewhat irregular longitudinal bands or strips, all along the body with the different colors extending in equal proportions. That is why the number of the scales of each color in a central ring of the body is a good descriptor of the entire body coloration.

A hand magnifier with a magnification of 10x was used. If a scale had more than one color (not altogether infrequent), the most prevalent color was considered. As the number of scales of each color may vary greatly, depending on the row studied (due to the irregular distribution of the markings of each color), the count was carried out on at least two rows of non-consecutive scales. A third ring was counted if the values obtained in the first two were significantly different. Subsequently, the average number of scales of each color for each individual was calculated.

In contrast to the green or black pigmentation, brown coloration is markedly variable between the different individuals or depending on the dorsal region considered, especially in *Iberolacerta monticola*. In this species very light brown or ochre colorations in the dorsal area and dark brown colorations on the flanks are predominant. However, in this study, they were all grouped together in a single brown coloration category, clearly distinguishable from the black and green colorations.

This study did not consider the blue markings exhibited by most of the *I. monticola* adults in the axillary region (axillary ocelli) and on the external ventral scales, as a function of already-known individual recognition (López et al., 2004). In the corporal region where they are located (axillae and ventral scales), they did not influence the color counts carried out on the dorsal scales. In all the population and morphological studies, *P. bocagei* has never been found to show blue ocelli.

Preference of females for the greener males

This part of the study was carried out only on the *Iberolacerta monticola*, as male *Podarcis bocagei* adults showed no dorsal coloration variation during their adult life (see Results). The aim was to estimate the preference of *I. monticola* females for adult males with a different dorsal coloration pattern by means of field observations.

In the populations of *Iberolacerta monticola* studied, the adult males exhibited mate guarding behaviour after mating with the females (Rúa and Galán, 2003; Galán, unpublished data). On the basis of observations, after copulation the male remains with the female for a period ranging from minutes to hours. No different-sex adult individuals were seen together unless they had mated. When a male approached a female and courtship was not accepted on her part, the female moved away and did not remain in the proximity of the male. Therefore, as an approximation towards

quantifying mating success in the different adult males of the populations studied, observations of males in close proximity to a female (< 10 cm, usually in contact) were used as an indication that these animals had mated and that the male in question had not been rejected by the female he remained beside (Olsson and Shine, 1998; Moreira and Birkhead, 2003; Todd, 2005). Therefore, during the months of May and June, the most intense period of mating of *I. monticola* in the study area, the adult males observed to have mated with an adult female (exhibiting male mate guarding behaviour) were collected by noosing and data on their biometrical parameters and coloration, as indicated above, were recorded (number of green, black and brown dorsal scales in a ring in the center of the body and areas of the body in which these colorations were concentrated in relation to four categories). As a comparative sample, several adult males observed to be on their own, with no females in the vicinity, were randomly collected by noosing from the same populations and over the same time period. Data identical to the males exhibiting mate guarding behaviour were recorded.

The number of dorsal scales of each color as well as the corporal marks, which allow us to determine an individual's age, can only be identified in animals that were collected and then observed in the hand. Hence, I also counted individuals not able to be captured, but observed in the field and classified into one of the four categories in keeping with the degree of brown and green dorsal coloration (B-B, B-BG, BG-G and G-G), in addition to animals that were captured but not marked (age unknown). However, in these cases only the following information was recorded: dorsal coloration category and whether or not they had mated or were alone. These observations took place in the Eume and Mandeo populations every year from 1989–2004.

Statistical analyses

In the text and tables, mean values are cited ± standard errors (SE). When an analysis of variance and covariance was used, normality was confirmed first. Homogeneity among variances was tested with the Kruskal-Wallis test and normality was tested with the Kolmogorov-Smirnov test. Data on the variables tested did not differ significantly from a homogenous and normal distribution of independent data. Data analysis was carried out with SPSS 11.0 software.

To test the increase of SVL with age, polinomial regression (x = age in years, y = SVL) was used. One-factor ANOVAs were used to compare differences in green, brown and black coloration (number of dorsal scales of each color in a ring in the center of the body) with the age (in years) of the adult males of both species. I also used ANCOVAs to test these differences in the number of green, brown and black scales with age in years using size (SVL) as a covariate. Regression analyses were used to test the increase in the number of green, brown and black dorsal scales with age (in years) and size (SVL) of males. To determine if the *I. monticola* males with green dorsal coloration showed courtship behaviour to the same extent as those with brown dorsal coloration, the Chi-square test (χ^2) was used. Finally, the difference in frequencies of *I. monticola* males observed paired with females and alone in relation to four categories of dorsal coloration (B-B, B-BG, BG-G and G-G) was tested using contingency table analysis (G statistic).

Results

Growth, sexual maturity and longevity of the males

On the basis of the data obtained from the recaptures of males belonging to the two species and marked in the year of their birth, the age of several specimens was ascertained and related to their body size (SVL).

Iberolacerta monticola

SVL increases significantly with age (polynomial regression, x = age in years, y = SVL; $r^2 = 0.921$; $F_{2, 141} = 810.7$; $P < 0.0001$), especially during the first 3 years of life. The increase in size diminishes and growth is practically zero after 6-7 years of age. In spite of this, a significant overlapping of sizes (SVL) between different ages was observed, leading us to the conclusion that, except in the first years of life, size alone is not a suitable way to estimate age. For this reason, the variation in the dorsal coloration was analyzed separately, with both size (SVL) and age (in years) of the individuals. According to recapture data on the individuals marked as juveniles in the year of their birth, males were found to reach sexual maturity at two years of age (third calendar year, 41%, n = 27) or three years of age (fourth calendar year, the remaining 59%) in the sample under study (combined data from all the populations studied). According to the information gathered, maximum longevity of the males from these populations was 8 years of age. In other populations higher maximum longevity figures were obtained (12 years of age in the population from the Lambre River, A Coruña).

