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Colour variation and alternative reproductive strategies in females of the common lizard *Lacerta vivipara*

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Abstract

Within-sex colour variation is a widespread phenomenon in animals that often plays a role in social selection. In males, colour variation is typically associated with the existence of alternative reproductive strategies. Despite ecological conditions theoretically favourable to the emergence of such alternative strategies in females, the social significance of colour variation in females has less commonly been addressed, relative to the attention given to male strategies. In a population of the common lizard, females display three classes of ventral colouration: pale yellow, orange and mixed. These ventral colours are stable through individual's life and maternally heritable. Females of different ventral colourations displayed different responses of clutch size, clutch hatching success and clutch sex-ratio to several individual and environmental parameters. Such reaction patterns might reflect alternative reproductive strategies in females. Spatial heterogeneity and presence of density- and frequency-dependent feedbacks in the environment could allow for the emergence of such alternative strategies in this population and the maintenance of colour variation in females.

Introduction

Variation in colour is an intriguing phenomenon found in a widespread number of animal taxa, particularly vertebrates (Galeotti *et al.*, 2003). Animal colour patterns are potentially used in intraspecific communication, thermoregulation and predation avoidance (Endler, 1990; Forsman & Shine, 1995). For these last two functions, variation in colouration is essentially found on a large geographical scale in response to variations in climate, habitat and predators (Galeotti *et al.*, 2003). Syntopic variation in colouration occurs much less frequently (Thompson & Moore, 1991), and is more likely to convey socially important information regarding sex (Cooper & Burns, 1987; Andrés *et al.*, 2002), reproductive condition (Weiss, 2002), social status (Dawkins & Krebs, 1978; Thompson & Moore, 1991) and, in some cases, competitive ability (Cooper & Burns, 1987). Syntopic variation can arise from between-sex, or within-sex differences, or both. If sexual dimorphism is related to mate choice (Mazer & Damuth, 2001), within-sex polymorphism is expected to be more related to social interactions than to ecological functions such as climate, habitat or anti-predator strategies (Forsman & Shine, 1995; Gross, 1996), and within-sex polymorphism is often associated with alternative reproductive strategies (in birds, Tuttle, 2003; in fishes, Hutchings & Myers, 1994; in insects, Ahnesjö & Forsman, 2003; in reptiles, Rand, 1988).

The determinism of a colour variation can be genetically based (true polymorphism) or condition-dependent (Gross, 1996). In the latter case, the phenotype that develops depends on the individual's condition (like the reproductive state, Weiss, 2002), or on an environmental factor (like population density, Eadie & Fryxell, 1992). Colour signals are assumed to be costly (e.g. carotenoid-based colouration, Olson & Owens, 1998), and thus are

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expected to be displayed by the most physiologically vigorous individuals who would also adopt a high-performance reproductive strategy. In the case of a genetic polymorphism, allelic variation can be maintained if the alternative strategies achieve equal mean fitness (Ryan *et al.*, 1992; Calsbeek *et al.*, 2001). Variation can also be maintained if the environment is heterogeneous (different phenotypes have unequal fitness under different environmental conditions, but the environment is variable enough spatially or temporally for all alternative phenotypes to persist, Mazer & Damuth, 2001), or if there is negative frequency-dependent selection (the rare phenotype gains a fitness advantage over the common phenotype, Gross, 1996). Finally, variation might also be maintained by overdominance of heterozygous genotypes relative to homozygous genotypes, or through an interaction between overdominance and frequency-dependent selection (Sinervo & Zamudio, 2001).

