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GREEN TAILS IN LIZARDS OF THE GENUS *PODARCIS*: DO THEY INFLUENCE THE INTENSITY OF PREDATION?

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ABSTRACT: Juveniles of a variety of lizard species exhibit bright tail colors that contrast clearly to the cryptically colored body. The "predator escape" hypothesis suggests that bright tail colors deflect the attack of a predator towards the lizard's tail, which can be autotomised, and hence increase the probability of surviving a predatory attack. Although this hypothesis is widely accepted, surprisingly few empirical data exist to support it. Here, we examined the relative frequencies of predatory attack on plasticine replicas of juvenile lizards in the genus *Podarcis* with either green or brown tails in nine areas of Spain. Replicas with bright green tail color experienced, over a one-week period, the same rates of attack by birds and other predators as replicas with cryptic brown tails. However, the proportion of replicas that showed bill markings on the tail only was highest for the green-tailed replicas. In contrast, the frequency of predatory attacks towards the head or body was similar in the two groups of replicas. Our experiment appears to support the classical prediction of the adaptive value of a green autotomic tail in lizards. However, lizard species with multiple tail colors may also represent alternative anti-predator strategies that may have arisen by different selective pressures between habitats. We also suggest that the evolution of bright tail coloration in juveniles of *Podarcis* as an antipredator mechanism may be favored by the correlated evolution of morphological, physiological, and behavioral characteristics

Key words: Antipredator mechanisms; Lizards; *Podarcis*; Predation; Tail coloration; Spain

STUDIES of animal coloration, color patterns, and their significance are important in the history of evolutionary biology (Booth, 1990). Although many recent studies have explored the significance of coloration related to sexual selection and

sexual dimorphism (references in Booth, 1990), very little attention has been paid to ontogenetic color changes that are unrelated to reproduction. However, such changes are widespread among reptiles (Cooper and Greenberg, 1992).

In a variety of phylogenetically diverse lizard species (e.g., members of the families Scincidae, Gymnophthalmidae, Teiidae,

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and Lacertidae), the tail of juveniles is green, blue, or red and contrasts clearly to the cryptically colored body. These bright tail colors fade and become similar to overall body colors when lizards approach the minimum size of sexual maturity (Arnold, 1984; Cooper and Greenberg, 1992). Several hypotheses have been suggested to explain the function of bright tail colors in juvenile lizards. The most widespread and widely accepted is the "predator escape" hypothesis, which suggests that bright tail colors deflect the attack of a predator towards the lizard's tail, which can be autotomised, and hence increases the probability of escape (Arnold, 1984; Cooper and Vitt, 1985). The "aposematic (unprofitable) prey" hypothesis states that brightly colored prey signal their unpalatability and thereby reduce the incidence of predatory attacks (Arnold, 1984; Cooper and Vitt, 1985). Finally, the "conspecific signalling" hypothesis proposes that bright tails signal the juvenile status and hence decrease conspecific aggression, or even cannibalistic attacks (Arnold, 1984; Clark and Hall, 1970; Arnold, 1984; Cooper and Vitt, 1985).

The hypothesis that brightly colored tails enhance the probability of escaping predation has been the subject of surprisingly few studies. These were conducted under captive conditions, exclusively on skinks of the genus *Eumeces*, and they examined responses of only a few predatory species (Clark and Hall, 1970; Cooper and Vitt, 1985; Vitt and Cooper, 1986). The studies of Cooper and Vitt showed that (1) blue tails provide hatchling of *Eumeces* with significant protection against predation by kingsnakes, (2) the tail's chromatic properties do not have a strong predation inhibiting effect against conspecific adults, and (3) the blue tail is not aposematic for the predators tested (one kingsnake, one frog, and one shrew). Contrary to these authors, Clark and Hall (1970) indicated that blue coloration in young of *Eumeces* inhibit attack by aggressive conspecific adults, and they considered the "predator escape hypothesis" inadequate to account for the evolution of the blue tail coloration.

