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Ecological correlates of colour pattern polymorphism along the transition zone between two morphs of the common wall lizard, *Podarcis muralis*

M. CAPULA[1], L. RUGIERO[2], & L. LUISELLI[2]*

[1]*Museo Civico di Zoologia, Roma, Italy, and* [2]*Centro di Studi Ambientali 'Demetra s.r.l.', Roma, Italy*

Abstract
The ecological correlates of dorsal colour pattern polymorphism were studied along the transition zone between two supposed subspecies (=colour pattern types in this article) of the common wall lizard, *Podarcis muralis*, in a hilly area of Latium, Central Italy. In this area two supposed subspecies, i.e. *P. m. brueggemanni* and *P. m. nigriventris*, are known to occur. Lizards were studied along 500 m long transects within three different habitat types, i.e. wood, wall, and bushy pasture. A total of 279 adult lizards (154 males, 125 females) were examined. Three colour morphs were observed at each site, i.e. *brueggemanni* type (brown–green upper parts), *nigriventris* type (black–green upper parts), and a colour morph intermediate between the two. The distribution and abundance of *brueggemanni* and *nigriventris* colour morphs was clearly non-random across habitat types: *brueggemanni* was abundant in walls and bushy pastures, and *nigriventris* in wood. To explain the observed pattern we tested the hypothesis of a differential predation exposure by the various colour morphs in different habitats by analysing the differences between colour morph frequencies of lizards with intact tail and with broken/regenerated tail in the various habitats of the study area. Our analysis would not support the differential predation-risk hypothesis, because the frequency of individuals with broken tails was very similar in the three colour morphs among different habitats.

Keywords: Podarcis muralis, *Lacertidae, colour polymorphism, Latium, Central Italy*

Introduction

Many studies have been devoted to investigate the correlates of colour pattern polymorphism in reptiles and to explain their ecological causes and consequences (see e.g. Camin & Ehrlich 1958; Andrén & Nilson 1981; Fernandez & Collins 1988; Malohtra & Thorpe 1991; Luiselli 1992; Capula & Luiselli 1994; Monney et al. 1995). The Mediterranean lacertid lizards seem to be particularly useful for this type of investigation because they are normally characterized by high inter- and intra-population variability in colour pattern (e.g. Arnold & Ovenden 2002; Corti & Lo Cascio 2002). The evolutionary significance of the high colour pattern polymorphism of the Lacertidae has been unstudied for most taxa. However, there is evidence that colour pattern polymorphism is influenced by habitat constraints and complex interactions between environmental pressures and physiological traits in at least some lizard species (e.g. Martin & Forsman 1999; Lopez

et al. 2004; Stuart-Fox et al. 2006; Sacchi et al. 2007). In *Podarcis muralis* (Laurenti, 1768), it has been demonstrated that immune responsiveness is morph-specific in males, suggesting that this physiological trait could play an important role in maintaining colour polymorphism in this species (Sacchi et al. 2007). In some cases at least it was pointed out that species which are characterized by a high degree of phenotypic plasticity in the pattern of the upper parts may have levels of genetic variability higher than those found in the morphologically low variable species (see e.g. Selander 1976; Capula 1994, 1996, 1997; Losos et al. 1997; Capula & Ceccarelli 2003). For instance, this is the case of the island populations of *P. muralis* occurring in the Tuscan Archipelago, which are characterized by high genetic and morphometric variability (Capula 1997). Moreover, it must be stressed that the results of mtDNA analysis (Caputo et al. 2008) indicate highly subdivided geographical and genetic structure of the *P. muralis* populations occurring in the Italian

peninsula. In this paper we analysed a transition zone between the ranges of two colour pattern types of the common wall lizard, *Podarcis muralis*, in northern Latium (Central Italy) to study the ecological correlates of their colour pattern polymorphism. *Podarcis muralis* occurs in central Italy with at least two colour pattern types: one was described as typical for *P. muralis brueggemanni* (Bedriaga, 1879) and the other for *P. muralis nigriventris* Bonaparte, 1836. The former colour pattern type is widespread in Tuscany, Umbria, Marche, Romagna, Liguria, and in the northern part of Latium (Capula 2000; Corti & Lo Cascio 2002); the latter is present only in Latium, where it is widespread in the central and southern parts of the region (Capula 2000). The two colour pattern types are clearly different especially in the upper parts. The '*brueggemanni*' type has a dark ground colour with a very variable pattern of brown blotches; the '*nigriventris*' type is characterized by a black ground colour with green blotches, which are normally small and relatively sparse. It must be noted that the taxonomic status of the two subspecies is still under debate (see Capula 2000; Corti & Lo Cascio 2002), and that some authors (e.g. Gruschwitz & Böhme 1986) do not recognize *brueggemanni* as a valid subspecies.

