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Does a polymorphic species have a 'polymorphic' diet? A case study from a lacertid lizard

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Lizards are ideal for studying colour polymorphism, because some species are polymorphic and the morphs often have different ecological or reproductive strategies. We studied the feeding habits of six polymorphic populations of *Podarcis muralis* to test whether morphs differed in their diet. Some taxa were selected in a similar way by all morphs, but selection on other taxa varied and was characteristic of each morph. Diet was most different for the red and yellow morphs. Two hypotheses could explain these differences: active segregation in the trophic niche or active segregation in space dependent on spatial heterogeneity in prey availability. The former is improbable because *P. muralis* is considered an opportunistic feeder, whereas the latter could occur if the morphs adopted alternative territorial strategies with consequent spatial segregation. © 2015 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2015, **00**, 000–000.

ADDITIONAL KEYWORDS: colour polymorphism – feeding habits – *Podarcis muralis* – trophic niche.

INTRODUCTION

Colour polymorphism, i.e. the coexistence in one interbreeding population of two or more distinct and genetically determined colour forms (Huxley, 1955), has attracted increasing interest over the past two decades, particularly with respect to the function of colours and ongoing selection on these traits in the wild (Gray & McKinnon, 2007; McKinnon & Pierotti, 2010; Olsson, Stuart-Fox & Ballen, 2013). Indeed, identifying the processes that lead to the evolution and maintenance of links between colour morphs and behavioural strategies is one of the most interesting topics in evolutionary biology (Gray & McKinnon, 2007), due to implications to the maintenance of genetic variation and the evolution of reproductive isolation and speciation processes (West-Eberhard, 1989; Pryke & Griffith, 2006; McKinnon & Pierotti, 2010). There is general agreement that the occurrence in the same population of different morphs reveals the occurrence of alternative ecological and reproductive strategies, which involve complex combinations of behavioural, morphological, physiological and life-history characteristics (Sinervo & Lively, 1996; Svensson, Sinervo & Comendant, 2001; Sacchi *et al.*, 2007a, 2009, 2015).

Lizards offer an ideal model to investigate the relationships between colour polymorphism and the ecological processes undergoing morph evolution and maintenance, as some lizard species show a significant colour polymorphism, such as *Urosaurus ornatus* (Thompson & Moore, 1991), *Uta stansburiana* (Sinervo & Lively, 1996), *Podarcis melisellensis* (Huyghe *et al.*, 2007), *Podarcis muralis* (Sacchi *et al.*, 2007b) and *Quedenfeldtia trachyblepharus* (Blouin-Demers *et al.*, 2013). Colour polymorphism

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*Corresponding author. E-mail: stefano.scali@comune.milano.it in those lizards has been shown to relate to alternative reproductive strategies (Sinervo & Lively, 1996; Zamudio & Sinervo, 2000, 2003; Galeotti *et al.*, 2013; Olsson *et al.*, 2013) that lead to different exploitation of available resources in heterogeneous habitats (Zamudio & Sinervo, 2003), even if contrasting data were obtained for some species (Huyghe *et al.*, 2007). Colour polymorphism has been also related to predation avoidance (Capula, Rugiero & Luiselli, 2009; Ortega, López & Martín, 2014). Surprisingly, very few studies have analysed the relationship between feeding habits and colour polymorphism (Huyghe *et al.*, 2007) although the alternative strategies adopted by morphs may be expected to have some effect on prey selection and diet composition (Roulin, 2004). This kind of information is needed, as some mechanisms driving the evolution and maintenance of colour polymorphism rely on habitat heterogeneity (Thompson & Moore, 1991; McLean & Stuart-Fox, 2014), which may be directly related to trophic heterogeneity among morphs. Indeed, if morphs differently exploit available microhabitats, they could differently access trophic resources causing divergences in diets.

The feeding habits of European lacertid lizards are well known (Di Palma, 1984; Arnold, 1987; Castilla *et al.*, 1989; Avery, Basker & Corti, 1993; Avery & Tosini, 1995; Angelici, Luiselli & Rugiero, 1997; Gvozdik & Boukal, 1998; Verwaijen & Van Damme, 2008). Lacertid lizards have often been regarded as opportunistic feeders (Mou & Barbault, 1986; Carretero & Llorente, 1991), although several studies based on sampling of prey availability contrasted this opinion and suggested that prey choices might depend on prey size, season, nutrient constraints, predation risk or body temperature (Mou, 1987; Díaz, 1995; Carretero, 2004).

Podarcis muralis (Laurenti, 1768) (common wall lizard) is a medium-sized lacertid, occurring in many south-western European countries (Sillero *et al.*, 2014), that shows a high ecological plasticity that allows the colonization of many different habitats, from urban areas to natural environments, including cultivated areas. The species exhibits a striking colour polymorphism, with three syntopic morphs that differ in throat and belly colorations (white, yellow and red) (Sacchi *et al.*, 2013a, b). They also show differences in body size, parasite load, immunological response, femoral gland secretions and homing behaviour (Sacchi *et al.*, 2007a, b; Calsbeek, Hasselquist & Clobert, 2010; Scali *et al.*, 2013; Pellitteri Rosa *et al.*, 2014). Previous studies have demonstrated that colour polymorphism of this species is associated with alternative reproductive strategies (Galeotti *et al.*, 2013) and that all the traits listed above could be correlated with reproduction. Interestingly, the relationship between polymorphism and the ecology of the common wall lizard remains largely understudied. The trophic ecology of common wall lizards has been extensively studied since the 1980s in France, Italy and Spain (Avery, 1978; Mou & Barbault, 1986; Mou, 1987; Avery *et al.*, 1993; Scali *et al.*, 2008; Verwaijen & Van Damme, 2008; Biaggini *et al.*, 2011) and all studies describe it as a generalist predator.

In this study, we compared the diet of the three morphs of *Podarcis muralis* in six polymorphic populations from northern Italy to assess if feeding habits differ among morphs. Specifically, we hypothesized that the three morphs of *P. muralis* would show differential resource use irrespective of site features, as morphs are thought to represent alternative ecological optima.

