

Article

Morph-specific assortative mating in common wall lizard females

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Abstract

Color polymorphism often is associated with alternative reproductive strategies and may reflect different adaptive optima that coexist within populations. The equilibrium among morph frequencies is maintained by the occurrence of opposite selective pressures (disruptive vs. stabilizing), which promote polymorphism while preserving gene flow. Sexual selection may contribute on both sides, particularly when morphs do not mate randomly. Reptiles offer a good model, notably lizards. Nevertheless, previous studies on mate choice in polymorphic lizards have generated contrasting results, with some studies suggesting that female morphs might tune their preference depending on environmental/social conditions such as crowding. We experimentally manipulated the number of individuals a female common wall lizard *Podarcis muralis* perceives around her, to test if females of different morphs (white or yellow) tune their choice for white and yellow males in order to maximize the probability that hatchlings follow the strategy best adapted to the population density. Results showed that crowding experienced by females did not affect mate choice, arguing against a flexible choice strategy by females. However, white females significantly associated with white males, whereas yellow females did not significantly associate with yellow males. Thus, sexual selection could contribute to the maintenance of color polymorphism in this species by a mix of assortative and non-assortative mating strategies, which could maintain the equilibrium between gene divergence and gene flow among morphs.

Key words: flexible female choice, population density, color polymorphism, sexual selection.

Color polymorphisms often associate with alternative reproductive strategies, which involve specific trade-offs among behavioral, morphological, physiological, and life history characteristics (Sinervo and Lively 1996; Svensson et al. 2001; Sacchi et al. 2007a, 2009), and represent different adaptive optima that may coexist within populations (Calsbeek et al. 2010). The evolutionary stable co-occurrence of these alternative optima within a single species is generally regarded as the result of the equilibrium between opposite selective pressures: disruptive selection (i.e., correlational selection), which promotes the association between life history traits and coloration, and the stabilizing selection (e.g., frequency-dependent

selection), which preserves gene flow among morphs (Sinervo and Svensson 2002). There is substantial evidence that natural selection maintains color morphs, notably negative frequency-dependent selection (reviewed in Gray and McKinnon 2007).

Sexual selection may also promote heritable color polymorphism, particularly when individuals of alternative morphs do not mate randomly (Wellenreuther et al. 2014). In particular, a strong sexual selection pressure may reinforce the divergence among alternative morphs, promoting morph maintenance (Corl et al. 2010; Pérez i de Lanuza et al. 2017), and a variation in the intensity of sexual selection could drive inter-population differences in color morph

frequencies (McLean and Stuart-Fox 2014). Furthermore, the intensity of sexual selection could differ in males and females resulting in different morph composition between sexes (Pérez i de Lanuza et al. 2017). However, assortative mating alters the genotype frequencies without favoring one allele with respect to another one, and consequently it cannot maintain color polymorphism alone in the absence of other micro-evolutionary forces. In particular, positive assortative mating requires the simultaneous presence of heterozygote advantage or some other form of selection (such as the negative frequency-dependent selection) to maintain the polymorphism. On the contrary, disassortative mating (i.e., negative assortative mating) can by itself prevent the loss of rare phenotypes, maintaining morphs within populations (Wellenreuther et al. 2014).

Lizards offer a good model to investigate the evolution and maintenance of color polymorphism, because polymorphic systems are quite common and some underlying mechanisms have been already hypothesized and tested (Thompson and Moore 1991; Thompson et al. 1993; Sinervo and Lively 1996; Zamudio and Sinervo 2000; Sinervo et al. 2001; Sinervo and Zamudio 2001; Huyghe et al. 2007; Sacchi et al. 2007b; Runemark et al. 2010; Galeotti et al. 2013). Some studies have explored the contribution of sexual selection on color polymorphism maintenance, specifically that of female preference, but with contrasting results (Alonzo and Sinervo 2001; Healey et al. 2008; Lattanzio and Miles 2014; Sacchi et al. 2015). For example, female side-blotched lizards *Uta stansburiana* choose males, but do not mate following a strictly assortative pattern and adopt a flexible mate choice rule according to population density (Alonzo and Sinervo 2001). By contrast, females of the Australian painted dragon *Ctenophorus pictus* do not discriminate between single males of different head color, but preferentially associate with polymorphic as opposed to monomorphic male dyads, possibly to increase the likelihood of mating with different males (Healey et al. 2008). Furthermore, female morphs of the tree lizard *Urosaurus ornatus* actually discriminate male partners, but mate preference does not relate with the color of male dewlap, but rather with the secretions of their femoral pores (Lattanzio and Miles 2014).