Podarcis bocagei

SVL also increases significantly with age (polynomial regression, $r^2 = 0.869$; $F_{2, 95} = 309.4$; $P < 0.0001$) especially during the first two years of life. The increase in size diminishes and growth is practically zero after three years of age. According to recapture data, males reached sexual maturity at one year of age (second calendar year, 33%, n = 43) or at two years of age (third calendar year, the remaining 67%). According to maximum longevity data, the males from these populations reached 4 years of age. In other populations higher maximum longevity figures were obtained (6 years of age in the population from the Tower of Hercules, A Coruña).

Differences in coloration between age and sex classes

Iberolacerta monticola

The dorsal coloration of immature individuals (juveniles and subadults) and adult females is brown, whereas in adult males it is variable, with different degrees of brown and green pigmentation (table 1). Ventral coloration varies in the immature individuals and adult females, but in this case all the adult males have the same green ventral coloration (table 1). A high percentage of the adult females has a ventral coloration similar to that of adult males. In the case of males, the onset of sexual maturity involves a change in ventral coloration, but not in dorsal color, which remains brown, as in immature individuals, the year they reach maturity. The green pigmentation appears

Table 1.
Percentages of juveniles, subadults, adult females and males assigned to the different categories of dorsal (back and flanks), ventral, and tail color in *Iberolacerta monticola*. The black pattern appearing on the brown, green or whitish coloration has been omitted.

		Adult males (N=108)	Adult females (N=92)	Subadults (N=72)	Juveniles (N=90)
Dorsal color					
Back	Flanks				
Green	Green	21.2	0	0	0
Green and brown	Green	27.4	0	0	0
Brown	Green and brown	16.8	0	0	0
Brown	Brown	34.5	100	100	100
Ventral color					
White or whitish		0	0	33.8	100
Pale yellow		0	0	24.6	0
Pale green		0	7.3	41.5	0
Green		100	92.7	0	0
Tail color					
Green and brown		34.5	0	0	0
Brown		65.5	100	83.1	0
Blue or blue-green		0	0	16.9	100

gradually, over the course of their lifetime. The coloration of the integer tail is relatively constant in adults, variable in sub-adults, and has a bright blue or blue-green color in juveniles, during their first calendar year.

Podarcis bocagei
The dorsal coloration of the immature individuals is also brown, but in this species the adult females are the ones that show varying degrees of brown and green pigmentation, whereas all of the adult males have a green dorsal coloration (table 2).

   The ventral coloration is variable in immature individuals and adult females, but all the adult males have the same yellow ventral coloration. A high percentage of the adult females has a ventral coloration similar to that of adult males (table 2). In males, the onset of sexual maturity involves a change in the dorsal coloration of all the individuals from brown to green. The coloration of the integer tail is relatively constant in adults, variable in subadults, and has a bright green color in juveniles.

Differences in coloration between adult males

Iberolacerta monticola
The dorsal coloration (back and flanks) of adult males (age ≥2 years; SVL ≥ 54 mm) changed notably over the course of the individuals' lifetime. The extension of the green dorsal coloration (number of green-colored scales in a ring in the center of the body) varied significantly with age (in years) in the adult individuals (ANOVA, $F_{5, 88}$ = 101.4,

Table 2.
Percentages of juveniles, subadults, adult females and males assigned to the different categories of dorsal (back and flanks), ventral, and tail color in *Podarcis bocagei*. The black pattern appearing on the brown, green or whitish coloration has been omitted.

		Adult males (N=113)	Adult females (N=109)	Subadults (N=65)	Juveniles (N=89)
Dorsal color					
Back	Flanks				
Green	Brown	100	20.7	0	0
Brown	Brown	0	79.3	100	100
Ventral color					
White or whitish		0	0	30.6	92.2
Pale yellow		0	27.2	69.4	7.8
Yellow		100	72.8	0	0
Tail color					
Brown		100	100	80.6	0
Green and brown		0	0	15.3	0
Green		0	0	4.2	100

$P < 0.0001$). The number of green dorsal scales increased significantly, with both age (polynomial regression, $r^2 = 0.815$; $F_{2, 88} = 189.3$; $P < 0.0001$) and size (SVL, $r^2 = 0.831$; $F_{2, 96} = 230.3$; $P < 0.0001$) (table 3, figs. 1 and 2). Using size (SVL) as a covariate, the number of green scales increased significantly with age in years (ANCOVA, $F_{6, 81} = 8.49$, $P = 0.005$). The green coloration appears first on the flanks, and then on the back, starting at a certain size (SVL > 65 mm) and age (4th-5th year). After five years of age and SVL ≥ 70 mm, the green coloration extends over a larger area than the brown coloration and individuals with completely green backs can be seen.

The number of brown-colored scales also varied significantly throughout the lifetime of the *I. monticola* adult males (ANOVA, $F_{5, 88} = 42.73$, $P < 0.0001$), but, contrary to what occurs with the green coloration, the amount of brown dorsal coloration (number of brown-colored scales) decreased significantly, with both age ($r^2 = 0.691$; $F_{2, 83} = 93.79$; $P < 0.0001$; fig. 2) and size (SVL, $r^2 = 0.673$; $F_{2, 94} = 94.83$; $P < 0.0001$; fig. 1). Using size (SVL) as a covariate, the number of brown scales decreased significantly with age in years (ANCOVA, $F_{6, 81} = 3.83$, $P = 0.04$). After monitoring the marked individuals, the brown-colored scales were found to turn green with age. Therefore green scales increase in number while the brown scales decrease as the animals grow older.