MATERIAL AND METHODS

STUDY AREA

Data were collected in six sites in Lombardy (northern Italy) from 2005 to 2006, which included one anthropic and five agricultural sites, briefly described below (see also Table 1).

Site A

The Borromeo Park (CSM) is an urban garden in the Municipality of Cesano Maderno, near Milan. It is an anthropogenic habitat in the centre of the town and it is used by citizens for recreational activities. The park is surrounded by a brick wall with many refuges suitable for lizards; in this study we considered only the inner southward face (500 m long and 3.5 m high) and a poplar tree-line facing the wall.

Table 1. List and location of study areas

Site ID	Altitude (m a.s.l.)	Extension (ha)	Coordinates
CSM	200	0.20	UTM 32T 511782E, 5052935N
CMG	60	2.77	UTM 32T 507032E, 5003401N
CAN	80	6.09	UTM 32T 514492E, 5006360N
SET	80	1.95	UTM 32T 517137E, 5011521N
BRU	60	4.19	UTM 32T 507998E, 5003675N
COR	80	5.11	UTM 32T 517653E, 5010265N

Sites B–F

Campomaggiore (CMG), Cantugno (CAN), Settimo (SET), Brunoria (BRU) and Corbesate (COR) are farms, located near the city of Pavia, characterized by houses, barns, cattlesheds and scattered trees and surrounded by rice fields. Some features vary among the farms (e.g. building sizes, dunghill extension, number of cattle) and this could cause some differences in the availability of invertebrates.

All the populations are polymorphic, and the three morphs are syntopic in each site (see Sacchi *et al.*, 2007b for details).

FIELD AND LABORATORY TECHNIQUES

Lizards were caught by noose and they often defecated following capture. Faeces were collected and preserved in 70% alcohol. The analysis of faecal pellets for the study of lizard feeding habits is widely used and considered to be fully reliable by most authors (Angelici *et al.*, 1997; Pérez-Mellado *et al.*, 2011). However, other authors suggest that faecal analysis underestimates soft-bodied organisms, which are almost completely destroyed by digestive processes (Pincheira-Donoso, 2008). This kind of bias could lead to an underestimation of the trophic niche width of morphs, but it is unlikely to affect the differences among their niches. For each individual we recorded date, site, sex, snout–vent length (SVL), and morph coded as white, yellow or red according to throat and belly coloration (Sacchi *et al.*, 2013a, b). All the lizards were released at the capture site after measuring and after being marked with dorsal paintings; they were also photographed for individual recognition during the short period to avoid pseudoreplication (Sacchi *et al.*, 2010). The faeces were dissolved in a Petri dish to separate all the prey items, which were identified using a stereomicroscope by one of the authors (MP), who is an expert entomologist. Prey items were recognized at the lowest taxonomic level, but were grouped at the order level for statistical analyses. Overall, we collected data from 249 lizards, including 121 faeces from the white morph (99 males and 22 females), 87 faeces from the yellow morph (64 males and 23 females), and 41 faeces from the red morph (38 males and three females) (Data S1). The number of individuals for morph and site is summarized in Table 2.

Table 2. Number of individuals for each morph and each site

Morph	CMG	SET	BRU	CAN	COR	CSM	Total
White	15	14	22	6	15	49	121
Yellow	5	14	5	4	35	24	87
Red	1	13	2	2	12	11	41
Total	21	41	29	12	62	84	249

STATISTICAL ANALYSES

A summary of prey items found in the faeces was made reporting the number and percentage of individuals for each site. A preliminary analysis using Pianka’s symmetric index (Pianka, 1974a, b) was conducted to verify the similarity of males’ and females’ diet. The overlap for the whole sample was very high ($O_{jk} = 0.97$) and a randomization test confirmed that the probability of observing values lower than 0.97 was 0.232 (permutations = 999). The samples from both sexes were therefore combined for all the subsequent analyses to improve the statistical power.

Niche breadth was calculated for all the morphs using the Shannon–Weaver index (Shannon & Weaver, 1949) and niche overlap among morphs was estimated using Pianka’s symmetric index. These indices were calculated under the R statistical environment (R Development Core Team, 2012) with the package ‘pgirmess’ (Giraudoux, 2014). Diet similarity among morphs was estimated by means of a correspondence analysis (CA), using the R package ‘ca’ (Nenadic & Greenacre, 2007).

To assess if diet similarity between sites was correlated with morph composition of different populations, we first computed a distance matrix among sites according to morph frequencies in both sexes using a Euclidean distance, and then performed a Mantel test to correlate this matrix with that of prey distance among sites. A partial Mantel test was also used to control for the effects of geographical distances on the correlation between diet and morph composition matrices. The Mantel tests were performed using the R package ‘vegan’ rel. 2.0-10 (Oksanen *et al.*, 2013).

Differences in prey item use among morphs were also assessed using compositional analysis (Aebischer, Robertson & Kenward, 1993), which was originally designed to compare a matrix of habitat use with a matrix of habitat availability to detect if a given species uses the habitats differentially from availability. Habitats are disposed in a ranking matrix that orders them from the most to the least preferred. Compositional analysis, however, has also been used to investigate components other than habitats, such as prey or behavioural displays (Aebischer *et al.*, 1993; Sacchi *et al.*, 2013a, b). A further application of compositional analysis is when investigators are interested in the relative differences occurring in one species with respect to another. In this case the analysis compares the matrix of component use by the first species with the mean frequencies of component use by all individuals of the second species (Sacchi *et al.*, 2013a, b). The resulting ranking matrix arranges the component according to the use by the first species relative to the second species, from the relatively more to the relatively less used. We followed this last procedure to compare the resource use by a morph relative to that of the other two and to identify differences in feeding habits among morphs. The matrices of diet composition for each morph were compiled and used to establish resources use; then, prey availability for each morph was calculated independently using diet composition of the two other morphs (i.e. the mean frequencies of resource use by all individuals of the other morphs). To account for sites, the resource use matrix of a morph was compared with the resource use by the other morphs computed within the same site. This way of estimating resource availability is considered superior to other methods in more direct but less unbiased ways (Winemiller & Pianka, 1990). Minor prey categories (fewer than ten specimens) were grouped for the analysis in a group called 'Other'. All three possible paired comparisons within sex were assessed (white morph vs. both yellow and red morphs; yellow morph vs. both white and red morphs; and red morph vs. both white and yellow morphs). Wilk's lambda determined by randomization tests (number of permutations = 500) was used to assess the significance of the ranking matrices (Aebischer *et al.*, 1993), and analyses were performed using the R package 'adehabitatHS' (Calenge, 2013).

