

Females that Imitate Males: Dorsal Coloration Varies with Reproductive Stage in Female *Podarcis bocagei* (Lacertidae)

PEDRO GALÁN

Adults of Bocage's Wall Lizard (*Podarcis bocagei*), a lacertid endemic to the northwestern Iberian Peninsula, generally show marked sexual dichromatism with males having green dorsal coloration and females brown dorsal coloration. In some populations, however, some adult females show dorsal coloration similar to that of males. I used mark-recapture methods to study a population of this type on a coastal promontory in A Coruña. A proportion of adult females showed green dorsal coloration during the reproductive period (April–July), but not during the rest of the year. Green dorsal coloration was most frequent among females with oviductal eggs, whereas preovulatory females with vitellogenic follicles in all cases showed brown dorsal coloration. These findings suggest that the green dorsal coloration observed in some females may be related to stage in the reproductive cycle, with green coloration developing during the gravid phase (i.e., with fertilized eggs). The findings also raise the possibility that the function of this coloration may be to avoid harassment and copulation attempts by males following fertilization. According to this hypothesis, females show brown dorsal coloration during the receptivity period (and during the nonreproductive period). Following fertilization, and possibly as a result of the hormonal changes that accompany ovulation and fertilization, they develop green dorsal coloration. This suggests that coloration, in these lacertids as in other reptiles, plays an important role in social communication.

La lagartija de Bocage (*Podarcis bocagei*) es un lacértido endémico del noroeste de la Península Ibérica que presenta generalmente un marcado dicromatismo sexual, teniendo los machos adultos una coloración dorsal verde y las hembras parda. Sin embargo, en determinadas poblaciones, algunas hembras adultas muestran una coloración dorsal verde, similar a la de los machos. Se han utilizado métodos de marcaje/recaptura para estudiar una población de este tipo en una localidad costera de A Coruña. Un porcentaje de hembras adultas de esta población mostró coloraciones dorsales verdes durante el período reproductor (abril-julio), pero no durante el resto del año. La coloración dorsal verde fue más frecuente en las hembras que tenían huevos oviductales, mientras que las hembras aún no ovuladas, con folículos en vitelogénesis, presentaron en todos los casos coloraciones dorsales pardas. Estos cambios sugieren que la coloración dorsal verde observada en algunas hembras puede estar relacionada con un período determinado del ciclo reproductor, desarrollándose durante la fase de gravidez (con huevos fertilizados en su interior). Estas observaciones también permiten plantear la hipótesis de que este cambio de coloración en las hembras puede tener la función de evitar las persecuciones y los intentos de cópula por parte de los machos una vez que ya han sido fertilizadas. De acuerdo con esta hipótesis, las hembras muestran una coloración dorsal parda durante el período de receptividad (así como durante el período no reproductor), mientras que después de la fertilización, y posiblemente como consecuencia de los cambios hormonales que siguen a la ovulación y fertilización, desarrollan una coloración dorsal verde. Esto sugiere que la coloración juega un importante papel en el reconocimiento sexual en estos lacértidos, al igual que sucede en muchos otros reptiles.

ADULTS of Bocage's Wall Lizard (*Podarcis bocagei*), a lacertid endemic to the northwestern Iberian Peninsula, typically show pronounced sexual dichromatism: males have green dorsal coloration, whereas females are brownish (Arnold and Burton, 1978; Galán,

1986, 1995). In some populations in Galicia, however, some adult females have green dorsal coloration like that of males. This coloration appears to develop during the reproductive period, between April and July (Galán, 1995, 1996a). The proportion of adult females show-

ing such coloration varies among populations. My observations indicate that green-backed females are most common in coastal populations (including populations on coastal islands and islets); inland, such females are less frequent (< 10% of the adult female population; Galán, 1995) or absent (unpubl. data). Here, I report a study of dorsal coloration among adult females in a population in which green-backed females occur frequently.

