Oecologia (2010) 162:49–58
DOI 10.1007/s00442-009-1442-6

POPULATION ECOLOGY - ORIGINAL PAPER

Frequency-dependent reproductive success in female common lizards: a real-life hawk–dove–bully game?

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Received: 3 February 2009 / Accepted: 1 August 2009 / Published online: 17 September 2009

Abstract Alternative strategies are characterised by context-dependent fitness payoffs, which means that their fitness depends on the frequency and the nature of their interactions with one or more strategies. The analysis of the variation of the fitness of each strategy in different social environments can elucidate the evolutionary dynamics played by the strategies. In the common lizard, three female colour types (yellow, orange and mixed) are associated with alternative reaction norms in reproduction and social behaviour that signal alternative strategies. To clarify the nature of colour-specific interactions and their influence on female fitness, we analysed the response of female reproductive success to an experimental manipulation of colour frequencies in natural populations. We found that juvenile body condition at birth for all colour types was negatively affected by the local frequency of yellow females. In addition, we found that mixed females had higher clutch hatching success in the populations where orange females were frequent. These results prove that female reproduction is sensitive to the social environment, and are consistent with a scenario of a hawk–dove–bully game, in which yellow females are aggressive hawks, orange females non-aggressive doves, and mixed females have a context-dependent bully strategy. In this system, the plastic bully strategy would confer a reproductive advantage to putative heterozygotes in some social environments, which could allow the maintenance of the system through context-dependent overdominance effects.

Keywords Colour signals · Social environment · Game theory · Alternative strategies · Overdominance

Communicated by Raoul Van Damme.

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Introduction

Colour signals are known to be of major importance in both inter- and intra-sexual selection, and can signal alternative reproductive or behavioural strategies in reptiles (Thompson and Moore 1991), birds (Roulin 2004), insects (Sirot et al. 2003) and fishes (Gross 1991). Indeed, colour signals are often correlated with morphological, physiological or behavioural traits and such syndromes can be characteristics of alternative strategies (Fisher 1930; Roulin 2004). For instance, in the side-blotched lizard (*Uta stansburiana*), males display three colour morphs signalling three alternative reproductive strategies: sneaker, aggressive territorial and cooperative territorial (Sinervo and Lively 1996). In female damselflies (*Ischnura elegans*), three female colour morphs have been identified that differ in their reproductive strategies (andromorph or gynomorph) and probably in their dispersal pattern (Svensson and Abbott 2005).

Social interactions are expected to drive the evolution of alternative strategies (Gross 1996). If the different strategies interact frequently, the fitness payoffs associated with a strategy are expected to be context dependent, which means they depend on how often this strategy competes with the other strategies (Henson and Warner 1997; Gross and Repka 1998; Brockmann 2001). To understand the nature of the social interactions between the different strategies in natural populations, and the dynamics of these systems, it is necessary to compare the fitness response of the strategies in different social environments characterised by different local colour type frequencies (Emlen 1997; Sirot and Brockmann 2001). However, fitness responses are difficult to analyse through correlative approaches because of many confounding factors (Svensson et al. 2005), which makes experimental approaches particularly relevant for the analysis of colour-specific fitness responses in different social environments (Brockmann 2001). Surprisingly, up to now very few studies (for instance Sinervo et al. 2001; Bleay et al. 2007) have experimentally manipulated colour-type frequencies and examined the consequences on each type's fitness.

In female common lizards (*Lacerta vivipara*), there is significant variation in ventral colouration within most populations. One way to describe and analyse this variation is to classify females into three discrete colour classes: yellow, pure orange or a mixed colouration. Females belonging to these three colour classes display different reaction norms in reproduction (Vercken et al. 2007) and offspring dispersal (Vercken et al., unpublished data). These responses were characterised by non-linear patterns as the responses of mixed females were never intermediate between the responses of yellow and orange females. Therefore, these colour-based differences in many traits were considered as alternative life history strategies (Vercken et al. 2007, 2008). Behavioural experiments in the laboratory showed that females used the information carried by other females' colour to adjust their behaviour in a competitive context (Vercken and Clobert 2009) and that yellow females were likely to be stronger competitors and socially dominant over other colour types (Vercken and Clobert 2008). However, because competitive relationships between alternative female strategies are still poorly documented (apart from behavioural dominance relationships in cooperatively breeding species, e.g. Bell 1983; Aubin-Horth et al. 2007), it was difficult to accurately predict the consequences of such differences in competitive ability for the dynamics of natural populations and the evolutionary stability of alternative female strategies. Yet two main scenarios resulting from classic game theory systems could be considered:

