TABLE 1. The frequencies of wins, losses, or draws after 300 min for territorial residents of *Plethodon cinereus* (34–36 mm SVL, N = 26) tested against three size classes of intruders. Exclusive occupancy of the food-rich side was scored as either a win (occupancy by a resident) or a loss (occupancy by an intruder). Shared occupancy was scored as a draw.

SVL intruder (mm)	No. wins	No. losses	No. draws
37–39	6	2	18
40–42	8	3	15
43–46	8	3	15

smaller residents were more successful at expelling the larger intruders than the intruders were at expelling the residents. Nonetheless, the smaller residents were unable to expel larger intruders successfully in more than half of the trials, regardless of the magnitude of the asymmetry in body size. Thus, territorial contests between rival male red-backed salamanders resemble Maynard Smith and Parker's (1976) "pay-off asymmetry" game, in which one contestant (e.g., a territory resident) may have more to gain by winning (maintenance of an established territory) or more to lose by accepting defeat (loss of that marked territory).

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Ontogenetic, Sexual, and Microgeographic Variation in Color Pattern within a Population of the Lizard *Podarcis lilfordi*

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Lizard species inhabiting islands and islets within the Mediterranean typically exhibit striking among population variation in morphological characteristics, most notably coloration, body size, and body proportions. This "rassenkreis" is especially prominent in several species of the lacertid genus *Podarcis* (e.g., Eisentraut, 1928, 1950; Cheylan, 1988; Cirer and Martínez-Rica, 1990). The lizard *Podarcis lilfordi*, which inhabits islets situated off the coast of the Balearic Islands of Mallorca and Menorca (Spain), provides an extreme example. It has a very restricted world range (<1700 ha) that is scattered over ca. 35 islets that vary in size between 0.1 and 1155 ha. The distinct populations exhibit important differences in coloration and body size. For instance, dorsal color is uniformly brown or greenish brown in some populations, in others it is green with dark blotches, whereas all individuals have black dorsal colors in several other populations. Samples of adult males from different islets vary in average snout–vent length (SVL) between 57 and 70 mm and in mean body mass between 4.2 and 9.5 g (Salvador, 1979; Pérez-Mellado and Salvador, 1988). This variation has led to the description of numerous subspecies, most of which are confined to single islets (Eisentraut, 1950; Salvador, 1979; Pérez-Mellado and Salvador, 1988).

The radiation of the *P. lilfordi* populations presumably took place after they became isolated by the rising of the sea level (Pérez-Mellado and Salvador, 1988), which occurred as recently as the end of the last quaternary glaciations (ca. 8000–10,000 yr ago). The inevitably small population sizes and the reproductive isolation of populations inhabiting small islets enhance the evolution of morphological traits through natural selection and genetic drift (Futuyma, 1986). Initial variation in population composition may arise, at least in part, by sampling accidents (genetic drift) during the foundation of populations by a small number of individuals ("founder effect"; Mayr, 1963). An implicit assumption of the founder effect hypothesis is that the source population exhibited important individual and/or (micro)geographic variation in phenotypic characteristics. Alternatively, population differences may originate through *de novo* mutations within the respective populations; mutations may become fixed more easily in founder populations or in small populations on the smallest islets.

Here we address the validity of the assumption of the founder effect hypothesis that considerable phenotypic variation exists in the source population. Specifically, we examine variation in color pattern within the population of *P. lilfordi* that inhabits Cabrera, the largest island occupied by this species. The population of Cabrera was the putative source for the other islets of the Cabrera archipelago. During the last glaciations, these islands were all connected by land bridges and presumably inhabited by a single population. Because the size of Cabrera exceeds that of the other islets by a factor 10 to 10,000, it seems reasonable to assume that its lizard population retains characteristics of the historical source population. We provide quantitative information on the within population variation in dorsal and ventral coloration and examine three sources of individual differences in coloration: size related shifts, sexual differences, and microgeographic variation. We also develop hypotheses about the relationship between the observed within population variation and the among population differences in color patterns.

