Evol Biol
DOI 10.1007/s11692-012-9222-3

RESEARCH ARTICLE

Colour Polymorphism and Alternative Breeding Strategies: Effects of Parent's Colour Morph on Fitness Traits in the Common Wall Lizard

Paolo Galeotti · Roberto Sacchi · Daniele Pellitteri-Rosa · Adriana Bellati · Walter Cocca · Augusto Gentilli · Stefano Scali · Mauro Fasola

Received: 9 November 2012 / Accepted: 21 December 2012

Abstract Colour polymorphism (CP) is widespread in animals, but mechanisms underlying morph evolution and maintenance are not completely resolved. In reptiles, CP is often genetically based and associated with alternative behavioural strategies, mainly in males for most cases. However, female colour morphs also display alternative reproductive strategies associated with behavioural and physiological traits, which may contribute to maintain CP in the population. Both sexes of the common wall lizard (*Podarcis muralis*) show three pure colour morphs, white, yellow and red. Here, we looked for the effects of male and female colour morphs on fitness traits of captive-breeding pairs. All yellow-throated females laid clutches of many small eggs and produced many light offspring, behaving as r-strategists, whereas white-throated females laid clutches of few large eggs and produced few heavy offspring, behaving as K-strategists. Red-throated females adopted a conditional Kr-strategy depending on their size/age. These basic female strategies were modulated in relation to mate morph: white females had the best fitness gain in terms of viable offspring when mated to red males; mating between yellow morphs yielded a greater breeding success than all other morph crosses, but also lighter offspring; finally, red females produced heavy progeny when paired with red or white males, and light offspring in pair with yellow males. Thus, correlation between CP and traits relevant to fitness combined with non-random mating, either assortative or disassortative, could increase the potential for CP to contribute to divergent evolution in the common wall lizard.

Keywords Clutch size · Colour polymorphism · Breeding strategies · Breeding success · Egg size · Morph combination · Kr-strategy · *Podarcis muralis*

Introduction

Identifying the processes maintaining both phenotypic and genetic variability in wild populations is a major challenge in conservation and evolutionary biology, since phenotypic variation is the raw material upon which natural and sexual selection work. A stimulating topic in this field research is to unravel the mechanisms that generate and maintain intra-specific colour variation, i.e. colour polymorphism (hereafter CP, Ford 1945), and its functions. In fact, although several processes definitely contribute to CP development and maintenance, such as genetic drift and gene flow, disruptive selection, heterosis, apostatic selection, sexual selection, sensory bias (Sinervo and Zamudio 2001; Galeotti et al. 2003; Roulin 2004; Gray and McKinnon 2007), their relative importance and/or how they might interact remain largely unknown. The functional significance of CP may be linked to the mechanism maintaining it (e.g. Widemo 1998). However, discrete colour signals as those found in polymorphic species, may represent non-adaptive correlates of physiological or fitness characters of selective value (Huxley 1955), or may simultaneously accomplish different functions, such as status signalling, crypsis, mimicry, thermoregulation and habitat use (Cooper and Burns 1987; Thompson and Moore

P. Galeotti (✉) · R. Sacchi · D. Pellitteri-Rosa · A. Bellati · W. Cocca · A. Gentilli · M. Fasola
Dipartimento di Scienze della Terra e dell'Ambiente, Laboratorio di Eco-Etologia, Università degli Studi di Pavia, Via Ferrata 9, 27100 Pavia, Italy
e-mail: galeozot@unipv.it

S. Scali
Museo Civico di Storia Naturale, C.so Venezia 55, 20121 Milan, Italy

1991; Martin and Forsman 1999; Weiss 2002; Andrés et al. 2002; Galeotti et al. 2003; Galeotti and Rubolini 2004; Lopez et al. 2004; Stuart-Fox et al. 2006).

If the expression of colour morphs is mainly under genetic control, as occurs in many taxa (mammals, Majerus and Mundy 2003; birds, Lank 2002; Mundy 2006; Nadeau et al. 2007; reptiles, Shine et al. 1998; anurans, Hoffman and Blouin 2000; fish, Gross 1985, 1991; insects, Majerus 1998), the costs of producing alternative colourations may be very similar (Roulin et al. 1998; Roulin and Dijkstra 2003). Therefore, rather than signal individual quality, discrete colour morphs may advertise different life history and behavioural traits (Lepetz et al. 2009), for example alternative reproductive strategies (fish, Hutchings and Myers 1994; reptiles, Rand 1988; birds, Tuttle 2003; insects, Ahnesjö and Forsman 2003). Alternative strategies among morphs may lead to evolution of morph-specific optimal trait combinations, which represent alternative solutions to fitness optimization in the face of trade-offs in resource allocation (Sinervo 2000; Roulin 2004). Eventually, this process may result in differences among morphs in morphological, physiological, life history or behavioural traits, such as body size, clutch size, immune function, and antipredatory behaviour, that may prelude to species divergence (Sinervo and Svensson 2002; Galeotti and Sacchi 2003; Sacchi et al. 2007a; Calsbeek et al. 2010).

Lizards offer an excellent model to investigate the evolution and maintenance of CP as they often show a high intraspecific variability of colour patterns (Cooper and Burns 1987; Rand 1992; Thompson et al. 1993; Forsman and Shine 1995; Sinervo and Lively 1996; Weiss 2002; Vercken et al. 2007). In many species, individuals occur in discrete, stable, mainly genetically-based colour morphs, which coexist at different equilibrium levels within the same population (Thompson and Moore 1991; Carpenter 1995; Sinervo and Lively 1996; Sinervo et al. 2001, 2006; Sacchi et al. 2007b). Since CP is often expressed only ventrally, rather than accomplishing antipredatory or thermoregulatory functions, it may be associated with alternative behavioural (territorial/reproductive) strategies in males as well as in females; these strategies may be cyclically favoured by different selection mechanisms (e.g. density- and frequency-dependent selection, *Uta stansburiana,* Sinervo and Lively 1996; Zamudio and Sinervo 2003; Sinervo et al. 2007; *Lacerta* [*Zootoca*] *vivipara,* Vercken et al. 2007; Sinervo et al. 2007).