In reptiles, variation in colour pattern is common (Cooper & Burns, 1987; Rand, 1988; Thompson *et al.*, 1993; Forsman & Shine, 1995; Sinervo & Lively, 1996; Weiss, 2002) and in several cases this variation is genetically based (Thompson *et al.*, 1993; Sinervo *et al.*, 2001; Sinervo & Zamudio, 2001). Such colour polymorphism is often associated with the existence of alternative behavioural strategies (Rand, 1988; Thompson *et al.*, 1993; Sinervo & Lively, 1996) but only in males for most cases, whereas female colour pattern polymorphism is usually related to thermoregulation or predation avoidance (Forsman & Shine, 1995). However, increasing awareness of an active female mating choice (Olsson *et al.*, 2003; Richard *et al.*, 2005) suggests that intrasexual competition and therefore alternative tactics should be common in females (Gross, 1996). As colour variation often reflects alternative tactics in males, we expect the same pattern to be found in females. In *Uta stansburiana*, female colour morphs actually display alternative reproductive strategies (Sinervo *et al.*, 2000), associated with complex behavioural and physiological syndromes (Sinervo *et al.*, 2001; Svensson *et al.*, 2001). But apart from this example (and a few in insects, see Sirot *et al.*, 2003; Svensson *et al.*, 2005), there seems to be a striking lack of information on such alternative female strategies and the genetic or environmental causes of such variation.

The common lizard (*Lacerta vivipara*) is a well-documented species, as many aspects of its demography (Massot *et al.*, 1992), ecology (Lorenzon *et al.*, 2001), behaviour (Léna *et al.*, 2000) and life-history (Pilorge, 1987) have been extensively studied. However, colour variation in this species has not yet been considered, even though females display conspicuous ventral colourations ranging from pale yellow to bright orange. As this colour pattern is ventral, we do not expect it to play any role in thermoregulation (even a minor role in thigmothermy, see Belliure & Carrascal, 2002) or in predation avoidance and, therefore, it is more likely to act as a social cue. As females have strong control over reproductive decisions by mate choice (direct or indirect) and through various maternal effects (Massot *et al.*, 2002; Meylan *et al.*, 2002; Belliure *et al.*, 2004), they have the opportunity to adopt different reproductive strategies. In addition, males could select their mates upon their ventral colour depending on their own individual strategy.

Populations of this species are subject to strong density feedback effects (Massot *et al.*, 1992; Clobert *et al.*, 1994; Lecomte *et al.*, 1994; Aragon *et al.*, in press), a situation that may open the field for alternative demographic strategies to evolve (Heino *et al.*, 1997). The first objective of this study was to describe female colour variation and to characterize alternative phenotypes using visual classification and spectrophotometry measures. We then examined colour stability throughout life as well as its heritability. The second objective was to look for life-history differences between colour variants, which can reveal alternative strategies. The morphology, reproduction and survival were compared between colour phenotypes, in particular the interactions with time, density and space. These analyses might help to answer questions about the nature of the maintenance of a colour variation in this species of lizard.

Methods

The species

Lacerta vivipara is a small [adult snout-vent length (SVL) from 50 to 70 mm], live bearing lacertid lizard, which is found throughout Europe and Asia. The population we studied is located on Mont Lozère (Southern France, altitude 1420 m), and is divided into two contiguous zones that differ in structural diversity of the microhabitat (Clobert *et al.*, 1994): a zone with high structural diversity and high lizard densities (high quality zone), and a zone with low structural diversity and lower lizard densities (low quality zone). In this population, adult males emerge from hibernation in mid-April, followed by yearlings, and adult females in mid-May. Mating occurs at female emergence, and gestation lasts for two months. Parturition starts in mid-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 life history can be found in Massot *et al.* (1992). In this population, adult females display a ventral colouration varying from pale yellow to bright orange, whereas adult males are almost always orange. Juveniles start by being melanic, and slowly turn to a pale green ventral colouration when yearlings. Stability of ventral colour arises with sexual maturity (usually at 2 years in the Mont Lozère population).