MATERIALS AND METHODS

Bocage's wall lizard, *P. bocagei*, is a small (adult snout-vent length 45–65 mm), diurnal, insectivorous lizard of the family Lacertidae. The study population occupies the Torre de Hércules promontory, a coastal site within the city limits of A Coruña. Within this area, the lizards occupy low *Ulex europaeus* scrub that alternates with *Koeleria* and *Dactylis* grassland. The shoreline is rocky. The microhabitats most frequently occupied by lizards are rocky outcrops, stone walls, and paths with bare soil.

Adult females were captured by hand or with nooses throughout 1990 and 1991. Sex was determined independently of color, in view of the marked sexual dimorphism shown by this species in body proportions: notably, the relative volume of the head is much lower in females. Only females with SVL > 55 mm were included in the analysis. In a previous study of other populations, minimum SVL at sexual maturity was 44–45 mm in females and 46–51 mm in males, whereas average SVL at sexual maturity was 46 mm in females and 50 mm in males (Galán, 1996b). In the present study population, by contrast, minimum SVL at sexual maturity was 46–48 mm in females and 47–53 mm in males, whereas average SVL at sexual maturity was 48 mm in females and 52 mm in males (unpubl. data).

All lizards were individually marked on capture by toe-clipping, and I recorded reproductive status (see below) and dorsal coloration (dorsal band and dorsolateral lines). In some cases, I was unable to determine reproductive state accurately because the animals were not killed for examination. Marking was done to allow identification of recaptured animals and, thus, assessment of whether dorsal coloration changes over time.

Colors were recorded by reference to Pantone standards, used previously in studies of this species (Galán, 1995), and the standard color sheets of Küppers (1994). In view of the effects of the angle of incident light on perceived col-

or, coloration was in all cases assessed under good light conditions with the lizard in hand, perpendicular to the observer at waist level at a distance of about 30 cm, so that the observer saw the maximum possible area of the lizard's back, on which light fell at 90°. All assessments were done by the same person. In the present study, I considered all females showing some degree of green pigmentation in the dorsal area to be "green-backed." In terms of the coordinates of Küppers' (1994) *Color Atlas*, "green" was defined as N_{00} – N_{20} , $> A_{50}$, $> C_{00}$, and A_{40} – A_{99} , $> C_{50}$, $< M_{30}$, whereas "brown" was defined as N_{30} – N_{80} , $> A_{50}$, $> C_{00}$, and A_{40} – A_{99} , $< C_{60}$, $> M_{20}$.

Reproductive status was assessed by ventral palpation and visual examination of external characters (see Galán, 1997). This approach allows assessment of stage in the reproductive cycle, namely (1) undeveloped gonads, (2) vitellogenic follicles, (3) oviductal eggs, and (4) eggs laid recently. Signs of recent copulation (i.e., inguinal marks; Galán, 1997) were also taken into account. Females that could not be clearly assigned to one or more of these categories were excluded from the analysis ($n = 4$). Whenever courtship or pairing behavior was observed, I tried to catch the female to determine her dorsal coloration and reproductive status. When an adult male remained in the immediate proximity of a female during the reproductive period, forming an evident pair, this was considered as evidence of mate-guarding by the male and, thus, as an indicator that copulation had taken place previously. This behavior is common in lacertids (see Olsson, 1993) including *P. bocagei* (Galán, 1995). Mate-guarding behavior following copulation was observed on numerous occasions. The fact that the members of each pair typically remain in close proximity, together with the absence of other stereotyped behavior patterns within pairs, meant that mate-guarding was readily distinguishable from courtship (see Galán, 1995).

RESULTS

The females of the study population may produce several clutches in a single season. Mark-recapture records for a number of females caught during the breeding season of 1990 and 1991 provided information on clutch frequency. During the laying period, 17.1% of reproductive females produced three clutches, 54.3% two clutches, and 28.6% one clutch ($n = 35$, pooled data for 1990 and 1991). Only large females (> 55 mm SVL) appear to be able to lay three

