

Morphology, performance, behavior and ecology of three color morphs in males of the lizard *Podarcis melisellensis*

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Synopsis Males of a Croatian population of the lacertid lizard *Podarcis melisellensis* exhibit a striking polymorphism, with coloration of the throat and abdomen ranging from completely white, to yellow or orange. In a first attempt to explore the potential ecological and evolutionary significance of this polymorphism, we compared the three forms of males in aspects of their morphology, whole-animal performance, behavior, and ecology. Orange males are, on average, larger in snout-vent length and have disproportionately larger heads than either white or yellow males. This is reflected in orange males having higher bite force capacity and theoretically an increased access to harder prey. Residual limb length, maximal sprint speed and maximal exertion do not differ among color morphs. Body temperatures in the field are similar in the three morphs, but yellow males are caught at sites with slightly higher air temperatures than are orange and white males. Behavioral observations show no differences in time budgets or in the timing of activities among morphs. Microhabitat use is also similar in the three color morphs, but orange males were more often initially seen on rocky substrates. Our findings suggest that the observed polymorphism likely does not originate from a divergence in niche or use of resources, but possibly reflects an underlying polymorphism in mating tactics.

Introduction

The co-existence of two or more morphs within a population is a challenge to evolutionary theory, because a single morph should prevail unless morphs either have exactly equal fitness or an advantage in fitness when rare (Sinervo and Lively 1996). If the polymorphism is selectively neutral, the respective morphs will have the same fitness and will continue to exist side-by-side until stochastic processes cause one of them to become fixed (e.g., Fincke 1994; Hoffman et al. 2006). Alternatively, polymorphisms can be maintained by temporal or spatial heterogeneity in selective pressures. The morphs can then be considered alternative products of disruptive selection, each specialized in the exploitation of different niches. While the idea of polymorphisms evolving from temporally varying selection regimes is usually deemed unlikely (Barton and Turelli 1989; Roulin 2004a), spatial variation in the direction and magnitude of selection may play a significant role (Roulin 2004a). Morphs of many vertebrate species differ in aspects of their trophic niche or use of microhabitat (review by Skúlason and Smith 1995). In models of frequency-dependent (or density-dependent) selection, the

frequencies of the morphs are in a dynamic equilibrium, and high abundance of one morph results in a fitness advantage to the other morph(s). A well-known example is apostatic selection, in which the existence of a search image in a predator results in disproportional killing of the most common prey morph, and relaxation of predation upon the rare morph (review by Allen 1988). Similarly, density-dependent recognition and avoidance of predators by prey can maintain color polymorphism in the predatory species (the “alternative foraging strategies hypothesis”) (Paulson 1973; Roulin and Wink 2004). In other examples involving frequency-dependent selection, color polymorphism is linked to a parallel polymorphism in life-history strategies (e.g., Sinervo et al. 2001) or mating tactics (Sinervo and Lively 1996), the success of which is influenced by the frequency of players with alternative strategies. Other (less supported) mechanisms that have been proposed to explain color polymorphism include heterosis (Cook and Gao 1996) and selection balanced by continued immigration or mutation (Cook 1998; Roulin 2004a).

Deciding which of these mechanisms is maintaining a specific case of polymorphism is difficult as it

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requires long-term field data on gene frequencies, color-specific survival, migration, reproductive success, and choice of mates, in combination with carefully planned experiments (Roulin 2004a). Some of these hypotheses however, generate predictions that can be readily tested with natural history data. In particular, the disruptive-selection hypothesis requires some aspect of the environment to vary persistently in time and space and predicts the morphs to have different phenotypic optima, tuned to their respective niches (Day 2000; Roulin 2004a). For instance, in contrast to the “typical” zooplankton-eating morphs, the “cannibalistic” morphs of larval tiger salamanders (*Ambystoma tigrinum*) are equipped with broader mouths and enlarged vomerine teeth that allow them to feed on conspecifics (Collins and Holomuzki 1984). Apostatic selection is likely to result in differential coloration of body parts visible to predators and should be reflected in differential vulnerability to predation. For instance, in mosquitofish (*Gambusia holbrooki*), rare melanic morphs suffer less predation from bass, crayfish, and dragonflies than do silver morphs (Horth 2004). The “alternative foraging strategies hypothesis” would predict morphs to differ in their ability to obtain certain prey types, and this should be reflected in their diet. For instance, dark-colored and light-colored morphs of owls (*Tyto alba*) consume voles (*Microtus arvalis*) and field mice (*Apodemus* spp.) disproportionately (Roulin 2004b). In cases where color polymorphisms signal different reproductive strategies, morph-specific selection should induce differences in morphology, behavior, and physiological performance in accordance with the specific requirements of these alternative strategies. In the lizard *Uta stansburiana*, orange-throated (“ultra-dominant”, territorial) males have higher plasma testosterone levels, endurance and activity than do blue (mate-guarding) and yellow-throated (“sneaky”) males (Sinervo et al. 2000). Examining differences in the morphology, performance, and ecology of morphs may thus provide valuable first insights into the nature of the mechanism maintaining a particular color polymorphism.