Data set

From 1989 to 2002, 1009 females were temporarily removed from the population. Each year, from the beginning of July, females were kept in the laboratory until parturition. At capture, females were measured (SVL) and weighed. Corpulence was calculated as the residual from the relationship between body mass and SVL. Females were housed in plastic terraria with damp soil, a shelter and water *ad libitum*. Two feeding treatments were applied: females on 'full rations' were offered one larva of *Pyralis farinalis* every week, and females on 'half-rations' had one every two weeks. They were exposed to natural daylight and were heated 6 h per day with an electric bulb. Female ventral colouration was estimated visually using a colour reference, and fell into three distinct classes: pale yellow, bright orange and mixed colouration (intense yellow or mixture of yellow and orange).

At birth, offspring were individually marked by toe-clipping and sexed by counting ventral scales (Lecomte *et al.*, 1992). Offspring and their mother were measured and weighed. They were then released at the mother's last capture point.

Spectrophotometry measures

In 2004, 246 adult females were captured at other study sites on Mont Lozère and their ventral colouration has been both estimated visually and measured with a spectrophotometer (Ocean Optics USB2000; Ocean Optics Inc., Dunedin, FL, USA). Data analysis was handled with the aid of the COLOR PROJECT 1 software, developed by Jean-Marc Rossi (Laboratoire d'Ecologie, Université Pierre et Marie Curie, Paris). The software allowed us to calculate several parameters quantifying colour: (i) the hue, which is the everyday meaning of 'colour' (e.g. blue, green, yellow, red, purple, etc.) and which is correlated with the wavelength of the maximum slope of the colour spectrum; (ii) the chroma, which is a measure of the saturation of a colour and a function of how rapidly intensity changes with wavelength; (iii) the classification segments LM and MS described by Endler (1990) which are the differences in brightness between binned segments of the spectral range and; (iv) the wavelength for which the reflectance is the highest (peak wavelength).

Density and survival analysis

Annual densities were estimated by mark-recapture methods, using the software CAPTURE in the computer program MARK (White, 1998). To estimate density, several capture sessions were organized within each year. The capture sessions were concentrated in time such that we could assume no mortality, emigration or immigration between sessions (closed populations). Colour morph frequencies in the population were estimated from the sub-sample of females captured in summer and brought to the laboratory (more than half of the adult female population). We verified (see *Apparent survival rates* section) that the capture probability was not colour morph-dependent.

Females were captured annually in spring, so we had a data set of 867 capture histories constituting of 14 capture occasions. The females apparent survival rate (including mortality and emigration) was estimated using the Cormack–Jolly–Seber model (Cormack, 1964; Jolly, 1965; Seber, 1965) extended to group effects (Clobert *et al.*, 1988; Lebreton *et al.*, 1992). As migration rate is low in this population (Massot *et al.*, 1992), we considered the apparent survival rate as representative of the actual survival rate. The computer program MARK (White, 1998) was used to fit models. Models were compared by Akaike information criterion (AIC) and we retained the most parsimonious of them (lowest AIC, Anderson *et al.*, 1994). We tested the effects of colour and year, and their interactions independently on survival and capture probabilities. We also replaced the year effect on survival by an effect of female density, male density, yellow female frequency, orange female frequency and the various interactions between density and frequency. These variables can be considered as statistically independent since the total density, the female morphs frequency and the survival probability have been estimated on different data set.

Statistical analysis

To verify that our visual classification was relevant, we conducted a discriminant analysis on the variables from an analysis of the spectrum. We used the DISCRIM procedure of the statistical package of SAS Institute (SAS, 1992) to calculate the discriminant power of variables, a canonical discriminant function, and a discriminant score by re-classifying individuals of known visual colour with the discriminant function. To avoid a bias in the reclassification process, we used the cross-validate option of the DISCRIM procedure, which allowed us to classify each individual using a discriminant function calculated from all others. We selected the combination of variables that led to a minimum of errors in the re-classification process.

For the analysis of morphology (SVL or corpulence, corpulence being calculated as the residual from the relationship between body mass and SVL) and reproduction, we only retained 1 year of data for the females that had been recaptured several times in order to avoid individual effects (we randomly chose one year in order to have a sample representative of all age classes). A total of 730 females was used for the analysis of morphology. For the analysis of reproduction, many females had missing values for at least one of the variables, and were thus excluded from the analyses. A total of 409 females was retained for the analysis of reproduction.