Our goal was to answer to the following key questions: (1) Can colour pattern be informative enough to clearly discriminate among adult individuals and between the two supposed colour pattern types? (2) If yes, are there differences in the frequency of occurrence of the two colour morphs among habitat types? (3) If yes, what reasons can be invoked to explain a habitat-dependent variation in the frequency of occurrence of the various morphs? That is, can predation risks explain an inter-habitat differential frequency of occurrence of the various colour morphs? We tested the latter question by analysing the differences between colour morphs frequencies of lizards with intact tail and with broken/regenerated tail in the various habitats of the study area.

Materials and methods

Study area

The field study was carried out during July and August 2007. All lizards were captured in the vicinities of Oriolo Romano (450 m a.s.l., about 50 km north of Rome, Central Italy), a hilly village situated in the transition zone between the ranges of the colour pattern types *P. m. brueggemanni* and *P. m. nigriventris*. Three habitat types were surveyed during the present study: (a) shady, dense, and wet mixed oak forest dominated by *Quercus* spp. and

Fagus sylvatica, with a canopy cover of approximately 60–80% (WOOD); (b) grassy territory interspersed by bushes (*Rubus* spp., *Cytisus scoparius*), with a canopy cover of approximately 20–40% (BUSHY PASTURE); (c) human-made stony or cement walls delimiting gardens, roads, etc., very often in proximity of human settlements (WALL). In order to avoid problems in assigning lizard individuals to the correct habitat type, we did not survey sites with habitat features intermediate among the three selected habitats, or where these habitats do alternate at the local scale. Within each habitat type, we walked appropriate transects of 500 m each. The transect sites used for the three habitats were ⩽ 1 km each from another, in order to avoid that inter-habitat colour pattern differences might be due to excessive geographic distance among sites rather than to micro-geographic and ecological factors. A habitat unsuitable to lizards was always present between two transects, i.e. buildings without gardens and roads. Hence, all transects were certainly independent of each other in terms of lizard movements.

Protocol

Each 500 m transect was surveyed only once by walking very slowly in one direction, and recording all lizard sightings. Lizards were captured and identified to sex by their secondary sexual characters (enlarged femoral pores). In addition, the capture habitat was recorded. Pseudo-replication of data was avoided by monitoring each transect only once and only in one direction, thus never replicating the eventuality of capturing the same lizard more than once.

Each captured lizard was assigned to one of the following colour morph categories, based on the colour pattern of the upper parts: (1) *brueggemanni* type (brown–green upper parts); (2) *nigriventris* type (black–green upper parts); (3) intermediate type (upper parts intermediate between *brueggemanni* and *nigriventris*). For this study we considered only adult individuals, i.e. individuals with snout–vent length ⩾ 5 cm, because juveniles of both *brueggemanni* and *nigriventris* have a similar colour pattern and this cannot be assigned to one of the three colour morph categories described above. The tail status (intact or broken/regenerated) was also recorded for each lizard captured at the study area.

Statistical analyses

The differences among habitats in the frequency of occurrence of colour morphs were analysed by a

Monte Carlo randomization procedure for χ^2 test, with 10,000 permutations of the whole data matrix prior to apply the calculations. Then, the observed value was compared with the mean and the variance of the simulated matrices (Gotelli & Graves 1996). Non-parametric tests were used in all cases because data variables were neither normally distributed nor were normalized with appropriate transformations. Non-parametric Spearman's rank correlation coefficient was used to test for the correlation between percentages of lizards with intact tail and sample sizes, habitat types, and colour pattern types. Differences in frequency of lizards with broken/regenerated tails among colour morphs within each habitat type were tested by χ^2 test. All tests were two-tailed and alpha was set at 5%. Statistical analyses were performed using STATISTICA 7.1 software. Monte Carlo analysis was performed after having generated the permutated matrices with Ecosym software 700 version.