We noticed a striking polymorphism in ventral coloration in a population of the lizard *Podarcis melisellensis* on the Croatian island of Lastovo (Fig. 1). Males can have bright white, yellow or orange throats, trunks and bellies. We present data here on the morphology, behavior, performance and ecology of the male morphs, and then relate our findings to predictions of several models invoked to explain the maintenance of color polymorphisms within natural populations.

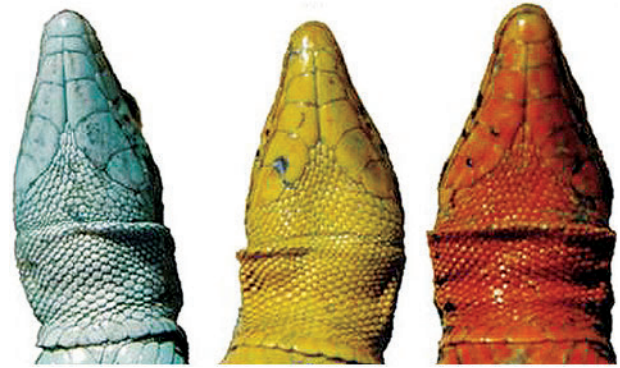


Fig. 1 Three male color morphs of *Podarcis melisellensis*, the Dalmatian wall lizard.

Materials and methods

Study species and study site

The Dalmatian wall lizard, *P. melisellensis*, is a medium-sized lacertid (adult snout-vent length (SVL) up to 70 mm) inhabiting a variety of dry habitats along the east Adriatic coast and on islands in the Adriatic Sea. We studied a population of this species in the center of the island of Lastovo (Croatia, 42°16'N, 16°54'E). The animals were observed and caught by noose or hand along a dirt road lined by stonewalls (~600 m long) and in an abandoned olive orchard (~50 × 55 m), in Spring and early Summer 2005 and 2006. Other reptiles encountered at this site were the European glass lizard (*Ophisaurus apodus*), the sharp-snouted rock lizard (*Lacerta oxycephala*) and the Balkan whip snake (*Dolichophis caspius*). All lizards used for the study were given a unique toe-clip code (to avoid repeated measurement of the same individual) and were put back at the exact place of capture as soon as possible. We here present data for adult males (SVL > 55 mm) only. Male *P. melisellensis* can be readily distinguished from females by the bulging of the hemipenes at the base of the tail.

Morphometrics

We measured the following distances to the nearest 0.01 mm, using digital calipers (Mitutoyo). SVL was measured from the tip of the snout to the posterior edge of the anal scale. Head length was taken as the distance between the tip of the snout and the caudal edge of the occipital scale. Head width was taken at the widest point of the head, and includes the bulging of the *Musculus pterygoideus*. Head height was measured at the highest point of the skull, just posterior of the orbit. Lower-jaw length was defined as the distance between the anterior end of the

dentary bone and the posterior edge of the retro-articular process. Separate measurements of the humerus (femur), radius (tibia), metacarpus (metatarsus) and toes were summed to obtain estimates of forelimb length and hind limb length. Individuals were weighed to the nearest 0.1 g using a Scout Pro balance.

Performance

All measurements of performance were conducted with lizards having body temperatures at or near the mean body temperature ($34 \pm 1^\circ\text{C}$) of animals active in the field.