The common wall lizard *Podarcis muralis* is an European lacertid lizard showing a striking color polymorphism in both sexes, with 6 distinct morphs, including 3 pure (i.e., white, yellow, and red) and 3 intermediate phenotypes (white-red, yellow-red, and white-yellow, Figure 1 in Sacchi et al. (2013) shows a picture of male and female morphs). Morphs occur within the same population, but their relative frequencies are highly variable among populations (Sacchi et al. 2007a, 2007b). Field observations of morph's mating behavior suggest that assortative mating between color morphs should actually occur (Pérez i de Lanuza et al. 2013). However, experimental tests failed to demonstrate that females really choose males according to their morph in a color assortative way (Sacchi et al. 2015), despite the fact that females might be able to detect morph by only smelling male scents (Pellitteri-Rosa et al. 2014).

Female morphs display different reproductive partitioning of reproductive output, with yellow-throated females producing many small eggs and white-throated females producing few large eggs. This pattern has been assimilated to K/r strategies, in which yellow females have been described as r-strategists, while white females as K-strategists (Sinervo and Zamudio 2001; Galeotti et al. 2013). In this scenario, a fixed preference for a given morph would not be the best choice for females if population density changes over time. Given that color morphs in lizards apparently follow a simple Mendelian inheritance—that is, 3 alleles on 1 single locus or 2 alleles on 2 loci, without

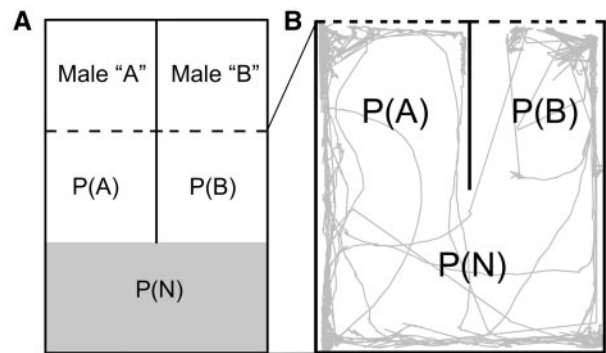


Figure 1. (A) The 2-choice arena used to test the female preference for white and yellow males. P(N): neutral area for the female; P(A) and P(B): preference compartments for male A or male B, respectively; the dashed lines represent the transparent plexiglas dividers separating male compartments from the female preference compartments. (B) An example of the trajectory of a female within the arena during the entire experiment produced by idTracker. Symbols as in panel A.

sex linkage (Sinervo et al. 2001, Rankin et al. 2016) - white females mating consistently with white males will always produce a white offspring, which best performs solely in high-density contexts. By contrast a “flexible choice strategy” (*sensu* Alonzo and Sinervo 2001) would be a more profitable solution for females in response to fluctuations in population density. In this case, mating with a white male will increase the proportion of white individuals among offspring, and mating with a yellow male will increase that of yellow ones. Hence, females may use local cues to project future conditions their offspring will experience and, consequently, tune their preference from one morph to the other. Therefore, in this article, we experimentally manipulated the population density in order to test whether the reproductive partitioning strategies of white and yellow females were tuned according to male morph in order to improve the proportion of hatchlings expressing the morph adapted more closely to the demographic conditions of the population. Our specific predictions are: 1) white females should prefer white males when reared in high-density condition; 2) yellow females should select yellow males when reared under low population density.