Finally, the number of black dorsal scales did not vary significantly with age in adult individuals (ANOVA, $F_{5, 86} = 1.88$, $P = 0.11$). The number of black dorsal scales undergoes a slight increase with age and SVL (figs. 1 and 2), although the difference in number is barely significant (age in years – no. black scales: $r^2 = 0.09$; $F_{2, 86} = 4.52$; $P = 0.02$; SVL – no. black scales: $r^2 = 0.075$; $F_{2, 94} = 3.72$; $P = 0.03$). ANCOVA, SVL as a covariate, $F_{6, 81} = 2.39$, $P = 0.13$.

Table 3.
Number of dorsal scales, green, brown and black in color, in a ring in the center of the body, at each year of age, sexual maturity (see methods), and SVL in males of _Iberolacerta monticola_ in A Coruña. Indicated in each case are the mean ± 1 standard error, the variation range and sampling size (N). To calculate the variation in the dorsal coloration of males, only adult specimens were used, 2 years of age and older (in the 2-year-old age class, only the 11 mature individuals were considered). The colors dark chestnut, dark brown, light brown and light ochre were grouped together in the count of brown-colored scales.

Age (years)	Sexual maturity	SVL (mm) Average ± 1 SE	SVL (mm) Range	No green scales Average ± 1 SE	No green scales Range	No brown scales Average ± 1 SE	No brown scales Range	No black scales Average ± 1 SE	No black scales Range	N
0	NO	29.0 ± 0.6	24 – 34	0	–	42.3 ± 1.1	33 – 50	15.3 ± 0.9	8 – 22	20
1	NO	41.6 ± 1.4	28 – 56	0	–	41.8 ± 0.8	33 – 48	15.4 ± 0.7	8 – 23	33
2	59% NO	51.0 ± 0.6	46 – 55	0	–	42.0 ± 0.8	37 – 47	16.2 ± 0.7	11 – 21	16
2	41% YES	58.1 ± 0.9	54 – 65	0	–	40.3 ± 2.1	24 – 48	15.5 ± 1.8	7 – 28	11
3	YES	62.8 ± 0.5	59 – 68	4.5 ± 1.0	0 – 19	34.5 ± 1.9	22 – 49	15.1 ± 1.5	6 – 26	22
4	YES	67.9 ± 0.3	65 – 71	19.1 ± 1.0	11 – 28	19.1 ± 2.1	4 – 42	17.9 ± 1.6	3 – 29	25
5	YES	70.9 ± 0.4	69 – 73	24.4 ± 1.1	20 – 31	7.8 ± 2.2	0 – 28	20.4 ± 2.6	4 – 31	11
6	YES	73.6 ± 0.2	72 – 74	26.4 ± 1.4	23 – 34	7.0 ± 2.2	0 – 20	21.5 ± 3.3	8 – 32	8
7	YES	74.6 ± 0.2	74 – 75	29.0 ± 2.1	22 – 37	5.9 ± 2.6	0 – 19	19.9 ± 4.3	6 – 34	7
8	YES	74.7 ± 0.3	74 – 75	31.6 ± 1.9	25 – 36	4.0 ± 1.8	0 – 9	24.8 ± 3.4	16 – 31	5
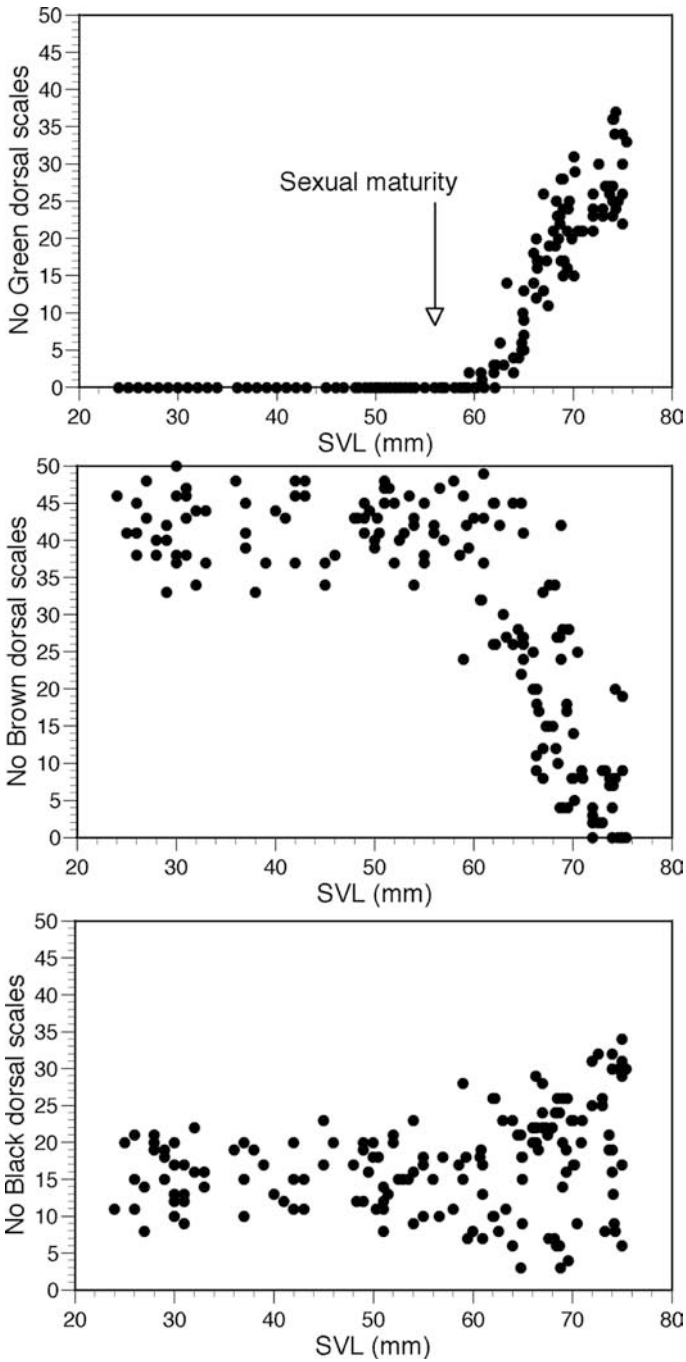
Figure 1. Relationship between the number of green, brown and black dorsal scales counted in a ring in the center of the body and body size (snout-vent length) in males of *Iberolacerta monticola* from A Coruña. The arrow indicates the size (SVL) at the onset of sexual maturity.
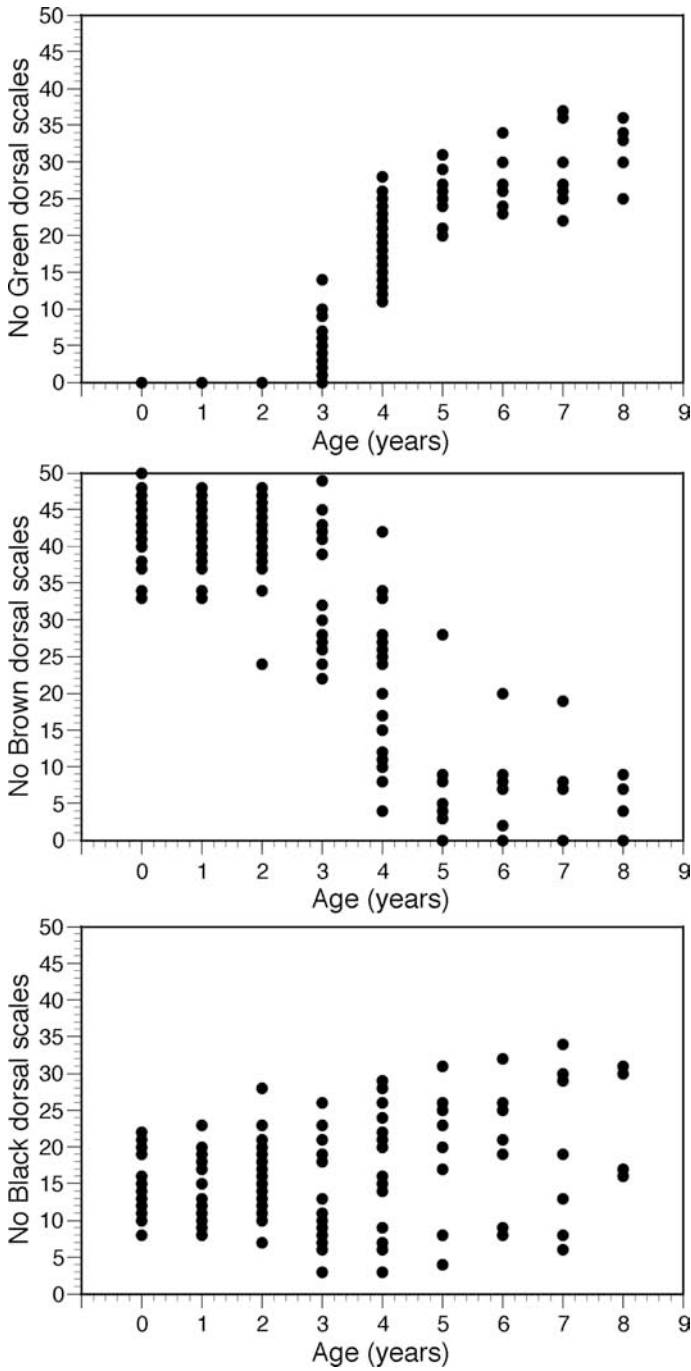
Figure 2. Relationship between the number of green, brown and black scales counted in a ring in the center of the body and age in years of *Iberolacerta monticola* males from A Coruña.