Maximal sprint speed was estimated by chasing lizards down a 2 m racetrack with a cork substrate. Eight pairs of photocells, placed at 25 cm intervals along the track, signaled passing times to a computer. The highest speed over 25 cm recorded from three trials was used as an estimate of an individual's maximal sprinting speed. Lizards were allowed to rest and to thermoregulate for at least an hour prior to a trial.

Bite force was estimated by inducing lizards to bite on two metal plates connected to an isometric force transducer and a charge amplifier (see Herrel et al. 1999 for more details). The highest of five recordings of bite force was taken as an estimate of maximal performance.

Maximal capacity for exertion was estimated by chasing lizards around a circular track (diameter 100 cm, width 15 cm) until exhaustion. Lizards were considered exhausted when they did not show an immediate righting response after being placed on their backs. The longest time to exhaustion out of two or three measurements was considered an individual's maximal capacity of exertion. Before every trial, lizards were allowed to rest and thermoregulate for at least an hour.

Body temperatures and environmental temperatures in the field

Body temperatures of active lizards in the field were recorded with an electronic thermometer (precision 0.1°C), by inserting the thermocouple into the cloaca within 15 s following capture. Immediately thereafter, air temperature was measured at the site where the lizard was first seen, with the thermocouple 1 cm above the substrate and shaded. Because both air and body temperatures are likely to vary across the day, we noted the time at which each measurement was taken. To facilitate analysis, we later grouped the measurements into four time intervals: between 7 and 10 h, 10 and 13 h, 13 and 16 h, and later than

16 h, Central European Time (CET). We also noted whether lizards were sitting in full sun, mosaic (patches with sun and shade), or full shade.

Activity and behavioral observations

To test whether color morphs varied in activity times, we compared the proportion of morphs observed in the four time intervals delineated earlier. We also noted the behavior of each undisturbed lizard when first observed ("basking": evidenced by the positioning with respect to the sun, dorso-ventral flattening; "no-move": sitting still but not basking; "moving": walking or running) and checked whether timing of these behaviors varied among time periods or morphs.

We performed more detailed behavioral observations on a smaller set of animals by filming them continuously for at least 10 min, using a digital video camera (Sony, 50 Hz). All observations were made on fully active lizards, between 9.30 and 12.00 CET, and during sunny weather. From the recordings, we estimated the time budget of each focal animal (proportion of time spent "basking", "no-move", "moving"). We also calculated the mean duration of bouts for each behavioral category. Finally, we noted the proportion of the total time that the focal animal engaged in displaying its ventral color.

Microhabitat use

We adopted the method described by Castilla and Bauwens (1992) to compare the structural features of the microhabitats used by the three color morphs. In a circle of 0.5 m radius around the site where an undisturbed lizard was first noticed, we estimated the proportion of the ground surface covered by rocks and stones (1), sand (2), herbs (3), shrubs (4), and trees (5). We assessed the vertical structure of the vegetation by estimating the proportion covered by plants smaller than 10 cm (6), between 10 and 25 cm (7), between 25 and 50 cm (8), and taller than 50 cm (9). We also measured the maximum height of the vegetation (10) and noted the distances to the nearest patch of vegetation and to the nearest rock. Subsequently, we walked 2 m in a random direction (settled by dropping a pen) and determined variables 1–10 for a second circle of 1 m radius. We then returned to the initial spot and walked 2 m in an angle at 120° of the first direction to measure habitat structure in a third circle. Finally, this procedure was repeated for a fourth circle. We used the means for the variables 1 through 10 over all four circles to describe the microhabitat within the home range of the lizards.

Diet

We stomach-flushed freshly caught lizards to assess differences in diet between morphs. A small plastic ring was placed between the lizard's jaws and a ball-tipped steel needle mounted on a syringe was slowly pushed through the oesophagus into the stomach. Then water was gently squeezed out of the syringe while massaging the stomach of the lizard. This always resulted in the lizard regurgitating its stomach contents. The contents were stored in individual vials with a 70% aqueous ethanol solution. Following procedures outlined by Herrel et al. (2006), we later determined each prey item to taxonomic order. The hardness of each item was then categorized as "soft", "intermediate", or "hard" on the basis of criteria established previously from a large sample with a great variety of arthropods (Aguirre et al. 2003, Herrel et al. 2006). We used the number of prey items present and the sum of the lengths of all prey in the stomach as an index of stomach fullness.