1. If the competition within a strategy is stronger than between different strategies, i.e. if females exploit different ecological niches, then we expect negative frequency dependence to apply to all female colour types. In the case of three distinct genetic strategies, this relationship is characteristic of a "rock–paper–scissors" game (Sinervo and Calsbeek 2006), where each strategy does better against the others than against itself, which thereby confers a fitness advantage to the rare strategy (Sinervo and Lively 1996).
2. If yellow females are strictly behaviourally dominant, then competition should be stronger when they are frequent in the populations, with negative effects on fitness for all strategies. We should thus observe a global negative effect of the frequency of yellow females, with no or little difference between strategies. Such dynamics would rather correspond to a "hawk–dove" game, where one strategy is aggressive or territorial and the other is non-aggressive and avoids physical confrontation. In this game, all strategies suffer from decreased fitness when hawks are frequent: indeed, hawks suffer the cost from frequent aggressive competition with other hawks and doves cannot access the resource whenever they encounter hawks (Maynard-Smith 1982, see Table 1).

In order to discriminate between these alternative scenarios of frequency dependent selection, we experimentally modified the local frequency of the different colour types around resident females and monitored the consequences of this manipulation on their reproductive success in several natural populations. A previous correlative study showed that female reproductive success was sensitive to variations in the environment, with different responses for each strategy (Vercken et al. 2007), so this parameter seemed especially relevant when estimating the impact of the composition of the social environment on the global fitness of females.

Table 1 Payoff matrix of the hawk–dove game with three strategies: hawk, dove and bully

	When it plays against		
	Hawk	Dove	Bully
Fitness payoffs for			
Hawk	v-c	2v	2v
Dove	0	v	0
Bully	0	2v	v

The exploitation of a resource provides a gain 2v and the cost of losing an aggressive contest is 2c. Two doves or two bullies encountering each other share the resource; when a hawk encounters another hawk, it wins the contest and takes over the resource or loses the confrontation with equal probability (after Maynard-Smith 1982)

Materials and methods

The species

Lacerta vivipara is a small [adult snout-vent length (SVL) 50–70 mm] live-bearing lacertid lizard, found throughout Europe and Asia. We studied four populations located on Mont Lozère (southern France, altitude 1,420 m). In these populations, adult males emerge from hibernation in mid-April, followed by yearlings, and adult females in May. Mating occurs at female emergence, and gestation lasts for 2 months. Parturition starts in July and lasts for 2 or 3 weeks. Females lay an average clutch of five soft-shelled eggs (range 1–12). Offspring hatch within 1 or 2 h after laying and are immediately independent of their mother. The activity season ends in late September and juveniles are the last to enter hibernation. A more detailed description of this species' life history can be found in Massot et al. (1992). In these populations, adult females display a ventral colouration varying from pale yellow to bright orange with some females displaying a mixed colouration, whereas adult males are almost always orange (this sexual dimorphism is almost reversed in rare oviparous populations, where males display a polymorphism of colour and strategies that resembles a rock–paper–scissors mating system; see Sinervo et al. 2007). Juveniles start by being melanic, and when they are yearlings the ventral colouration slowly turns to a pale green. Stability of ventral colour arises with sexual maturity (usually at 2 years in the Mont Lozère populations).

Frequency experiment

The four populations we studied are distributed along a linear axis (road), two successive populations on the axis being separated by 1.2 km on average (minimum 800 m, maximum 2 km). These populations are not differentiated genetically (estimation of F_{st} using microsatellite data; M. Richard, unpublished data). As the maximum dispersal distance for a lizard is around 100 m (Massot 1992), the study populations are not connected directly through migratory fluxes. Female density and relative frequency of colour types have been estimated by mark-recapture analyses. The four study populations differed in female density, and in female colour type frequencies. The respective values of density (estimated from the recapture rate by the Lincoln–Petersen index) and colour type frequency in the different populations at the beginning of the study in 2004 are given in Table 2. We distinguished two populations with a high frequency of orange females relative to yellow females ("high-orange" populations; A and B) from two populations with high frequency of yellow females relatively to orange females ("high-yellow" populations; C and D).