Results

A total sample of 279 adult lizards, 154 males and 125 females (sex ratio 1.23:1, not different from equality at binomial test) were analysed. The distribution of observations of lizards by colour morph and by habitat type is given in Figure 1. Details of lizard distribution by sex and by habitat and the relative frequency of individuals with intact tail by sex, colour morph, and habitat type is shown in Table I. The three colour morphs were always clearly recognizable at the study area. The distribution of the three colour morphs was non-random across habitat types (Monte Carlo randomization procedure for χ^2 test: Observed index=147.308; mean $\pm$ variance of simulated indices=8.110 $\pm$ 15.975, $P<0.00001$), with *brueggemanni* accounting for the majority of *P. muralis* individuals in WALL ($N=80$) and BUSHY PASTURE ($N=41$), and *nigriventris* accounting for the majority of individuals in WOOD ($N=114$; Figure 1).

Intermediate individuals accounted for a percentage of individuals less than *brueggemanni* and *nigriventris*, and were observed in all habitat types (Figure 1).

There was no inter-sexual difference in the frequency of occurrence of a given colour morph within each habitat type apart from WOOD (Table I). In this latter habitat the colour morph *nigriventris* was significantly more associated to males than to females ($\chi^2=4.246$, df=1, $P<0.039$).

Transect-by-transect (total $N=17$), the percentage of individuals with intact tail (Table I) was not correlated with sample size (Spearman's $r=-0.030$, $P=0.908$), sex (Spearman's $r=0.399$, $P=0.113$), habitat type (Spearman's $r=-0.322$, $P=0.207$), and colour morph (Spearman's $r=0.076$, $P=0.771$). The frequencies of lizards with broken/regenerated tails did not differ significantly among colour morphs within each habitat type, either if sexes were pooled or entered separately in the analyses (in all cases, at least $P>0.255$ at χ^2 test).

Discussion

Within the studied geographic transition zone three colour morphs (*brueggemanni*, *nigriventris*, intemedi-
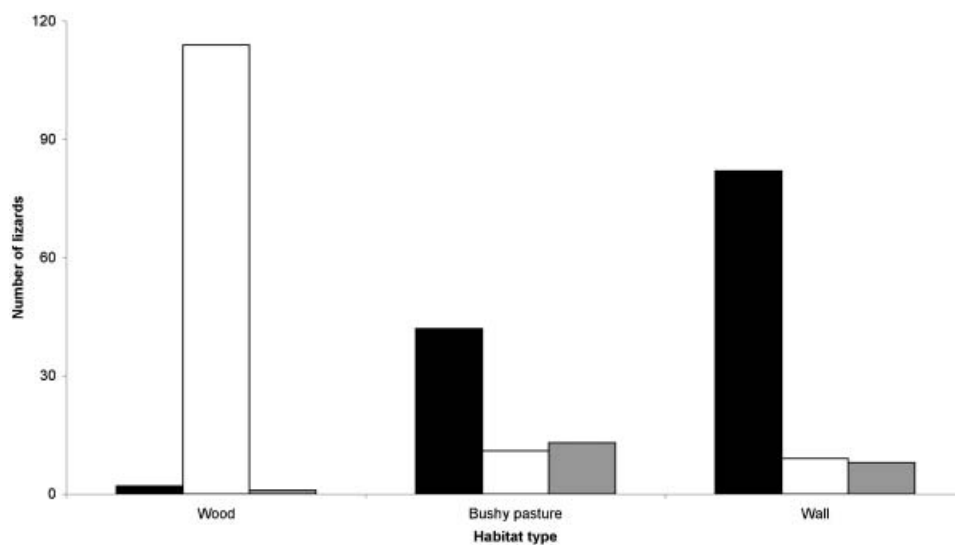

Figure 1. Distribution of observations of lizards by colour morph in the three habitat types. White bar: *nigriventris* type; black bar: *brueggemanni* type; grey bar: intermediate type.

Table I. Colour morph categories, sex, habitat type, and frequency of occurrence of intact/regenerated tails in *Podarcis muralis* from the study area. Numbers indicate individuals examined for each column category. Numbers in parentheses indicate individuals with broken/regenerated tail.

