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Risk of predation may explain the absence of nuptial coloration in the wall lizard, *Podarcis muralis*

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ABSTRACT

Males of many species show conspicuous breeding colours that are important in social contexts, whereas other species are dull coloured. Bright coloration may be selected against if it renders males more conspicuous and results in a higher susceptibility to predators. We tested this hypothesis experimentally by manipulating in the field the coloration of the heads of live common wall lizards, *Podarcis muralis*. Probably because of the small sample size, we did not detect a significant difference in the survivorship of control individuals (painted brown to resemble their natural dull coloration) and that of experimental individuals (painted orange to resemble nuptial coloration of related species). However, within the individuals that survived, experimental lizards suffered a significantly greater loss of relative body mass than controls. We conclude that, even if bright coloration does not increase mortality directly, it may result in increased predation risk, which would force lizards to use anti-predatory behaviours, with their increased associated costs.

Keywords: costs of refuge use, lizards, nuptial coloration, *Podarcis muralis*, predation risk.

INTRODUCTION

Among vertebrates, males of many species use conspicuous body coloration to convey information about the sender, such as fighting ability, sex recognition or reproductive status (e.g. Cooper and Greenberg, 1992; Andersson, 1994). This raises the question of why males of some species have bright colours, whereas others, even in the same genus, are dull coloured. Female choice and male–male competition generally favour bright coloration in males. However, predation is often assumed to constrain the evolution of more elaborate male ornaments because, as males evolve brighter coloration, they are assumed to be easier to detect and to face increased predation risk (Kirkpatrick *et al.*, 1990; Andersson, 1994). Therefore, the signal may be selected against and could only be maintained by an adaptive benefit outweighing the effect of increased risk of predation (Reimchen, 1989; Zuk and Kolluru, 1998).

Predation is often difficult to study in the wild. Some research has quantified the risk of predatory attacks by using artificial models or mounts of birds (Götmark, 1993,

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1994), snakes (Andrén and Nilson, 1981; Brodie, 1993) or lizards (Olsson, 1993; Castilla and Labra, 1998). Although these studies may have clarified components of the predation process, their relevance to predation on live prey is unclear (Slagsvold *et al.*, 1995; Götmark and Olsson, 1997). Live animals are not static but show flexible anti-predatory behaviours. More conspicuous individuals, or those assessing an increase in predation risk, are often able to compensate for it by modifying their anti-predatory responses (Lima and Dill, 1990; Martín and López, 1999a). Therefore, studies of the predation rate on live prey in relation to different coloration are required to establish how predation influences the evolution of male secondary sexual characters.

Males of many species of lizards also show breeding colours during the mating season that are important for sex recognition or status signalling (for a review, see Cooper and Greenberg, 1992), which renders them more conspicuous, possibly resulting in a greater susceptibility to predators (e.g. Forsman and Shine, 1995; but see Olsson, 1993). In the present study, we manipulated experimentally in the field the coloration of the heads of live common wall lizards, *Podarcis muralis*, to test the hypothesis that bright coloration influences the risk of predation. *Podarcis muralis* is a small lacertid lizard (60–76 mm adult snout–vent length) that is widespread in Central Europe. It is restricted to the mountain areas of the northern half of the Iberian Peninsula, where it occupies soil dwellings, taluses and walls extending into forests (Martín-Vallejo *et al.*, 1995). We chose this species because its dorsal coloration is rather inconspicuous and, although males do not have brightly coloured heads, they still show bright colours on the ventrolateral surfaces that may be important in some social contexts, but might be hidden except during displays, as occurs in other lizards (e.g. Cooper and Burns, 1987). With this pattern of coloration, males may reduce the probability of detection by visually guided predators when on exposed rocky surfaces (their preferred microhabitat), where otherwise they could be easily detected. In such ecological circumstances, the risk of predation on male *P. muralis* may have precluded the appearance, or favoured the loss, of bright nuptial coloration of the head. In contrast, males of other sympatric and closely related species of lacertid lizards (e.g. *Psammodromus algirus* and *Lacerta schreiberi*) that occur in microhabitats with more visual cover show bright nuptial coloration. Similarly, a comparative analysis among species of phrynosomatid lizards has shown that repeated losses of conspicuous male coloration during evolutionary time are associated with differences in microhabitat use (Wiens, 1999).