The study lasted from May 2004 to September 2006. Each year, in June, females were captured in the different populations and kept in the laboratory until parturition (251 females in 2004, two hundred and eighty-two in 2005 and 240 in 2006; see "Measurement of female characteristics and juvenile morphological traits" for details on rearing conditions). Females were then released with their offspring after parturition in July, according to our experimental design. Indeed, in 2004 and 2005, a portion of the female population was released with their offspring into another population in order to increase the local frequency of yellow females in the "high-orange" populations (and decrease the frequency of orange females), and to increase the local frequency of orange females in the "high-yellow" populations (and decrease the frequency of yellow females), the remaining females being released into their population of origin. Orange females from population A were exchanged with yellow females from population D, and orange females from population B were exchanged with yellow

Table 2 Female density (estimated from the Lincoln–Petersen index), orange and yellow female frequencies for the four studied populations (*pop.*) before any manipulation in 2004, number of transplanted females in 2004, orange and yellow female frequency in 2005 after the first manipulation, number of transplanted females in 2005, orange and yellow female frequency in 2006 after the second manipulation

Population	A	B	C	D
Adult female density in 2004	160	140	175	100
Orange/yellow female frequency in 2004	0.42/0.36	0.4/0.25	0.2/0.37	0.21/0.42
Number of transplanted females in 2004	25 Orange females to pop. D	26 Orange females to pop. C	26 Yellow females to pop. B	25 Yellow females to pop. A
Orange/yellow female frequency in 2005	0.34/0.44	0.31/0.34	0.33/0.3	0.27/0.3
Number of transplanted females in 2005	19 Orange females to pop. D	23 Orange females to pop. C	23 Yellow females to pop. B	19 Yellow females to pop. A
Orange/yellow female frequency in 2006	0.28/0.5	0.25/0.4	0.44/0.19	0.31/0.26

females from population C (Table 2). Total population densities were not modified, therefore the frequencies of mixed females were not modified either. In their new population, immigrant females were released at the capture point of a native female that had been transplanted, in order not to modify female density at the local scale.

Therefore, in 2005 and 2006, females were exposed to two different treatments: females from populations A and B experienced an "increased-yellow" treatment (Y+ treatment), whereas females from populations C and D experienced an "increased-orange" treatment (O+ treatment). Because there were two transplantation events in 2005 and 2006, the modification of local colour type frequencies was additive (see Table 2 for the colour type frequencies after the first transplantation event and after both transplantation events).

We did not include an undisturbed population as control, because we could not follow the dynamics of more than four populations simultaneously. However, the reproductive parameters observed in 2004 were used as references as they were obtained in undisturbed populations, before any experimental manipulation. We analysed the difference between the parameters in 2004 and the following years to estimate the effect of the experimental manipulation (see "Statistical analyses"), independently of annual effects related to the natural variations of the environment that are expected to be the same for all populations regardless of their experimental treatments. This experimental design has been used in this species with success on several occasions and it has allowed us to study individual responses to variation in two different types of parameters of the environment, social (Meylan et al. 2007) and abiotic factors (Lorenzon et al. 2001; Massot et al. 2002).

Control of transplantation effects

In a previous experiment of reciprocal transplants in this species, the majority of transplanted females were found to remain around their release site (Massot et al. 1994). In our experiment, 24 out of 98 females released into their natal site after parturition and 22 out of 102 transplanted females in 2004 were captured again in 2005. We tested for the effect of transplantation on fitness by comparing survival, body condition and reproductive success between resident and transplanted females in 2005 in all populations [for body condition and clutch size, GLM procedure (SAS Institute); for survival rate and clutch hatching success with binomial distribution and logit link function, GENMOD procedure (SAS Institute)]. There was no effect of population in any of the comparisons (all $P > 0.6$). There was no difference in apparent survival rate between resident and transplanted females ($P = 0.84$) and we did not find any effect of transplantation on other fitness-related traits like female body condition ($P = 0.10$), clutch size ($P = 0.67$), clutch hatching success ($P = 0.88$) or juvenile asymmetry ($P = 0.11$). We did not find either any interaction between transplantation and female colour (all $P > 0.7$). In addition, most transplanted females (91%) were captured within 20 m of their release site, and 36% within 10 m. As common lizards are sedentary as adults, the stability of the territories of transplanted females suggests that they managed to settle successfully in their new population. Therefore, we may assume that the reciprocal transplant experiment had persistent effects on the social structure of the populations, while preserving their spatial structure.