Podarcis bocagei

Unlike the species described above, the amount of green dorsal coloration in adult males (age ≥1 year; SVL ≥50 mm) did not vary significantly with age (ANOVA, $F_{3,\,49}$ = 1.54, P = 0.21). The young adults (1-2 years old), with a smaller body size (average SVL 53-57 mm) have a similar number of green dorsal scales as the older adults (3-4 years old), of a larger size (average SVL 60-62 mm). No increase was observed with either age (r^2 = 0.09; $F_{2,\,49}$ = 2.35; P = 0.11) or size (SVL, r^2 = 0.09; $F_{2,\,49}$ = 2.47; P = 0.10) (table 4, figs. 3 and 4). Using the size (SVL) as a covariate, the number of green scales did not vary significantly with the age in years either (ANCOVA, $F_{3,\,40}$ = 0.93, P = 0.34).

Nor did the number of brown and black-colored dorsal scales vary throughout the lifetime of the adults. Number of brown scales: ANOVA, $F_{3,\,44}$ = 1.13, P = 0.35 (age: r^2 = 0.01; $F_{2,\,44}$ = 0.18; P = 0.83; SVL: r^2 = 0.03; $F_{2,\,44}$ = 0.65; P = 0.52; ANCOVA, SVL as a covariate, $F_{3,\,40}$ = 2.07, P = 0.16) (figs. 3 and 4). Number of black scales: ANOVA, $F_{3,\,44}$ = 0.73, P = 0.54 (ANCOVA, SVL as a covariate, $F_{3,\,40}$ = 0.54, P = 0.47) (figs. 3 and 4).