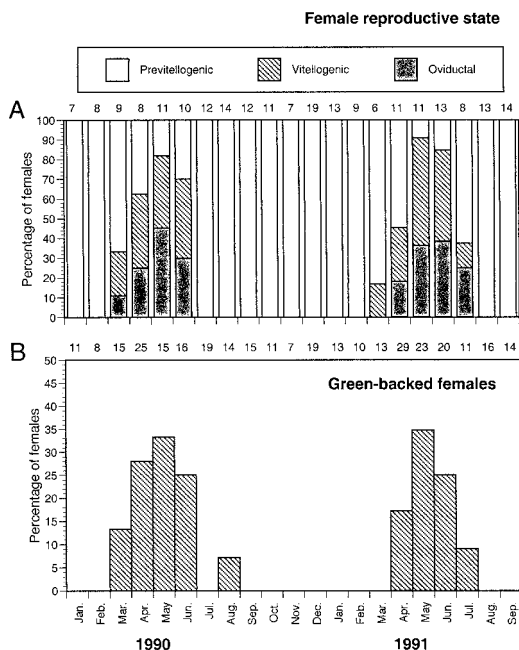


Fig. 1. (A) Frequency of adult females of *Podarcis bocagei* in three categories of reproductive state, over the 21-month study period. (B) Frequency of green-backed females in the adult female population, in the same period. Bars show the percentage of the adult female sample for that month with green dorsal coloration. Sample size for that month is shown at top of both figures.

clutches per year, and, in general, single clutches were produced by small females (< 50 mm SVL; unpubl. data; see also Galán, 1997).

Green-backed females were observed mainly between March and June 1990 and between April and July 1991 (Fig. 1), though small numbers of green-backed females were also observed in August 1990. The dorsal coloration of green-backed females is much more variable than that of males. In males, dorsal coloration is intense green in all individuals and throughout the reproductive season. In green-backed females, by contrast, coloration ranges from greenish brown (because of the presence of both brown and green scales) to the intense green observed in males (Galán, 1995). The green dorsal coloration was not acquired simultaneously by all females (Fig. 1B). Even during the months of the reproductive period, a part of the population remained without such coloration.

I compared the percentage of adult females at different stages of the reproductive cycle (previtellogenic, vitellogenic, and oviductal-mat-

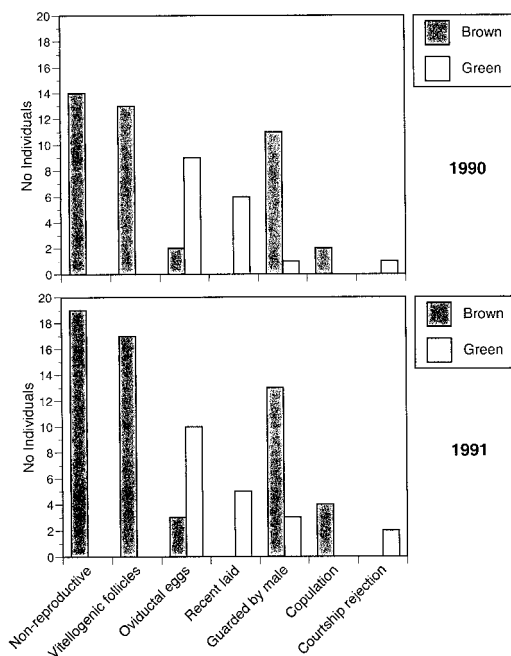


Fig. 2. Numbers of observations of brown- and green-backed females at different stages in the reproductive cycle and showing reproductive behavior.

ed) in each month of the study period (Fig. 1A). The distribution by months of proportion of green-backed females did not differ significantly from that of females with oviductal eggs, either in 1990 ($\chi^2 = 2.61$, $df = 3$, $P = 0.46$) or in 1991 ($\chi^2 = 1.80$, $df = 3$, $P = 0.62$).

The mark-recapture data revealed that dorsal coloration changes over the year within certain individuals. Marked individuals who had shown brown dorsal coloration during the nonreproductive period (second half of the summer, autumn, and winter) showed green dorsal coloration when recaptured during the reproductive period and then brown dorsal coloration once again after this period had ended.

Green dorsal coloration is not an ontogenetic character that develops, or is more frequent, in older/larger individuals. The SVL of green-backed females ranged from 55.6–63.5 mm (mean 60.5 mm, $n = 34$). During the same reproductive period, a sample of brown-backed females exhibited similar SVL characteristics (range 55.5–63.2 mm, mean 58.7 mm, $n = 38$). The two means do not differ significantly ($t = 1.76$, $df = 33$, $P > 0.05$).