Measurement of female characteristics and juvenile morphological traits

From 2004 to 2006, 773 females were removed temporarily from the four populations. Each year, from the end of June, females were captured and kept in the laboratory until parturition. At capture, females were measured (SVL), weighed and marked individually by toe-clipping. Female ventral colouration was estimated visually using a colour reference, and were categorised into three distinct classes: pale yellow, bright orange and mixed colouration. Although spectrum components like chroma and hue vary continuously along the colour range (Vercken et al. 2007; Cote et al. 2008), visual classification of females into three discrete colour classes (yellow, orange, and mixed) provides a good characterisation of the ecological significance of colour variation in this species (Vercken et al. 2007, 2008). Female ventral colour was also measured with a spectrophotometer (Ocean Optics USB2000). Data analysis was handled with the aid of the Color Project 1 software, developed by Jean-Marc Rossi (Laboratoire Ecologie et Evolution, Université Pierre et Marie Curie, Paris). The software allowed us to calculate several parameters quantifying colour, in particular the hue and the chroma. Females were housed in plastic terraria with damp soil, a shelter and water ad libitum. They were exposed to natural daylight and were heated 6 h per day with an electric bulb. All animals were treated in accordance with the *National Institutes of Health Guide for Care and Use of Laboratory Animals*. At birth, offspring were individually marked by toe-clipping and sexed by counting ventral scales. This method allows the determination of juvenile sex with 95% precision (Lecomte et al. 1992). Offspring asymmetry, which is thought to reflect developmental stress (Moller and Swaddle 1997), was estimated by the absolute value of the difference between the number of left and right ventral scales. Offspring and their mothers were measured and weighed. They were then released in the field either in their population of origin or in another population (see Frequency experiment).

Statistical analyses

We tested the stability of female colouration using both visual classification and colour spectrum. Ninety-four females were captured at least twice throughout the study. The stability of ventral colour class was estimated by a GLM procedure (SAS Institute) testing for the effect of the ventral colour on the first capture occasion on the ventral colour on the second capture occasion, with ventral colours being additively scored as 0 = yellow, 1 = mixed and 2 = orange (following Sinervo et al. 2001). The stability of the colour spectrum was estimated by paired *t*-tests (TTEST procedure; SAS Institute) comparing the measures of chroma and hue made on the first capture occasion with the measures made on the second capture occasion. The effects of frequency treatment and transplantation on the stability of colour were assessed with GLMs analysing the difference between the two successive measures of chroma and hue (GLM procedure, SAS Institute).

We analysed the response of resident female reproduction [clutch size, clutch hatching success (number of living juveniles on total number of embryos) clutch sex ratio (proportion of males), mean juvenile SVL, mean juvenile weight, mean juvenile body condition (residual from the relationship between body mass and SVL), mean juvenile asymmetry] to several factors: year (coded as a class factor), frequency treatment (Y+ vs. O+), female ventral colour and female SVL. Population was considered as a random factor nested within the frequency treatment. We analysed the reproductive traits of resident females only (i.e. females that had not been transplanted) in order to avoid confounding effects related to transplantation. We tested for all simple effects and for the following interactions: year by treatment, year by ventral colour, ventral colour by treatment, and year by ventral colour by treatment. A significant year effect alone would mean that only annual effects related to the natural variations of the environment are responsible for differences between the parameters observed in 2004 and the parameters observed in 2005 or 2006. A significant year by treatment effect would mean that the frequency treatments have modified the reproduction of resident females in comparison with the reference year, with different effects for the two treatments that cannot be explained by annual variation only. A significant year by ventral colour by treatment effect would mean that the reproduction of the resident females of different colour types has been affected differently by the two experimental treatments, i.e. that the social context affected female reproductive success, with different effects for the different colour types.