Materials and Methods

Subjects and housing conditions

Between February and March 2015, we captured sexually mature lizards (SVL > 50 mm, Sacchi et al. 2012) by noosing in 4 sites in the surrounding of Pavia (Lombardy, Northern Italy), which were at least 5 km apart each other. We collected only not-mated females as determined by the lack of male's bite signs on their belly (typically being present after copulation, Bauwens and Verheyen 1985; Sacchi et al. 2015). Each individual was measured by a digital caliper for SVL, weighed, and transferred to the laboratory within 2 h from capture. Overall, we housed 46 females (23 for each morph) and 31 males (16 yellow and 15 white). We housed females in opaque plastic cages (60 × 50 × 50 cm), provided with a paper sheet as substratum and two 4-hole bricks covered by a tile as shelter. We set 2 different density treatments: 1) in the “high-density” treatment, we randomly assigned 24 females (12 for each morph) to 4 cages with 6 individuals in each one (3 for each morph); 2) in the “low-density” treatment, we randomly assigned 22 females (11 for each morph) to 11 cages with 2 individuals each (1 for each morph). We housed

males individually in plastic cages (20 × 30 × 20 cm), provided with a paper sheet as substratum and 2 small tiles as basking site and shelter. Cages were maintained at ambient temperature in a range that promotes lizard activity (15–30 °C) and under natural photoperiod (daylight). We maintained and fed all lizards for at least 1 week before trials started and released them in their capture sites at the end of the experiment. Before release, we weighed the females again and found that all of them maintained their original body mass (change: −0.10 g, paired-sample *t*-test; $t_{43} = -1.19$, $P = 0.24$).

Experimental design

We formed 44 dyads of males by randomly choosing 1 male of each color morph. Mean SVL of males was 62.3 ± 1.1 mm (range 50.0–69.6 mm) and did not differ between morphs (2-sample *t*-test: $t_{29} = 0.43$, $P = 0.66$). The mean size difference between males within dyad was 9.0% of SVL (range: 0.1–29.6%). Mean SVL of females was 60.8 ± 0.6 mm (range 53.8–69.1 mm) and did not differ among morphs (2-sample *t*-test: $t_{42} = 0.38$, $P = 0.70$). We randomly assigned each female a dyad, and we experimentally tested the female preference for males using a 2-choice arena. The arena was modified after LeBas and Marshall (2000) and Bajer et al. (2010) and was composed of a rectangular compartment (20 × 40 cm side) connected to 2 20 × 20 cm compartments (Figure 1). The rectangular compartment was regarded as neutral area for the female, while the 2 annexed compartments were defined as the preference ones (Figure 1A). The 2 preference compartments were separated by a transparent plexiglas divider from the male compartments (20 × 20 cm, Figure 1). The temperature was kept constant using a 45-W heat mat at 33 °C. We placed each lizard in a thermostated terrarium (20 × 30 × 20 cm, 33 °C) for 10 min before starting trial, then we gently moved individuals from pre-heating cages into the arena: males were assigned randomly among preference compartments, while females were placed in the center of the rectangular compartment within an opaque small box 5 min before the trial started. The box was then removed and female behavior was observed and videotaped with a SONY Super Night Vision Camera (M020-s53-001) connected by a 20-m isolated wire to a laptop PC located in a room adjacent to the one housing the arena. We observed females continuously for 1 h, and trials were carried out using 2 identical arenas. After each trial, we carefully washed the arena with detergent in order to remove any chemical stimuli left by lizards from the previous trial. A trial was invalidated if the female had not approached any of the preference compartments at least once, and consequently we excluded 2 recordings (1 for each morph), and the sample size for the analysis included 44 females (11 females for each morph in each treatment).