We analysed continuous variables (morphological variables and clutch size) with general linear models (GLM procedure, SAS Institute). For variables that constituted proportions (clutch hatching success, sex-ratio), we used logistic-linear regression analyses (GENMOD procedure, SAS Institute). 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 started with a general model including all the potential effects and their interactions (up to three-way interactions with habitat zone and ventral colour): year (or annual female density), habitat zone, annual orange female frequency, annual yellow female frequency, ventral colour, SVL, age (logarithm and squared logarithm), corpulence and feeding treatment. We then dropped the nonsignificant effects (backward selection), starting with the most complex interaction terms. Only the results of the final model are reported. Colour effects were interpreted by alternately comparing the three different colour pairs. In that case, we used a Bonferroni correction to assess significance of effects (the significance threshold for the critic probability being lowered to 0.017). Colour effects were graphically represented with conditional plots: only the effect of one covariate on the response variable is represented, all other covariates being replaced by their mean values in the multivariate model.

The stability of ventral colour at the individual level was estimated on 611 females by a general linear model (GLM procedure, SAS Institute) testing for the effect of the ventral colour in the first capture occasion on the ventral colour in the second capture occasion, with ventral colours being additively scored as 0 = yellow, 1 = mixed and 2 = orange (following Sinervo *et al.*, 2001). We tested for the effects of several environmental variables: year effect, annual density, orange and yellow females frequencies, and feeding treatment. Heritability of ventral colour was estimated by a general linear model testing for the additive effects of maternal ventral colour on daughter ventral colour (when recaptured as adult) on 136 mother–daughter pairs, and we tested for the environmental effects noted above to estimate the potential source of maternal effect variation.

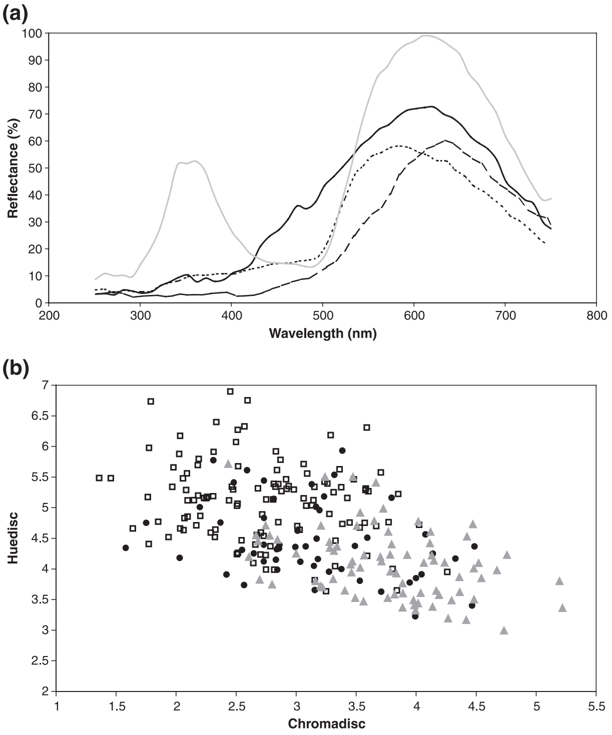

Fig. 1 (a) Examples of reflectance spectra: for yellow females (black solid line), for orange females (short-dashed line), for mixed females (long-dashed line) and for males (grey solid line). (b) Discriminant analysis of colour parameters. Distribution of yellow (white squares), orange (grey triangles) and mixed-coloured (black circles) females in function of their values of chroma and hue multiplicated by the discriminant coefficients.