In this study, we used the polymorphic common wall lizard (*Podarcis muralis*), as a model to investigate the relationships between colour morphs and breeding investment strategies. In this species both sexes exhibit three pure colour morphs differing in throat and belly colouration (i.e. red-, yellow- and white-throated, Sacchi et al. 2007b; Calsbeek et al. 2010, see Fig. 1 in Galeotti et al. 2010); in addition, two intermediate phenotypes (white-red and yellow–red) regularly occur in both sexes, and therefore a maximum of five morphs are recognizable in this species, the "white-yellow morph" representing in fact the sub-adult colour-phase of yellow individuals (Bellati 2012). Juveniles show monomorphic white ventral colour at hatching, while the final, adult colour pattern develops in the second year of life, when individuals attain sexual maturity (Cheylan 1988; Barbault and Mou 1988). Noteworthy, males are more coloured than females, which express colouration only on the throat and not on the belly.

Considering that CP is expressed ventrally in this lizard, colour pattern should be involved in social communication, possibly signalling life-history traits and related behavioural strategies, upon which reciprocal mate selection could be based (Galeotti and Sacchi 2003; Galeotti et al. 2010; Calsbeek et al. 2010). Alternatively, ventral CP may be simply a neutral or non-adaptive correlated trait of a physiologically or ecologically adaptive one.

In fact, ventral colour pattern in common wall lizards appears to be unimportant in inter-male fighting (Sacchi et al. 2009), thus not accomplishing any status-signalling function, at least among males. However, a morph-specific immune responsiveness in males of this species exists, since yellow morphs have a lower immune response compared to both red and white males, whose immune response is similarly high (Sacchi et al. 2007a). We also recently observed a morph-, sex- and size-specific susceptibility to stress measured by haematological variables in wall lizards kept in captivity for breeding experiments. Specifically, red and yellow females respond differently from white ones to long-term stressful conditions depending on individual size/age, and thus morphs have different physiological profiles (Galeotti et al. 2010).

Taken together, these findings suggest that multiple phenotypic optima exist in the population, and they may be associated with alternative behavioural or reproductive strategies, which in turn may be involved in the processes of maintaining CP in this species. In fact, coadapted trait complexes may arise from disruptive selection associated with colour-based assortative mating (Bolnick 2012; Bolnick and Kirkpatrick 2012).

Here, we present a 2-year study on captive breeding of wall lizards aimed to compare primary reproductive investments (clutch and egg size), and breeding success (viable young produced) among all pair-combinations of different colour morph individuals, in order to ascertain: (1) if morphs reflected different parental strategies as occurs in other lizards (Sinervo and Lively 1996; Sinervo et al. 2000, 2001, 2006, 2007), and (2) what are the effects of parental colour morphs on life-history traits, such as clutch size, egg size, breeding success and offspring quality.

Methods

Study Species

The common wall lizard is a small lizard (snout-vent length, SVL, 45–75 mm) widespread in southern and central Europe, which mates multiply and produces two clutches per year on average (range 1–3, Sacchi et al. 2012) during its life (max lifetime 5 years, Barbault and Mou 1988; pers. obs.). Breeding season extends from late February to July in our study areas (Northern Italy). Larger females lay larger clutches of smaller eggs and thus trade between quantitative and qualitative breeding investments (Barbault and Mou 1988; Ji and Braña 2000; Sacchi et al. 2012). Eggs are hidden in sandy substrates and neither parent provides parental care to progeny. Larger juveniles, hatching from larger eggs, show higher survival probability in the wild, as they exhibit faster growth, better condition in the autumn and improved survival during winter season (Van Damme et al. 1992).

Subjects and Housing

In spring 2009 and 2010 (February to March), we captured by noosing (i.e. using a slip knot of sewing thread attached to the end of a 2-m pole, Blomberg and Shine 1996) sexually mature lizards (SVL >50 mm, Sacchi et al. 2012) in 11 sites located in Pavia town and in the surroundings (Lombardy, Northern Italy, 80 m a.s.l.). Most of them were farms with cows and all have ancient brick walls plenty of shelters. In each site, we captured males and virgin females (i.e. females that had not mated yet in the current season as determined by the lack of male's scars on their belly, typically being present after copulation, Bauwens and Verheyen 1985), in order to obtain mating and egg laying in captivity. Each individual was measured by a digital calliper (accuracy ±0.1 mm) for SVL, weighed (accuracy ±0.1 g), and transferred to our laboratory within 2 h from capture (Table 1). Overall, we housed 124 adult lizards in 2009 and 128 lizards in 2010 for a total of 252 individuals (sex-ratio 1:1). Pairs were formed soon after the arrival to our laboratory (see "Experimental Design" below for details on pair formation) and maintained indoor under a natural light–dark cycle in transparent plastic jars ("mating jars", 20 × 30 × 20 cm, a pair per jar) provided with a newspaper sheet as substratum, a water tank and a shelter, and fed with 3 mealworms *Tenebrio molitor* each day. Mating jars were placed under an UV-B lamp (18 W) in order to provide the daily UV requirements for calcium and vitamin D fixation, and an incandescent lamp (25 W) for heating. UV lamps were switched on for 3 h a day (from 10.00 to 13.00), while incandescent lamps were set alight for 6 h a day (from 11.00 to 17.00).

Table 1 Means and (SE) of morphological measures of lizards collected in the 2 years of study (ANOVA test)

	2009	*n*	2010	*n*	*F*	*P*
SVL ♀ mm	62.58 (0.44)	62	60.36 (0.51)	64	10.69	0.001
Body mass ♀ g	5.2 (0.13)	62	4.6 (0.12)	64	11.29	0.001
SVL ♂	64.79 (0.58)	62	62.54 (0.54)	64	8.03	0.005
Body mass ♂	6.83 (0.18)	62	5.99 (0.14)	64	13.44	<0.001

At the end of the experiment (late June) all lizards were returned to their capture sites and all animals increased their body mass between capture and release (Galeotti et al. 2010).

Experimental Design

In this study, we used only pure colour morph individuals, which are more frequent in our populations than intermediates.

Each female, either white, yellow and red, was mated twice in the breeding season with two differently coloured males according to a balanced design, which included all the possible colour combinations between male and female morphs (3 × 3 = 9 colour morph combinations: WW, WY, WR, YW, YY, YR, RW, RY and RR, Table 2). We used the same males in both mating, but they were paired to a different female at each mating. After the first clutch was completed, the first-mating male was removed from the mating jar and held isolated for a week. Then, he was paired to a different female which had already completed its first clutch from at least a week. Pairs were assorted at random as far as size and body mass were concerned.

Each mating jar was supplied with a small plastic box (10 × 10 × 5 cm) filled by wet sand to allow egg laying.