Colour morph	Wood Males	Wood Females	Bushy pasture Males	Bushy pasture Females	Wall Males	Wall Females
Brueggemanni type	1 (1)	1 (0)	18 (4)	23 (10)	38 (14)	42 (9)
Nigriventris type	68 (27)	46 (11)	9 (2)	2 (0)	6 (1)	3 (1)
Intermediate type		1 (0)	10 (2)	3 (2)	4 (0)	4 (1)

ate type) are always recognizable. The morphs *brueggemanni* and *nigriventris* are clearly linked to different habitat types, although sharing their habitat with individuals of the intermediate colour pattern. The morph *brueggemanni* is extremely rare in WOOD habitats, and very abundant in WALL and in BUSHY PASTURE habitats. On the other hand, the morph *nigriventris* is especially associated with wet, dense and shady wooded portions of territory (WOOD), where it represents over 95% of the common wall lizard population. These inter-habitat differences between colour morphs are clearly unrelated to sex or sample size.

Differential habitat use among colour morphs of certain reptile species has been sometimes reported, and is generally attributed to predation avoidance by the least cryptic morph in the suboptimal habitat (e.g. Kjaergaard 1981). However, there is no univocal pattern in this regard, and some experimental studies have shown that different colour morphs may be nearly identical in terms of habitat choice, including even the choice of background colour (see e.g. Luiselli et al. 1994; Capula & Luiselli 1995). To explain the observed pattern in *P. muralis*, we hypothesized a differential predation exposure by the various colour morphs in different habitats: e.g. the *nigriventris* colour morph would be dominant over the *brueggemanni* one within wooded habitats because the former is more cryptic, that is less exposed to predators; the reverse might be true in wall and bushy pasture habitats. We tested this hypothesis comparing the frequency of occurrence of lizards with intact tail and with broken/regenerated tail. Since in reptiles frequency of tail damage and predation intensity are positively correlated (Capula et al. 1997; Luiselli et al. 2005; Placyk & Burghardt 2005), our assumption was that in inter-morph comparisons for a given habitat type higher percentages of lizards with broken tails would indicate higher risk of predation for a given morph. However, our analysis would not support the differential predation-risk hypothesis, because the frequency of individuals with broken tails was very similar in the three colour morphs among different habitats. The

lack of significance in these analyses may, however, have been caused by the unbalanced, small sample sizes. Indeed, in suboptimal habitats for a certain morph, the number of individuals for that morph was much smaller than that of individuals for the other morph (e.g. in WOOD the sample size for *brueggemanni* was 2 versus 1 of intermediate morph and 114 of *nigriventris*), thus possibly biasing the statistical significance of comparisons. This obviously indicates that further data on several ecological aspects (e.g. thermal and reproductive ecology) are required to explain how the high degree of morphological variation observed in *P. muralis* is maintained by selection for different habitats in the absence of barriers to gene flow between adjacent populations.

References

Andrén C, Nilson G. 1981. Reproductive success and risk of predation in normal and melanistic colour morphs of the adder, *Vipera berus*. Biological Journal of the Linnean Society 15:235–246.

Arnold EN, Ovenden D. 2002. A field guide to the reptiles and amphibians of Britain and Europe. London: Harper Collins.

Camin J, Ehrlich P. 1958. Natural selection in water snakes (*Natrix sipedon* L.) on islands in Lake Erie. Evolution 12:504–511.

Capula M. 1994. Population genetics of a colonizing lizard: Loss of genetic variability in introduced populations of *Podarcis sicula*. Experientia 50:691–696.

Capula M. 1996. Evolutionary genetics of the insular lacertid lizard *Podarcis tiliguerta*: Genetic structure and population heterogeneity in a geographically fragmented species. Heredity 77:518–529.

Capula M. 1997. High genetic variability in insular populations of the lacertid lizard, *Podarcis muralis*. Biochemical Systematics and Ecology 25:411–417.

Capula M. 2000. *Podarcis muralis* (Laurenti, 1768). In: Bologna MA, Capula M, Carpaneto GM, editors. Anfibi e Rettili del Lazio. Roma: Fratelli Palombi Editori. pp. 84–85.

Capula M, Ceccarelli A. 2003. Distribution of genetic variation and taxonomy of insular and mainland populations of the Italian wall lizard, *Podarcis sicula*. Amphibia–Reptilia 24:483–496.