We analysed continuous variables (clutch size and juvenile morphology) with mixed linear models (MIXED procedure, SAS Institute). We also analysed clutch size and juvenile asymmetry as Poisson variables with mixed log–regression analyses, which did not affect the results with comparison with a model of continuous distribution. For variables that constituted proportions (clutch hatching success and clutch sex ratio), we used mixed logistic regression analyses (GLIMMIX procedure; SAS Institute). Estimations and test statistics were calculated with a restricted maximum likelihood approach. When random effects did not account for a significant part of variance, GLM procedure (SAS Institute) and logistic regression analyses (GENMOD procedure, SAS Institute) were used. *F*-tests and log-likelihood ratio tests (χ^2-values) were used to assess significance of effects. Type III sum of squares was used in all cases. We selected the best model using lowest Akaike information criterion. Only the results of the selected models are reported. Colour effects and year effects were interpreted by comparing alternately the three different colour or year pairs. For this, we used a Bonferroni correction to assess significance of effects (the significance threshold for the *P*-value being lowered to 0.017).

Results

Stability of colour

The classification of ventral colour on a second capture occasion was highly dependent on the classification made on the first capture occasion ($F_{1,92} = 197.27$, $P < 0.0001$) and only three females out of 94 were classified differently in different occasions. The measure of hue made on the second capture occasion was not significantly different from the measure made on the first capture occasion ($t = -1.39$, $P = 0.17$), but the two measures of chroma were significantly different ($t = -4.15$, $P < 0.0001$). Neither the frequency treatment (Y+ or O+) nor the transplantation (resident females versus transplanted females) significantly affected the probability for spectrum components to change (for chroma, effect of treatment $P = 0.19$, effect of transplantation $P = 0.64$; for hue, effect of treatment $P = 0.54$, effect of transplantation $P = 0.99$).

Female reproductive success

Clutch size depended on year and female SVL (see Table 3 for probabilities), but it was not affected by population ($P = 0.14$) or by frequency treatment ($P = 0.99$). Clutch hatching success did not depend on population ($P = 0.43$), but it was affected by the interaction between year, ventral colour and frequency treatment (Table 3). There was a significant difference in the interaction between colour types and treatments in 2004 when compared with 2005 and 2006 (interaction colour by treatment by year in 2004 and 2005,

Table 3 Significant effects on responses of female reproductive parameters

Reproductive parameter	Explanatory variables	Statistics
Clutch size	Year	$F_{2,721} = 16.73$, $P < 0.0001$
	Female SVL	$F_{1,721} = 335.87$, $P < 0.0001$
Clutch hatching success	**Year × female colour × frequency treatment**	$\boldsymbol{\chi^2_4 = 27.01}$, $\boldsymbol{P < 0.0001}$
Juvenile SVL	Year	$F_{2,689} = 71.20$, $P < 0.0001$
	Female SVL	$F_{1,689} = 10.26$, $P = 0.014$
Juvenile weight	Female SVL	$F_{1,686} = 20.54$, $P < 0.0001$
	Year × frequency treatment	$F_{2,688} = 2.70$, $P = 0.0676$
Juvenile body condition	Female SVL	$F_{1,686} = 15.04$, $P < 0.0001$
	Year × frequency treatment	$\boldsymbol{F_{2,686} = 5.68}$, $\boldsymbol{p = 0.046}$
Juvenile asymmetry	Year	$F_{2,684} = 6.69$, $P = 0.0013$
	Female colour × female SVL	$F_{2,684} = 6.80$, $P = 0.0012$

Effects involving the frequency treatments are in *bold*. *SVL* Snout–vent length

$\chi^2_2 = 14.64$, $P = 0.0007$, $n = 501$; in 2004 and 2006, $\chi^2_2 = 21.69$, $P < 0.0001$, $n = 449$; in 2005 and 2006, $\chi^2_2 = 4.3$, $P = 0.117$, $n = 476$). Mixed females had a higher clutch hatching success in O+ populations in 2005 and 2006 than in Y+ populations, whereas this was not the case for orange or yellow females (interaction colour by treatment for yellow and mixed females when pooling 2005 and 2006 data, $\chi^2_1 = 8.21$, $P = 0.0042$, $n = 335$; for yellow and orange females, $\chi^2_1 = 1.28$, $P = 0.26$, $n = 298$; for orange and mixed females, $\chi^2_1 = 15.62$ $P < 0.0001$, $n = 319$; see Fig. 1). Clutch sex ratio did not respond to any of the factors tested in this study (all $P > 0.2$).