Reproductive status and reproductive behavior covaried during March–July in both years of the study (Fig. 2). Reproductive state (vitellogenic follicles or oviductal eggs) was significant-

ly associated with dorsal coloration (brown or green; $\chi^2 = 36.64$, $df = 1$, $P < 0.0001$). All females with vitellogenic follicles showed brown dorsal coloration. After ovulation, 79.2% (both years together; $n = 24$) showed green dorsal coloration. All nonreproductive females showed brown dorsal coloration, and the frequency of brown-backed individuals among nonreproductive females was markedly and significantly higher than among females with oviductal eggs ($\chi^2 = 39.2$, $df = 1$, $P < 0.0001$) and among females who had just laid ($\chi^2 = 44.0$, $df = 1$, $P < 0.0001$). The frequency of brown-backed individuals was also significantly greater for vitellogenic females than for females who had just laid ($\chi^2 = 41.0$, $df = 1$, $P < 0.0001$). However, there was no significant difference in this characteristic between females who had just laid and females with oviductal eggs ($\chi^2 = 2.67$, $df = 1$, $P = 0.1$).

All females seen copulating ($n = 6$) showed brown dorsal coloration (binomial test: $z = 2.45$, $P < 0.001$). Similarly, most females accompanied by an adult male (i.e., "guarded" females who can be assumed to have mated previously with that male) showed brown dorsal coloration (85.7%, $n = 28$; binomial test: $z = 3.78$, $P < 0.05$). All females who had just laid (i.e., who had marked lateral folds; $n = 11$) showed green dorsal coloration (binomial test: $z = -3.32$, $P < 0.001$).

Courtship rejection behavior was observed on three occasions, in all cases by green-backed females. On all three occasions, the female's behavior in response to the approaching male included the following components: (1) stop-alert with raised head; (2) tail lashing; (3) raising and rapid movement of the forelegs ("Treteln"); and (4) running away. The male was never observed to pursue the fleeing female.

DISCUSSION

The months during which females with greenish dorsal coloration were observed largely coincided with the reproductive period (Galán, 1995, 1996a, 1997). It thus seems likely that the observed change in dorsal coloration is related to the reproductive cycle. Because adult coloration during the reproductive period in lacertids and other lizards sometimes plays an important role in sex recognition (Bauwens et al., 1987; Díaz, 1993; Olsson, 1994b), the color change might be related to reproductive behavior.

The green dorsal coloration of females is similar to that of sexually mature adult males. In

some species of insects, there have been reports of populations in which a proportion of females have the same coloration as the male (androchrome females), whereas the remainder have a different coloration (gynochrome females; Hilton, 1987). In such cases, however, females do not change color once they have reached maturity (Robertson, 1985; Cordero, 1992), and these color variants have been shown to have a genetic basis (Johnson, 1966; Cordero, 1990).

In reptiles, color changes occurring over periods of days, weeks, or months are classed as morphological color changes and are typically related to hormonal changes associated with growth and seasonal reproductive periods (Cooper and Greenberg, 1992). The development of bright coloration during the reproductive period is well documented in many lizard species, particularly among males (Cooper and Vitt, 1988; Cooper and Greenberg, 1992; Olsson, 1994a). Reproductive-period coloration in males of lizard species showing sexual dichromatism may play an important social role (Cooper and Greenberg, 1992). In the family Lacertidae, the importance of such coloration in sex recognition has been demonstrated experimentally (by painting lizards the color of the opposite sex) in several species. Faced with males painted like females, males initiate courtship behavior; faced with females painted like males, they initiate agonistic behavior (Kitzler, 1941; Bauwens et al., 1987; see also Olsson, 1994a).

The development of bright coloration in female lizards during the reproductive season has been described in a number of phrynosomatid, tropidurid, and crotaphytid species, which develop red or orange coloration during ovulation and pregnancy (Ferguson, 1976; Cooper et al., 1983; Watkins, 1997). Such color changes are induced by sex steroids (Cooper and Greenberg, 1992).