Results

Spectrophotometrical characterization of colour morphs

Individuals of different colour classes display different reflectance spectra (Fig. 1a). Yellow females are characterized by a large peak between 400 and 750 nm, the climax being around 620 nm, with a small bump around 480 nm. Orange females display a steeper slope leading to a narrower peak between 500 and 750 nm, the climax being around 590 nm. Mixed females have a spectrum with characteristics from both the yellow and the orange spectra, but sometimes arranged in different ways depending on the individual. On average, the peak starts around 400 but with a low slope at first, the slope increasing around 500 nm, and a slight change of inclination around 550 nm. For males, the spectrum is composed of a major peak similar to the orange females peak, and a smaller peak between 300 and 400 nm, corresponding to the ultraviolet A wavelength. From the discriminant analysis, we retained only the chroma and the hue among the various coefficients describing the reflectance spectrum, because this combination led to a minimum of errors in the re-classification process. These two variables have a very strong discriminant power ($F_{2,243}$ equal to 63.16 and 63.84, respectively, both probabilities being <0.0001) and allow us to separate well all three of the colour classes (the squared Mahalanobis distance between groups is different from 0, all probabilities being inferior to 0.0001 and Fig. 1b). Although the mixed colouration category appeared a bit less well discriminated, the hit score (which is the proportion of correctly classified individuals) nevertheless reaches 0.67 with a net gain of 0.81 yielding to a highly significant discrimination of the mixed class from the yellow and orange classes ($P < 0.0001$).

The different colour morphs are actually better characterized by the global shape of the reflectance spectrum than by the wavelengths, as the chroma and the hue are the most discriminating variables. With that criterion, orange and yellow spectra are always distinguishable, but the mixed spectrum can sometimes be confused with an orange or a yellow one even if the visual inspection clearly classified these individuals in the mixed-coloured category.

Stability and heritability of colour

Individual colour was stable through life ($F_{1,478} = 923.55$, $P < 0.0001$, $n = 611$). Only in 25% of cases did the colour change in the course of an individual life, and in most cases that change occurred between two nearby colour classes. Transitions from pale yellow to bright orange or vice versa concerned less than 2% of individuals (eight cases), and are likely to be mistakes in recording the colour pattern. No effect of year ($F_{8,470} = 0.33$, $P = 0.96$), density($F_{1,421} = 0.05$, $P = 0.82$), morph frequencies ($F_{1,465} = 0.02$, $P = 0.89$ for yellow female frequency, and $F_{1,465} = 0.1$, $P = 0.75$ for orange female frequency) or feeding treatment ($F_{1,477} = 1.46$, $P = 0.23$) was found on the stability of colour.

The regression between mother's and daughter's ventral colour was significant ($F_{1,134} = 8.17$, $P < 0.01$, $n = 136$), with a regression coefficient of 0.24, leading to an estimation of heritability equal to 0.48. Again, no environmental effect could be found on the heritability of colour (for year $F_{5,129} = 0.71$, $P = 0.62$; for density $F_{1,106} = 0.81$, $P = 0.37$; for yellow female frequency $F_{1,123} = 0$, $P = 0.99$; for orange female frequency $F_{1,123} = 0.43$, $P = 0.51$; for feeding treatment $F_{1,133} = 0.61$, $P = 0.43$). If heritability of colour is calculated on yellow or orange individuals only, maternal heritability increases slightly up to 0.62 ($F_{1,72} = 7.9$, $P < 0.01$, $n = 74$). Mixed-coloured individuals are not significantly altering the heritability score, which strongly suggests that they are not a simple alteration of pale yellow or orange colour but rather a true category, intermediate in colour spectrum.