RESULTS

PREY SPECTRUM

An overall sample of 1468 prey items was obtained from the six sites and the prey spectrum for each one is summarized in Table 3. Hemiptera constituted the most important category (21.80%), followed by Hymenoptera (21.59%), Coleoptera (21.46%) and Araneae (11.17%). The relative importance of different taxa changed among sites: Hymenoptera were the main prey taxa at CSM, substituted by Hemiptera at CMG, SET and BRU, by Coleoptera at CAN, and by Diptera at COR ($\chi^2 = 315.56$; d.f. = 25; $P < 0.001$).

NICHE BREADTH AND OVERLAP

Shannon's diversity indices calculated for the whole sample were similar for the three morphs ($H_w = 2.85$; $H_y = 2.78$; $H_r = 2.87$; one-way ANOVA: $F_{2,15} = 1.794$, $P = 0.20$).

A higher variability was found in niche overlap, with a maximum value for the overlap between white and red lizards ($O_{jk} = 0.94$), an intermediate value for white/yellow lizards ($O_{jk} = 0.85$), and a minimum overlap between red and yellow lizards ($O_{jk} = 0.74$).

The CA used to evaluate the affinities among morphs separated the three groups quite well: white lizards were associated mainly with Coleoptera, Dermaptera, Lepidoptera and Mecoptera; yellow lizards were associated with Orthoptera, Hymenoptera and Diptera; and red lizards were associated with Psocoptera, Araneae and plants (mainly *Rubus* sp. fruits). The scores of the first and second components, explaining respectively 67.95 and 32.05% of variance, are shown in Figure 1.

SITE AND MORPH COMPARISON

Three distance matrices were calculated respectively for diet composition, morph composition and geographical distance among sites (Table 4). They were used to evaluate the correlation between diet and morph, controlling for geographical position using a partial Mantel test and the correlation was significant ($r = 0.5264$; $P < 0.05$).

The analysis highlighted a significant difference in prey composition based on morph composition and a compositional analysis was applied to the data to verify which kind of prey were more frequently consumed by each morph. The results were significant (white: Lambda = 0.2838, $P < 0.01$; yellow: Lambda = 0.4403, $P < 0.01$; red: Lambda = 0.4176, $P < 0.01$), confirming the differences in diet among morphs. The simplified ranking matrices of resource use for each morph are reported in Table 5. Many differences can be observed in the relative use of prey taxa: (1) white lizards consumed proportionally more Lepidoptera, Coleoptera and Diptera than the other morphs, (2) yellow lizards preyed more upon Orthoptera, and to a lesser extent Araneae, and (3) red lizards ate more Dermaptera and plants.

DISCUSSION

It is widely accepted that lacertid lizards are opportunistic feeders (Mou & Barbault, 1986; Arnold, 1987; Carretero & Llorente, 1991) and this is probably true as a general rule, although there are different opinions (Mou, 1987; Díaz, 1995; Carretero, 2004). Our data supported the former theory. In particular, we found that the diet of *P. muralis* at each site examined comprised a wide range of prey, with the most common terrestrial taxa being Hemiptera, Hymenoptera, Coleoptera and Araneae. Their relative importance varied among sites, and this could reflect their relative abundance at the sites, although

Table 3. Number of faeces analysed for each site and diet composition of all the studied populations summarized by prey frequency and abundance (percentage of a given prey item relative to the total number of prey items, in parentheses)

Taxa	CSM (*N* = 84)	CMG (*N* = 21)	CAN (*N* = 12)	SET (*N* = 41)	BRU (*N* = 29)	COR (*N* = 62)	Total (*N* = 249)
Plant	27	3	1	10	8	23	72
	3.73%	2.33%	1.49%	6.58%	8.89%	7.49%	4.90%
Arachnida	65	27	12	17	11	32	164
	8.99%	20.93%	17.91%	11.18%	12.22%	10.42%	11.17%
Chilopoda	2	0	0	0	0	0	2
	0.28%	0.00%	0.00%	0.00%	0.00%	0.00%	0.14%
Coleoptera	170	25	16	38	25	41	315
	23.51%	19.38	23.88%	25.00%	27.78	13.36%	21.46%
Diptera	16	2	3	16	10	97	144
	2.21%	1.55%	4.48%	10.53%	11.11%	31.60%	9.81%
Hymenoptera	204	17	8	10	10	68	317
	28.22%	13.18%	11.94%	6.58%	11.11%	22.15%	21.59%
Lepidoptera	3	3	6	1	2	3	18
	0.41%	2.33%	8.96%	0.66%	2.22%	0.98%	1.23%
Orthoptera	5	0	0	1	1	0	7
	0.69%	0.00%	0.00%	0.66%	1.11%	0.00%	0.48%
Dermaptera	52	10	4	6	0	1	73
	7.19%	7.75%	5.97%	3.95%	0.00%	0.33%	4.97%
Collembola	6	0	0	0	0	0	6
	0.83%	0.00%	0.00%	0.00%	0.00%	0.00%	0.41%
Raphidioptera	1	0	0	0	0	0	1
	0.14%	0.00%	0.00%	0.00%	0.00%	0.00%	0.07%
Neuroptera	1	0	0	0	0	0	1
	0.14%	0.00%	0.00%	0.00%	0.00%	0.00%	0.07%
Mecoptera	0	0	1	0	8	0	9
	0.00%	0.00%	1.49%	0.00%	8.89%	0.00%	0.61%
Psocoptera	0	2	2	2	0	4	10
	0.00%	1.55%	2.99%	1.32%	0.00%	1.30%	0.68%
Thysanoptera	0	0	1	0	0	0	1
	0.00%	0.00%	1.49%	0.00%	0.00%	0.00%	0.07%
Hemiptera	167	39	12	50	14	38	320
	23.10%	30.23%	17.91%	32.89%	15.56%	12.38%	21.80%
Insecta n.d.	4	0	0	1	1	0	6
	0.55%	0.00%	0.00%	0.66%	1.11%	0.00%	0.41%
Gastropoda	0	1	1	0	0	0	2
	0.00%	0.78%	1.49%	0.00%	0.00%	0.00%	0.14%
Total no.	723	129	67	152	90	307	1468