Preference of Iberolacerta monticola females: field observations

The percentages obtained for the males paired with a female in relation to the type of dorsal coloration are very similar in the individuals whose ages were known (table 5) and in specimens observed and not collected and/or of unknown age (table 6). These frequencies do not differ significantly (χ^2 = 4.48; df = 2; P = 0.106). According to the data from both tables, frequencies of individuals observed paired with females differ significantly between the four categories of dorsal coloration (specimens of known age: G = 15.23; df = 3; P = 0.0016; table 5; specimens of unknown age: G = 18.28; df = 3; P = 0.0004; table 6). In both cases, post-hoc analyses show that the observed values of paired males were higher than the values expected in the greener ones (G-G and BG-G). The only males that were observed paired with females had a green dorsal coloration, while those with a brown dorsal coloration were never seen beside a female. Furthermore, males with a greater amount of green dorsal coloration (green back and flanks, G-G) were observed paired with a female a significantly higher number of times than those with a smaller amount of green dorsal coloration (tables 5 and 6); specimens of known age: G = 11.01; df = 2; P = 0.0089; specimens of unknown age: G = 11.13; df = 2; P = 0.005).

All the males that carried out mating in the study area (N = 10) had a green dorsal coloration (type G-G, eight times, and BG-G, twice).

Discussion

No comparisons between two such phylogenetically different species such as *Iberolacerta monticola* and *Podarcis bocagei* can be established (Bauwens and Díaz-Uriarte, 1997; Arnold, 2004; Carranza et al., 2004). However, differences in the life history of these two species, (particularly, those related to adult life span and longevity) may help explain the differences observed in the changes in the dorsal coloration patterns of males.
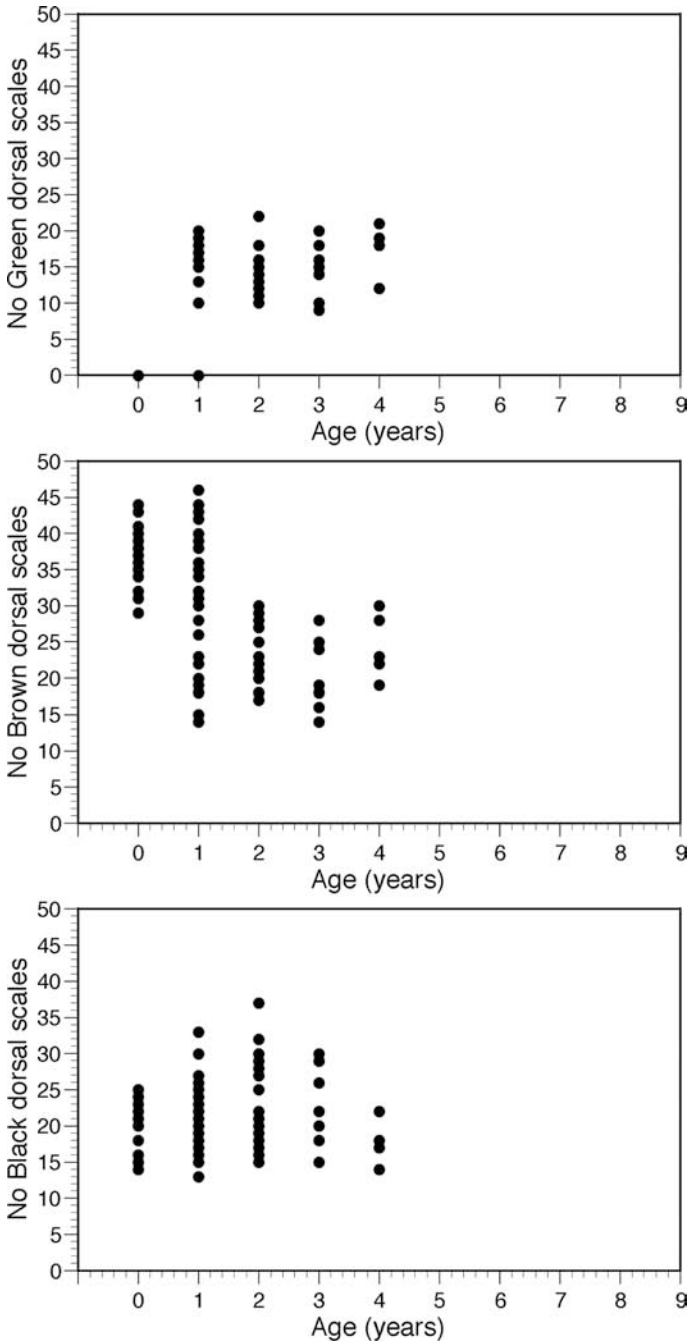
Table 4.

Number of dorsal scales, green, brown and black in color, in a ring in the center of the body, at each year of age, sexual maturity (see methods), and SVL in males of *Podarcis bocagei* in A Coruña. Indicated in each case are the mean ± 1 standard error, the variation range and sampling size (N).