Female preference variables

Video recordings of female behavior were analyzed automatically using the software idTracker (Pérez-Escudero et al. 2014), which automatically tracks the movements in 2D of the target lizard and supplies its position in each frame in terms of horizontal and vertical coordinates (expressed in pixels). Since the resolution of recordings was 25 frames/s, the position of the target female was obtained with the same frequency, supplying, therefore, a set of 90,000 locations for each lizard. Those locations were used to build the female trajectory within the arena during the entire experiment (Figure 1B). By counting the number of locations in each compartment of the arena and converting it in seconds (1 frame = 1/25 s), we obtained the total time spent by each female in the 2 choice compartments. These times

were interpreted as a measure of interest in the male and, thus, an evaluation of the female choice. People who analyzed videos (M.B. and A.J.C.) were “blind” with respect to both female treatment (i.e., low vs. high density) and the morph of males kept in the 2 preference compartments. In order to check whether idTracker was giving accurate results, we manually analyzed 6 randomly selected recordings, and we compared the estimates between the 2 methods. The correlation was extremely high (Pearson’s correlation coefficient, $r_p = 0.988$), confirming that the estimates of the times spent by females within the choice compartment obtained by idTracker were fully reliable.

Statistical analyses

As we simultaneously collected 2 measures (1 for each male morph) for each trial, we used a multivariate analysis of covariance (MANCOVA) to compare the total time spent in the choice compartments between female morphs. In this analysis, the matrix of the 2 measures was the dependent variable, whereas the female morph, the female body size (SVL), the density treatment, and the difference in size between males were the predictors. The female morph × density treatment interaction was also added to check for different pattern of choice by females. Finally, the arena was included among predictors to control for the 2 experimental sets. Multivariate homogeneity of variance was achieved, so raw data were used in the analyses. Finally, we used univariate analyses of covariance (ANCOVA) as post hoc test to the MANCOVA, in order to disentangling the groups responsible for significant multivariate effects. We ran 2 separate ANCOVAs, both including the same predictors as in the MANCOVA. The dependent variables were, respectively, the time spent in the choice compartment associated with the white (first model) and yellow (second model) males. We performed all the analyses using R version 3.1.0 (R Core Team 2016), and otherwise stated, reported values represent mean and standard errors.

Results

Contrary to any expectation, the density treatment did not affect female choice. Indeed, the time females spent in each of the 2 choice compartments did not significantly differ according to density treatment or the density treatment × morph interaction (Table 1). Similarly, females spent the same amount of time in the 2 choice compartments regardless of body size and the arena used for the trial (Table 1). However, we found a significant main effect of the female morph (Pillai’s $trace = 0.241$, $P = 0.0069$). The first post hoc ANCOVA showed that white females spent on average more time than yellow ones with the white male (contrast between white and yellow females: $\beta = 14.5 \pm 4.2$ min, $t = 3.42$, $P = 0.0015$, Figure 2), whereas the second post hoc ANCOVA did not find any difference between female morphs for the time spent in association with the yellow male (contrast between white and yellow females: $\beta = -5.1 \pm 3.6$ min, $t = 1.44$, $P = 0.16$, Figure 2). Consequently, white females spent more time in the white male side than in the yellow male one irrespective of the treatment (2-sample *t*-test: $t_{42} = 3.906$, $P = 0.00033$, Figure 2), whereas yellow females did not show any difference (2-sample *t*-test: $t_{42} = 0.807$, $P = 0.42$, Figure 2).

Discussion

In this article, we looked if female morphs of the common wall lizards associate with male morphs in an assortative way. Since yellow

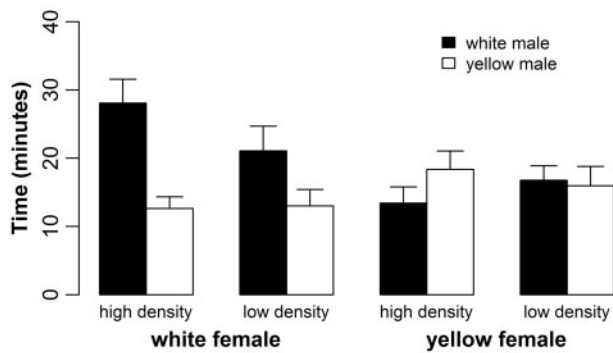


Figure 2. Mean time spent by white and yellow females in the 2-choice compartments depending on the 2 density treatments. Bars represent standard errors.