we do not have detailed information regarding this (e.g. the massive dunghills occurring in COR attracted many flies – family Muscidae – that were the main prey taxon in that study area).

The most interesting result is the different feeding habits of the three morphs. This result does not emerge from the niche breadth indices, which were very similar among white, yellow and red lizards, but rather from differences in the overlap indices. In fact, they highlighted an almost complete overlap between white and red morphs, whereas the similarity decreased when white/yellow and red/yellow pairs of morphs were compared. The correlation between some prey taxa and morphs was confirmed also by the correspondence analysis, which clearly confirmed the segregation of the three morphs in the trophic niche.

Further confirmation came from direct comparison of the morphs’ diet composition via the compositional analysis. The proportional use of some prey taxa, such as Orthoptera, Diptera, Coleoptera, Lepidoptera, Dermaptera and plants, differed widely among morphs. We can reliably exclude the possibility that the observed patterns arise from among-site variability in prey availability because (1) morphs are strictly

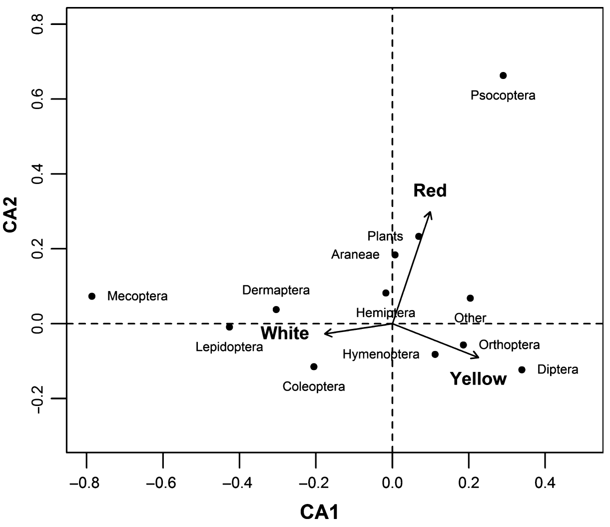

Figure 1. Results of the correspondence analysis for diet composition and morphs.

Table 4. Matrix distance between sites based on prey composition (Prey), morph frequency composition (i.e. number of individuals assigned to white, red and yellow morphs) (Morph), and geographical distances (km) among study sites

	Distance	CSM	CMG	CAN	SET	BRU
CMG	Prey	0.57				
	Morph	0.40				
	km	49.76				
CAN	Prey	0.42	0.66			
	Morph	0.25	0.67			
	km	46.65	8.03			
SET	Prey	0.46	0.71	0.25		
	Morph	0.62	0.65	0.45		
	km	41.76	12.96	5.8		
BRU	Prey	0.69	0.85	0.46	0.38	
	Morph	0.51	0.84	0.59	0.60	
	km	49.91	1.00	7.03	12.04	
COR	Prey	0.60	0.80	0.33	0.39	0.31
	Morph	0.68	0.51	0.32	0.78	0.48
	km	43.07	12.65	5.02	1.36	11.69

syntopic, so within-site prey availability is the same for all morphs, and (2) all the analyses were conducted comparing morphs within a site. A cautionary approach should be adopted for the outcome of the red morph, because of the small sample size from some sites. Nevertheless, our analyses clearly support the occurrence of different prey exploitations among morphs, at least for yellow and white lizards.

Two hypotheses can be proposed to explain the differences in feeding habits among morphs: an active segregation in the trophic niche or an active segregation in space with spatial heterogeneity in prey availability. The first hypothesis assumes that each morph evolved a specific preference for certain kind of prey taxa, only partially shared by other morphs. Such a pattern is quite common in animals and often evolves in response to a high level of competition for food (Huyghe *et al.*, 2007; but see Sinervo, 1997 for a review). Segregation in the trophic niche in fact reduces competition for resources, thus promoting coexistence in the same locality (Pianka, 1974b). For instance, sexual size dimorphism in reptiles frequently evolves through such segregation between sexes (Parker & Pianka, 1975; Carretero, 2004; Vincent & Herrel, 2007; Amat *et al.*, 2008). Moreover, previous studies have demonstrated the occurrence of morphological differences among morphs of a polymorphic lizard, particularly in head morphology, with consequent differences in bite force that are probably associated with the choice of harder or softer prey (Huyghe *et al.*, 2007, 2009). However, the common wall lizard is an opportunistic feeder (Avery, 1978; Mou & Barbault, 1986; Mou, 1987; Biaggini *et al.*, 2011), and our data as well as the literature did not reveal any kind of specialization. We therefore regard this hypothesis as not realistic for the common wall lizard, although we cannot exclude that some degree of specialization could occur at levels lower than that of the species.