Age (years)	Sexual maturity	SVL (mm)		No green scales		No brown scales		No black scales		N
		Average ± 1 SE	Range	Average ± 1 SE	Range	Average ± 1 SE	Range	Average ± 1 SE	Range	
0	NO	27.4 ± 0.9	22 – 35	0	–	36.6 ± 1.0	30 – 44	20.6 ± 1.0	14 – 25	25
1	67.4% NO	43.6 ± 1.0	34 – 52	0	–	38.1 ± 0.8	30 – 46	20.3 ± 0.7	15 – 30	29
1	32.6% YES	52.8 ± 0.3	51 – 55	15.7 ± 0.8	10 – 20	21.7 ± 1.4	14 – 32	22.1 ± 1.5	13 – 33	14
2	YES	57.4 ± 0.3	54 – 59	14.4 ± 0.7	10 – 22	23.9 ± 1.1	18 – 30	21.5 ± 1.4	15 – 32	23
3	YES	60.3 ± 0.2	59 – 62	16.6 ± 1.0	14 – 20	19.8 ± 2.8	14 – 28	24.0 ± 2.8	15 – 30	8
4	YES	62.4 ± 0.7	61 – 64	17.0 ± 2.6	12 – 21	25.7 ± 3.4	19 – 30	17.7 ± 2.3	14 – 22	5
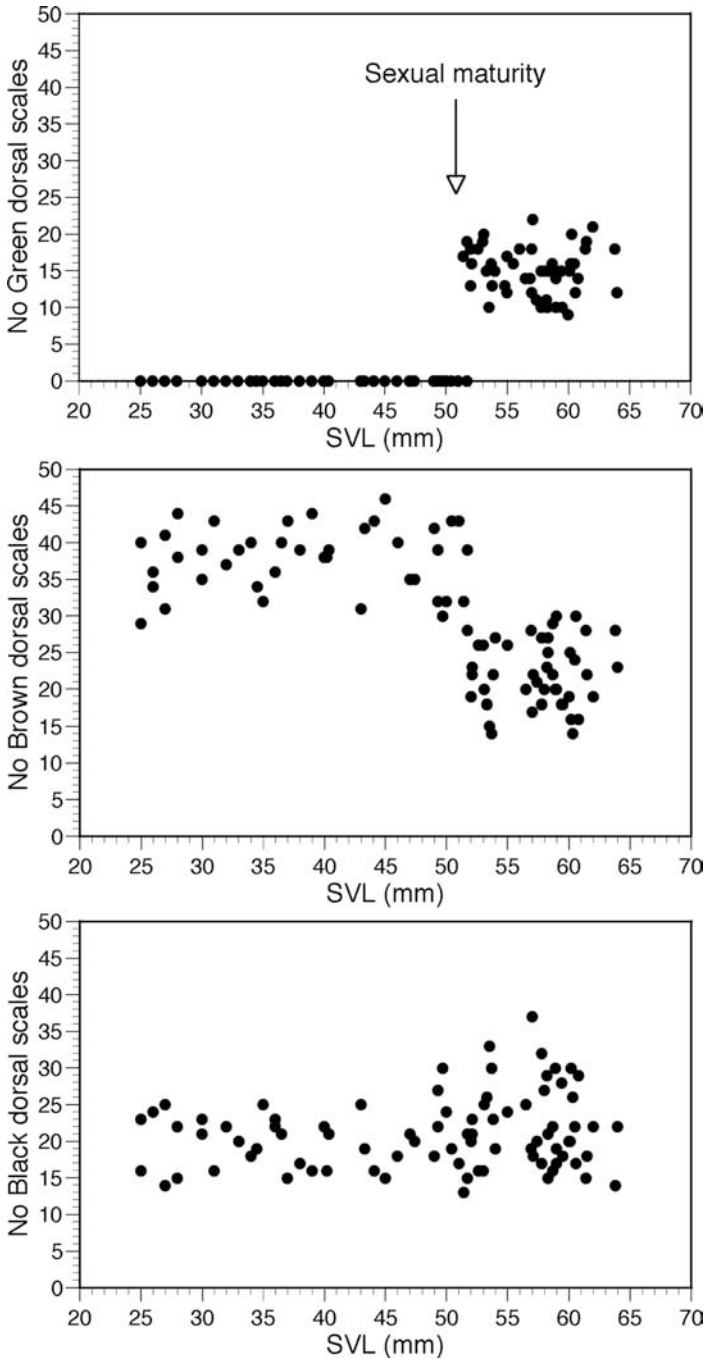
Figure 3. Relationship between the number of green, brown and black scales counted in a ring in the center of the body and body size (snout-vent length) in males of *Podarcis bocagei* from A Coruña. The arrow indicates the size (SVL) at the onset of sexual maturity.

Figure 4. Relationship between the number of green, brown and black scales counted in a ring in the center of the body and age in years of *Podarcis bocagei* males from A Coruña.

Table 5.
Field observations of adult *I. monticola* males having varying expanses of green dorsal coloration paired with a female (carrying out "male mate guarding" behaviour) and alone. (a) The general coloration is indicated, not the pattern of black spots. (b) The number of green scales was counted in a transversal ring of dorsal scales in the center of the body.

Dorsal coloration (a)	Flanks coloration (a)	No of green dorsal scales (b)	SVL average ± 1 ES (mm)	Age (years)	No of males alone	No of males paired with a female	% Paired
Green	Green	26 – 35	74.2 ± 0.2	6 – 8	12	8	40.0
Brown and Green	Green	18 – 25	69.6 ± 0.3	4 – 5	19	7	28.0
Brown	Brown and Green	7 – 17	64.7 ± 0.5	3 – 4	26	1	3.7
Brown	Brown	0	58.6 ± 0.6	2 – 3	16	0	0
Total					73	16	

The most constant body coloration in the adult males of both species, at least in terms of hue characteristics, is the ventral color. In the two cases, the onset of sexual maturity involves the development of a constant, bright ventral coloration during the reproductive period, which, in the populations studied, is green in *I. monticola* and yellow in *P. bocagei*. Therefore, the ventral coloration of adult males is clearly related to maturity. In other lizard species, males were also observed to acquire a characteristic ventral coloration upon reaching maturity (Lemos-Espinal et al., 1996; Pinto et al., 2005), a phenomenon which has been related to the influence of androgenic sexual hormones (Rand, 1992; Abell, 1998). Nevertheless, some minor differences between individuals with regard to the intensity of the ventral coloration have been observed. They may be related to differences in sexual hormone levels, as has been suggested for other species of lacertids (Bauwens and Castilla, 1998), and possibly induced by genetic differences between individuals (Thompson et al., 1993) or by different blood parasite loads and immune system levels.