My data indicate that green dorsal coloration in females of *P. bocagei* is most frequent among females with oviductal eggs, whereas such coloration was not observed among females that had not yet ovulated. These data are consistent with induction by steroids such as progesterone and androgens, both of which are produced by lacertid ovaries (Mosconi et al., 1991). In some species of lizard, such as *Holbrookia propinqua*, female coloration of this kind and aggressive courtship rejection behavior toward males are induced by progesterone and testosterone, as well as estradiol (Cooper and Crews, 1987). The same authors have also detected relationships between steroid levels and behavior in nonmanipulated females of

this species (i.e., females not subjected to experimental hormone treatment). Studies of the relationships between steroid hormone (progesterone) levels and bright coloration in female lizards have also been performed in other species, including *Crotaphytus collaris* (Cooper and Ferguson, 1972) and *Petrosaurus mearnsi* (Cooper and McGuire, 1993). In both species, the bright coloration develops during gravidity (i.e., when fertilized oviductal eggs are present). In view of these results, the green dorsal coloration observed in females of *P. bocagei* may be the result of steroid hormones.

In my study population, green or greenish dorsal coloration in adult females, similar to that observed in adult males, develops after ovulation (luteal phase) and possibly after fertilization because most individuals in which such coloration was observed had oviductal eggs and showed copulation marks. The small percentage of females with oviductal eggs but brown dorsal coloration may reflect a methodological problem: the presence of follicles or eggs was in all cases determined by ventral palpation (not dissection), so that incorrect interpretation of large follicles as eggs may possibly have occurred. If this were the case, the proportion of females with oviductal eggs that show green dorsal coloration may in fact be even higher. Alternatively, some females may have been palpated during a period after ovulation, but prior to color change. It is also possible that the wide range of color variation in females is due to individual differences in the factors responsible for color change in this sex. It is also possible that the various degrees of green pigmentation observed in females may be partially because of observations of individuals undergoing transition from one coloration to another (i.e., from brown to green, then green to brown).

A function of the green dorsal coloration might be to avoid harassment and copulation attempts by males once fertilization has occurred (rejection hypothesis; Cooper, 1984). In lacertids, as in many other reptiles, copulation involves repeated biting of the female by the male (Verbeek, 1972), and this behavior is observed in *P. bocagei* (Galán, 1995). The biting leaves marks on the female's body; it may cause her some degree of trauma and could increase risk of infection. All females observed copulating, and most females guarded by males, were brown-backed. This is consistent with reduced postfertilization harassment by males in response to green dorsal coloration, since, in lacertids as in other lizards, coloration has a sex-recognition function (Bauwens et al., 1987; Díaz, 1993; Olsson, 1994a). However, there is no

evidence for such harassment by lizards such as lacertids and skinks, in which females produce sex pheromones that stimulate courtship (Mason, 1992; Cooper, 1994).

My three observations of courtship rejection behavior in all cases involved green-backed females, although the number of observations is of course insufficient for definitive conclusions to be drawn. The "fast movement of forelegs" behavior ("Treteln"; Verbeek, 1972) seen on these occasions is considered a courtship rejection behavior in another lacertid, *Lacerta vivipara* (Heulin, 1988). However, this nonaggressive behavior differs dramatically from the aggressive rejection signaled by bright coloration in phrynosomatid, tropidurid, and crotaphytid lizards.

The data available indicate that *P. bocagei* is nonterritorial (unpubl. data) like the closely related Iberian species *P. hispanica* (Gil et al., 1988). Male-male aggression appears to be relatively infrequent, so that green-backed females would not be expected to suffer frequent aggression from males who mistake them for males. However, male aggression toward green-backed females cannot be ruled out and may be an important cost of the color change. At short range, males may recognize females largely by chemical cues (tongue-flicking); at greater distances, however, green dorsal coloration might reduce recognition as females, thus reducing the likelihood of approach. This might be beneficial during gravidity, when females of *P. bocagei* suffer increased mortality and become markedly less mobile, presumably because the weight of their eggs makes them more vulnerable to predators (Galán, 1999). Sedentary behavior in gravid females has been described for many other lizard species (e.g., Bauwens and Thoen, 1981; Brodie, 1989; Braña, 1993) and has been interpreted as an adaptation favoring predator evasion and energy conservation during the critical egg-laying period. The approach of males would be another risk during this period of maximum vulnerability, and it is therefore perhaps beneficial to avoid it. In a study of the lizard *Microlophus occipitalis*, in which females change color when gravid, it was suggested that the color change might reduce the costs associated with social interactions during this period by signaling nonreceptivity (Watkins, 1997).