The second hypothesis assumes that diet differences among morphs are not a consequence of feeding behaviour, but rather of differences in the spatial distribution of morphs linked to habitat heterogeneity. Previous studies of polymorphic species have shown that male morphs might adopt alternative territorial strategies, implying different kinds of movement and spatial distribution of individuals. For instance, the three morphs of male side-blotched lizards (*Uta stansburiana*) follow three different strategies; individuals of one morph defend their territories whereas the other two are mate-guarders or sneakers (Zamudio & Sinervo, 2003). Consequently, the three morphs move around and also spread out differently, using different habitats. The occurrence of such alternative territorial strategies has not been yet demonstrated in *Podarcis muralis* as clearly as in *Uta stansburiana*. However, some indication that morphs do not share a unique strategy has been found (Sacchi *et al.*, 2007a; Scali *et al.*, 2013) and homing ability has been shown to be morph-specific, which suggests that each morph might keep a different connection with the territory (Scali *et al.*, 2013). Consequently, each morph might prevail over the others in different habitats, leading to habitat partitioning and consequently to different prey availability and exploitation. Roulin (2004) argued that a

Table 5. Simplified ranking matrices of resource use for each morph

	Orthoptera	Lepidoptera	Coleoptera	Diptera	Hemiptera	Dermaptera	Araneae	Hymenoptera	Plants	Other	Rank
White											
Orthoptera	0	+	+	+	+++	+++	+++	+++	+++	+++	9
Lepidoptera	–	0	+	+	+	+++	+++	+++	+++	+++	8
Coleoptera	–	–	0	+	+	+	+	+	+++	+++	7
Diptera	–	–	–	0	+	+	+	+	+++	+++	6
Hemiptera	–	–	–	–	0	+	+	+	+++	+++	5
Dermaptera	–	–	–	–	–	0	+	+	+++	+++	4
Araneae	–	–	–	–	–	–	0	+	+++	+++	3
Hymenoptera	–	–	–	–	–	–	–	0	+	+++	2
Plants	–	–	–	–	–	–	–	–	0	+++	1
Other	–	–	–	–	–	–	–	–	–	0	0

	Orthoptera	Hemiptera	Hymenoptera	Diptera	Coleoptera	Araneae	Other	Dermaptera	Plants	Lepidoptera	Rank
Yellow											
Orthoptera	0	+++	+++	+++	+++	+++	+++	+++	+++	+++	9
Hemiptera	–	0	+	+	+	+	+++	+++	+++	+++	8
Hymenoptera	–	–	0	+	+	+	+	+++	+++	+++	7
Diptera	–	–	–	0	+	+	+	+++	+++	+++	6
Coleoptera	–	–	–	–	0	+	+	+	+	+++	5
Araneae	–	–	–	–	–	0	+	+	+	+++	4
Other	–	–	–	–	–	–	0	+	+	+	3
Dermaptera	–	–	–	–	–	–	–	0	+	+	2
Plants	–	–	–	–	–	–	–	–	0	+	1
Lepidoptera	–	–	–	–	–	–	–	–	–	0	0

	Orthoptera	Dermaptera	Plants	Hemiptera	Hymenoptera	Lepidoptera	Araneae	Other	Coleoptera	Diptera	Rank
Red											
Orthoptera	0	+	+++	+++	+++	+++	+++	+++	+++	+++	9
Dermaptera	–	0	+	+	+	+++	+++	+++	+++	+++	8
Plants	–	–	0	+	+	+	+	+	+++	+++	7
Hemiptera	–	–	–	0	+	+	+	+	+	+	6
Hymenoptera	–	–	–	–	0	+	+	+	+	+	5
Lepidoptera	–	–	–	–	–	0	+	+	+	+	4

Table 5. *Continued*

	Orthoptera	Dermaptera	Plants	Hemiptera	Hymenoptera	Lepidoptera	Araneae	Other	Coleoptera	Diptera	Rank
Araneae	−	−	−	−	−	−	0	+	+	+	3
Other	−	−	−	−	−	−	−	0	+	+	2
Coleoptera	−	−	−	−	−	−	−	−	0	+	1
Diptera	−	−	−	−	−	−	−	−	−	0	0

Prey taxa are sorted so that the left type is the most preferred and the right type is the most avoided. Prey taxa for which the intensity of selection is similar (no significant difference) are highlighted in grey. The signs '+' and '−' indicate a proportional use of a resource greater and smaller than the resource in a column. The triple signs represent significant deviation from random at $P < 0.05$ (Aebischer *et al.*, 1993). The rank column reports the relative ranking of each resource for each morph.

similar mechanism could have caused a trophic specialization of morphs in barn owls *Tyto alba*, thanks to different conspicuousness to some prey taxa. In agreement with this hypothesis, chemical polymorphism in male femoral gland secretions has been recently shown to match polymorphic coloration in *P. muralis* (Pellitteri Rosa *et al.*, 2014). Diet influences femoral gland secretions and lizards are known to allocate steroids from the diet (e.g. vitamin E in *Lacerta schreiberi*; Kopena, López & Martín, 2014). Therefore, differentiation among chemical cues might be the result of trophic niche segregation, which in turn could be the outcome of the adoption of alternative reproductive strategies.

Different patterns of spatial distribution could also be explained by the evolution of distinct physiological optima among morphs (Calsbeek *et al.*, 2010). In some species individuals belonging to various morphs have been shown to have specific microclimatic needs to optimize their physiological efficiency and thus segregate in different microhabitats. Such segregation could lead them to feed on different prey. An example of the influence of climatic parameters in polymorphic lizards comes from a previous study on *Zootoca vivipara*, in which the frequency of morphs varied according to a warming trend and, even if the underlying mechanisms remain unexplained, they are thought to be correlated to physiological optima (Lepetz *et al.*, 2009). Furthermore, climatic conditions directly affect physiological parameters, such as hormonal concentrations in blood, inducing lizard morphs to change their territorial behaviour and causing spatial segregation, as in *Urosaurus ornatus* (Knapp *et al.*, 2003). Previous studies demonstrated significant differences in immunological response (Sacchi *et al.*, 2007a) and homing behaviour (Scali *et al.*, 2013) among ventral morphs of *P. muralis* that seem to endorse the occurrence of alternative territorial strategies. Furthermore, preliminary data seem to confirm the occurrence of a certain degree of habitat partitioning, probably correlated with habitat thermal stability (Mangiacotti *et al.*, 2015). That correlation could be a possible explanation for differential prey availability and feeding differences among morphs.