Despite the lack of empirical evidence, it is generally assumed that bright tail colors have evolved to increase the probability of surviving a predatory attack (Arnold, 1984; Cooper and Vitt, 1985, 1991). Moreover, geographic variation in the occurrence of bright tail coloration has been attributed to putative selective differences (e.g., Brown and Thorpe, 1991).

We are unaware of studies that examine whether or not free-ranging predators direct their attacks towards brightly colored lizard tails. Such studies are hampered by the difficulties of observing juvenile lizards and, especially, predator-prey interactions in natural conditions. However, this problem can be circumvented through the use of soft plasticine replicas of the prey. Because these replicas retain on their surface the impressions of bills and teeth, they can be used to survey the frequency of predatory attacks under different conditions (Brodie, 1993; Castilla and Labra, 1998).

Here we report results of a study designed to test a prediction of the "predator escape" hypothesis, that bright tail colors will induce an increased frequency of predatory attacks towards the tail. We used plasticine replicas of juvenile lizards in the genus *Podarcis* to survey the frequency of attacks by free-ranging predators in different study areas, on replicas with bright green or cryptic brown tail colors. *Podarcis* is ideal for examining this hypothesis, because juvenile tail colors are variable across populations (Barbadillo, 1987). In *Podarcis bocagei*, juveniles have green tails, in *P. muralis* and *P. atrata* (Castilla et al., 1998), the tail of juveniles is grey-brown, and tail coloration of juveniles of *P. hispanica* ranges from grey-brown to a spectrum of blue-green, depending upon population location.

MATERIALS AND METHODS

We performed the study in nine areas located in Spain (Table 1). The study areas differ in habitat structure, diversity and abundance of predatory and sympatric species (Castilla and Bauwens, 1996; Elósegui, 1985; Escala et al., 1997; Galán and Fernández-Arias, 1993; Gosá and Bergerandi, 1994; Herrero, 1984; Penas-Patiño et

TABLE 1.—Location and characteristics of the study areas. We indicate whether the study area is situated on the mainland (M), continental island (CI), or oceanic island (I); the altitude (Alt; in meters); the number of lizard replicas used (NR); the date of the experiment; the species of *Podarcis* present in each study area (Sp: Pb = *P. bocagei*, Ph = *P. hispanica*, Pa = *P. atrata*, Pm = *P. muralis*); and the tail colors in juveniles (Tc: G = bright greenish, contrasting with the brown body colors; B = grey-brownish, not contrasting with coloration of the body); the type of habitat (Hb: mx = mixture of open and cover, op = open areas); the number of lacertid lizard species (Lz) and the number of predator species: lizards (L), snakes (S), mammals (M), birds (B) and total (T) in each area.

Note that in areas 6 and 7, juveniles of different sympatric species have either a green, brown, or reddish tail. Area 1 is an open shrubland (*Ulex*, *Cytisus*, *Adenocarpus*) and grassland (*Agrostis* and *Vulpia*). Area 2 is a dense grassland (*Dactylis*) with bushes (*Ulex*) and open rocky areas. Area 3 is a mountainous grassland (*Festuca*, *Trifolium*, *Bellis*) with sparse low bushes (*Sambucus*) and rocky grasslands (*Plantago*, *Setum*). Area 4 is a forest of *Fagus* with dispersed bushes (*Crataegus*, *Prunus*, *Rubus*). Area 5 is a xeric beechwood (*Fagus*) and pine forest (*Pinus nigra*) with bushes (*Quercus humilis*, *Crataegus*, *Juniperus*, *Malus*, *Prunus*, *Rubus*, *Erica*) and sparse rocky areas. Area 6 is a rocky open area with sparse low bushes (*Erica*, *Cistus*, *Larandata*). Area 7 is a degraded oak (*Quercus ilex*) woodland with bushes (*Prunus*, *Salix*), herbs and rock walls. Area 8 is a volcanic rocky area with low bushes, herbs and grasses (*Suaeda vera*, *Lobularia*, *Lavatera*, *Malva*). Area 9 is an open limestone rocky area with sparse low bushes (*Suaeda*, *Atriplex*, *Malva*).