Cabrera (39°09′N, 2°56′E) is the largest island (1155 ha) of the Cabrera Archipelago, located in the Mediterranean, south of Mallorca (Spain). The archipelago, which has been declared a National Park, is composed of 19 islets (all except two are ≤10 ha), is virtually uninhabited (except for the Park wardens, a small military unit, and a single farmer that reside on Cabrera) and its access is controlled and restricted. Cabrera and 16 of the other islands of the archipelago are occupied by *P. lilfordi*.

Data were collected on Cabrera during 3–9 September 1996; we also made brief exploratory visits to eight neighboring islets. Lizards were caught with a noose or in traps (plastic or metal cans baited with tomatoes). For each lizard we recorded age-class (juvenile or adult), sex of adults, snout–vent length (SVL; to nearest 0.1 mm) and coloration of the dorsum, vent and throat, and tail. Although variation in color and pattern is continuous, we grouped individual lizards into following categories. Dorsal color: (1) brown: the back and flanks are brown or brown-green; the color pattern, that consists of dark, bluish and/or light spots, blotches and lines is clearly visible from a distance; (2) dark: the back and flanks are dark brown or dark blue; the color pattern is barely visible from a distance (i.e., these individuals appear to be uniformly black) but is readily discernible at close sight; (3) black: dorsal coloration is uniformly black; no pattern is perceivable. Tail color: (1) green or blue-green; (2) brown; (3) dark; (4) black. Color of vent and throat: (1) white; (2) pale blue; (3) blue; (4) deep blue. The blue colors represent variation in amount of darkening (pigmentation) rather than different hues.

All lizards (N = 206) were caught at three different sites, that are <1 km apart and not separated by unfavorable lizard habitat. The first two sites ("Campamento" and "Can Felíu") have vegetation dominated by *Pistacea lentiscus* shrubs; their soils are formed by Eocene or Quaternary deposits (Rodríguez-Perea and Servera, 1993) and have a predominantly brownish coloration. The third area ("La Miranda") has more heterogeneous vegetation with various shrubs (e.g., *Olea europea, Pistacea lentiscus, Phillyrea* spp., *Ephedra fragilis*); the soil consists of conspicuous white limestone. Within each site, all lizards were caught within a restricted area (ca. 30 × 30 m).

Coloration of the lizards differed clearly among age and sex groups (Table 1). Juveniles had brown dorsal colors and a green tail; their vent was either white or pale blue. Although we captured only a small number of juveniles (N = 17), observations of many others in the field confirm these findings. Most adult females had brown dorsal colors and a blue-green tail; the coloration of the belly was more variable (Table 1). Dorsal coloration was most variable within the adult males (Table 1). The belly and throat of most adult males were blue or deep blue. Males with brown dorsal coloration had ventral colors that were either pale blue (20%), blue (42%) or deep blue (38%), whereas virtually all (96%) of the males with dark or black dorsal colors had a deep blue venter.

The fact that all juveniles had brown dorsal colors, whereas some of the females and half of the adult males were dark or black (Table 1), indicates that lizards change dorsal colors during their ontogeny. A similar statement can be made for the ventral colors, which are white or pale blue in juveniles, but often blue or deep blue in the adults. In the absence of repeated records of growing individual lizards, we further examine the change in coloration by comparing

TABLE 1. Percentages of juveniles, adult females and males assigned to the different categories of dorsal, ventral and tail color.

	Juveniles (N = 17)	Adult females (N = 99)	Adult males (N = 90)
Dorsal color			
brown	100	94	50
dark	0	6	34
black	0	0	16
Ventral color			
white	59	1	0
pale blue	41	25	10
blue	0	36	23
deep blue	0	37	67
Tail color			
green or blue-green	100	63	40
brown	0	33	29
dark	0	3	19
black	0	0	12

the body length of males and females that differed in coloration. We note that observations in captivity on a small group of full-grown adult lizards (four males, four females) indicate that their coloration did not change over a period of 16 months, including a breeding season.