Statistical analyses

All morphometric and performance variables were log-10 transformed before analysis. Proportional data were arcsine transformed. We used the Shapiro-Wilk

statistic to test for normality. If transforming the data did not result in a normal distribution, we used nonparametric tests. When performing analyses of covariance, we tested for parallelism by inspecting the significance of the interaction between the main factor(s) and the covariate(s). Interaction terms that were significant are mentioned in the text; otherwise, we report the significance of the factors in a model with the interaction terms removed. We used principal components analysis to reduce the number of variables in our analyses of head dimensions, behavior, and microhabitat use. In all three cases, the analysis was performed on the correlation matrix, using the Varimax rotation. We used scree-plots to decide how many composite variables to keep.

Results

Morphometrics

Mean SVL varied among color morphs (ANOVA, $F_{2,410}=6.99$, $P=0.001$, Table 1). White and yellow males were similar in size (Tukey HSD test, $P=0.38$), but orange males were on average larger than either white ($P=0.02$) or yellow males ($P=0.002$). After correcting for SVL, differences in body mass among morphs fell just short

Table 1 Descriptive statistics (means, standard errors and sample sizes) for the morphometric, performance, thermal ecology and diet of three color morphs of the lizard *Podarcis melisellensis*

| Trait | White | | | Yellow | | | Orange | | |
|-----------------------|----------|------|----------|----------------|------|----------|----------------|------|----------|
| | <i>x</i> | SE | <i>n</i> | <i>x</i> | SE | <i>N</i> | <i>x</i> | SE | <i>n</i> |
| SVL (mm) | 63.64 | 0.27 | 187 | 63.02 | 0.46 | 78 | 64.67 | 0.23 | 148 |
| Mass (g) | 5.41 | 0.21 | 69 | 4.69 | 0.31 | 23 | 5.31 | 0.16 | 66 |
| Head length (mm) | 14.84 | 0.07 | 168 | 14.60 | 0.12 | 61 | 15.13 | 0.05 | 133 |
| Head width (mm) | 8.75 | 0.07 | 97 | 8.43 | 0.12 | 45 | 9.04 | 0.07 | 91 |
| Head height (mm) | 6.99 | 0.06 | 97 | 6.74 | 0.09 | 45 | 7.20 | 0.05 | 91 |
| Lower jaw length (mm) | 15.80 | 0.09 | 97 | 15.48 | 0.15 | 45 | 16.19 | 0.07 | 91 |
| Forelimb (mm) | 17.66 | 0.14 | 61 | 17.50 | 0.20 | 37 | 18.14 | 0.12 | 64 |
| Hind limb (mm) | 26.43 | 0.21 | 61 | 25.60 | 0.26 | 37 | 26.79 | 0.23 | 64 |
| Bite force (N) | 12.09 | 0.32 | 60 | 11.49 197.8 | 0.50 | 37 | 13.98 202.4 | 0.34 | 64 |
| Speed (cm/s) | 201.4 | 6.08 | 59 | 9 | 7.45 | 37 | 0 | 6.19 | 63 |
| Exertion capacity (s) | 30.95 | 1.97 | 24 | 29.90 | 1.49 | 9 | 29.86 | 2.33 | 18 |
| Body temperature (°C) | 33.49 | 0.15 | 180 | 33.60 | 0.25 | 40 | 33.88 | 0.30 | 53 |
| Air temperature (°C) | 25.92 | 0.20 | 179 | 27.77 | 0.77 | 38 | 26.87 | 0.51 | 53 |
| Number of prey items | 6.90 | 1.10 | 42 | 6.30 | 2.00 | 9 | 4.60 | 0.60 | 26 |
| Total prey size | 31.99 | 3.56 | 42 | 30.60 | 4.94 | 9 | 25.74 | 3.42 | 26 |

of statistical significance (ANCOVA, $F_{2,154}=2.85$, $P=0.061$). Residuals of the $\log(\text{mass})$ - $\log(\text{SVL})$ regression were smallest for the yellow males, intermediate for the orange and highest for the white males, but only the difference between yellow and white males approached statistical significance ($P=0.056$). Neither hind limb length ($F_{2,158}=1.72$, $P=0.18$) nor forelimb length ($F_{2,158}=2.05$, $P=0.13$) differed among color morphs after correction for SVL.