A more detailed analysis of the questions raised by the present study will require endocrinological studies aimed at identifying the factors causing color change in females and manipulative painting studies aimed at determining the effects of green dorsal coloration

on males' responses to females. In the absence of evidence for aggression toward courting males or reduction of approach or courtship intensity by males attributable to green coloration, it remains possible that green dorsal coloration is simply an epiphenomenon of genetic correlation between the sexes or physiological responses of pigmentation to steroid hormones.

LITERATURE CITED

- ARNOLD, E. N., AND J. A. BURTON. 1978. Guía de campo de los reptiles y anfibios de España y Europa. Ed. Omega. Barcelona, Spain.
- BAUWENS, D., K. NUIJTEN, H. VAN WEZEL, AND R. F. VERHEYEN. 1987. Sex recognition by males of the lizard *Lacerta vivipara*: an introductory study. *Amphib.-Reptilia* 8:49–57.
- , AND C. THOEN. 1981. Escape tactics and vulnerability to predation associated with reproduction in the lizard *Lacerta vivipara*. *J. Anim. Ecol.* 50: 733–743.
- BRAÑA, F. 1993. Shifts in body temperature and escape behaviour of female *Podarcis muralis* during pregnancy. *Oikos* 66:216–222.
- BRODIE III, E. D. 1989. Behavioral modification as a means of reducing the cost of reproduction. *Am. Nat.* 134:225–238.
- COOPER JR., W. E. 1984. Female secondary sexual coloration and sex recognition in the keeled earless lizard, *Holbrookia propinqua*. *Anim. Behav.* 32:1142–1150.
- . 1994. Chemical discrimination by tongue-flicking in lizards: a review with hypotheses on its origin and its ecological and phylogenetic relationships. *J. Chem. Ecol.* 20:439–487.
- , AND D. CREWS. 1987. Hormonal induction of secondary sexual coloration and rejection behaviour in female keeled earless lizards, *Holbrookia propinqua*. *Anim. Behav.* 35:1177–1187.
- , AND G. W. FERGUSON. 1972. Steroids and color change during gravidity in the lizard *Crotaphytus collaris*. *Gen. Comp. Endocrinol.* 18:69–72.
- , AND N. GREENBERG. 1992. Reptilian coloration and behavior, p. 298–422. *In: Biology of the Reptilia*. Vol. 18. Physiology E. Hormones, brain, and behavior. C. Gans and D. Crews (eds.). Univ. of Chicago Press, Chicago.
- , AND J. A. MCGUIRE. 1993. Progesterone induces bright orange throat coloration in female *Petrosaurus mearnsi*. *Amphib.-Reptilia* 14:213–221.
- , AND L. J. VITT. 1988. Orange head coloration of the male broad-headed skink (*Eumeces laticeps*), a sexually selected social cue. *Copeia* 1988:1–6.
- , C. S. ADAMS, AND J. L. DOBIE. 1983. Female color change in the keeled earless lizard, *Holbrookia propinqua*: relationship to the reproductive cycle. *Southwest. Nat.* 28:275–280.
- CORDERO, A. 1990. The inheritance of female polymorphism in the damselfly *Ischnura graellsii* Rambur (Odonata: Coenagrionidae). *Heredity* 64:341–346.
- . 1992. Density-dependent mating success and colour polymorphism in females of the damselfly *Ischnura graellsii* (Odonata: Coenagrionidae). *J. Anim. Ecol.* 61:769–780.
- DÍAZ, J. A. 1993. Breeding coloration, mating opportunities, activity, and survival in the lacertid lizard *Psammodromus algerus*. *Can. J. Zool.* 71:1104–1110.