Table 2 Experimental design: list of colour morph breeding combinations for common wall lizards used in this study

Female	First-mating male	Second-mating male
White	Red	Yellow
Red	Yellow	White
Yellow	White	Red
White	White	Red
Red	Red	Yellow
Yellow	Yellow	White
White	Yellow	White
Red	White	Red
Yellow	Red	Yellow

Table 3 Number and (%) of clutches according to colour mating combinations (e.g. WW: white female × white male, WY: white female × yellow male, and so on)

	Mating combinations									
	WW	WY	WR	YW	YY	YR	RW	RY	RR	Total
Laid clutches	26	27	25	23	25	23	23	20	18	210
Fertile clutches	23 (88)	27 (100)	21 (84)	20 (87)	21 (84)	22 (96)	22 (96)	20 (100)	17 (94)	193
Successful clutches	10 (43.5)	12 (44)	12 (57)	12 (60)	16 (76)	11 (50)	11 (50)	10 (50)	10 (59)	104

Boxes were carefully checked for eggs every morning, and laid eggs were gently removed, measured with a digital calliper (major diameter to the nearest 0.01 mm) and weighed (Sartorius R200D balance, accuracy 0.01 mg). Mean laying date for first clutches was 3 May in 2009, and 28 April in 2010, while for second clutches was 6 June in 2009 and 31 May in 2010. Overall, from 252 matings, we collected 229 clutches (2009: 108; 2010: 121), because 23 pairs (equally distributed among all colour combinations) failed to produce eggs (2009: 16; 2010: 7). Since we considered only pairs producing eggs in both matings, 19 further pairs (equally distributed among all colour combinations) were excluded due to failure in one or the other mating (12 in 2009 and 7 in 2010). Thus, our final sample comprised 210 clutches, 105 first clutches and 105 second clutches (numbers of clutches per colour combinations are reported in Table 3). Egg weight and egg length were collected for 193 clutches, because 17 clutches were wholly formed by decayed (presumably unfertilized) eggs and were not measured.

Fertile eggs of each clutch were inserted in small plastic tubes (an egg per tube) filled by wet sand and incubated at +28 °C (incubator MG316/REP). Hatched young were collected from 104 clutches, because 89 clutches failed to hatch; offspring were weighed, measured and photographed following standard techniques (Sacchi et al. 2010). Breeding success was estimated as the ratio of hatched young over fertile (and incubated) eggs produced by females.

Statistical Analyses

Preliminarily, we ran a Wilcoxon test for matched pairs to check for differences in reproductive parameters between the first and the second mating effected by the same female with two different males.

The relationships between normally distributed reproductive parameters (clutch size, fertile eggs, egg mass, egg size, newborn mass) and male and female colour morph were investigated separately by mixed models analyses (REML method), using collection year, female collection site and female identity as random factors, mating order (first or second) and colour morph of male and female as fixed factors. We also included female SVL as a covariate, since it is known that female size influences clutch size in this species (Ji and Braña 2000; Sacchi et al. 2012). All main effects and two-way interactions male morph × female morph, female morph × SVL, and mating × male morph (to take in account male turn-over between matings) were included in the models.

Breeding success (hatched young/fertile eggs) showed a binomial distribution and thus its relationship with male and female colour morph were investigated by a GLMM analysis with binomial error distribution and logit function. We included in the model the same factors and covariates as well as their interactions as above. Models were not subjected to any simplification procedure in order to reduce type 1 error.

Analyses were performed using SPSS 18.0, and R 2.14 (R Development Core Team 2011) statistical packages. Unless otherwise stated, parameter estimates and mean values are reported together with associated SE.

Results

All reproductive parameters, but egg length, differed significantly between first and second clutches, showing a general decline in all measures (Table 4). In both clutches, females traded egg size against egg number ($r_p = -0.554$ and -0.599, respectively, $P < 0.0001$, $n_1 = 100$, $n_2 = 93$).

The mixed model confirmed the decline in clutch size from first to second mating, and showed a significant effect of female morph × SVL interaction on clutch size (Table 5). Specifically, clutch size increased with female SVL in all morphs (white females: estimate 0.082 ± 0.03, $t = 2.73$, $P = 0.008$; yellow females: estimate 0.111 ± 0.03, $t = 3.40$, $P = 0.001$; red females: estimate 0.207 ± 0.04, $t = 5.44$, $P < 0.0001$), but yellow females of any size laid consistently more eggs than white females of any size; on the other hand, small red females laid significantly smaller clutches than the other morphs, while large red females laid larger clutches than the other morphs (Fig. 1). All random factors were non significant (P values >0.54), except for female identity (*Wald* $Z = 1.984$, $P = 0.047$).

Table 4 Breeding parameters for female lizards producing both first and second clutches (Wilcoxon test for matched pairs, *n* is the number of clutches, means are reported for simplicity)

	I° mating			II° mating			Z	P
	n	Mean	SE	*n*	Mean	SE		
Clutch size (*n*)	105	4.30	0.122	105	3.69	0.100	−4.698	**<0.001**
Fertile eggs (*n*)	100	4.10	0.145	93	3.47	0.109	−3.814	**<0.001**
Egg mass (g)	100	0.325	0.005	93	0.297	0.005	−4.247	**<0.001**
Egg length (mm)	100	11.45	0.079	93	11.28	0.088	−1.374	0.169
Hatched young (*n*)	65	3.62	0.188	39	2.72	0.172	−2.359	**0.018**
Breeding success	100	0.54	0.044	93	0.34	0.046	−3.291	**0.001**
Juvenile mass (g)	65	0.361	0.006	39	0.315	0.008	−3.484	**<0.001**

Significant values are in bold

Egg weight significantly decreased according to mating while increasing with female SVL, large females of all morphs, but red, producing heavier eggs than smaller females. No effects of male or female colour morph singly or in combination were evident (Table 5). All random factors were non significant (all P values >0.15).

Concerning egg length, the mixed model showed a significant effect of female morph × SVL interaction, i.e. egg size decreased with body size in red females (estimate -0.110 ± 0.03, $t = -3.715$, $P < 0.0001$), so that large red females laid smaller eggs while small red females laid larger eggs than both white and yellow females (Table 5; Fig. 2). This suggested an age-modulated strategy of breeding investments in red females. All random factors were non significant (all P values >0.11).