I	Study area										Predators						
	Location	Alt	NR	Date	Sp	Tc	Hb	Lz	L	S	M	B	T				
1	Cerdeña 43° 30' N, 8° 30' W	250	110	IX-96	Pb	G	mx	2	0	2	5	13	20				
2	Torre Hércules 43° 25' N, 8° 25' W	20	110	IX-96	Pb	G	mx	1	0	0	1	4	5				
3	Aralar I 43° 0' N, 2° 5' W	1020	40	VII-96	Ph	B	op	2	0	1	7	12	20				
4	Aralar II 43° 0' N, 2° 5' W	1020	20	VII-96	Pm	B	mx	2	0	1	7	13	21				
5	Beorburu 42° 50' N, 1° 40' W	780	110	IX-96	Pm	B	mx	4	0	3	6	3	12				
6	N. Francia 40° 30' N, 6° 5' W	1040	100	X-96	Ph	G	op	5	1	5	10	20	36				
7	El Pardo 40° 30' N, 3° 45' W	700	110	VII-96	Ph	G	mx	5	1	6	10	20	37				
8	Columbretes 39° 54' N, 0° 41' E	35	96	V-95	Pa	B	mx	1	1	0	0	8	9				
9	Chafarinas 35° 10' N, 2° 20' W	40	110	IX-96	Ph	G	op	1	1	0	0	9	10				

al., 1991), the species of *Podarcis* inhabiting the area, and coloration of the tail of the juveniles (Table 1). The experiments were carried out from late spring to autumn 1995–1996, when juvenile lizards are present in the study areas. We chose sunny and windless days to reduce natural variation in conditions that may affect the visibility of the replicas (Endler, 1978) and to avoid artefacts associated with searching behavior of predators.

We used a plaster mold and precolored non-toxic plasticine to obtain identical replicas of juvenile lizards [snout–vent length (SVL) = 30 mm; tail length = 52 mm]. We made total of 806 replicas, half of them with green tails that contrasted clearly to the brown body color, and half of them with brown tails and bodies. The body and tail of the replicas were uniformly colored, because it was impracticable to mimic the complex and highly variable color patterns of juvenile lizards, made up of various combinations of spots and stripes (Castilla and Bauwens, 1996). Because plasticine colors that matched those of the lizards were not commercially available, we mixed them to mimic the coloration of brightly colored green tails (Munsell hue = 2.5 G, value = 5, chroma = 8) and brown bodies and tails (Munsell hue = 7.5 YR, value = 4, chroma = 2). The resulting body and tail colors were within the range of the variation observed within and among natural populations of the study species. An implicit assumption of our approach is that the resemblance between replicas and lizards, which was apparent to the human eye, was also perceived as such by visually hunting predators.

In each study area, we positioned replicas, with color selected at random, at 5-m intervals along one or more transect lines. Each replica was placed against a natural background, on sites that appeared to be good basking spots for lizards. For each placement, we recorded substrate type (rock, ground, herb, litter, moss, log/branch) and background color (white–grey, yellow, brown–orange, green). Subsequently, all replicas were surveyed on each of seven consecutive days. During each survey, we recorded whether or not

the replica exhibited imprints, their positions on the replica (head, body, tail), the size and shape of the markings, and the suspected predator. Some replicas disappeared after one or more attacks, but others remained in their sites and received different attacks on successive days. Thus, for each replica, we only retained the information obtained when it was first attacked by a presumed lizard predator. A replica was considered as being attacked by a lizard predator when it exhibited bill marks of birds (characteristically paired V- or U-shaped), tooth marks of mammals, unidentifiable predators that eat lizards (e.g., square-shape tooth), or when the replica had disappeared. Replicas showing marks of only putatively non-lizard predators, such as small birds (with a thin insectivorous bill), insects and rodents (mice, rats, and rabbits), were analyzed as “other disturbances”.

Analyses were performed using the G-test with $\alpha = 0.05$. We used a log-linear analysis to examine the associations between study area, tail color, and the position of birds' bill markings on the replicas.