Morphology

Morphological characteristics were always affected by year (for SVL $F_{12,714} = 19.88$, $P < 0.0001$, $n = 730$; for weight $F_{12,71} = 4.56$, $P < 0.0001$, $n = 727$; for corpulence before treatment $F_{12,710} = 7.12$, $P < 0.0001$, $n = 727$), but only SVL was also affected by female age ($F_{1,714} = 197.36$, $P < 0.0001$, $n = 730$). We did not find any significant relationships between colour and morphological characteristics once the effects of year and age had been removed (for SVL $F_{2,714} = 0.12$, $P = 0.89$, $n = 730$; for weight $F_{1,710} = 0.45$, $P = 0.63$, $n = 727$; for corpulence before treatment $F_{1,710} = 0.45$, $P = 0.64$, $n = 727$). There was an effect of food treatment on corpulence after treatment (full-ration females being more corpulent than half-ration females $F_{1,455} = 20.74$, $P < 0.0001$, $n = 469$), but no interaction between colour and food treatment ($F_{2,455} = 0.16$, $P = 0.85$, $n = 469$).

Reproduction

Clutch size (number of juveniles, living or dead, and of aborted eggs) was affected by female SVL ($F_{1,397} = 352.88$, $P < 0.0001$, $n = 409$), corpulence before treatment ($F_{1,397} = 115.5$, $P < 0.0001$), female density ($F_{1,397} = 115.5$, $P < 0.0001$), feeding treatment ($F_{1,397} = 6.73$, $P < 0.01$), by the interactions of ventral colour with habitat zone ($F_{2,397} = 3.92$, $P < 0.05$), and of yellow female frequency with habitat zone ($F_{1,397} = 13.19$, $P < 0.001$). Large or corpulent females laid larger clutches than small or thin females, and females exposed to the 'half-ration' treatment laid larger clutches than females exposed to the 'full-ration' treatment. Female density had a negative effect on clutch size, but yellow female frequency had a positive effect, especially in the low-density zone ($F_{1,110} = 10.38$, $P < 0.01$, $n = 118$). Moreover, yellow females laid smaller clutches (mean 4.9) than orange (mean 5.6) or mixed (mean 5.4) females, especially in the low-density zone ($F_{2,110} = 2.86$, $P = 0.061$, $n = 118$ in the low-density zone; $F_{2,283} = 1.19$, $P = 0.31$, $n = 291$ in the high-density zone).

Clutch hatching success (number of living juveniles on the total number of eggs laid) was affected by female SVL ($\chi^2_1 = 34.8$, $P < 0.0001$, $n = 409$) and age ($\chi^2_1 = 61.54$, $P < 0.0001$), feeding treatment ($\chi^2_1 = 11.75$, $P < 0.001$), female ventral colour ($\chi^2_2 = 15.38$, $P < 0.001$), female density ($\chi^2_1 = 79.62$, $P < 0.0001$), yellow female frequency ($\chi^2_1 = 47.79$, $P < 0.0001$) and by the interaction of several variables (female age, female density and yellow female frequency) with ventral colour (see Table 1 for probabilities). Large females had a higher clutch hatching success than small females, and so did full-ration females in comparison with half-ration females. Mixed females had a higher clutch hatching success (mean = 0.84) than yellow (mean = 0.8) and orange (mean = 0.78) females. Orange and yellow females' clutch hatching success was negatively affected by yellow female frequency, whereas this was not the case for mixed females (see Table 1 for probabilities, and Fig. 2a). Female density had a strong negative effect on orange females' clutch hatching success, but a weaker effect for yellow and mixed females (Table 1, Fig. 2b). Finally, clutch hatching success of yellow females was negatively affected by female age, whereas the trend was less significant for orange and mixed females (Table 1, Fig. 2c).

Clutch sex-ratio was significantly affected by the interaction between ventral colour and female corpulence ($\chi^2_2 = 7.01$, $P < 0.05$, $n = 407$), and between habitat zone, female SVL and ventral colour ($\chi^2_2 =$