Table 1. Statistics of the MANCOVAs used to compare the responses of females to male color morphs

Variables	Pillai's trace	df	P
Morph	0.241	1	0.0069
Density	0.057	1	0.34
Morph × Density	0.052	1	0.38
Female SVL	0.008	1	0.86
Arena	0.066	1	0.29
Difference in SVL between males	0.072	1	0.26

and white females adopt r/K reproductive strategy (*sensu* Alonzo and Sinervo 2001; Galeotti et al. 2013), we tested if female mate preference changed depending on lizard density, in order to maximize the probability that hatchlings will express the morph adapted more closely to the demographic conditions of the population. Experimental manipulation of density did not give significant results, since it did not have any effect on mate preference by white and yellow females. Even if density was manipulated in laboratory and for short time, these results suggested that white and yellow females do not really tune mate preference according to the population density.

In the common wall lizard, alternative breeding strategies also occur in male morphs (Sacchi et al. 2007a; Calsbeek et al. 2010; Scali et al. 2013), and male and female strategies could couple in order to maximize the fitness of each player (Sinervo and Zamudio 2001). Since the cycles by which male and female morphs maximize their fitness are not necessarily synchronous (Sinervo and Zamudio 2001), females could tune their choice in a much more complex way than accordingly only to their own strategy. For example, females might also take into account the strategy adopted by males in order to maximize fitness for their offspring. For example, in side-blotched lizards orange females are r-strategists, and territorial orange males are a convenient choice at low density since hatchlings will share increased aggression and will better perform in defending territories and resources. But this choice will give different output for sons if orange is the most frequent morph in males due to the negative frequency-dependent selection working on male strategies (Sinervo and Lively 1996). Thus, the optimal choice for orange females at low density should be dependent also on the relative abundance of male morphs.

Nevertheless, white females significantly associated with white males irrespective of the density treatment, while yellow females did not respond at all to the males' color. In a previous experiment using

a 3-choice experimental arena, we did not detect any association between male and female morphs (Sacchi et al. 2015). This second experiment showed a positive assortative mating, but solely in white morphs, conflicting with our previous observations. However, the conflict is in appearance only. The experiment we did in 2015 was designed to check the occurrence of assortative mating in all female morphs and was likely not powerful enough to detect assortative mating in 1 morph only, when compared with the other 2. Conversely, this new experiment compared only 2 morphs (those whose breeding strategy are better known), thus providing a more stringent tool in highlighting assortative mating. The 2 experiments combined make some kind of morph-specific assortative mating possible in common wall lizards: white females prefer white males, whereas the other 2 morphs do not associate with their corresponding colors or they select male traits that are not strictly related with male breeding strategy (Perez i de Lanuza et al. 2014). From an evolutionary point of view, a complex scenario emerges. Sexual selection could be actually working in *P. muralis* (at least in 1 morph), but it still remains to be determined whether this is enough to maintain the color polymorphism in this species. Positive assortative mating cannot maintain polymorphism alone (Wellenreuther et al. 2014). Indeed, assortative mating in white morph should promote divergence (until to speciation) if not counterbalanced by gene flow among morphs (Rosenblum et al. 2004; Rosenblum 2006). Given the lack of choice in yellow females, a disassortative mating in red females with a preference for white males could be enough to ensure gene flow between morphs and, thus, maintain polymorphism. Gene flow could be even maintained either in the absence of choice (random mating) with respect to male morphs, if yellow and red females (at least 1 of them) would select males based on male quality (e.g., traits that are costly to produce thus revealing "good genes" of male, Zahavi 1975, 1977) rather than on male strategy.

In conclusion, our results support the hypothesis that sexual selection might play a relevant role in maintenance of the color polymorphism in the common wall lizard, but new controlled experiments specifically designed to decoupling the effects of female mate choice on the fitness of both male and female morphs are needed to enhance our understanding of how sexual selection operates on the strategies adopted by morphs.