Many authors have demonstrated ethological and physiological differences among morphs in polymorphic lizards, but these were always correlated with reproductive behaviours or with escape behaviour. For example, colour morphs adopt alternative reproductive strategies in some lizard species (Comendant *et al.*, 2003; Zamudio & Sinervo, 2003; Huyghe *et al.*, 2007; Vercken *et al.*, 2007), but they may also differ in immunological response (Sacchi *et al.*, 2007a; Calsbeek *et al.*, 2010; Huyghe *et al.*, 2010), survival (Calsbeek *et al.*, 2010; Paemelaere, Guyer & Dobson, 2011), health and parasite load (Calsbeek *et al.*, 2010; Huyghe *et al.*, 2010), morphology (Calsbeek *et al.*, 2010), mating patterns (Pérez i de Lanuza, Font & Carazo, 2012), fitness (Galeotti *et al.*, 2013) and mate choice (Healey, Uller & Olsson, 2008). Sometimes polymorphism could be correlated with anti-predatory behaviour, as in *Podarcis hispanicus*, where escape strategies are influenced by the interactions between dorsal patterns, size and tail conspicuousness (Ortega *et al.*, 2014).

Our study is one of the first to show that ecological differences, not correlated with reproductive behaviour or escape behaviour, can also occur in polymorphic lizards. Some ecological traits not related to reproduction in a polymorphic snake (*Python brongersmai*), including feeding and parasite loads, were described by Shine *et al.* (1998) and also in this case the authors hypothesized that they probably depended on the divergence of a single aspect such as habitat selection. This assumption is confirmed by bibliographic data that demonstrate that polymorphic species are often able to utilize a diverse range of habitats because different morphs are often adapted to different microhabitats (McLean & Stuart-Fox, 2014).

In conclusion, our study confirmed the high trophic plasticity of the common wall lizard, but it showed that many factors can affect diet composition, including polymorphism. This aspect is particularly intriguing, because it demonstrates that the evolution of colour polymorphism could be correlated with many biological features, not only linked to reproduction. It is often difficult to disentangle the effects of such features, so additional in-depth studies would be desirable to investigate some aspects such as thermal ecology or microhabitat selection of morphs.

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REFERENCES

Aebischer NJ, Robertson PA, Kenward RE. 1993. Compositional analysis of habitat use from animal radio-tracking data. *Ecology* **74:** 1313–1325.

Amat F, Pérez-Mellado V, Hernández-Estévez JA, García DT. 2008. Dietary strategy of a Pyrenean lizard, *Iberolacerta aurelioi*, living in a poor resources alpine environment. *Amphibia-Reptilia* **29:** 329–336.

Angelici FM, Luiselli L, Rugiero L. 1997. Food habits of the green lizard, *Lacerta bilineata*, in central Italy and a reliability test of faecal pellet analysis. *Italian Journal of Zoology* **64:** 267–272.

Arnold EN. 1987. Resource partition among lacertid lizards in southern Europe. *Journal of Zoology of London (B)* **1:** 739–782.

Avery RA. 1978. Activity patterns, thermoregulation and food consumption in two sympatric lizard species (*Podarcis muralis* and *Podarcis sicula*) from central Italy. *Journal of Animal Ecology* **47:** 143–158.

Avery R, Tosini G. 1995. Dynamics of predation in Lacertidae: the relation between locomotor pattern and prey-capture probability in three contrasted species. *Amphibia-Reptilia* **16:** 1–10.

Avery R, Basker A, Corti C. 1993. ‘Scan’ behaviour in *Podarcis muralis*: the use of vantage points by an actively foraging lizard. *Amphibia-Reptilia* **14:** 247–259.

Biaggini M, Bombi P, Capula M, Corti C. 2011. *Podarcis muralis* (Laurenti, 1768). In: Corti M, Capula M, Luiselli L, Razzetti E, Sindaco R, eds. *Fauna d'Italia. Reptilia*. Bologna: Calderini, 391–401.

Blouin-Demers G, Lourdais O, Bouazza A, Verreault C, El Mouden H, Slimani T. 2013. Patterns of throat colour variation in *Quedenfeldtia trachyblepharus*, a high-altitude gecko endemic to the High Atlas Mountains of Morocco. *Amphibia-Reptilia* **34:** 567–572.

Calenge C. 2013. *Package ‘adehabitatHS’ ver. 0.3.9*. Available at: https://trac.faunalia.it/animove/

Calsbeek B, Hasselquist D, Clobert J. 2010. Multivariate phenotypes and the potential for alternative phenotypic optima in wall lizard (*Podarcis muralis*) ventral colour morphs. *Journal of Evolutionary Biology* **23:** 1138–1147.

Capula M, Rugiero L, Luiselli L. 2009. Ecological correlates of colour pattern polymorphism along the transition zone between two morphs of the common wall lizard, *Podarcis muralis*. *Italian Journal of Zoology* **76:** 376–380.

Carretero MA. 2004. From set menu to a la carte. Linking issues in trophic ecology of Mediterranean lacertids. *Italian Journal of Zoology* **71**(Suppl. 2)**:** 121–133.

Carretero MA, Llorente GA. 1991. Alimentación de *Psammodromus hispanicus* en un arenal costero del noreste ibérico. *Revista Española de Herpetologia* **6:** 31–44.

Castilla AM, Bauwens D, Van Damme R, Verheyen RF. 1989. Notes on the biology of the high altitude lizard *Lacerta bedriagae*. *Herpetological Journal* **1:** 400–403.

Comendant T, Sinervo B, Svensson EI, Wingfield J. 2003. Social competition, corticosterone and survival in female lizard morphs. *Journal of Evolutionary Biology* **16:** 948–955.

Di Palma MG. 1984. Regime alimentaire de *Psammodromus algirus* (Reptilia Lacertidae) dans une population insulaire du Canal de Sicilie. *Revue d'Ecologie (Terre Vie), Paris* **39:** 225–230.