The number of fertile eggs (the productive clutch size) declined according to mating, and increased with female SVL (Table 5). Interestingly, there was an effect of female morph × male morph interaction on the number of fertile eggs, that is, white females laid significantly more fertile eggs when paired to red males than when paired to white male morphs (WR vs. WW: mean difference = 1.012, $P = 0.009$, LSD post hoc comparison); yellow females laid fewer fertile eggs when paired to red males than when paired to yellow male morphs (YR vs. YY: mean difference = −1.019, $P = 0.009$, LSD post hoc comparison); finally, red females tended to lay fewer fertile eggs when paired to yellow males than to other male morphs (RY vs. RW: mean difference = −0.636, $P = 0.105$; RY vs. RR: mean difference = −0.550, $P = 0.171$, LSD post hoc comparison; Fig. 3). All random factors were non significant (P values >0.56), except for female identity (*Wald* $Z = 1.96$, $P = 0.048$).

Breeding success (number of hatched eggs/fertile eggs) declined significantly from the first mating to the second one ($\beta = -2.36 \pm 0.60$., $Z = -3.94$, $P < 0.0001$) irrespective of male morph (logLik-$\chi^2 = 0.12$, $df = 2$, $P = 0.94$). Also, the interaction female morph × female SVL did not affect the breeding success (logLik-$\chi^2 = 0.073$, $df = 2$, $P = 0.96$), but there was a significant combined effect of female morph × male morph (logLik-$\chi^2 = 13.56$, $df = 4$, $P = 0.009$); in particular, yellow females produced significantly more viable offspring when mated to yellow males than to other male morphs (yellow female × yellow male: $\beta = 5.80 \pm 7.55$; yellow female × white male: $\beta = -2.43 \pm 0.77$, $Z = -3.15$, $P = 0.002$; yellow female × red male: $\beta = -1.75 \pm 0.81$, $Z = -2.16$, $P = 0.031$), while white and red females did not significantly vary their breeding success according to male morph (Fig. 4). In addition, the breeding success varied significantly in relation to female identity (logLik-$\chi^2 = 134.33$, $df = 1$, $P < 0.0001$) and to year of experiment (logLik-$\chi^2 = 5.34$, $df = 1$, $P = 0.021$), being higher in the first year of the study.

The mass of newborn young was affected by mating × male morph interaction, yellow males producing lighter offspring in their first clutches than the other male morphs (Table 5; Fig. 5a), and by male morph × female morph. In particular, yellow × yellow individuals produced lighter offspring than the mating crosses between white × red individuals (YY vs. WR: mean difference = −0.047, $P = 0.031$; YY vs. RW: mean difference = −0.052, $P = 0.018$, LSD post hoc comparison) and between red × red individuals (YY vs. RR: mean difference = −0.051, $P = 0.024$, LSD post hoc comparison); on the other hand, red females tended to produce lighter offspring when paired to yellow males than to other male morphs (RY vs. RW: mean difference = −0.046, $P = 0.054$; RY vs. RR: mean difference = −0.045, $P = 0.065$, LSD post hoc comparison, Fig. 5b). Finally, and most significantly, offspring mass was also influenced by female morph × SVL interaction (Table 5); newborn mass increased with female SVL in white and yellow females (white females: estimate 0.005 ± 0.002, $t = 2.47$, $P = 0.016$; yellow females: estimate 0.004 ± 0.002, $t = 2.04$, $P = 0.045$), while the opposite occurred in red females, with small females producing heavier offspring than large females (red females: estimate -0.006 ± 0.003, $t = -2.37$, $P = 0.021$, Fig. 5c). This last result was in accordance with the age-dependent investment in primary breeding efforts (clutch size and egg size) of red females. All random factors were non significant (all P values >0.746), except for female identity (*Wald* $Z = 3.104$, $P = 0.002$).

Table 5 Mixed model analyses of main reproductive traits of common wall lizards in relation to mating, male and female morph, female SVL and their interactions

Model	*F*	*df*	*P*
(a) Clutch size			
Mating	24.917	1.98	**<0.001**
Female morph	3.174	2.98	**0.046**
Male morph	0.217	2.139	0.806
Female SVL	47.593	1.96	**<0.001**
Female morph × male morph	1.360	4.139	0.251
Female morph × SVL	3.392	2.97	**0.038**
Mating × male morph	0.519	2.177	0.596
(b) Fertile eggs			
Mating	18.389	1.87	**<0.001**
Female morph	1.587	2.93	0.210
Male morph	0.137	2.123	0.872
Female SVL	32.808	1.90	**<0.001**
Female morph × male morph	4.256	4.123	**0.003**
Female morph × SVL	1.731	2.93	0.183
Mating × male morph	0.696	2.164	0.500
(c) Mean egg mass			
Mating	22.233	1.90	**<0.001**
Female morph	1.871	2.94	0.160
Male morph	0.575	2.130	0.564
Female SVL	8.773	1.90	**0.004**
Female morph × male morph	0.705	4.131	0.590
Female morph × SVL	1.988	2.94	0.143
Mating × male morph	1.102	2.157	0.335
(d) Mean egg length			
Mating	3.862	1.86	0.053
Female morph	7.435	2.90	**0.001**
Male morph	1.588	2.125	0.208
Female SVL	3.802	1.86	0.054
Female morph × male morph	0.705	4.125	0.590
Female morph × SVL	7.493	2.89	**0.001**
Mating × male morph	2.377	2.159	0.096
(e) Mean juvenile mass			
Mating	49.495	1.25	**<0.001**
Female morph	6.041	2.61	**0.004**
Male morph	3.251	2.45	**0.048**
Female SVL	0.567	1.61	0.454
Female morph × male morph	2.949	4.30	**0.036**
Female morph × SVL	5.938	2.61	**0.004**
Mating × male morph	4.141	2.82	**0.019**