Principal components analysis on the correlation matrix of the four original head measures yielded a single composite variable that explained 78.59% of the total variation (eigenvalue=3.14). This new variable (representing head size) correlated highly positively with all original variables (all $r>0.83$). The effect of SVL on overall head size differed among color morphs (ANCOVA, color \times SVL interaction effect: $F_{2,227}=3.66$, $P=0.012$), indicating morph-specific head-growth trajectories. Head size increases more slowly with SVL in orange males than in either white or yellow ones, but because young adult orange males start out with relatively large heads, they have on average larger heads than either of the other morphs (Fig. 2). When calculated over a common regression line (head size versus $\log(\text{SVL})$) for all males, residuals for the three males differ significantly ($F_{2,230}=9.02$, $P<0.001$). Residuals for yellow males are smaller than those of either white ($P=0.03$), or orange males ($P<0.001$).

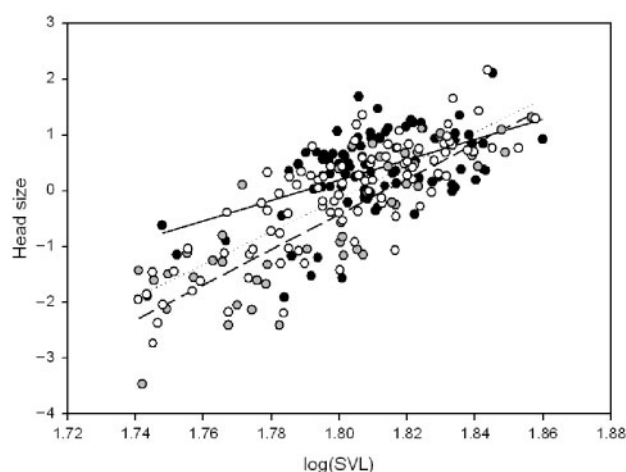


Fig. 2 Relationship between head size and snout-vent length in three male color morphs of the lizard *Podarcis melisellensis*. Head size is a composite measure obtained through principal components analysis on four linear dimensions of the head (see text for details). White morphs = white circles, dotted line; yellow morphs = grey circles, dashed line; orange morphs = black circles, solid line.

Performance

Maximal sprint speed ($F_{2,156}=0.09$, $P=0.91$) and exertion ($F_{2,48}=0.12$, $P=0.89$) did not differ between morphs. SVL (entered as a covariate) did not explain significant variation in either performance trait (both $P>0.67$). Morphs did differ in bite force ($F_{2,254}=6.38$, $P=0.002$), with orange ($P=0.001$) and white ($P=0.015$) males biting considerably harder than yellow morphs. The difference remained after correcting for SVL ($F_{2,254}=5.81$, $P=0.003$), but disappeared when both SVL and head size were entered as covariates ($F_{2,254}=0.34$, $P=0.72$).

Body temperatures and environmental temperatures in the field

Body temperatures varied slightly throughout the day (ANOVA, $F_{3,249}=2.70$, $P=0.047$) but we found no differences between morphs (Table 1, $F_{2,249}=0.29$, $P=0.75$) and the interaction effect also was not significant ($F_{2,249}=1.72$, $P=0.12$). Air temperatures followed a pattern of diurnal variation similar to that of body temperatures ($F_{3,247}=2.46$, $P=0.055$). Air temperatures differed marginally among color morphs (Table 1, $F_{2,249}=2.94$, $P=0.055$), with yellow males being observed at relatively higher air temperatures. The average difference between body temperature and air temperature varied among color morphs ($F_{2,246}=3.71$, $P=0.026$). It was least pronounced in yellow males, although only the difference with white males was significant ($P=0.008$; P -values for other combinations >0.15). The period and period \times morph effects were not significant (both $P>0.16$). We found no significant difference in the proportion of lizards observed in full sun, mosaic, or full shade among periods ($\chi^2_6=6.78$, $P=0.34$) or color morphs ($\chi^2_4=7.29$, $P=0.12$).

Activity and behavior

The proportion with which the different color morphs were observed did not vary among the four 3-hourly periods ($\chi^2_6=10.38$, $P=0.12$). The behavior of the lizards did vary, however, among the four periods considered ($\chi^2_9=31.51$, $P<0.001$), with a disproportionate high number of lizards basking in the early hours. Color morphs did not differ in the proportions of different behavioral acts exhibited ($\chi^2_4=4.13$, $P=0.38$) or in the timing of those acts throughout the day ($\chi^2_{12}=8.75$, $P=0.72$).