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References

- Alonzo SH, Sinervo BR, 2001. Mate choice games, context-dependent good genes, and genetic cycles in the side-blotched lizard *Uta stansburiana*. *Behav Ecol Sociobiol* 49:176–186.
- Bajer K, Molnár O, Török J, Herczeg G, 2010. Female European green lizards *Lacerta viridis* prefer males with high ultraviolet throat reflectance. *Behav Ecol Sociobiol* 64:2007–2014.

- Bauwens D, Verheyen RF, 1985. The timing of reproduction in the lizard *Lacerta vivipara*: differences between individual females. *J Herpetol* 19: 353–364.
- Calsbeek B, Hasselquist D, Clobert J, 2010. Multivariate phenotypes and the potential for alternative phenotypic optima in wall lizard *Podarcis muralis* ventral colour morphs. *J Evol Biol* 23:1138–1147.
- Corl A, Davis AR, Kuchta SR, Sinervo BR, 2010. Selective loss of polymorphic mating types is associated with rapid phenotypic evolution during morphic speciation. *PNAS* 107:4254–4259.
- Galeotti P, Sacchi R, Pellitteri-Rosa D, Bellati A, Cocca W et al., 2013. Colour polymorphism and alternative breeding strategies: effects of parent's colour morph on fitness traits in the common wall lizard. *Evol Biol* 40:385–394.
- Gray SM, McKinnon JS, 2007. Linking color polymorphism maintenance and speciation. *Trends Ecol Evol* 22:71–79.
- Healey M, Uller T, Olsson M, 2008. Variety is the spice of life: female lizards choose to associate with colour-polymorphic male dyads. *Ethology* 114: 231–237.
- Huyghe K, Vanhooydonck B, Herrel A, 2007. Morphology, performance, behavior and ecology of three color morphs in males of the lizard *Podarcis melisellensis*. *Int Comp Biol* 47:211–220.
- Lattanzio MS, Miles DB, 2014. Ecological divergence among colour morphs mediated by changes in spatial network structure associated with disturbance. *J Anim Ecol* 83:1490–1500.
- LeBas NR, Marshall NJ, 2000. The role of colour in signalling and male choice in the agamid lizard *Ctenophorus ornatus*. *Proc R Soc Lond B* 267: 445–452.
- McLean CA, Stuart-Fox DM, 2014. Geographic variation in animal colour polymorphisms and its role in speciation. *Biol Rev* 89:860–873.
- Pellitteri-Rosa D, Martín J, López P, Bellati A, Sacchi R et al., 2014. Chemical polymorphism in male femoral gland secretions matches polymorphic coloration in common wall lizards *Podarcis muralis*. *Chemoecology* 24:67–78.
- Pérez-Escudero A, Vicente-Page J, Hinz RC, Arganda S, de Polavieja GG, 2014. idTracker: tracking individuals in a group by automatic identification of unmarked animals. *Nat Methods* 11:743–748.
- Pérez i de Lanuza G, Carazo P, Font E, 2014. Colours of quality: Structural, but not pigment coloration informs about male quality in a polychromatic lizard. *Anim Behav* 90:73–81.
- Pérez i de Lanuza G, Carretero MA, Font E, 2017. Intensity of male-male competition predicts morph diversity in a colour polymorphic lizard. *Evolution* 71:1–9.
- Pérez i de Lanuza G, Font E, Carazo P, 2013. Color-assortative mating in a color-polymorphic lacertid lizard. *Behav Ecol* 24:273–279.
- R Core Team, 2016. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. URL <https://www.R-project.org/>.
- Rankin KJ, Mclean CA, Kemp DJ, Stuart-Fox DM, 2016. The genetic basis of discrete and quantitative colour variation in the polymorphic lizard, *Ctenophorus decresii*. *BMC Evol Biol* 16:179.
- Rosenblum EB, 2006. Convergent evolution and divergent selection: lizards at the White Sands Ecotone. *Am Nat* 167:1–15.