Juvenile morphology

Juvenile SVL did not depend on population ($P = 0.28$) or on frequency treatment ($P = 0.33$) but it was affected by year and female SVL (Table 3). Juvenile SVL was higher in the last year of the experiment than in the first year. Juvenile weight did not depend on population ($P = 0.26$), but it was affected by female SVL and marginally by the interaction between year and frequency treatment (Table 3). Juvenile body condition did not depend on population ($P = 0.34$), but it was affected by female SVL and by the interaction between year and frequency treatment (Table 3). There was a significant difference in juvenile body condition between experimental treatments in 2006, but not in 2004 or 2005 (interaction treatment by year in 2004 and 2005, $F_{1,487} = 0.35$, $P = 0.56$; in 2004 and 2006, $F_{1,426} = 8.79$, $P = 0.0032$; in 2005 and 2006, $F_{1,458} = 7.19$, $P = 0.0076$). Y+ treatment had a negative effect on juvenile body condition in comparison with O+ treatment in 2006 (effect of treatment in 2006, $F_{1,198} = 20.47$, $P < 0.0001$; Fig. 2).

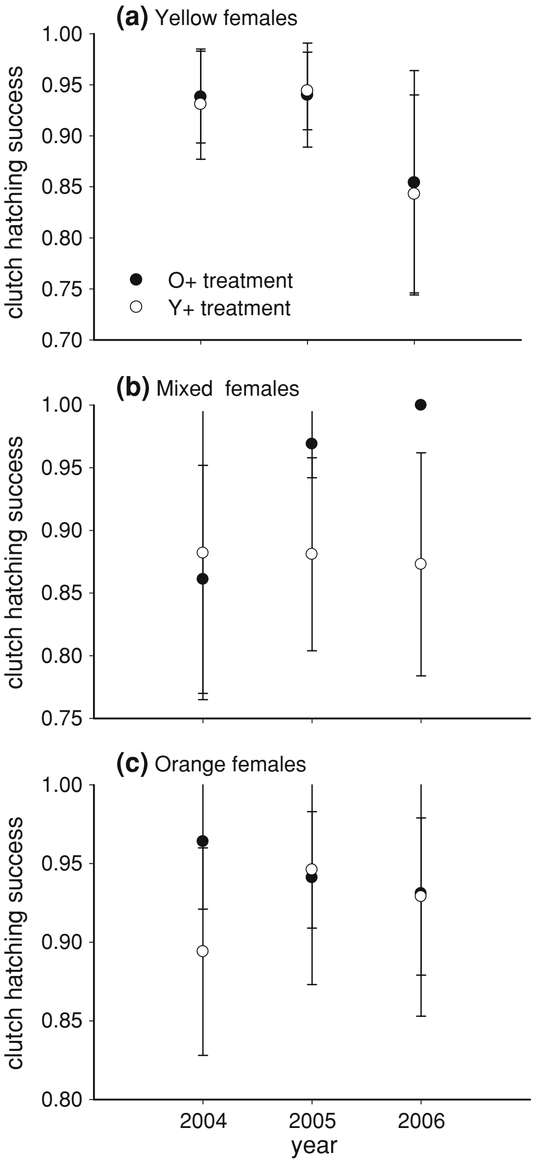

Fig. 1 Mean clutch hatching success for **a** yellow, **b** mixed, and **c** orange females in the "increased-orange" treatment (*O+*; *filled circle*) and in the "increased-yellow" treatment (*Y+*; *open circle*) populations in 2004 (reference year), 2005 and 2006. *Error bars* are 95% confidence intervals (CI)

Juvenile asymmetry did not depend on population ($P = 0.99$) or on frequency treatment ($P = 0.20$), but it was affected by year and the interaction of female colour and

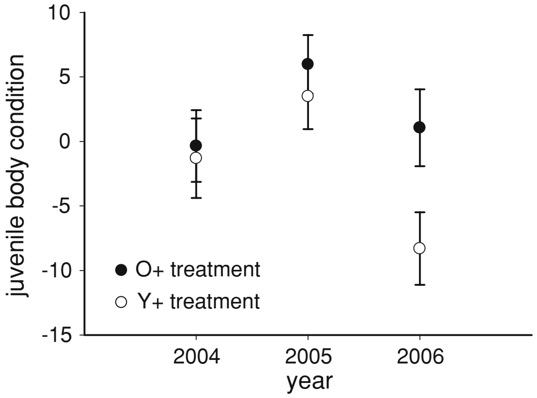

Fig. 2 Mean juvenile body condition in O+ (*filled circle*) and in Y+ (*open circle*) populations in 2004 (reference year), 2005 and 2006. *Error bars* are 95% CI. For abbreviations, see Fig. 1