Díaz JA. 1995. Prey selection by lacertid lizards: a short review. *Herpetological Journal* **5:** 245–251.

Galeotti P, Sacchi R, Pellitteri-Rosa D, Bellati A, Cocca W, Gentilli A, Scali S, Fasola M. 2013. Colour polymorphism and alternative breeding strategies: effects of parent's colour morph on fitness traits in the common wall lizard. *Evolutionary Biology* **40:** 385–394.

Giraudoux P. 2014. *pgirmess: Data analysis in ecology. 1.5.9*. Available at: http://perso.orange.fr/giraudoux

Gray SM, McKinnon JS. 2007. Linking color polymorphism maintenance and speciation. *Trends in Ecology & Evolution* **22:** 71–79.

Gvozdik L, Boukal M. 1998. Sexual dimorphism and intersexual food niche overlap in the sand lizard, *Lacerta agilis* (Squamata: Lacertidae). *Folia Zoologica* **47:** 189–195.

Healey M, Uller T, Olsson J. 2008. Variety is the spice of life: female lizards choose to associate with colour-polymorphic male dyads. *Ethology* **114:** 231–237.

Huxley J. 1955. Morphism in birds. *Acta International Congress of Ornithology*. **111:** 309–328.

Huyghe K, Vanhooydonck B, Herrel A, Tadic Z, Van Damme R. 2007. Morphology, performance, behavior and ecology of three color morphs in males of the lizard *Podarcis melisellensis*. *Integrative and Comparative Biology* **47:** 211–220.

Huyghe K, Husak JF, Herrel A, Tadić Z, Moore IT, Van Damme R, Vanhooydonck B. 2009. Relationships between hormones, physiological performance and immunocompetence in a color-polymorphic lizard species, *Podarcis melisellensis*. *Hormones and Behavior* **55:** 488–494.

Huyghe K, Van Oystaeyen A, Pasmans F, Tadić Z, Vanhooydonck B, Van Damme R. 2010. Seasonal changes in parasite load and a cellular immune response in a colour polymorphic lizard. *Oecologia* **163:** 867–974.

Knapp R, Hews DK, Thompson CW, Ray LE, Moore MC. 2003. Environmental and endocrine correlates of tactic switching by nonterritorial male tree lizards (*Urosaurus ornatus*). *Hormones and Behavior* **43:** 83–92.

Kopena R, López P, Martín J. 2014. Relative contribution of dietary carotenoids and vitamin E to visual and sexual signals of male Iberian green lizards: an experimental test. *Behavioral Ecology and Sociobiology* **68:** 571–581.

Lepetz V, Massot M, Chaine AS, Clobert J. 2009. Climate warming and the evolution of morphotypes in a reptile. *Global Change Biology* **15:** 454–466.

Mangiacotti M, Falaschi M, Scali S, Sannolo M, Sacchi R. 2015. Differenze di nicchia termica tra i morfi cromatici di *Podarcis muralis*. In: Doria G, Poggi R, Salvidio S, Tavano M, eds. *Atti X Congresso Nazionale della Societas Herpetologica Italica (Genova 15–18 October 2014)*. Pescara: Ianieri Edizioni, 115–116.

McKinnon JS, Pierotti ME. 2010. Colour polymorphism and correlated characters: genetic mechanisms and evolution. *Molecular Ecology* **19:** 5101–5125.

McLean CA, Stuart-Fox D. 2014. Geographic variation in animal colour polymorphisms and its role in speciation. *Biological Review* **89:** 860–873.

Mou YP. 1987. Ecologie trophique d'une population de lézards des murailles *Podarcis muralis* dans l'ouest de la France. *Revue d'Ecologie (Terre Vie), Paris* **42:** 81–100.

Mou YP, Barbault R. 1986. Regime alimentaire d'une population de Lézard des Murailles, *Podarcis muralis* (Laurenti, 1768) dans le Sud-Ouest de la France. *Amphibia-Reptilia* **7:** 171–180.

Nenadic O, Greenacre M. 2007. Correspondence analysis in R, with two- and three-dimensional graphics: the ca package. *Journal of Statistical Software* **20:** 1–13.

Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHM, Wagner H. 2013. *vegan: Community Ecology Package. R package version 2.0-10*. Available at: http://CRAN.R-project.org/package=vegan

Olsson M, Stuart-Fox D, Ballen C. 2013. Genetics and evolution of colour patterns in reptiles. *Seminars in Cell & Developmental Biology* **24:** 529–541.

Ortega J, López P, Martín J. 2014. Conspicuous blue tails, dorsal pattern morphs and escape behavior in hatchling Iberian wall lizards (*Podarcis hispanicus*). *Biological Journal of the Linnean Society* **113:** 1094–1106.

Paemelaere EAD, Guyer C, Dobson FS. 2011. Survival of alternative dorsal-pattern morphs in females of the anole *Norops humilis*. *Herpetologica* **67:** 420–427.

Parker WS, Pianka ER. 1975. Comparative ecology of populations of the lizard *Uta stansburiana*. *Copeia* **1975:** 615–632.

Pellitteri Rosa D, Martin J, Lopez P, Bellati A, Sacchi R, Fasola M, Galeotti P. 2014. Chemical polymorphism in male femoral gland secretions matches polymorphic coloration in common wall lizards (*Podarcis muralis*). *Chemoecology* **24:** 67–78.

Pérez i de Lanuza G, Font E, Carazo P. 2012. Color-assortative mating in a color-polymorphic lacertid lizard. *Behavioral Ecology* **24:** 273–279.

Pérez-Mellado V, Pérez-Cembranos A, Garrido M, Luiselli L, Corti C. 2011. Using faecal samples in lizard dietary studies. *Amphibia-Reptilia* **32:** 1–7.

Pianka E. 1974a. The structure of lizard communities. *Annual Review of Ecology and Systematics* **4:** 53–74.

Pianka E. 1974b. Niche overlap and diffuse competition. *Proceedings of the National Academy of Sciences of the United States of America* **71:** 2141–2145.