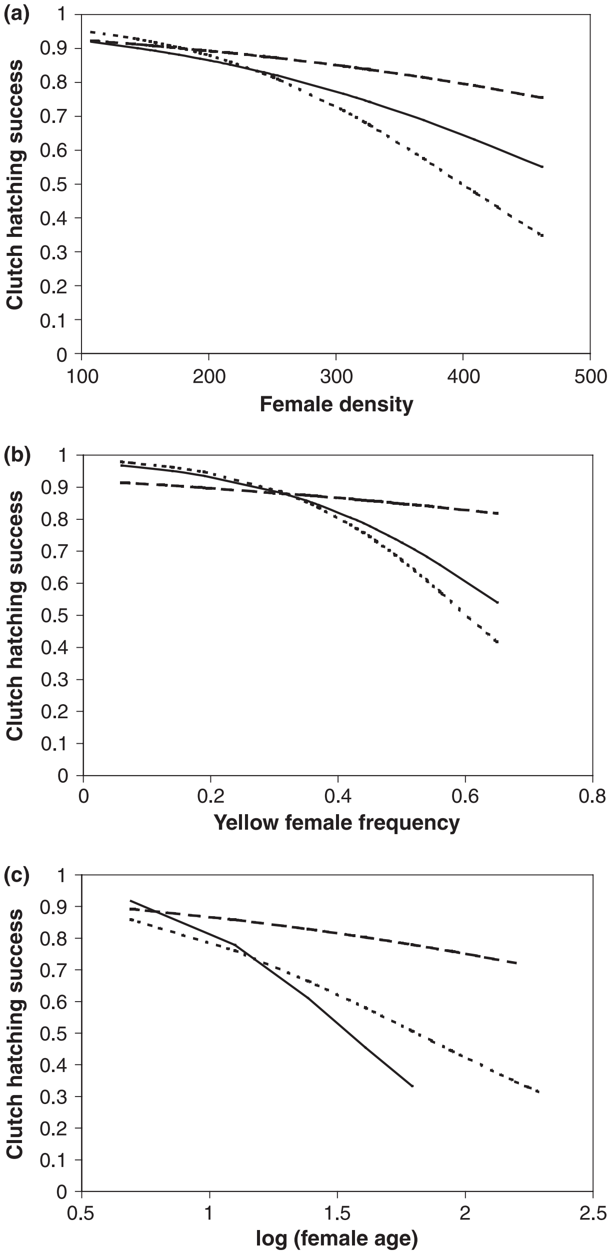

Fig. 2 Effect of various explanatory variables on clutch hatching success for yellow (solid line), orange (short-dashed line) and mixed-coloured (long-dashed line) females. (a) Effect of female density. (b) Effect of yellow females frequency. (c) Effect of female age.

14.98, $P < 0.01$). Yellow corpulent females produced clutches with a higher proportion of females (lower sex-ratio), whereas the opposite was true for orange females (Table 1 and Fig. 3a). The interaction between female SVL and ventral colour was significant in the low-density zone only ($\chi^2_2 = 7.851$, $P < 0.05$, $n = 110$). In the low-density zone, larger yellow females laid clutches with a higher proportion of males, whereas the opposite was true for orange and mixed females (Table 1 and Fig. 3b).

Apparent survival rates

Female survival probability was only affected by yellow female frequency (see Table 2 for models results). Female survival probability was positively correlated to yellow females frequency ($r = 0.99$).

Discussion

Significant variation in ventral colouration of the female common lizard is associated with patterns of reproduction and sex allocation. Colour variants are stable through an individual's life, heritable between mothers and daughters, and characterized by differences in reproductive output and different sensitivity to the environment. The ground is open for the existence of alternative reproductive strategies in females of this species.

Heritability and stability of colour

From field measurements, ventral colouration appeared in three distinctive colour classes: yellow, orange and mixed. However, the distribution of spectrophotometric variables seems to be continuous among and within the colour classes (Fig. 1b). Ventral colour may thus be a continuous trait, or a threshold trait, which appears as a discrete polyphenism to the human eye. Nevertheless, discriminant analysis of colour spectra allowed to efficiently separate the three colour classes on the basis of chroma and hue, which means that the ranking of colour into visual colour classes is representative of the continuous variation in colour spectrum.