Capula M, Luiselli L. 1994. Reproductive strategies in alpine adders, *Vipera berus*. The black females bear more often. Acta Oecologica 15:207–214.

Capula M, Luiselli L. 1995. Is there a different preference in the choice of background colour between melanistic and cryptically coloured morphs of the adder, *Vipera berus*? Bollettino di Zoologia 62:253–256.

Capula M, Luiselli L, Capanna E. 1997. The blue-spotted morph of the slow worm, *Anguis fragilis*: Colour polymorphism and predation risks. Italian Journal of Zoology 64:147–153.

Caputo V, Giovannotti M, Olmo E. 2008. Refugia-within-refugia: The case of *Podarcis muralis* (Laurenti, 1768) in the Italian Peninsula. Riassunti del 7° Congresso Nazionale della Societas Herpetologica Italica, 1–5 ottobre 2008, Oristano.

Corti C, Lo Cascio P. 2002. The lizards of Italy and adjacent areas. Frankfurt-am-Main: Chimaira Verlag. 165 pp.

Fernandez PJ Jr, Collins JP. 1988. Effect of environment and ontogeny on color pattern variation in Arizona tiger salamanders (*Ambystoma tigrinum nebulosum* Hallowell). Copeia 1988:928–938.

Gotelli NJ, Graves GC. 1996. Null models in ecology. Washington D.C.: Smithsonian Institution Press.

Gruschwitz M, Böhme W. 1986. *Podarcis muralis* (Laurenti, 1768) – Mauereidechse. In: Böhme W, editor. Handbuch der Reptilien und Amphibien Europas. 2/II, Echsen (Sauria) III (Lacertidae III: *Podarcis*). Wiesbaden: Aula. pp. 155–208.

Kjaergaard J. 1981. Udbredelsen af sort hugorm I Danmark. Flora og Fauna (Silkeborg) 87:27–29.

Lopez P, Martin J, Cuadrado M. 2004. The role of lateral blue spots in intrasexual relationships between male Iberian rocklizards, *Lacerta monticola*. Ethology 110:543–561.

Losos JB, Warheit KI, Schoener TW. 1997. Adaptive differentiation following experimental island colonization in *Anolis* lizards. Nature 387:70–73.

Luiselli L. 1992. Reproductive success in melanistic adders: A new hypothesis and some considerations on Andrén and Nilson's (1981) suggestions. Oikos 64:601–604.

Luiselli L, Angelici FM, Di Vittorio M, Spinnato A, Politano E. 2005. Analysis of a herpetofaunal community from an altered marshy area in Sicily; with special remarks on habitat use (niche breadth and overlap), relative abundance of lizards and snakes, and the correlation between predator abundance and tail loss in lizards. Contributions to Zoology 74:41–49.

Luiselli L, Capula M, Rugiero L, Anibaldi C. 1994. Habitat choice by melanistic and cryptically coloured morphs of the adder, *Vipera berus*. Bollettino di Zoologia 61:213–216.

Malhotra A, Thorpe RS. 1991. Experimental detection of rapid evolutionary response in natural lizard populations. Nature 353:347–348.

Martin J, Forsman A. 1999. Social costs and development of nuptial coloration in male *Psammodromus algirus* lizards: An experiment. Behavioural Ecology 10:396–400.

Monney JC, Luiselli L, Capula M. 1995. Correlates of melanism in a population of adders (*Vipera berus*) from the Swiss Alps and comparison with other alpine populations. Amphibia–Reptilia 16:323–330.

Placyk JS Jr, Burghardt GM. 2005. Geographic variation in the frequency of scarring and tail stubs in eastern gartersnakes (*Thamnophis s. sirtalis*) from Michigan, USA. Amphibia–Reptilia 26:353–358.

Sacchi R, Rubolini D, Gentilli A, Pupin F, Razzetti E, Scali S, Galeotti P, Fasola M. 2007. Morph-specific immunity in male *Podarcis muralis*. Amphibia–Reptilia 28:408–412.

Selander RK. 1976. Genic variation in natural populations. In: Ayala FJ, editor. Molecular evolution. Sunderland: Sinauer Associates. pp. 21–45.

Stuart-Fox DM, Firth D, Whiting MJ. 2006. Multiple signals in chameleon contests: Designing and analysing animal contests as a tournament. Animal Behaviour 71:1263–1271.