RESULTS

There were differences in substrate type ($G = 816.3$, $df = 32$, $P < 0.001$) and substrate color ($G = 827.0$, $df = 32$, $P < 0.001$) among study areas. However, in none of the nine study areas did the substrate color differ between sites where green or brown-tailed replicas were placed ($P > 0.06$ in all cases).

The nature and position of the imprints on the replicas suggested that they were identified and treated as potential prey, rather than non-prey items. A high overall proportion of the replicas experienced attack (75%, $n = 607$ of 806) within the short period (1 wk) of exposure. Attack rates varied from 20–100% among study areas ($G = 46.4$, $df = 8$, $P < 0.001$) (Fig. 1). Out of 607 replicas that were considered as being attacked, the majority (81%, $n = 493$) had disappeared, whereas the others were preyed upon by birds (14%, $n = 86$), mammals (1%, $n = 5$), or unidentified predators (4%, $n = 23$). Avian predators that could be identified were mainly

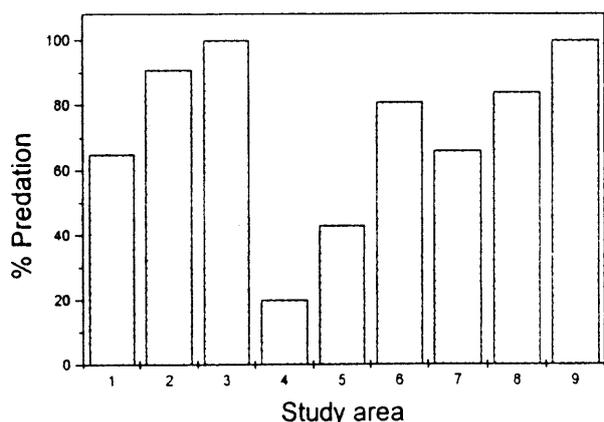


FIG. 1.—Total percentage of predation on lizard replicas in different study areas.

corvids (*Corvus corone*) and gulls (*Larus cachinnans*). Among mammals, we recognized imprints of foxes (*Vulpes vulpes*) and cats (*Felis catus*).

We found no evidence for a difference between green- and brown-tailed replicas in attack frequency by birds ($G = 0.74$, $df = 1$, $P > 0.30$), mammals and undetermined lizard predators ($G = 1.55$, $df = 1$, $P > 0.30$), and other disturbances ($G = 1.13$, $df = 1$, $P > 0.20$; Fig. 2).

To ensure that attacks followed visual detection of the replicas by the predator, we hereafter restrict analyses to the replicas that were attacked by birds. Attack frequencies on green- and brown-tailed replicas were similar not only after the 1 wk exposure period, but also after every single day of exposure to predators (Fig. 3). A log-linear analysis used to examine the associations between study area, tail color, and the position of the attack on the replicas revealed a significant interaction effect between study area and position of the bill markings ($\chi^2 = 24.77$, $df = 8$, $P < 0.01$). The number of replicas that had imprints on the tail only was higher in study areas 1 and 2 than in the others. This may be due to differences among areas in the species' composition of avian predators. However, this interpretation remains speculative, because we were unable to assign all the bill imprints on the plasticine to particular bird species. We also found a significant interaction between tail color and position of the bill markings ($\chi^2 = 6.22$, $df = 2$, $P < 0.05$; Fig. 4). The pro-

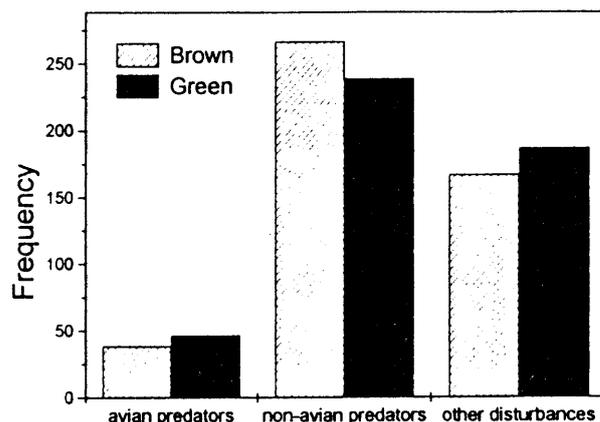


FIG. 2.—Number of lizard replicas with different tail coloration that were attacked by different agents after one week.

portion of replicas with bird imprints only on the tail was significantly higher in the green-tailed than in the brown-tailed replicas ($G = 5.33$, $df = 1$, $P = 0.02$; Fig. 4). In contrast, the proportion of lizard replicas attacked exclusively on the head and body parts was similar in both tail color morphs ($G = 0.55$, $df = 1$, $P > 0.40$).