Mean SVL differed significantly among the three dorsal color groups of adult males (ANOVA: $F = 6.8$, $df = 2, 87$, $P < 0.005$; Fig. 1A). Males with brown dorsal colors were on average smaller than were those with dark or black colors. Detailed examination of the data indicates that virtually all males with SVL ≤ 62 mm were brown, whereas all black males were ≥64 mm (Fig. 1A). This implies that some males acquire dark or black dorsal colors when they attain a SVL of ≥64 mm. However, not all males obtain dark or black colors when they surpass this size, because some of the larger males had brown dorsal colors (Fig. 1A).

Adult females with a dark dorsum were on average bigger than were those with brown dorsal coloration (brown: mean ± 1 SD = 57.8 ± 4.7, range = 46.5–67.5, N = 93; dark: mean ± 1 SD = 63.6 ± 3.6, range = 58.2–68.8, N = 6; ANOVA: $F = 8.9$, $df = 1, 97$, $P < 0.005$). Females with dark dorsal colors were all ≥58 mm, indicating that some individuals change dorsal

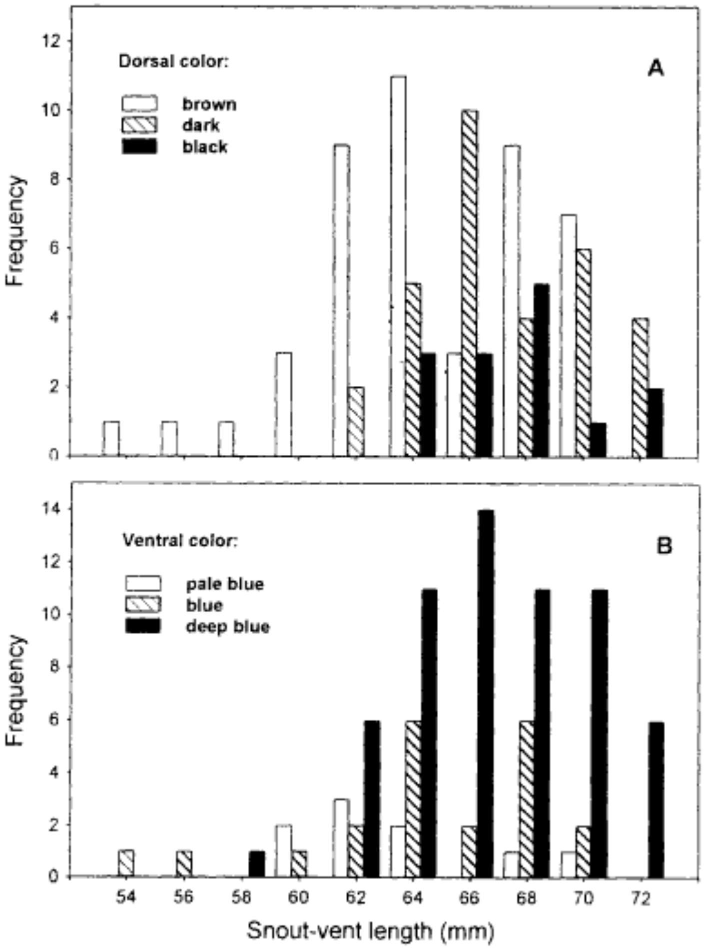

FIG. 1. Distribution of snout–vent length in adult male *Podarcis lilfordi* with different dorsal (A) and ventral (B) colorations.

TABLE 2. Percentage of adult males and females assigned to the different categories of dorsal coloration caught at three different areas within Cabrera.

	Campamento	Can Felíu	La Miranda
Males			
brown	55	71	30
dark	36	25	39
black	9	4	30
N	33	24	33
Females			
brown	100	96	87
dark	0	4	13
N	35	25	39

color from brown to dark as they attain or surpass this size.