Principal components analysis of the detailed behavioral variables (mean bout duration and proportion of time engaged in “bask”, “move”,

“no-move”, and “display”) resulted in three new axes that explained 33.96, 29.30, and 18.37% of the variation, respectively (eigenvalues 2.72, 2.34, and 1.47). The first axis distinguished lizards that engaged in “moving” ($r=0.85$ for proportion, $r=0.97$ for duration of bout) from lizards that exhibited “no-move” behavior ($r=-0.69$ for proportion). The second axis correlated positively with engagement in the “display” behavior ($r=0.89$ for proportion, 0.91 for bout duration). The third axis separated observations with extensive basking ($r=-0.83$ for proportion) from those with long bouts of “no-move” ($r=0.85$). Scores for the three colour morphs, however, did not differ on any of the three axes (all $P>0.28$).

Microhabitat use

Principal components analysis (Varimax Rotation) on the structural features of the microhabitat obtained from the central spot summarized the variation; there were three composite variables that jointly explained 69.21% of the variation. The first axis (eigenvalue 2.87, explaining 28.73%) was positively correlated with the percentage cover by shrubs ($r=0.80$) and vegetation between 25–50 cm ($r=0.76$), and negatively correlated with percentage of vegetation lower than 10 cm ($r=-0.89$). The second axis (eigenvalue=2.54, explaining 25.37%) was correlated with the percentage cover by trees ($r=0.82$) and tall vegetation (>50 cm, $r=0.83$) and it was negatively correlated with percentage of vegetation between 10–25 cm ($r=-0.72$). The third axis (eigenvalue=1.51, explaining 15.11%) was correlated positively with percentage cover by sand ($r=0.85$) and negatively with cover by rocks and stones ($r=-0.86$). The scores on the three new axes did not differ among color morphs (ANOVAs, all $P>0.063$).

A similar analysis on the data averaged over all four plots resulted in two composite variables that together explained 57.97% of the variation. The first axis (eigenvalue 3.42, explaining 34.21%) was positively correlated with the percentage cover by shrubs ($r=0.76$), percentage cover by vegetation higher than 50 cm ($r=0.80$), and the maximal height of the vegetation ($r=0.82$). It was negatively correlated with the percentage cover by herbs ($r=-0.57$) and vegetation below 10 cm high ($r=-0.78$). The second axis (eigenvalue 2.37, explaining 23.76%) was correlated positively with the percentage cover by rocks ($r=0.61$), vegetation between 10–25 cm ($r=0.83$), and vegetation between 25–50 cm ($r=0.73$). The scores of the individual

data on the axes did not differ among color morphs (ANOVAs, both $P>0.37$).

The distances to the nearest rock (Kruskal-Wallis test, $\chi^2_2=0.211$, $P=0.90$) and to the nearest patch of vegetation (Kruskal-Wallis test, $\chi^2_2=0.46$, $P=0.79$) did not differ among color morphs. The distance to the nearest rock varied between 0 and 6 m, but 75% of all lizards observed were within 67 cm of a rock. The distance to the nearest patch of vegetation varied between 0 and 150 cm, with $>90\%$ of lizards within 50 cm.

Substrate use varied with time of day ($\chi^2_4=19.54$, $P=0.003$). This seemed mainly due to an increased use of rocks in the late afternoon. Substrate use also varied among color morphs ($\chi^2_4=10.79$, $P=0.029$). In comparison with other males, orange morphs were more often seen on rocks, and less often on open ground or vegetation. The period \times morph interaction was not significant ($\chi^2_{12}=13.46$, $P=0.34$).

Diet

Lizards had between 0 and 42 prey items in their stomach. The mean number of prey items per stomach did not differ among color morphs ($F_{2,74}=0.75$, $P=0.34$), and neither did the total amount of prey per stomach ($F_{2,74}=1.22$, $P=0.47$). However, the proportions of soft, intermediate and hard prey items did differ among color morphs ($\chi^2_4=29.5$, $P<0.001$). The diet of orange males contained higher proportions of hard prey than did that of either white or yellow males (Fig. 3). Taxonomic distribution of prey did not differ among morphs (all $P>0.22$).