female SVL (Table 3). Juvenile asymmetry increased with female size for mixed females, whereas no such relationship was found for yellow or orange females (difference between yellow and mixed females, $F_{1,468} = 12.03$, $P = 0.0006$; difference between orange and mixed females, $F_{1,443} = 7.4$, $P = 0.0068$; difference between yellow and orange females, $F_{1,458} = 0.68$, $P = 0.41$).

Discussion

We did not find any difference between populations within treatments in female reproductive parameters. Thus treatment effects can be interpreted safely as they do not include any confounding replicate effect. Clutch hatching success, juvenile weight and juvenile body condition were affected by the local frequency of colour types. The social environment experienced by females at the beginning of gestation thus affects female reproductive allocation and ultimately female fitness.

Stability of female colouration

In our experiment, the measure of hue was repeatable through time while the measure of chroma was significantly different between two capture occasions, but this change was independent of our experimental manipulation. The effect of the experimental manipulation on the social structure of populations was not biased by an alteration of individual colour in response to the modification of the social environment. In addition, the visual classification of colour was not altered by the quantitative modifications of chroma, which confirms previous findings on the temporal stability of female colour class (Vercken et al. 2007).

We found a significant variation in chroma between years, and previous studies have demonstrated that several spectrum components are open to environmental influences [population density (Meylan et al. 2007); population sex ratio (Cote et al. 2008); corticosterone level (J. Cote, unpublished data)]. Colour is known to be a complex signal, and the different components of the spectrum might reflect different components of the phenotype (e.g. Andersson 2000; Weiss 2006). Thus, the colour class could be a stable, early determined signal of female strategy (either genetically determined or condition dependent with an early ontogenetic switch: irreversible strategy; Brockmann 2001), while quantitative spectrum components would give up-to-date information on more variable parts of the phenotype (as stress or age; Cote et al. 2008). However, because chroma was not affected either by transplantation or by the frequency treatment, it does not seem to respond to the particular social stress related to colour-specific competition between females.

Effects of female colour type frequencies on female reproductive success

Juvenile condition was significantly better in O+ populations than in Y+ populations, regardless of female ventral colour. Thus, resident females of all of the colour types experienced negative effects on juvenile condition at birth in the populations where the frequency of yellow females had been increased. Such negative effects of yellow female frequency on female reproductive success were also found in a long-term correlative study (Vercken et al. 2007). In other species, several studies showed that social and competitive interactions between female strategies cause colour-dependent effects on female fitness and juvenile phenotype (Comendant et al. 2003; Van Gossum et al. 2005). In laboratory experiments, female lizards of different ventral colour were found to differ in aggressiveness and probably in competitive ability (Vercken and Clobert 2008), and yellow females are thought to be stronger competitors and socially dominant. When a female of any colour experiences an increase in the frequency of her yellow neighbours she should suffer from increased social stress (even yellow females that would interact more with females with similar competitive abilities). On the contrary, a female of any colour surrounded by many orange neighbours should have higher reproductive success on average due to lower social stress. The negative effect of Y+ environments on juvenile phenotype at birth could thus result from increased social stress for gestational females in Y+ populations.

Frequency-dependent fitness effects support the hypothesis of a hawk–dove–bully game

We found a negative effect of an increased frequency of yellow females on offspring body condition for all strategies, and no negative effect of an increased frequency of orange females on the reproductive success of orange females (either clutch size, clutch hatching success or juvenile morphology). This result does not support the hypothesis of a "rock–paper–scissors game" stabilized by pure negative frequency-dependent selection.

In contrast, our results would be compatible with the hypothesis of a dynamic "hawk–dove–bully" game between female strategies. In such a system, the average fitness of all strategies is lower when they encounter the hawk strategy frequently (Table 1). Female reproductive success was lower in Y+ populations than in O+ populations, which suggests that yellow females play the role of hawks and orange females the role of doves. These strategies are also consistent with the behavioural observations made in laboratory conditions (Vercken and Clobert 2008, 2009).