An increase in predation risk does not necessarily imply an increase in predation rate (McNamara and Houston, 1987), because individuals might behave differently to cope with the temporal situation of higher predation risk (Lima and Dill, 1990). In fact, it has been shown previously that *P. muralis* is able to compensate for an increase in risk of predation by increasing its use of refuges. However, this anti-predatory strategy may entail costs that are reflected in the condition of the body (i.e. a loss of relative body mass) of individuals (Martín and López, 1999b). Thus, we hypothesized that, if bright coloration increases the probability of predatory attacks, experimental individuals might respond by increasing their use of refuges, and that there will be associated costs to their body condition.

In this experiment, we simulated the appearance of a novel bright nuptial coloration in this species by creating experimental individuals whose heads were painted orange (resembling the nuptial coloration shown by other related lizards species), and compared their survivorship with that of control individuals whose heads were painted brown to resemble their natural dull coloration. We hypothesized that, if bright coloration increases predation risk, experimental individuals should have lower survival rates than controls. We also assessed whether body condition or intersexual differences affect the probability of survivorship independently or in interaction with the experimental treatment. Finally, we examined the body condition of all surviving lizards at the end of the experiment to test for possible indirect effects of increased predation risk (Martín and López, 1999b). We show that mortality due to predators might not affect directly *P. muralis* with bright coloration. However, bright coloration may actually be costly and not be favoured because of the indirect effects of increased predation risk that would force lizards to increase their use of refuges, with their associated costs to the body condition of the lizards.

MATERIALS AND METHODS

Study site

The experiment was performed in the Guadarrama Mountains, in a pine forest at Cercedilla (Madrid Province, Central Spain) 1500 m above sea level. The dominant vegetation at this altitude consists of *Pinus sylvestris* forest, with shrubs such as *Juniperus communis* and *Cytisus scoparius*. We conducted the experiment at an artificial wall (120 m long and 5 m high) of granite rocks built to hold back a sandbank. Active lizards were found basking or walking on the wall, where they used the many crevices between rocks as refuges. Also, lizards regularly crossed at high speed a nearby bare soil track without cover (4 m wide) to enter the forest where they foraged. We often observed in the area visual guided predators known to predate on this lizard (Martín and López, 1990), such as jays (*Garrulus glandarius*), magpies (*Pica pica*), great grey shrikes (*Lanius excubitor*), buzzards (*Buteo buteo*), short-toed eagles (*Circaetus gallicus*), kestrels (*Falco tinnunculus*), little owls (*Athene noctua*) and tawny owls (*Strix aluco*), as well as the many feral cats that frequently chased and killed these lizards in this and other populations (Boag, 1973; Brown *et al.*, 1995).

Experimental procedure

During the second week of April 1999, we noosed lizards to record snout–vent length (to the nearest millimetre), tail length, body mass (to the nearest 0.1 g with a Pesola spring scale), sex and tail condition (only adult lizards with complete tails were used in the experiment). By experimentally manipulating phenotype, we created two groups: experimental individuals (with orange coloration on most of the head resembling related species) and controls (with brown coloration on most of the head resembling natural coloration). We used flexible non-toxic Testor's paints for model aeroplanes, mixing them to achieve good visual matches with the natural brown colour of the head of *P. muralis*, or with the breeding orange colour shown by males of the lacertid lizard *Psammodromus algirus* (Martín and Forsman, 1999). During recaptures, we did not observe any tissue necrosis due to the paint that could influence the behaviour or survivorship of the lizards. We painted both males and females to determine whether differences in behaviour (e.g. higher mobility of males searching for mates) between the sexes have a differential effect on predation risk independently of coloration (Magnhagen, 1991). Individual lizards of each sex were assigned alternately to the control ($n = 30$; 15 males and 15 females) and the experimental

($n = 30$; 15 males and 15 females) groups. Although males tended to be shorter than females, lizards from the control and experimental group did not differ in snout–vent length (two-way ANOVA: sex, $F = 3.86$, $P = 0.05$; colour, $F = 0.24$, $P = 0.63$; interaction, $F = 0.37$, $P = 0.55$) or body mass residuals (two-way ANOVA: sex, $F = 0.29$, $P = 0.60$; colour, $F = 1.46$, $P = 0.23$; interaction, $F = 0.26$, $P = 0.61$). Lizards were individually marked by toe clipping and released at the capture site within less than 5 min.