DISCUSSION

Birds, which have excellent color vision, are important lizard predators (Martin and López, 1990) and are suggested to be one of the most significant potential factors in the evolution of antipredator mechanisms in reptiles (Greene, 1988). Some of the most common bird species (different species of the genus *Milvus*, *Buteo*, *Falco*, *Corvus*, *Lanius*, *Turdus*, *Monticola*, and

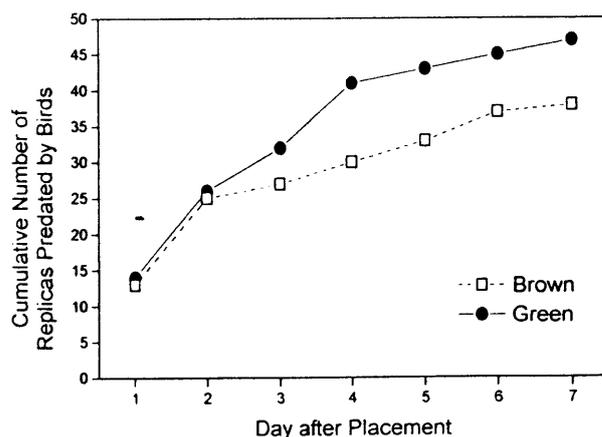


FIG. 3.—Cumulative number of green and brown tailed lizard replicas preyed upon by birds after each day of exposure to predators.

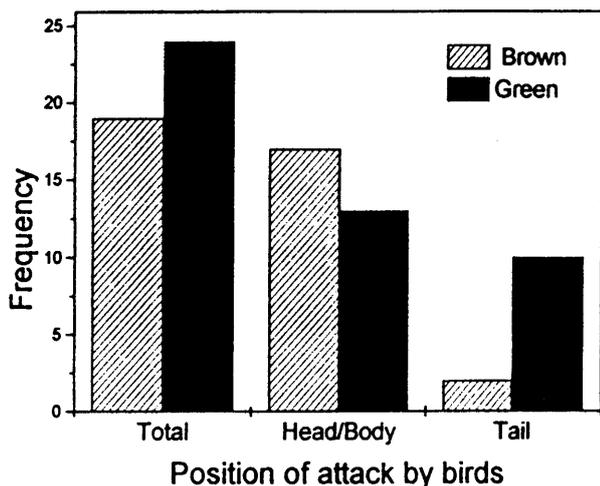


FIG. 4.—Number of replicas (green- and brown-tailed lizards) attacked by birds on different positions. We distinguished between replicas exhibiting imprints all over their surface, exclusively on the head and/or body, and exclusively on the tail.

the gull *Larus cachinnans michaelis*) in our study areas are known to prey on lizards (Castilla and Labra, 1998; Elósegui, 1985; Herrero, 1984; Penas-Patiño et al., 1991). In Spain, where several species of *Podarcis* are widespread and locally abundant (Barbadillo, 1987), the importance of reptiles as prey is higher than in other Mediterranean habitats (Jaksic and Delibes, 1987), and the incidence of predation on a lizard species may be correlated with its relative abundance (Jaksic et al., 1982).

Our results indicate that replicas in all study areas experienced high attack rates. The proportion of predated replicas among areas was not correlated with altitude, latitude, or with the number of predators in each area. Predation on islands, where the diversity of predators is low, was very high (92%) when compared to predation on mainland populations (67%).