What is more intriguing is the role played by mixed females in this system. Behavioural experiments suggested that these females were social challengers (Vercken and Clobert 2008), and we found here that mixed females had a different response than yellow and orange females for clutch hatching success. Mixed females had higher clutch hatching success in O+ populations than in Y+ populations, whereas no differences were found between treatments for yellow and orange females. This advantage of mixed females in O+ environments could correspond to a "bully" strategy (Maynard-Smith 1982), in which individuals play dove against hawks and hawk against doves. This strategy is associated with high average fitness payoffs (see Table 1) because it benefits from a dominance relationship over doves without paying the physiological cost of this social dominance. Indeed, yellow females have higher testosterone levels in plasma (E. Vercken, unpublished data) and seem to be more senescent than other females (Vercken et al. 2007), which suggest a strong physiological cost of "true" dominance in this species. If mixed females can dominate orange females without paying this physiological cost, they could increase more substantially their reproductive success relative to the other two types when shifting from a predominantly yellow to a predominantly orange frequency environment.

Maintenance of orange "dove" strategy by overdominance?

In hawk–dove–bully dynamics, the dove strategy is always outcompeted by the bully strategy (Table 1), which raises the issue of the maintenance of the dove strategy. If ventral colour is a genetic polymorphism, this apparent paradox can be solved by the action of overdominance. In the common lizard, the colour phenotype of mixed females is a mixture of the phenotypes of yellow and orange females, either with an intermediate colouration or with both yellow and orange scales. With our current knowledge of this system, the most likely scenario to explain the phenotype of mixed females would be that they are heterozygotes and display overdominant effects.

We showed here that mixed females had a higher reproductive success than other females in O+ environments, which can probably ensure a fitness advantage to this strategy on average if colour type frequency varies over time. Indeed, the mean reproductive success of mixed-coloured females calculated over 14 years (about four to five generations) is superior to those of the other two colour types (Vercken et al. 2007). Furthermore the hypothesis of mixed females being heterozygotes provides a direct explanation for their particular strategy. Indeed, if these females possess the genetic architecture for both a hawk and dove strategy, they are more likely to be able to switch from one strategy to the other as is expected in the bully strategy.

A comparable system of context-dependent overdominance has been documented in another lizard species with a comparable system of colour morphs (Sinervo and Zamudio 2001). In the side-blotched lizard, the fitness associated with specific alleles depends on the frequency of the different colour morphs in the population. Because they can express more or less of their different alleles, heterozygous individuals are advantaged at different phases of the frequency cycle. Although the nature of alternative strategies in these two species is different, context-dependent overdominance could be a general process implicated in the evolution and maintenance of polymorphisms of strategies, through the highest potential for plasticity conferred by heterozygosity.

Conclusion

The present research demonstrates that female reproductive success is affected directly by the relative frequency of female colour types in the environment. In particular, we found a negative effect of the frequency of yellow females on offspring body condition for all female strategies. These results support the hypothesis that female ventral colour in the common lizard signals alternative strategies with different dominance statuses, compatible with a classic "hawk–dove" game. In such a system, mixed females would adopt a plastic, high-benefits bully strategy. The hypothesis that mixed females are heterozygotes for the genetic loci determining female strategy is strongly supported, as it explains both the particular phenotype of mixed females and the maintenance of the low-performing orange strategy through overdominance effects.

However, in this study we only examined aspects of reproductive success. To fully understand the evolutionary game played by the different strategies, other fitness components (Widemo 1998) should be examined such as colour-dependent survival (Olendorf et al. 2006), or colour-dependent offspring dispersal strategies (Sinervo and Clobert 2003), which may respond more directly to colour-type frequencies. More work is also needed on the plasticity and heritability of colour to assess the relative importance of genetics and environment in the determinism of ventral colour in this species, and to confirm the potential role of overdominance in the maintenance of the strategies.

Acknowledgments We are indebted to several undergraduate students (C. Cansell, B. Chéron, B. Khoury, T. Le Mao, V. Lecat and E. Serres) for their help in the field and the laboratory during the study period. We thank the Parc National des Cévennes and the Office National des Forêts for providing logistical support. We are most grateful to Raoul Van Damme and two anonymous referees for their suggestions and comments that contributed greatly to the improvement of this manuscript. The reported experiments comply with the current laws of France concerning animal experimentation.

Conflict of interest statement The authors declare they have no conflict of interest.

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