Random effects are reported in the "Results" section

Significant values are in bold

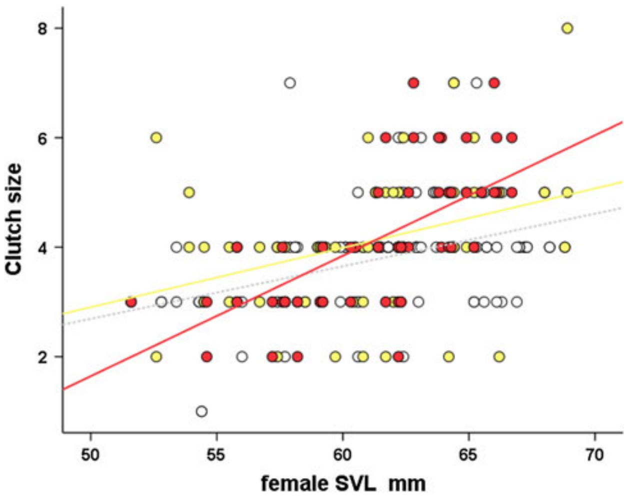

Fig. 1 Variation in clutch size of common wall lizards according to female morph and body size (SVL). *Colour dots* indicate the relative morph, *white*, *yellow* and *red*. *Regression lines* for each morph are also showed (*dashed grey line* indicates white morph)

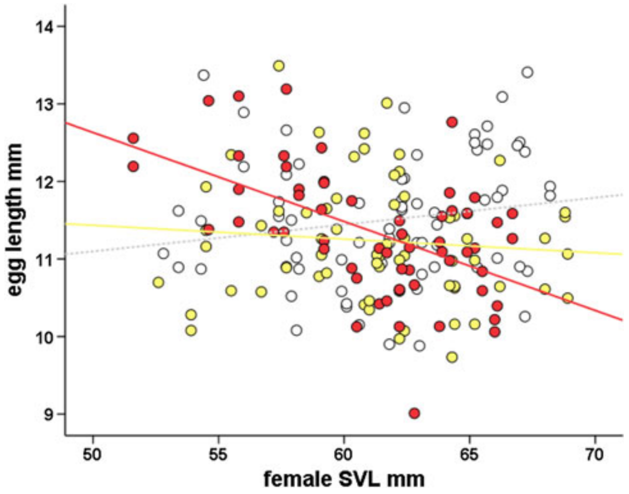

Fig. 2 Variation in egg length (major diameter) of common wall lizard according to female morph and SVL. *Colour dots* indicate the morph. *Regression lines* for each morph are also showed (*dashed grey line* indicates white morph)

Discussion

In this paper, we analysed the variation of investments in reproductive life-history traits among all possible colour morph mating combinations of the common wall lizard, and estimated the effects of parental colour morph on traits relevant to fitness.

First of all, our study revealed an association between female colour morph and primary reproductive efforts, namely clutch size and egg size (Sinervo 2001), after controlling for female SVL. Indeed, we found that yellow females produced always larger clutches of smaller eggs than white females independently of size; conversely red females laid smaller clutch of larger eggs or larger clutches of smaller eggs depending on their own body size (SVL), and therefore on their age (Stamp and Krishnan 1998). In

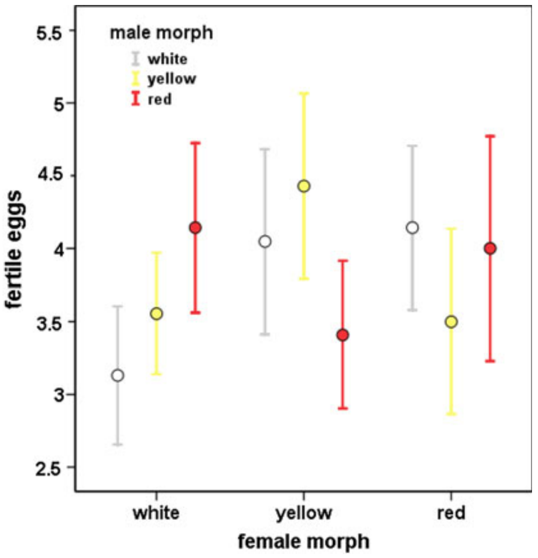

Fig. 3 Mean number of fertile eggs produced by the different *colour* morph mating combinations. *Bars* represent 95 % confidence intervals of the mean

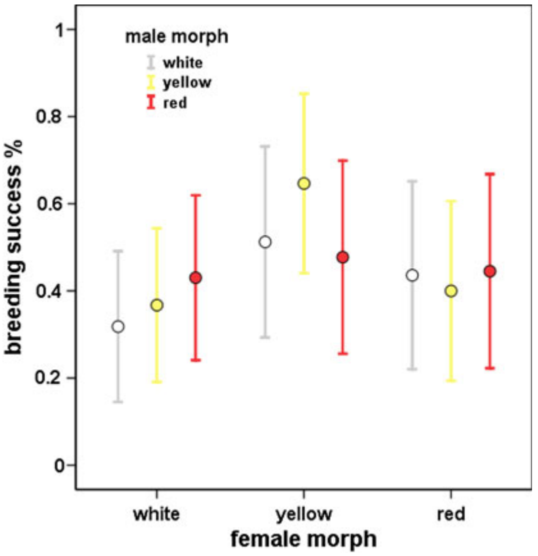

Fig. 4 Mean breeding success (no. of viable young/fertile eggs) of the different *colour* morph mating combinations. *Bars* represent 95 % confidence intervals of the mean

short, yellow females seemingly behaved as pure r-strategists and white females as pure K-strategists independently of size/age, while red females behaved as super K-strategists when small and as super r-strategists when large. Thus, red morph females were seemingly adopting a mixed, age-dependent Kr-strategy of reproductive allocation. The populations of wall lizards under study appeared therefore to be composed of two alternative pure-strategists (white and yellow females) and by mixed-strategists (red females). At low population density, r-strategists, i.e. yellow-throated females of any age and old red females, producing many small eggs (and lighter progeny) should be favoured when the intrinsic rate of increase, r, governs population growth, as occurs for example after a population crash (Pianka 1970; Sinervo et al. 2000). At peak density, white-throated females and young red-throated females, the K-strategists, producing fewer larger eggs (and large-mass progeny) should be favoured when the carrying capacity, K, is exceeded and the population crashes. In any case, if habitat conditions fluctuate over time and space favouring alternately a given breeding strategy and the associated morph, CP might be maintained over time, and morphs may coexist with different equilibrium levels according to density-dependent selection experienced in the different environmental conditions, as already reported for common and side-blotched lizards (Sinervo et al. 2000, 2001; Vercken et al. 2007).