The study site was not visited in the following months so as not to disturb the lizards or their potential predators. Thus, the experimental treatment ran for 2 months (middle of April to middle of June) without the experimenters being present. Finally, during the last 2 weeks of June 1999, we noosed all individuals found to identify them and record changes in snout–vent length and body mass. To ensure that non-recaptured lizards had not migrated to other locales, we surveyed the entire wall and also the surrounding areas, where occasionally a few isolated lizards, not previously marked, were found. Thus, we assumed that all unlocated individuals had not survived. Predation rate was measured indirectly from disappearing individuals; mortality was probably affected by factors other than predation. However, controls presumably had the same mortality factors as the experimental individuals. Thus, possible differences in survivorship between treatments were assumed to be due to increased predation by visually guided predators.

Data analyses

We used logistic regression analysis to test for independence of recapture status (i.e. survivorship), colour treatment and sex, and to test for a possible effect of body size (i.e. body mass residuals) on probability of recapture. Logistic regression is suitable for dichotomous dependent variables (e.g. alive *vs* dead), can handle categorical as well as continuous independent variables, and it is also possible to test for effects of interactions (Hosmer and Lemeshow, 1989). The data analyses were performed using SPSS for Windows (SPSS, 1993). This package provides a likelihood ratio statistic as a goodness-of-fit estimator for the model, and maximum likelihood estimators (β) and standard errors of the independent parameters. To assess the significance of the independent variables, we calculated the difference in deviation for a model with and without the variable of interest. The resulting difference in deviation between the two models follows a chi-square distribution with one degree of freedom (Hosmer and Lemeshow, 1989). We used the PASS 2000 computer software (Hintze, 2000) to calculate statistical power for tests yielding non-significant results (Cohen, 1988; Thomas and Juanes, 1996). Power estimates in logistic regression were based on sample size, the baseline probability $Y = 1$ (i.e. the probability that $Y = 1$ given that $X = 0$, $p(0)$) and odds ratios (i.e. the exponents of the partial regression coefficients, e^{β}) (Hintze, 2000).

We used a repeated-measures three-way analysis of covariance (ANCOVA) to test for changes in relative body mass ($\log_e$ transformed) between first capture and recapture (within-subjects factor). We used snout–vent length as the covariate and sex and colour manipulation as the between-subjects factors. Sex was included to adjust for possible size and behaviour differences between males and females (see above), which might affect how body mass changes. The interaction between colour and treatment (i.e. time between captures) tested for effects of the experimental manipulation on relative body mass of individuals that survived. Individual values of relative body mass were equivalent to the residuals from the regression equation of ln mass (g) on snout–vent length (mm), which may represent an index of the relative amount of fat stored and, hence, an estimation of individual physical condition or nutritional status (Bonnet and Naulleau, 1994). We first tested for slope heterogeneity, which we found not to be significant ($P > 0.60$). Significance levels for the multiple tests of the ANCOVA were calculated using the sequential Bonferroni adjustment of Rice (1989) for multiple comparisons (Chandler, 1995).

RESULTS

In total, 70 individuals were recaptured. Of the 60 individuals that were painted, marked and released at first capture, 20 (33%) were recaptured (Fig. 1). Logistic regression analysis showed no significant differences in probability of recapture between control and experimental lizards, or between males and females ($\chi^2_4 = 2.51$, $P = 0.64$) (Table 1). The interaction between colour treatment and sex was also not significant, showing that the relationship between probability of recapture and colour treatment was similar for both sexes. The initial body condition of the lizards did not influence significantly the probability of recapture.

Table 1. Results of logistic regression analysis of probability of recapture (i.e. survival) on experimental treatment (colour), sex and body mass residuals in *Podarcis muralis*

Source	β	SE	P
Colour	0.32	0.28	0.26
Sex	0.29	0.29	0.32
Body mass residuals	−0.01	0.04	0.81
Colour × sex	−0.02	0.28	0.93
Constant	−0.07	0.75	0.98

Note: The heads of experimental and control individuals were painted orange and brown, respectively. The maximum likelihood estimates (β), standard errors (SE) of the estimates and the level of significance (P) of each independent variable are shown.