Mean SVL also differed among groups of males with different ventral colors (ANOVA: $F = 5.9$, df = 2, 87, $P < 0.01$; Fig. 1B). Males with a deep blue vent were, on average, bigger than were those exhibiting a pale blue or blue vent. However, the three groups overlap considerably in body length, and the different vent colors were found among both the smallest and the largest males (Fig. 1B).

We found no difference in mean SVL among groups of females with different vent colors (white: 47.9, $N = 1$; pale blue: mean ± 1 SD = 58.7 ± 5.1, range = 48.0–68.8, $N = 25$; blue: mean ± 1 SD = 58.2 ± 4.7, range = 46.5–67.5, $N = 36$; deep blue: mean ± 1 SD = 58.1 ± 4.5, range = 47.3–65.7, $N = 37$; ANOVA: $F = 1.7$, df = 3, 95, $P > 0.10$). The range in SVL overlaps widely among the three groups of females, such that there is no indication for a progressive size related change towards darker blue vent colors in the adult females.

The relative frequency of adult males assigned to different dorsal color groups varied significantly among the three study sites ($G = 13.38$, 4 df, $P < 0.01$; Table 2): relatively more males had black dorsal colors at "La Miranda" than at the two other areas. A similar tendency towards a higher frequency of individuals with dark dorsal colors at "La Miranda" was also observed in the females ($G = 7.00$, 2 df, $P = 0.03$; Table 2), despite the overall low number of females with dark back colors. Because mainly the largest adults exhibit darker back colors, this result could be a secondary effect of possible differences among study sites in lizard body sizes. However, we found no differences in SVL among the three study areas (ANOVA; males: $F = 1.1$, df = 2, 87, $P > 0.30$; females: $F = 1.4$, df = 2, 96, $P > 0.20$).

Our results indicate that many lizards within this population acquire darker pigmentation during their ontogeny. Ventral colors change from white or pale blue to a darker blue color presumably before lizards reach adult size. Dorsal pigmentation also intensifies, probably mainly during the adult life stage, beginning at about 58 mm SVL in females and 64 mm SVL in males. Nevertheless, some of the largest individuals of each sex had brown dorsal and clear ventral colors that very much resembled the juveniles' coloration. Thus, variation in coloration within this population of *P. lilfordi* reflects both variation in body size and individual differences in the intensity of ontogenetic color changes. Our impression is that there is continuous variation, from individuals that maintain juvenile coloration throughout the life span to lizards that acquire blackish dorsal colors and darker blue vent colors as they grow in size. This interpretation of differences in the ontogeny of color changes is supported by the observation, in captivity conditions, that full-grown adults maintain their color pattern for periods >1 yr.

The individual differences in the intensity of color changes increase the phenotypic variation among the adults, especially adult males. The observed sexual difference in the frequency distribution of distinct color categories reflects the following two differences, which are quantitative rather than qualitative. First, there is a higher proportion of males—which also grow to a larger size—that develop blackish dorsal coloration. Second, some males acquire more intense dark dorsal pigmentation than do females, although no such difference in ventral colors was observed.

Many species of lacertid lizards exhibit some kind of ontogenetic color change. These changes most often reflect the development of permanent sexually dichromatic patterns (e.g., Kramer, 1937; Bauwens et al., 1987) and/or the acquisition of temporal breeding colors in males (e.g., Díaz, 1993; Olsson, 1994; Galán, 1995). An increase in dorsal pigmentation similar to that in *P. lilfordi*, has to our knowledge only been observed in several species of the genus *Gallotia* (Thorpe and Brown, 1989; R. Márquez, pers. comm.), wherein males become increasingly darker as they grow beyond the minimum adult size. However, we are unaware of individual variation in the intensity of darkening in *Gallotia*. It is worth mentioning that *Gallotia* and *Podarcis* are representatives of different phylogenetic lineages within the Lacertidae (Arnold, 1989).