Replicas in all study areas experienced high attack rates regardless of the contrast between tail and body color. This suggests that tail coloration of stationary lizards (e.g., basking) does not influence their overall conspicuousness to predators. However, the frequency of bird attacks exclusively directed towards the tail was highest in the replicas with brightly colored tails, indicating that at least some birds were attracted by the contrasting tail

color. Unfortunately, many replicas showed imprints all over their surface, such that it was impossible to determine whether the initial attack was directed towards the tail, body or head. On the other hand, other bird attacks were directly to the head or body of the replica and ignored the tail, regardless of its color. Directing the attack towards the head may reflect innate differences among species in hunting strategies. Alternatively, some bird predators could learn not to direct their attack towards the autotomous tails of lizards (e.g., Howard and Brodie, 1973; Huheey, 1960; Smith, 1973, 1976). Mammals, which also possess color vision and which tend to attacks the head of a prey (references in Green, 1988), directed their attacks to the head of some replicas. Some of the common mammalian species in our study areas are lizard predators (e.g., *Genetta genetta*, *Mustela nivalis*, *Felis catus*, *F. silvestris*, *Vulpes vulpes*: Delibes, 1978; García-Márquez et al., 1997; Mouches, 1981). Hence, for predators that guide their attacks toward the head of a prey, bright tail colors probably lack functionality for escaping predation, at least in stationary lizards. A bright tail may be thus effective only for escaping attacks by some bird species.

In addition to the results of our experiment, indirect evidence suggests that both bright and cryptic tail colors confer a selective antipredator advantage to lizards. Species of *Podarcis*, with different juvenile tail colors, overlap in distributional range and are similar in general behavior (e.g., thermoregulation, widely foraging). They are also similar in body size (SVL) at hatching (approximately 25 mm) and at sexual maturity (approximately 45–50 mm), so that attack frequency on different morphs cannot be biased by size. In areas where species that differ in juvenile tail colors occur sympatrically, and thus share the same predators, we expect that juveniles with different tail coloration would differ in antipredator behavior or in morphological and physiological characteristics. No information on antipredator behaviors in juveniles of *Podarcis* are available, except for the observation that hatch-

lings of *P. bocagei* agitate their green tail as a defense mechanism (Galán, 1994). Therefore, if the antipredator function of brightly colored tails is enhanced when it is accompanied by relevant tail display, movements of autotomised tails, or escape behavior, we suggest that the evolution of contrasting tail colors as an antipredator mechanism may be favored by the correlated evolution of behavioral and morphological characteristics. To examine these ideas, it is necessary to measure some of the morphological and physiological characteristics associated with tail moving behavior. The ease with which a tail breaks and the time an autotomised tail keeps moving is higher in lizards from areas with putatively stronger predation pressures (Pérez-Mellado et al., 1997). If predators are attracted by brightly colored and moving tails, we expect that green tails will show a higher breakage frequency and keep moving longer than brown tails. Hence, it would be interesting to measure the capacity to autotomise, the duration of movements by the broken tail, and the sprint speed of juveniles of both morphs.

If cost of colors varies between species and geographical areas, a complete understanding of the role of predation in the evolution of juvenile tail coloration in lizards will require replication and improvement of our experiment (e.g., through use of autotomous replicas) in a variety of habitats and species, as well as examining responses of caged lizards towards a variety of predators.

Our study did not address the "aposematic prey" hypothesis. Because lizards are unlikely to constitute unprofitable prey, there is no reinforcement for the supposed warning coloration of the tail, thus falsifying a basic assumption of the hypothesis. We have also not examined the "conspecific signalling" hypothesis, because we consider it as unlikely that bright tail colors would inhibit aggression or predation by conspecific adults of *Podarcis*. The incidence of cannibalism has only been shown to be high in *Podarcis atrata* (Castilla and Van Damme, 1996), a species with cryptic tail colors in juveniles and adults (Castilla and Bauwens, 1996). In ad-

dition, juveniles are consumed head-first (Castilla, 1995), and they either flee or freeze in the presence of cannibalistic adults. Therefore, the camouflaged grey-brown tail of juveniles of *P. atrata* may reduce detectability by conspecific adults. These observations, together with the results of our experiment, suggest that bright tail colors in juvenile lizards may be favored by predation in some species and populations and disfavored in others.

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