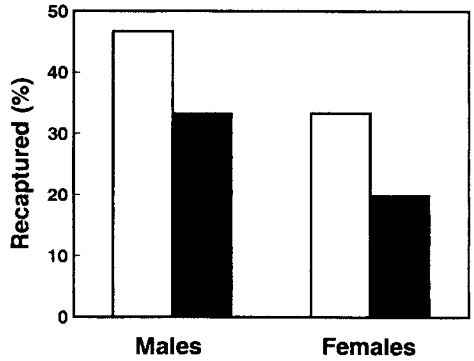

Fig. 1. Dependence of recapture probability (i.e. survival) on the colour of the head of male and female *Podarcis muralis*. The heads of experimental and control individuals were painted orange (■) and brown (□), respectively.

Given the small sample sizes, we calculated the statistical power of the logistic regression. For the colour treatment effect (odds ratio = 1.38), the power was only 0.03 (i.e. 3%). Assuming that the observed differences in survivorship were real, power calculations indicated that at least 330 or 25,437 lizards would need to be sampled to see a significant difference for this effect size at the $P = 0.05$ and $P = 0.01$ levels, respectively.

However, the ANCOVA of body mass indicated that lizards painted orange that survived to the end of the experiment had significantly lower relative body mass than lizards painted brown (treatment × colour effect) (Table 2). The interaction between colour and sex, although not significant after Bonferroni adjustments, suggested that the effect of colour manipulation differed between the sexes. Differences in body mass between colour groups were a consequence of experimental lizards suffering a significantly greater loss of relative body mass during the experiment than control lizards (two-way ANCOVA of differences between initial and final body mass with snout–vent length as the covariate: sex, $F = 0.47$, $P = 0.50$; colour, $F = 8.14$, $P = 0.011$; interaction, $F = 3.23$, $P = 0.09$) (Fig. 2).

DISCUSSION

The results of our experiment suggest that the appearance of a bright colour mutation on the heads of *P. muralis* would not translate immediately into an increase in mortality. This is consistent with the results of a study with model replicas of *Lacerta agilis* (Olsson, 1993). Nor was there support for the alternative hypothesis that a novel or rare colourful individual might be favoured by a reduction in predation risk because predators often avoid novel prey (Curio, 1993; Götmark, 1994), as experimental individuals did not suffer reduced predation. Thus, predation risk might be considered initially as unable to explain the

Table 2. Repeated-measures three-way ANCOVA examining colour, sex and treatment (time elapsed between initial capture and recapture) effects on body mass of lizards that survived ($n = 20$) at the end of the experiment

	d.f.	*F*	*P*
Between-subjects effects			
Colour	1,16	40.07	< 0.0001*
Sex	1,16	0.01	0.92
Colour × sex	1,16	7.42	0.015
Within-subjects effects			
Treatment	1,16	26.36	0.0001*
Treatment × colour	1,16	10.58	0.005*
Treatment × sex	1,16	0.78	0.39
Treatment × colour × sex	1,16	1.56	0.23

Note: Snout–vent length was the covariate. The repeated factor was body mass ($\log_e$ transformed) at the beginning and at the end of the experiment. *P*-values are unadjusted for multiple comparisons.

* Significant at $\alpha = 0.05$ using the sequential Bonferroni method with seven comparisons (Rice, 1989).

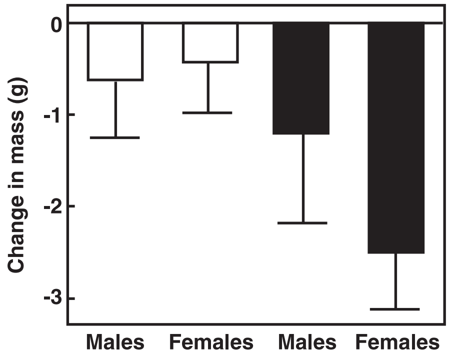

Fig. 2. Changes in body mass (mean and standard error) between initial capture and recapture of lizards with heads painted brown (□) or orange (■) that survived at the end of the experiment.

absence of bright coloration on the most visible parts of the body of this lizard. However, given the low power of our statistical tests, we cannot exclude the possibility that a larger sample size might have yielded significant results. In fact, the recapture rates of orange-painted individuals was lower than that of controls, suggesting that a bright colour on the head might actually increase the predation rate.