Based on the available data we cannot determine whether the individual variation in ontogenetic color changes reflects genetic differences or is influenced by environmental conditions. Physiological color changes, which are reversible and take place over seconds or hours, often occur in response to environmental factors, in particular the social context (Cooper and Greenberg, 1992). By contrast, in several species of fish, birds and lizards, long-term individual differences in the expression of ontogenetic color changes do not seem to be influenced by environmental conditions (e.g., van Rhijn, 1983; Gross, 1991; Thompson et al., 1993). Thus, we cannot dismiss the possibility that the observed individual variation in *P. lilfordi* is induced, at least in part, by genetic differences.

The increase of the dorsal pigmentation during the adult life stage may indicate that this morphological color change is controlled by cumulative hormonal action, comparable to the hormonal influence of temporary, breeding-season color changes observed in many lizards. For instance, in male *Sceloporus occidentalis* the effects of androgens on melanophores induce ventrolateral darkening (Kimball and Erpino, 1971). This effect may be either direct or indirect, through the activation of melanophore stimulating hormone secretion by the pituitary (Cooper and Greenberg, 1992). We suggest that individual variation in the intensity of color changes in *P. lilfordi* may result from different levels of circulating hormones, or alternatively from the deposition of different amounts of melanine in response to particular hormone levels. This putative variation could be induced by individual genetic differences (Thompson et al., 1993).

Our preliminary data indicate the existence of microgeographic variation within Cabrera in the proportion of lizards with different dorsal coloration. Lizards with dark or black dorsal colors were more frequent at one site than in two other areas. Because we found no differences in mean body length among the three sites, the observed variation in coloration cannot be considered as an artifact induced by possible differences in body size. This microgeographic variation in colors is remarkable, given the proximity of the three sites and the lack of intermediate barriers. We note that Eisentraut (1928, 1950) mentioned a comparable between site difference within the island of Cabrera: he observed a higher frequency of black-colored lizards near the lighthouse (an area that we did not sample), than in other parts of the island. Based on the available information, we can only speculate on the proximate and ultimate causes of these among-site differences. Nevertheless, the data underscore the manifestation of microgeographic variation in coloration within this species.

Extant populations of *P. lilfordi* exhibit important differences in coloration and other phenotypic characteristics. Given the short separation times (i.e., <10,000 years) of the distinct insular populations, we hypothesized that the among-population differences reflect, at least in part, a considerable amount of individual variation in the source population. Our data confirm this presumption for the population of Cabrera, the largest islet actually occupied by *P. lilfordi.* This population presumably acted as a source for the populations that inhabit the other islets of the Cabrera archipelago. How do the among population differences in the Cabrera archipelago relate to the within-population variation at Cabrera Island? Of the 16 populations of *P. lilfordi* that inhabit the archipelago's islets, three are characterized by the simultaneous presence of brown, dark and black colored individuals (Salvador, 1979; pers. obs.), a situation that is highly similar to that on Cabrera Island. In all other populations, except one, adult lizards have uniform black dorsal colors and have been labeled as "melanistic" (Eisentraut, 1950; Salvador, 1979). However, our anecdotal observations in some of these populations indicate that the juveniles have brown or dark dorsal colors. This suggests that the black adult coloration results from an ontogenetic color change, very much resembling that observed in a fraction of the lizards on Cabrera Island. If true, much of the among-population differences in dorsal coloration at the Cabrera archipelago could be reduced to variation in the proportion of individuals that develop black dorsal colors and, perhaps, in the timing of the color change.