Table 6.
Field observations of adult *I. monticola* males having varying expanses of green dorsal coloration paired with a female (carrying out "male mate guarding" behaviour) and alone. Observations of specimens with an unknown age (not marked) and/or observed without being captured.

Dorsal coloration	Flanks coloration	No of males alone	No of males paired with a female	% Paired
Green	Green	14	11	44.0
Brown and Green	Green	25	6	19.4
Brown	Brown and Green	34	2	5.6
Brown	Brown	24	0	0
Total		97	19	

Dorsal coloration, however, shows a different variation pattern depending on the species. In *P. bocagei* maturity brings about the same type of change as in ventral coloration, with the brown dorsal color typical of immature individuals changing to green, a color exhibited by all the adult individuals during the reproductive period. This green-colored covering (the number of green scales) does not change significantly once the animals reach maturity (at 1-2 years of age) until the end of their life, which has a relatively short longevity (4 years of age). By contrast, in *I. monticola* males, dorsal coloration does not change when sexual maturity is reached; it continues to be brown, like in the immature individuals. In the males of this species, the green dorsal coloration is acquired gradually after maturity is reached, over a period of several years. The number of green dorsal scales increases significantly with the size-age of the individuals, while the number of brown dorsal scales diminishes. Only the older (≥5-6 years of age) and larger (SVL ≥70 mm) individuals have a predominantly green dorsal coloration.

Although in Lacertidae species having a marked sexual dichromatism, green dorsal colorations are traditionally associated with adult males during the reproductive period, and brown coloration with the females (e.g., Olsson, 1994), even in the species studied here (*I. monticola*, Moreira et al., 1999; *P. bocagei*, Galán, 1995), variations to this general pattern have been found in these populations. Thus, a percentage of *P. bocagei* females had a green dorsal coloration, similar to that of males during the reproductive period while, on the other hand, a percentage of *I. monticola* adult males had a brown dorsal coloration, similar to that of the immature individuals and the females.

The presence of green dorsal colorations in some *P. bocagei* females has been discussed elsewhere (Galán, 2000). In this study, which focuses on adult males, an interesting observation was the fact that in one of the species (*P. bocagei*), the onset of maturity led to the development of a bright mating coloration in all the individuals, which did not change for the rest of their adult lives. In the other species (*I. monticola*), however, this did not occur. The bright dorsal mating coloration of the males did not appear after maturity, rather there was a period of several years, during which the brown scales gradually turned green. In this species, only the larger and older males have a green dorsal coloration.

There is a third dorsal color (black), appearing in the dorsal scales along with the green and brown colors, which showed no significant variation over the lifetime of the individuals of both species. It may, however, show changes in the amount of relative cover, especially in *I. monticola*, as well as marked differences in the number and arrangement of the black marks between the individuals of the two species. So it is possible that different proportions of the blackish marking pattern over the colored (i.e. green) part of the male dorsum, may affect the perception of a female sighting the male in question.

Other colors, such as the blue ocelli in the lateral areas of the body, generally found in the axilliary areas, and blue spots on the lateral ventral scales (both only present in *I. monticola*), have not been taken into account in this study, although significant changes in either their number or the amount of relative cover throughout the lifetime of the individuals were not observed (Galán, unpublished; see, however, López et al., 2004).

It is important to note that the relationship observed between the increase in the green dorsal coloration in *I. monticola* and the size and age of the individuals may vary among populations. There are isolated populations of the Iberian rock lizard in several low altitude locations in the north of Galicia (Galán, 1982, 1999b). In this study, two of these populations (Eume and Mandeo) were examined, although others are know to exist where the increase in the green coloration and the decrease in the brown coloring occur at a faster (males take on a green dorsal coloration at a smaller size and earlier age) or slower rate (some brown coloration still remains even in larger and older individuals) (Galán, unpublished). The populations studied here would fall somewhere in the middle between these two extremes. Variations in life history between the different populations which affect, for example, longevity and age at sexual maturity, as well as population density, mortality rates, etc., could be related to differences in the speed with which changes take place in the dorsal coloration of adult males (Sinervo et al., 2001; Taylor and Caraveo, 2003; Macedonia et al., 2004).

The complex coloration patterns, as shown by the adult males of these two species, can generally be explained, in adaptive terms, as an interaction between the sexual selection of bright, conspicuous colorations and the natural selection of cryptic colorations (e.g., Stuart-Fox et al., 2004 and references included in this article). In this study the hypothesis was put forward that this balance between the need to be conspicuous as a sexual signal and the need to be cryptic in order to avoid predation, is fulfilled by the dorsal coloration pattern of the adult males of these two lacertid species. The green coloration, which is either acquired abruptly after maturity in *P. bocagei*, or varies throughout the lifetime of the individual, increasing with age and size in *I. monticola*, would have a conspicuous role, as a sexual signal. On the other hand, the black dorsal coloration, in the form of irregular or reticulated markings, would have a cryptic function, and therefore its relative cover did not vary significantly throughout the lifetime of these animals.