The recapture rate of marked individuals was relatively low, in spite of search efforts to locate marked individuals that might have dispersed. However, the recapture rate (i.e. survivorship) was similar to that found in unmanipulated individuals in this and other populations (Barbault and Mou, 1988; unpublished data). It is probable that predation is the main cause of mortality in *P. muralis*. For example, predation by visually guided predators has been observed in other populations of this lizard; when safe refuges were taken away from resident lizards, several individuals were observed being stalked and killed by cats (Brown *et al.*, 1995). Mortality risk is probably dependent on the availability of refuges as well as on conspicuousness to predators. Thus, the susceptibility of bright individuals to predation might differ between populations or species inhabiting microhabitats with different numbers of refuges, or with different densities of predators. Differences in microhabitat use have been used to explain the loss of conspicuous male coloration over evolutionary time among phrynosomatid lizards (Wiens, 1999).

Like many other animals, lizards often respond to the presence of predators by increasing their use of refuges. The results of a previous study showed that *P. muralis* identified a higher rate of simulated predatory attacks as an increase in predation risk, and that they were able to compensate for it by increasing the time they spent in refuges (Martín and López, 1999b). In the present study, if lizards with orange heads were more conspicuous and thus suffered more attempts of capture from predators, they may have realized that predation risk had increased and thus modified their refuge use or escape behaviour. Therefore, the experimental lizards may actually have suffered a higher predation risk without significant changes in mortality. Patterns of covariance between colour pattern and anti-predatory behaviour have been observed among and within species of other lizards and snakes (Heatwole, 1968; Brodie, 1992). For example, male *Psammodromus algirus* lizards with natural bright nuptial coloration are able to compensate for increased predation risk by adjusting their escape response, which may contribute to the maintenance of bright coloration in this species (Martín and López, 1999a).

Because we did not find an effect of coloration on mortality rate does not necessarily mean that a bright coloration is not costly and thus not favoured by *P. muralis*. An increase in predation risk may force animals to use anti-predatory behaviours that have increased associated costs (e.g. more time spent in refuges). The results of this and a previous experiment further indicate that lizards who increase their use of refuges may incur a cost (Martín and López, 1999b). Experimental lizards did not need to be aware of the colour manipulation. However, their bright coloration may have caused an increase in the frequency of unsuccessful predation attempts. Thus, lizards respond to an increase in predation risk with an increase in the use of refuges. As a consequence, at the end of the treatment, the experimental lizards that survived had a poorer body condition and lower stores of fat than control lizards. The cause of a lower body mass in the experimental lizards could be a reduction in the time available for foraging (i.e. more time spent in refuges avoiding predators), resulting in a reduced food intake (e.g. Ballinger, 1977), or thermoregulatory costs (i.e. more time spent at unfavourable body temperatures), which may lower the speed at which food is processed and the energy available for storage (Harwood, 1979). In addition, a threatening situation often induces a physiological stress response, which involves the production of hormones such as cortisol or epinephrine, which, in excess, can cause stress-induced diseases or immunosuppression (Weiner, 1992).

An alternative explanation to the absence of coloration is that bright colours may not benefit a male if the development of orange head coloration does not translate into increased social dominance or mating success. Also, the display of nuptial coloration may have additional costs related to the immunosuppressive consequences of high testosterone concentrations associated with the development of nuptial coloration that may render males more susceptible to parasites (Salvador *et al.*, 1996). Although male *P. muralis* do not display bright colours on their heads, they still do have bright colours on their ventrolateral surfaces. While displaying, a lizard may flatten its body laterally and tilt its side towards the recipient of his display to reveal ventrolateral colours (Cooper and Burns, 1987). Although there is no experimental evidence in this species, this bright ventral coloration could be important in some social contexts, but might be hidden except during displays. Therefore, it is probable that, if there were no other costs, coloration on the head might be important in social encounters signalling status, as occurs in other lizards (Martín and Forsman, 1999).

We conclude that mortality due to predators does not affect directly *P. muralis* lizards with bright coloration. Wearing a bright coloration may actually be costly and thus not be favoured because of the indirect effects of increased predation risk that would force lizards to use anti-predatory behaviours, thus increasing the associated costs. Therefore, predation risk might be considered a selective factor to explain the absence of nuptial coloration in *P. muralis*.

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