Second and most interesting, our study showed that these basic female strategies were modulated in relation to mate colour morph. In particular, while primary reproductive efforts (clutch and egg size) were apparently a female's affair only in this lizard, indicating no occurrence of female differential allocation in relation to male phenotype, important effects of male morph were evident when considering the other breeding traits relevant to fitness. Actually, the productive clutch size (fertilized eggs within each clutch), the hatching success (viable offspring) and the newborn quality (juvenile mass) varied according to morph mating assortment, some colour combinations working significantly better than others. Specifically, the better crosses in terms of productive clutch size were those between white × red individuals, yellow × yellow individuals and red × red individuals, while the worst was that between white × white and yellow × red colour morphs. Mating cross between yellow individuals led to the highest number of viable offspring than all other mating combinations, but also to a lighter progeny than those between red × red and red × white individuals; this was not surprising since yellow females behaved as pure r-strategists at any age. On the other hand, red females produced lighter or heavier offspring as a consequence of the mixed Kr-strategy they adopted depending on age (Fig. 5c).

Taken together, these results highlighted four points: (a) yellow × yellow mating combination had the highest hatching success, but produced also the lightest offspring; i.e. a progeny of low quality since mass at birth enhances offspring survival in species without parental care such as the common wall lizard, (b) white × red crosses produced mean numbers of large offspring, (c) red × red mating produced many light or few large offspring depending on female age, (d) white × white and red × yellow crosses appeared to be the worst mating combinations, since produced relatively few and light offspring. Therefore, we may hypothesize that white lizards should mate disassortatively in the wild (red favoured), while yellow individuals assortatively, and red individuals should adopt a mix of assortative and disassortative (white favoured) mating to obtain the best fitness gain. On the other hand, red individuals should avoid mating with yellow individuals and viceversa. Noteworthy, our conclusions agree with previous studies, which demonstrated assortative mating according to colour morph in other *Podarcis* species (e.g. *Podarcis melisellensis*, Huyghe et al. 2010). This non-random mating in the population of the common wall lizard, beside helping to maintain CP, may enhance genetic divergence in sympatry among morphs (Huyghe et al. 2010). Recent results from genetic structure analysis on the populations under study strongly suggests the presence of partly distinct reproductive groups based on colour within the same population (i.e. yellow morph shows a significant genetic divergence from both white and red morphs, Bellati 2012).

To the best of our knowledge, this is the first study documenting differential effects of parental colour morphs on primary and secondary reproductive efforts of a polymorphic lizard species. Correlation between CPs and traits relevant to fitness combined with non-random mating, either assortative or disassortative, could increase the potential for CP to contribute to divergent evolution in the common wall lizard, which may be considered as an evolutionarily dynamic species. In case of morph-specific habitat use (red morphs are more frequent in natural habitats and at higher altitude, Sacchi et al. 2007b) and reduced gene flow between habitats, spatial segregation may lead to monomorphic metapopulations (Van Valen and Grant 1970; Gray and McKinnon 2007) and sympatric species differentiation could eventually be promoted according to "morphic" speciation (Corl et al. 2010).

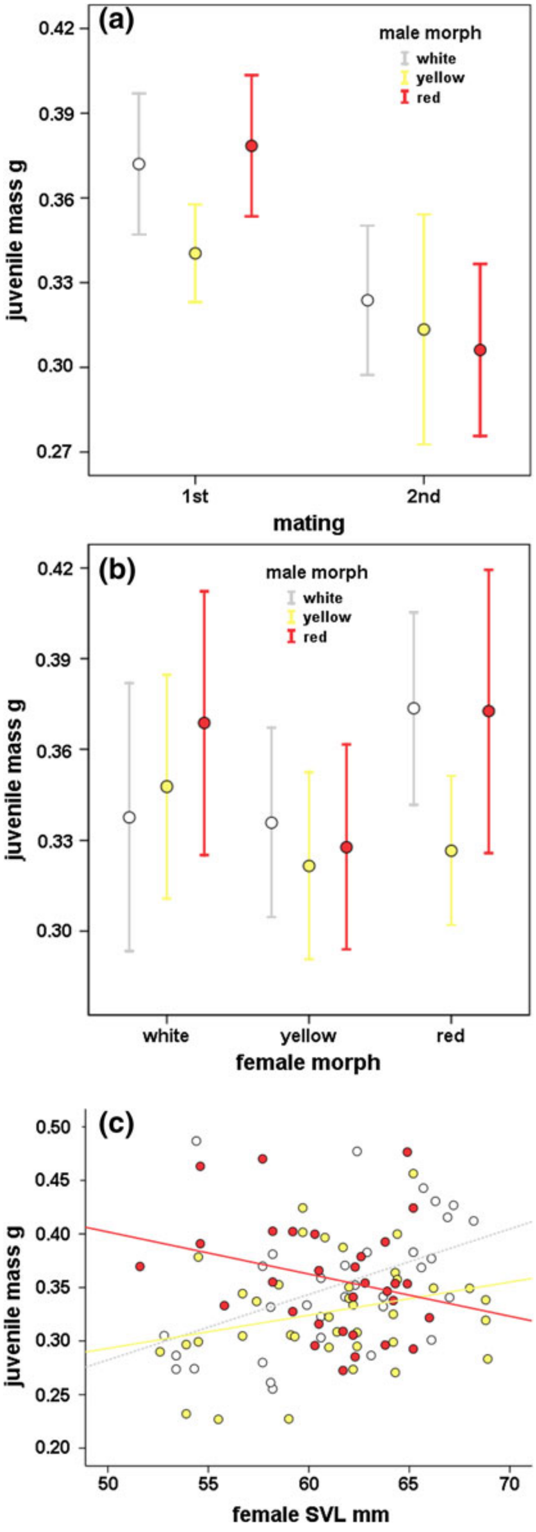

Fig. 5 **a** Mean mass (g) of juveniles originating from first and second mating of different male colour morphs; *bars* represent 95 % confidence intervals of the mean. **b** Mean mass of juveniles produced by the different *colour* morph mating combinations; *bars* represent 95 % confidence intervals of the mean. **c** Variation in juvenile mass according to female morph and SVL. *Colour dots* indicate the morph. *Regression lines* for each morph are also showed (*dashed grey line* indicates white morph)

Acknowledgments We wish to thank Drs. F. Pupin, M. Melpignano, and M. Teofilo Pignati for their help with field and laboratory work. Many thanks are also due to Prof. M. B. Rasotto for her useful comments on an early draft of the paper. Research was supported by PhD grants (Doctorate in Experimental Ecology and Geobotany) from the University of Pavia to D. P.-R. and A. B. The study was carried out in conformity with the Italian current laws for lizard collection and detention.

Ethical note The study was carried out with the agreement of the Ministero dell'Ambiente Italiano (Aut. Prot. DPN no. 2009-0016034, validity 2009–2011).