Pincheira-Donoso D. 2008. Testing the accuracy of fecal-based analyses in studies of trophic ecology in lizards. *Copeia* **2008:** 322–325.

Pryke SR, Griffith SC. 2006. Red dominates black: agonistic signalling among head morphs in the colour polymorphic Gouldian finch. *Proceedings of the Royal Society B-Biological Sciences* **273:** 949–957.

R Development Core Team. 2012. *R: a language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing. Available at: http://www.R-project.org.

Roulin A. 2004. Covariation between plumage colour polymorphism and diet in the Barn Owl *Tyto alba*. *Ibis* **146:** 509–517.

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

Sacchi R, Scali S, Pupin F, Gentilli A, Galeotti P, Fasola M. 2007b. Microgeographic variation of colour morph frequency and biometry of common wall lizards. *Journal of Zoology* **273:** 389–396.

Sacchi R, Pupin F, Gentilli A, Rubolini D, Scali S, Fasola M, Galeotti P. 2009. Male–male combats in a polymorphic lizard: residency and size, but not color, affects fighting rules and contest outcome. *Aggressive Behavior* **35:** 274–283.

Sacchi R, Scali S, Pellitteri-Rosa D, Pupin F, Gentilli A, Tettamanti S, Cavigioli L, Racina L, Maiocchi V, Galeotti P, Fasola M. 2010. Photographic identification in reptiles: a matter of scales. *Amphibia-Reptilia* **31:** 489–502.

Sacchi R, Pellitteri-Rosa D, Marchesi M, Galeotti P, Fasola M. 2013a. A comparison among sexual signals in courtship of European tortoises. *Journal of Herpetology* **47:** 215–221.

Sacchi R, Pellitteri-Rosa D, Bellati A, Di Paoli A, Ghitti M, Scali S, Galeotti P, Fasola M. 2013b. Colour variation in the polymorphic common wall lizard (*Podarcis muralis*): an analysis using the RGB colour system. *Zoologischer Anzeiger* **252:** 431–439.

Sacchi R, Mangiacotti M, Scali S, Sannolo M, Zuffi MAL, Pellitteri-Rosa D, Bellati A, Galeotti P, Fasola M. 2015. Context-dependent expression of sexual dimorphism in island populations of the common wall lizard (*Podarcis muralis*). *Biological Journal of the Linnean Society* **114:** 552–565.

Scali S, Spadola F, Di Toro F, Gentilli A, Mangiacotti M, Tettamanti S, Cavigioli L. 2008. Plasticità trofica di due Lacertidi italiani: casi di predazione anomala in *Lacerta bilineata* e *Podarcis muralis*. In: Corti C, ed. *Herpetologia Sardiniae*. Latina: Societas Herpetologica Italica/Edizioni Belvedere, 435–438.

Scali S, Sacchi R, Azzusi M, Daverio S, Oppedisano T, Mangiacotti M. 2013. Homeward bound: factors affecting homing ability in a polymorphic lizard. *Journal of Zoology* **289:** 196–203.

Shannon CE, Weaver W. 1949. *The mathematical theory of communication*. Urbana, IL: University of Illinois Press.

Shine R, Ambariyanto, Harlow PS Mumpuni. 1998. Ecological divergence among sympatric colour morphs in blood pythons. *Python brongersmai. Oecologia* **116:** 113–119.

Sillero N, Campos J, Bonardi A, Corti C, Creemers R, Crochet PA, Crnobrnja Isailovic J, Denoël M, Ficetola GF, Gonçalves J, Kuzmin SL, Lymberakis P, de Pous P, Rodríguez A, Sindaco R, Speybroeck J, Toxopeus B, Vieites DR, Vences M. 2014. Updated distribution and biogeography of amphibians and reptiles of Europe. *Amphibia-Reptilia* **35:** 1–31.

Sinervo B. 1997. *Chapter 6: Optimal foraging theory: constraints and cognitive processes*. Course: Behavioral Ecology 2013. Department of Ecology and Evolutionary Biology, UCSC. Available at: http://bio.research.ucsc.edu/~barrylab/classes/animal_behavior/FORAGING.HTM

Sinervo B, Lively CM. 1996. The rock–paper–scissors game and the evolution of alternative mating strategies. *Nature* **380:** 240–243.

Svensson E, Sinervo B, Comendant T. 2001. Density-dependent competition and selection on immune function in genetic lizard morphs. *Proceedings of the National Academy of Sciences of the United States of America* **98:** 12561–12565.

Thompson CW, Moore MC. 1991. Syntopic occurrence of multiple dewlap color morphs in male tree lizards, *Urosaurus ornatus*. *Copeia* **1991:** 495–503.

Vercken E, Massot M, Sinervo B, Clobert J. 2007. Colour variation and alternative reproductive strategies in females of the common lizard *Lacerta vivipara*. *Journal of Evolutionary Biology* **20:** 221–232.

Verwaijen D, Van Damme R. 2008. Foraging mode and its flexibility in lacertid lizards from Europe. *Journal of Herpetology* **42:** 124–133.

Vincent SE, Herrel A. 2007. Functional and ecological correlates of ecologically-based dimorphisms in squamate reptiles. *Integrative and Comparative Biology* **47:** 172–188.

West-Eberhard MJ. 1989. Alternative adaptations, speciation, and phylogeny (a review). *Proceedings of the National Academy of Sciences of the United States of America* **83:** 1388–1392.

Winemiller KO, Pianka E. 1990. Organization in natural assemblages of desert lizards and tropical fishes. *Ecological Monographs* **60:** 27–55.

Zamudio KR, Sinervo B. 2000. Polygyny, mate-guarding, and posthumous fertilization as alternative male mating strategies. *Proceedings of the National Academy of Sciences of the United States of America* **97:** 14427–14432.

Zamudio KR, Sinervo B. 2003. Ecological and social contexts for the evolution of alternative mating strategies. In: Fox SF, McCoy JK, Baird TA, eds. *Lizard social behavior*. Baltimore: The Johns Hopkins University Press, 83–106.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Data S1. Dataset used for the analyses.