- Rosenblum EB, Hoekstra HE, Nachman MW, 2004. Adaptive reptile color variation and the evolution of the Mc1r gene. *Evolution* 58:1794–1808.
- Runemark A, Hansson B, Pafilis P, Valakos ED, Svensson EI, 2010. Island biology and morphological divergence of the Skyros wall lizard *Podarcis gaigeae*: a combined role for local selection and genetic drift on color morph frequency divergence? *BMC* 10:269.
- Sacchi R, Ghitti M, Scali S, Mangiacotti M, Zuffi MAL et al., 2015. Common wall lizard females *Podarcis muralis* do not actively choose males based on their colour morph. *Ethology* 121:1145–1153.
- Sacchi R, Pellitteri-Rosa D, Bellati A, Di Paoli A, Ghitti M et al., 2013. Colour variation in the polymorphic common wall lizard *Podarcis muralis*: an analysis using the RGB colour system. *Zool Anz* 252:431–439.
- Sacchi R, Pellitteri-Rosa D, Capelli A, Ghitti M, Di Paoli A et al., 2012. Studying the reproductive biology of the common wall lizard using ultrasonography. *J Zool* 287:301–310.
- Sacchi R, Pupin F, Gentilli A, Rubolini D, Fasola M et al., 2009. Male-male combats in a polymorphic lizard: Residency and size, but not color, affect fighting rules and contest outcome. *Aggress Behav* 35:274–283.
- Sacchi R, Rubolini D, Gentilli A, Pupin F, Razzetti E et al., 2007a. Morph-specific immunity in males of the common wall lizard *Podarcis muralis*. *Amphibia-Reptilia* 28:408–412.
- Sacchi R, Scali S, Pupin F, Gentilli A, Galeotti P et al., 2007b. Microgeographic variation of colour morph frequency and biometry of common wall lizards. *J Zool* 273:389–396.
- Scali S, Sacchi R, Azzusi M, Daverio S, Oppedisano T et al., 2013. Homeward bound: factors affecting homing ability in a polymorphic lizard. *J Zool* 289: 196–203.
- Sinervo BR, Bleay C, Adamopoulou C, 2001. Social causes of correlational selection and the resolution of a heritable throat color polymorphism in a lizard. *Evolution* 55:2040–2052.
- Sinervo BR, Lively CM, 1996. The rock-paper-scissors game and the evolution of alternative male strategies. *Nature* 380:240–243.
- Sinervo BR, Svensson EI, 2002. Correlational selection and the evolution of genomic architecture. *Heredity* 89:329–338.
- Sinervo BR, Zamudio KR, 2001. The evolution of alternative reproductive strategies: fitness differential, heritability, and genetic correlation between the sexes. *J Heredity* 92:198–205.
- Svensson EI, Sinervo BR, Comendant T, 2001. Condition, genotype-by-environment interaction, and correlational selection in lizard life-history morphs. *Evolution* 55: 2053–2069.
- Thompson CW, Moore IT, Moore MC, 1993. Social, environmental and genetic factors in the ontogeny of phenotypic differentiation in a lizard with alternative male reproductive strategies. *Behav Ecol Sociobiol* 33:137–146.
- Thompson CW, Moore MC, 1991. Syntopic occurrence of multiple dewlap color morphs in male tree lizards *Urosaurus ornatus*. *Copeia* 1991: 493–503.
- Wellenreuther M, Svensson EI, Hansson B, 2014. Sexual selection and genetic colour polymorphisms in animals. *Mol Ecol* 23:5398–5414.
- Zahavi A, 1975. Mate selection: a selection for a handicap. *J Theor Biol* 53: 205–214.
- Zahavi A, 1977. The cost of honesty, further remarks on the handicap principle. *J Theor Biol* 67:603–605.
- Zamudio KR, Sinervo BR, 2000. Fertilization as alternative male mating strategies. *Proc Nat Acad Sci USA* 97:14427–14432.