References

Ahnesjö, J., & Forsman, A. (2003). Correlated evolution of colour pattern and body size in polymorphic pygmy grasshoppers, *Tetrix undulata*. *Journal of Evolutionary Biology, 16*, 1308–1318.

Andrés, J. A., Sanchez-Guillén, R. A., & Cordero-Rivera, A. (2002). Evolution of female colour polymorphism in damselflies: Testing the hypotheses. *Animal Behaviour, 63*, 677–685.

Barbault, R., & Mou, Y. P. (1988). Population dynamics of the common wall lizard, *Podarcis muralis*, in southwestern France. *Herpetologica, 44*, 38–47.

Bauwens, D., & Verheyen, R. F. (1985). The timing of reproduction in the lizard *Lacerta vivipara*: Differences between individual females. *Journal of Herpetology, 19*, 353–364.

Bellati, A. (2012). *Intra-and inter-population analysis of colour polymorphism in Podarcis muralis* (*Sauria: Lacertidae*) *using mitochondrial and nuclear markers*. PhD thesis, University of Pavia.

Blomberg, S., & Shine, R. (1996). Reptiles. In W. J. Sutherland (Ed.), *Ecological census techniques: A handbook* (pp. 218–226). Cambridge: Cambridge University Press.

Bolnick, D. I. (2012). Sympatric speciation in threespine stickleback: Why not? *International Journal of Ecology, 2011* (Article ID 942847), 15. doi:10.1155/2011/942847.

Bolnick, D. I., & Kirkpatrick, M. (2012). The relationship between intraspecific assortative mating and reproductive isolation between divergent populations. *Current Zoology, 58*, 484–492.

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.

Carpenter, G. C. (1995). Modeling dominance: The influence of size, coloration, and experience on dominance relations in tree lizards (*Urosaurus ornatus*). *Herpetological Monographs, 9*, 88–101.

Cheylan, M. (1988). Variabilité phénotypique du Lézard des murailles *Podarcis muralis* sur les îles de la côte provençale, France. *Revue d'Ecologie-Terre et Vie, 43*, 287–321.

Cooper, W. E., & Burns, N., Jr. (1987). Social significance of ventrolateral coloration in the fence lizard, *Sceloporus undulatus*. *Animal Behaviour, 35*, 526–532.

Corl, A., Davis, A. R., Kuchta, S. R., & Sinervo, B. (2010). Selective loss of polymorphic mating types is associated with rapid phenotypic evolution during morphic speciation. *Proceedings of the National Academy of Sciences United States of America, 107*, 4254–4259.

Ford, E. B. (1945). Polymorphism. *Biological Reviews and Biological Proceedings of the Cambridge Philosophical Society, 20*, 73–88.

Forsman, A., & Shine, R. (1995). The adaptive significance of colour pattern polymorphism in the Australian scincid lizard *Lampropholis delicata*. *Biological Journal of Linnean Society, 55*, 273–291.

Galeotti, P., Pellitteri-Rosa, D., Sacchi, R., Gentilli, A., Pupin, F., Rubolini, D., et al. (2010). Sex, morph- and size-specific susceptibility to stress measured by haematological variables in captive common wall lizard *Podarcis muralis*. *Comparative Biochemistry and Physiology A, 157*, 354–363.

Galeotti, P., & Rubolini, D. (2004). The niche variation hypothesis and the evolution of colour polymorphism in birds: A comparative study of owls, nightjars and raptors. *Biological Journal of Linnean Society, 82*, 237–248.

Galeotti, P., Rubolini, D., Dunn, P. O., & Fasola, M. (2003). Colour polymorphism in birds: Causes and functions. *Journal of Evolutionary Biology, 16*, 635–646.

Galeotti, P., & Sacchi, R. (2003). Differential parasitaemia in the tawny owl (*Strix aluco*): Effect of colour morph and habitat. *Journal of Zoology, 261*, 91–99.

Gray, S. M., & McKinnon, J. S. (2007). Linking color polymorphism maintenance and speciation. *Trends in Ecology & Evolution, 22*, 71–79.

Gross, M. R. (1985). Disruptive selection for alternative life history in salmon. *Nature, 313*, 47–48.

Gross, M. R. (1991). Evolution of alternative reproductive strategies: Frequency-dependent sexual selection in male bluegill sunfish. *Philosophical Transaction of the Royal Society B, 1262*, 59–66.

Hoffman, E. A., & Blouin, M. S. (2000). A review of colour and pattern polymorphisms in anurans. *Biological Journal of the Linnean Society, 70*, 633–665.

Hutchings, J. A., & Myers, R. A. (1994). The evolution of alternative mating strategies in variable environments. *Evolutionary Ecology, 8*, 256–268.

Huxley, J. S. (1955). *Morphism in birds. Acta 6th international ornithological congress* (pp. 309–328). XI Basel 1954.

Huyghe, K., Small, M., Vanhooydonck, V., Herrel, A., Tadic, Z., Van Damme, R., et al. (2010). Genetic divergence among sympatric colour morphs of the Dalmatian wall lizard (*Podarcis melisellensis*). *Genetica, 138*, 387–393.

Ji, X. A., & Braña, F. (2000). Among clutch variation in reproductive output and egg size in the wall lizard (*Podarcis muralis*) from a lowland population of northern Spain. *Journal of Herpetology, 34*, 54–60.

Lank, D. B. (2002). Diverse processes maintain plumage polymorphisms in birds. *Journal of Avian Biology, 4*, 327–330.

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

Lopez, P., Martin, J., & Cuadrado, M. (2004). The role of lateral blue spots in intrasexual relationships between male Iberian rock-lizards, *Lacerta monticola*. *Ethology, 110*, 543–561.

Majerus, M. N. (1998). *Melanism: Evolution in action*. Oxford: Oxford University Press.

Majerus, M. N., & Mundy, N. I. (2003). Mammalian melanism: Natural selection in black and white. *Trends in Genetics, 19*, 585–588.

Martin, J., & Forsman, A. (1999). Social costs and development on nuptial coloration in male *Psammodromus algirus* lizards: An experiment. *Behavioral Ecology, 10*, 396–400.

Mundy, N. Y. (2006). Genetic basis of color variation in wild birds. In G. E. Hill & K. J. McGraw (Eds.), *Bird coloration, mechanisms and measurements* (pp. 469–506). Cambridge, USA: Harvard University Press.