- FERGUSON, G. W. 1976. Color change and reproductive cycling in female collared lizards (*Crotaphytus collaris*). *Copeia* 1976:491–494.
- GALÁN, P. 1986. Morfología y distribución del género *Podarcis* Wagler, 1830 (Sauria, Lacertidae) en el noroeste de la Península Ibérica. *Rev. Esp. Herpetol.* 1:85–142.
- . 1995. Cambios estacionales de coloración y comportamiento agonístico, de cortejo y de apareamiento en el lacértido *Podarcis bocagei*. *Ibid.* 9:57–75.
- . 1996a. Reproductive and fat body cycles of the lacertid lizard *Podarcis bocagei*. *Herpetol. J.* 6:20–25.
- . 1996b. Sexual maturity in a population of the lacertid lizard *Podarcis bocagei*. *Ibid.* 6:87–93.
- . 1997. Reproductive ecology of the lacertid lizard *Podarcis bocagei*. *Ecography* 20:197–209.
- . 1999. Demography and population dynamics of the lacertid lizard *Podarcis bocagei* in Northwest Spain. *J. Zool., Lond.* 249:203–218.
- GIL, M. J., V. PÉREZ-MELLADO, AND F. GUERRERO. 1988. Estructura del hábitat y dominios vitales en *Podarcis hispanica* (Steindachner, 1870). *Misc. Zool.* 12:273–281.
- HEULIN, B. 1988. Observations sur l'organisation de la reproduction et sur les comportements sexuels et agonistiques chez *Lacerta vivipara*. *Vie Milieu* 38: 177–187.
- HILTON, D. F. J. 1987. A terminology for females with color patterns that mimic males. *Entomol. News* 98: 221–223.
- JOHNSON, C. 1966. Genetics of female dimorphism in *Ischnura demorsa*. *Heredity* 21:453–459.
- KITZLER, G. Z. 1941. Die Paarungsbiologie einiger Eidechsen. *Z. Tierpsychol.* 4:355–402.
- KÜPPERS, H. 1994. Atlas de los colores. Ed. Blume. Barcelona, Spain.
- MASON, R. T. 1992. Reptilian pheromones, p. 114–228. *In: Biology of the Reptilia*. Vol. 18. Physiology E. Hormones, brain, and behavior. C. Gans and D. Crews (eds.). Univ. of Chicago Press, Chicago.
- MOSCONI, G., O. CARNEVALI, AND A. M. POLZONETTI. 1991. Ovarian development and sex steroid hormones during the reproductive cycle of *Podarcis s. sicula* Raf. *Gynecol. Endocrinol.* 5:7–13.
- OLSSON, M. 1993. Contest success and mate guarding in male sand lizards, *Lacerta agilis*. *Anim. Behav.* 46: 408–409.
- . 1994a. Nuptial coloration in the sand lizard, *Lacerta agilis*: an intra-sexually selected cue to fighting ability. *Ibid.* 48:607–613.
- . 1994b. Rival recognition affects male contest behavior in sand lizard (*Lacerta agilis*). *Behav. Ecol. Sociobiol.* 35:249–252.
- ROBERTSON, H. M. 1985. Female dimorphism and mating behaviour in a damselfly, *Ischnura ramburi*:

- females mimicking males. *Anim. Behav.* 33:805–809.
- VERBEEK, B. 1972. Ethologische untersuchungen an einigen europäischen Eidechsen. *Bonn. Zool. Beitr.* 23:122–151.
- WATKINS, G. G. 1997. Inter-sexual signalling and the functions of female coloration in the tropidurid lizard *Microlophus occipitalis*. *Anim. Behav.* 53:843–852.
- DEPARTAMENTO DE BIOLOGÍA ANIMAL, BIOLOGÍA VEXETAL E ECOLOGÍA, FACULTADE DE CIENCIAS, UNIVERSIDADE DA CORUÑA, CAMPUS DA ZAPATEIRA, S/ N, 15071 A CORUÑA, SPAIN. E-mail: pgalan@udc.es. Submitted: 2 Nov. 1998. Accepted: 17 Nov. 1999. Section editor: A. H. Price.