Discussion

Male *P. melisellensis* morphs with orange-colored throats and abdomens tend to be larger than white or yellow-colored males. In principle, this observation could be explained by (1) ontogenetic changes in ventral coloration (males turning orange as they grow older); (2) differential growth of color morphs (orange males growing faster) or (3) differential survival of color morphs (orange males surviving better). Ontogenetic change in color pattern is widespread in lizards in general (Cooper and Greenberg 1992) and in lacertid lizards in particular (e.g., Huey and Pianka 1977; Diaz 1993; Castilla et al. 1999). In the Iberian rock lizard, *Lacerta* (now *Iberolacerta*) *monticola*, sexually mature males can be dull brown or bright green, depending on their status. The brown males are smaller and younger and have lower competitive abilities than did the bright

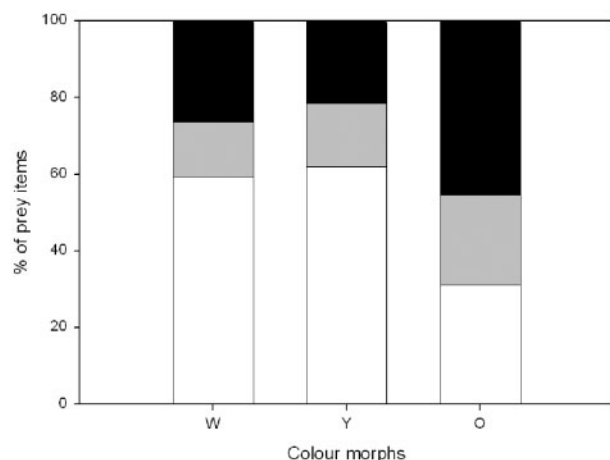


Fig. 3 Proportion of hard (black bars), intermediate (grey bars) and soft prey items (white bars) eaten by the three male morphs (W = white; Y = yellow; O = orange).

green males into which they develop in subsequent activity seasons (Aragón et al. 2004). In another lacertid, *Psammotromus algirus*, larger and older males exhibit orange nuptial coloration on the head, while younger males, albeit sexually mature, do not (Martin and Forsman 1999). However, several considerations suggest that color morphs in *P. melisellensis* are fixed early in life. First, of the individuals that were caught in two successive activity seasons, none changed color between years. Second, the overlap in SVL among color morphs is considerable, with some yellow and some white males reaching SVLs of the largest orange males. This contrasts with the more disparate size distribution of color morphs in *Lacerta monticola* (Aragón et al. 2004) and *P. algirus* (Martin and Forsman 1999). If the three male *P. melisellensis* morphs are, on average, the same age, the size difference could be due to orange males growing faster. In several other, nonrelated lizard species, orange coloration is associated with social dominance (e.g., *Uta stansburiana*: Sinervo et al. 2000; *Platysaurus degressii*: Whiting et al. 2006). Since body size is by far the most important determinant of fighting ability in most lizard species studied (reviewed by Olsson and Madsen 1998), a connection between large body size and orange coloration makes sense evolutionarily. Mechanistically, such a connection could arise through the combined effects of sex steroids such as testosterone on body growth (e.g., Cox and John-Alder 2005; Cox et al. 2005a, but see e.g., Salvador and Veiga 2000), coloration (e.g., Hews 1994; Sinervo 2000; Cox 2005b) and aggressiveness (e.g., Crews 1975; Klukowski and Nelson 1998)

in lizards. These ideas seem in agreement with the hypothesis that the color polymorphism in *P. melisellensis* is maintained by frequency-dependent selection for a coupled polymorphism in mating tactics. Alternatively, the difference in body size could be due to orange males surviving better. This option seems counterintuitive, because there is no reason to believe that ventral coloration has a direct effect (either positive or negative) on vulnerability to predation. However, the development of bright (orange) colors in lizards may come at the expense of susceptibility to parasites (e.g., Schall 1986; Ressel 1989; Salvador et al. 1996).