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Neopalatine Odontoids in *Bufo alvarius* (Anura: Bufonidae)

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The lack of teeth among all species in the family Bufonidae is considered a synapomorphy to support the monophyly of this nearly cosmopolitan group (Ford and Cannatella, 1993; Graybeal and Cannatella, 1995). Odontoids occur in many frogs (e.g., the mandible of the hylid *Hemiphractus*; Shaw, 1989) but are simple tooth-like projections of bone and, thus, differ from true pedicellate, dentine-covered, amphibian teeth (Duellman and Trueb, 1986). No bufonid has been reported to have teeth or odontoids. Thus we were surprised to observe, in *Bufo alvarius*, discrete tooth-like odontoids on the ventral surface of the neopalatine. The proper name (i.e., neopalatine or palatine) for these paired bones which brace the anterior maxilla medially was discussed by Trueb (1993). Neopalatine odontoids have been reported in several other neobatrachian taxa (e.g., *Hemiphractus*, many species of *Hyla*) but such structures have never been reported in a bufonid. In this paper we present the first report of tooth-like structures in any bufonid and describe variation in size, number, and form among individuals of *B. alvarius*.

All nine specimens of *Bufo alvarius* that we examined had a prominent bony ridge on the ventral surface of the neopalatine. The odontoids protrude from this bony ridge and were found to be variable in size and number. The following description is based on an adult female (KU 14082). The paired neopalatines are robust elements that contact the sphenethmoid medially and both the maxilla and the anterior ramus of the pterygoid laterally. At midlength, in cross section, the bone has the shape of an asymmetrical V, the anterior flange being higher than the posterior flange (Fig. 1). The ventral surface of the dextral neopalatine is studded with 12 conical odontoids which protrude from the ventral ridge. These odontoids are accompanied by several smaller bumps. Among *B. alvarius* there is much variation in the size and number of odontoids. An adult male specimen (KU 25204), comparable in size to the previously described female, has only three odontoids per neopalatine, producing an overall smoother appearance to the ventral ridge.

We surveyed the skulls of all *Bufo* in The University of Kansas Natural History Museum (KU) anuran osteological collection. Because we used only available material, our survey is incomplete and non-random with respect to total bufonid diversity. The ventral surface of the neopalatine of *Bufo* may be smooth (e.g., *B. americanus*), may bear a transverse, thin bony ridge that may be smooth (e.g., *B. marmoreus*) or distinctly serrate (e.g., *B. luetkeni*). Our survey suggests that the distinct odontoids described above are unique to *B. alvarius*. It is tempting to speculate that similar structures are present in the closest relative of *B. alvarius* (i.e., these structures are a synapomorphy for a group of species). However, the phylogenetic relationships of *B. alvarius* have never been clear (Blair, 1972) and Graybeal's (1997) phylogenetic analyses suggested that *B. alvarius* has no living sister-species, rather it is the sister to a lineage comprising the *B. valliceps* group. Despite the uncertainty of its phylogenetic position among bufonids, neopalatine odontoids seem to be an autapomorphy for *B. alvarius*. Tihen (1972) summarized the literature on fossil bufonids and none with neopalatine odontoids was reported, nor have any been described since that time.

Several speculative hypotheses are available to explain the unusual occurrence of odontoids in *Bufo alvarius*. One hypothesis would propose that these odontoids are correlated with hyper ossification and large size. However, other large species (e.g., *B. marinus, B. blombergi*) with highly ossified skulls lack neopalatine odontoids. A second hypothesis would suggest that these odontoids are adaptations for prey handling. *Bufo alvarius* has a varied diet that includes relatively large vertebrate prey (Degenhardt et al., 1996), and perhaps the odontoids are utilized in prey capture or manipulation. However, we note that other species of *Bufo* that lack odontoids consume an equally diverse diet that also includes vertebrates (e.g., *B. marinus*; Zug and Zug, 1979).

Among frogs that have teeth and/or odontoids, the size and shape of these structures varies considerably (Trueb, 1993). Presumably, the function and utility of anuran teeth and odontoids during feeding varies as well, but their specific function, beyond simple prey-holding, is unknown (Duellman and Trueb, 1986; Stebbins and Cohen, 1995). Thus, although it is tempting to speculate that the neopalatine odontoids of *Bufo alvarius* are functionally adaptive for a unique method of prey capture or manipulation, no evidence exists that the feeding ecology and behavior of this species differs in any great way from that of other large—and totally edentate—toads.

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