Assuming a cryptic function of the black (and brown) dorsal pattern, related to camouflage and the survival of the individual, and a conspicuous function of the green dorsal coloration, related to intraspecific recognition cues, why in one of the two species (*P. bocagei*) is the green dorsal coloration of the males acquired abruptly with the onset of sexual maturity, while in the other (*I. monticola*) it is acquired progressively over the years, after maturity? This may be explained by differences in longevity between the two species. *Podarcis bocagei* males belonging to the populations studied live for a maximum of 4 years, and have only 2-3 years of adult life. On the contrary, *I. monticola* males can live for up to 8 years, 5-6 of which are adulthood. In *P. bocagei* there are few differences, in both body size and years of life, between a "young" and an "old" adult male. Furthermore, considering that adult males of this species have an annual probability of survival of around 0.45 (Galán, 1999a), the proportion of "old" males in the population is scarce. Therefore, a cue, such as the green dorsal coloration, which would indicate size-age differences between adult males would not be of great importance. By contrast, in the most long-lived species (*I. monticola*), there would be important differences between the different adult males of the population in years of age. Hence, in this species, it would make more sense to have some kind of signal that

would make it possible for females to be able to clearly differentiate between young and old males. Female *Iberolacerta cyreni* (former *I. monticola cyreni*) showed a strong preference for the scents of older and larger males (López et al., 2003). In other lizard species, females also select older males (Martín and Forsman, 1999; Irschick and Lailvaux, 2006).

In *I. monticola*, the conspicuous green dorsal coloration increases throughout the lifetime of the lizards at the expense of the brown coloration, which decreases, i.e. the initially brown-pigmented scales turn green over the years. In this way, there is a transition between a principally brown coloration, very similar to that of immature and female individuals, which the younger adult males have, towards a mainly green coloration found in larger-sized and older males. The change in the dorsal coloration of the males after they reach sexual maturity has been described for other species of lacertids, both insular, *Gallotia galloti* (Thorpe and Brown, 1989) and *Podarcis lilfordi* (Bauwens and Castilla, 1998). In these two species, which are also longevous (*Gallotia galloti* reaches 8-9 years of age, Castanet and Báez, 1988), an increase in the dark dorsal pigmentation of the males occurs as they grow, continuing after the minimum adult size has been acquired. Bauwens and Castilla (1998) suggest that these changes could be due to the accumulative action of sexual hormones, with individual differences being the result of the genetic differences between individuals.

Since Darwin (1871) it has generally been acknowledged that the secondary sexual characteristics of males may have evolved for selection by females (sexual selection). Many subsequent studies have confirmed this, revealing that the selection by females is a powerful evolutionary force which has modified the behaviour and morphology of many species (Andersson, 1994). However, as Olsson and Madsen (1995) have pointed out, selection by females has scarcely been described in lizards, a taxon which has been the subject of a considerable number of studies (Cooper and Vitt, 1993, for example, showed that the females of the non-territorial scincid, *Eumeces laticeps*, prefer to mate with the larger males). Furthermore, in territorial lizard species, such as the majority of iguanids (Stamps, 1983), and many lacertids (Bauwens, 1999), it is very difficult to show unequivocally if selection by the female is governed by characteristics of the male or by the quality of the territory (Hews, 1990). In this respect, it must be remembered that *I. monticola* is a territorial species (Moreira et al., 1999). In some lizard species, the conspicuous color of the males has evolved for aggressive intrasexual competition and not for mate selection by the female. In these species, in agonistic encounters between males, the success of an individual increases in proportion to the amount of green pigmentation cover (Olsson, 1994; Olsson and Madsen, 1995).

In territorial lizard species an increase in conspicuous green coloration in the older males may imply a change in strategy, i.e. to visible stand out from other competitive males. The younger individuals, on the contrary, would tend to maintain less conspicuous (brown) colorations to call less attention to themselves. These changes in coloration and strategy in the use of space with age have been described in *Iberolacerta cyreni* in Guadarrama (Aragón et al., 2004) and in other species of lacertids, such as in *Psammodromus algirus* (Díaz, 1993; Martín and López, 1999; Carretero, 2002).

In these species, the change in coloration is linked to different mating strategies: the older individuals carry out mate guarding of the female after copulation, while the younger ones would have to move away after copulating with the female, as they are in the territory of another male (sneakers versus territorial strategy). This change in strategy means that in the field, only the greenest males would be carrying out mate guarding, although this is not necessarily related to mating success.

This paper does not examine the relationship between coloration changes in adult males and their success in aggressive encounters or in obtaining and maintaining a territory. Therefore, the close relationship between the green dorsal coloration cover and body size in *I. monticola* may, in turn, be related to the aggressive behaviour and fighting capacity against other males, as occurs in other lacertids (Olsson, 1994). In this case, field observations of green males (not brown males) mating with females would not be related to a selection made by the females based on the color of the male but, more importantly, on the quality of the territory conquered by the male displacing other smaller (and brown) males.

Given the high level of correlation between body size and age with the amount of green dorsal color, it could also be argued that, if the female does indeed make a selection, this would be based on size (or other attributes related to size) and not color. In order to see whether or not the female makes a selection based on color it would be necessary to include experiments where the dorsal color of the males would be changed with paint. With the results obtained, these findings can only be considered provisional. However, the importance of the changes in dorsal coloration observed in *I. monticola* adult males throughout their growth after maturity would indicate an interesting line of research on the social and sexual meaning of these colors, non-exclusive of the use of other communication signs, such as chemical signals, for example (López et al., 2003).

In conclusion, on the basis of field observations, I cannot state with certainty whether it is coloration or age (and size) that is the most important trait in determining the pairing success of *I. monticola* males. Nevertheless, the younger, smaller, brown-colored males could still enjoy reproductive success to that of the older, bigger and greener ones if the younger males carried out different reproductive strategies (sneakers vs. mate guarding).

Acknowledgements

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