A second striking morphological difference among male morphs is the disproportionately larger head of orange males. Although this should be verified by including data on juvenile and sub-adult animals in the future, our data suggest that orange males acquire these larger heads soon in life (even prior to maturation), indicating an early allometric shift. It is tempting to interpret this as a consequence of increased testosterone during development, but data on the organizational effects of hormones, such as testosterone, on the dimensions of lizards' heads are unavailable (Perry et al. 2004). The observed difference in head size is in agreement with predictions of both the disruptive-selection hypothesis and the frequency-dependent-selection hypotheses for the maintenance of color polymorphism. With their relatively large head, and increased bite capacity, orange males can eat harder prey than can the other morphs, and the differences among morphs therefore could be mediated by disruptive selection operating on the trophic niche. Alternatively, head size (and its functional correlate, bite-force capacity) may be under sexual selection, rather than under natural selection (*sensu stricto*). In many lizard species, head size and bite force are important determinants of fighting ability and dominance (e.g., Alberts et al. 2002; López and Martín 2002; Huyghe et al. 2005) and the larger heads of orange males may thus correlate with a putative territorial or dominant morph. In this case, the observed expansion of the trophic niche would constitute a bonus, rather than the actual target of selection. One argument in favor of the idea that bite force is primarily under sexual selection is the fact that crushing even the hardest prey items consumed by these lizards does not require the bite forces measured (pers obs).

We found no differences in average sprint speed or exertion among color morphs. Accordingly, relative limb lengths did not differ. Differences in locomotor performance were expected under the

hypothesis of a polymorphism in escape tactics and/or mating strategy. Although the exact mechanistic link remains uncertain (Lailvaux and Irschick 2006), both sprint speed (e.g., Garland et al. 1990; Robson and Miles 2000) and endurance (e.g., Robson and Miles 2000; Perry et al. 2004) correlate with social dominance in several lizard species. Speed and stamina are presumed to aid a dominant male in patrolling its territory, in chasing away intruders, or in direct combat (e.g., Husak et al. 2006). The link between social dominance and locomotor capacity, however, is not universal. Several other studies on lizards have found no correlation (e.g., Miles et al. 2001; Huyghe et al. 2005) and López and Martín (2002) found that in male *Lacerta monticola*, sexual selection for increased head size comes at the expense of decreased performance in locomotion. Likely, environmental conditions affect the intensity of selection on particular attributes of respective morphs in different species. Superior locomotor performance may be more important for territorial males in open habitats than for those in densely vegetated habitats (as that of *P. melisellensis*).

Body temperatures in the field did not differ among the three color morphs. Although differences in thermal requirements are a popular way of explaining variation in body coloration in lizards (e.g., Norris 1965; Rosenblum 2005), we did not expect to find a direct effect of coloration on body temperature in *P. melisellensis* because the difference between the morphs is restricted to the venter, a side of the animal that is not typically exposed to direct solar radiation. However, we did want to consider the option that the color polymorphism reflects disruptive selection with respect to the use of the thermal niche. Unexpectedly, our results indicate that yellow males, while having body temperatures similar to those of orange males and white males, were active at somewhat higher air temperatures. Since morphs do not differ in (structural) microhabitat use, activity patterns or behavior (e.g., basking frequency), difference may be due to selection of slightly hotter sites within the habitat. At our study site, structural complexity of the habitat is high and the presence of stone walls, rocks, and different types of vegetation likely results in considerable thermal heterogeneity that can be exploited by the lizards. The functional significance (if any) of this difference in the use of the thermal environment is unclear but unlikely to be driving divergence between morphs.

Microhabitat use was highly similar in all three color morphs. This seems to negate the possibility of divergent adaptation of the respective morphs to

different types of microhabitats. Within their home ranges, orange males were observed more often on rocky substrates than were other morphs. Although at first sight this might indicate that they use these perches to survey their territory, or to advertise their status, behavioral observations suggest this is not the case. The average distance to the nearest available hiding place was equally small in all three morphs.

In conclusion, we found differences in body size and in some aspects of body shape, performance, and ecology among the male color morphs of *P. melisellensis*. The fact that morphs show little divergence in dimensions of their niches renders the disruptive-selection hypotheses less likely. Additionally, it seems unlikely that apostatic selection would be involved, as the ventral color would be visible to aerial predators rarely, if at all. Our observations suggest that a polymorphism in mating tactics may potentially underlie the color polymorphism. More generally, future investigations of the genetics, ontogeny and the behavioral, physiological, and life-history correlates of the three morphs will be necessary to conclude whether the striking polymorphism in this lacertid is indeed related to different mating tactics.

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