Nadeau, N. J., Burke, T., & Mundy, N. I. (2007). Evolution of an avian pigmentation: Gene correlates with a measure of sexual selection. *Proceedings of the Royal Society of London Series B-Biological Sciences, 274*, 1807–1813.

Pianka, E. R. (1970). On r- and K-selection. *American Naturalist, 104*, 592–597.

R Development Core Team. (2011). *R: A language and environment for statistical computing*. Vienna, Austria: The R Foundation for Statistical Computing. ISBN: 3-900051-07-0. Available online at http://www.R-project.org/.

Rand, M. S. (1988). Courtship and aggressive behavior in male lizards exhibiting two different sexual colorations. *American Zoologist, 28*, 153A.

Rand, M. S. (1992). Hormonal control of polymorphic and sexually dimorphic coloration in the lizard *Sceloporus undulatus erythrocheilus*. *General and Comparative Endocrinology, 88*, 461–468.

Roulin, A. (2004). The evolution, maintenance and adaptive function of genetic colour polymorphism in birds. *Biological Review, 79*, 1–34.

Roulin, A., & Dijkstra, C. (2003). Genetic and environmental components of variation in eumelanin and phaeomelanin sex-traits in the barn owl. *Heredity, 90*, 359–364.

Roulin, A., Richner, H., & Ducrest, A. L. (1998). Genetic, environmental, and condition-dependent effects on female and male ornamentation in the barn owl *Tyto alba*. *Evolution, 52*, 1451–1460.

Sacchi, R., Pellitteri-Rosa, D., Capelli, A., Ghitti, M., Di Paoli, A., Bellati, A., et al. (2012). Studying the reproductive biology of the common wall lizard using ultrasonography. *Journal of Zoology, 287*, 301–310.

Sacchi, R., Pupin, F., Gentilli, A., Rubolini, D., Scali, S., Fasola, M., et al. (2009). Male-male combats in a polymorphic lizard: Residency and size, but not color, affect fighting rules and contest outcome. *Aggressive Behaviour, 35*, 274–283.

Sacchi, R., Rubolini, D., Gentilli, A., Pupin, F., Razzetti, E., Scali, F., 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., & Fasola, M. (2007b). Microgeographic variation of colour morph frequency and biometry of common wall lizards. *Journal of Zoology, 273*, 389–396.

Sacchi, R., Scali, S., Pellitteri-Rosa, D., Pupin, F., Gentilli, A., Tettamanti, S., et al. (2010). Photographic identification in reptiles: A matter of scales. *Amphibia Reptilia, 31*, 489–502.

Shine, R., Ambariyanto, Harlow, P. S., & Mumpuni. (1998). Ecological divergence among sympatric colour morphs in blood pythons, *Python brongersmai*. *Oecologia, 116*, 113–119.

Sinervo, B. (2000). Adaptation, natural selection, and optimal life history allocation in the face of genetically-based trade-offs. In T. Mousseau, B. Sinervo, & J. A. Endler (Eds.), *Adaptive genetic variation in the wild* (pp. 41–64). Oxford: Oxford University Press.

Sinervo, B. (2001). Runaway social games, genetic cycles driven by alternative male and female strategies, and the origin of morphs. *Genetica, 112–113*, 417–434.

Sinervo, B., 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, B., Calsbeek, R., Comendant, T., Both, C., Adamopoulou, C., & Clobert, J. (2006). Genetic and maternal determinants on effective dispersal: The effect of sire genotype and size at birth in side-blotched lizards. *American Natutalist, 168*, 88–99.

Sinervo, B., Heulin, B., Surget-Groba, Y., Clobert, J., Miles, D. B., Corl, A., et al. (2007). Models of density-dependent genic selection and a new rock-paper-scissors social system. *American Naturalist, 170*, 663–680.

Sinervo, B., & Lively, C. M. (1996). The rock–paper–scissors game and the evolution of alternative mating strategies. *Nature, 380*, 240–243.

Sinervo, B., & Svensson, E. (2002). Correlational selection and the evolution of genomic architecture. *Heredity, 89*, 329–338.

Sinervo, B., Svensson, E., & Comendant, T. (2000). Density cycles and an offspring quantity and quality game driven by natural selection. *Nature, 406*, 985–988.

Sinervo, B., & Zamudio, K. R. (2001). The evolution of alternative reproductive strategies: Fitness differential, heritability, and genetic correlation between sexes. *Journal of Heredity, 92*, 198–205.

Stamps, J. A., & Krishnan, V. V. (1998). Territory acquisition in lizards: I First encounters. *Animal Behaviour, 47*, 1375–1385.

Stuart-Fox, D. M., Firth, D., & Whiting, M. J. (2006). Multiple signals in chameleon contests: Designing and analysing animal contests as a tournament. *Animal Behaviour, 71*, 1263–1271.

Thompson, C. W., & Moore, M. C. (1991). Synthopic occurrence of multiple dewlap color morphs in male Tree Lizards, *Urosaurus ornatus*. *Copeia, 1991*, 493–503.

Thompson, C. W., Moore, I. T., & Moore, M. C. (1993). Social, environmental and genetic factors in the ontogeny of phenotypic differentiation in a lizard with alternative male reproductive strategies. *Behavioral Ecology and Sociobiology, 33*, 137–146.

Tuttle, E. M. (2003). Alternative reproductive strategies in the white-throated sparrow: Behavioral and genetic evidence. *Behavioral Ecology, 14*, 425–432.

Van Damme, R., Bauwens, D., Braña, F., & Verheyen, R. F. (1992). Incubation temperature differentially affects hatching time, egg survival, and hatchling performance. *Herpetologica, 48*, 220–228.

Van Valen, L., & Grant, P. R. (1970). Variation and niche width reexamined. *American Naturalist, 104*, 589–590.

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.

Weiss, S. L. (2002). Reproductive signals of female lizards: Pattern of trait expression and male response. *Ethology, 108*, 793–813.

Widemo, F. (1998). Alternative reproductive strategies in the ruff, *Philomachus pugnax*: A mixed ESS? *Animal Behaviour, 56*, 329–336.

Zamudio, K. R., & Sinervo, B. (2003). Ecological and social contexts for the evolution of alternative mating strategies. In S. F. Fox, J. K. McCoy, & T. A. Baird (Eds.), *Lizard social behavior* (pp. 83–106). Baltimore and London: John Hopkins University Press.