Although stability and maternal heritability of colour were both statistically significant, they appeared lower than what could be expected under the hypothesis of pure genetic polymorphism, especially when we consider that the heritability calculated on mother–daughter regression is likely to be overestimated by the presence of maternal effects. The determinism of ventral colour may be condition-dependent with respect to individual condition (yellow or orange colouration is most probably carotenoid-based, Gray, 1996; Bartolotti *et al.*, 2000), but we did not find any morphological difference between females of different colours, weakening the support for condition-dependence. Colour determinism could also include a part of phenotypic plasticity, or other non-genetic or perigenetic mechanisms. As the stability through life and the heritability have not been affected by the environmental factors that were found in previous studies to affect many aspects of this species' life, environmental effects do not seem to influence the development of ventral colouration. This strongly

Table 1 Results of likelihood-ratio tests for colour effects on different variables.

Effect	Difference between yellow and mixed females	Difference between yellow and orange females	Difference between orange and mixed females
Female density on clutch success	$\chi^2_1 = 2.44$ $P = 0.12$ $n = 290$	$\chi^2_1 = 5.29$ **$P = 0.021$** (marginal) $n = 294$	$\chi^2_1 = 10.68$ **$P = 0.001$** $n = 234$
Yellow female frequency on clutch success	$\chi^2_1 = 5.77$ **$P = 0.016$**	$\chi^2_1 = 0.63$ $P = 0.43$	$\chi^2_1 = 11.74$ **$P = 0.0006$**
Female age on clutch success	$\chi^2_1 = 17.45$ **$P < 0.0001$**	$\chi^2_1 = 6.89$ **$P = 0.0087$**	$\chi^2_1 = 2.6$ $P = 0.107$
Female corpulence on clutch sex-ratio	$\chi^2_1 = 1.21$ $P = 0.27$	$\chi^2_1 = 6.98$ **$P = 0.0082$**	$\chi^2_1 = 2.26$ $P = 0.13$
Female SVL on clutch sex-ratio in the low-density zone	$\chi^2_1 = 7.76$ **$P = 0.0053$** $n = 45$	$\chi^2_1 = 2.62$ $P = 0.106$ $n = 34$	$\chi^2_1 = 0.96$ $P = 0.327$ $n = 31$

Values shown in bold are significant *P*-values.

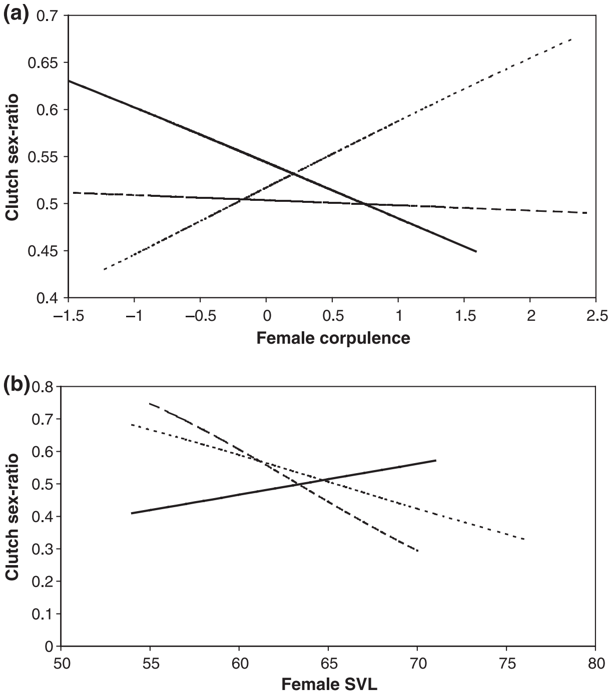

Fig. 3 Effect of maternal morphological traits on clutch sex-ratio for yellow (solid line), orange (short-dashed line) and mixed-coloured (long-dashed line) females. (a) Effect of female corpulence. (b) Effect of female SVL in the low-density zone.

Table 2 Results of model selection for survival and capture rate, AIC (number of estimable parameters).

Capture rate (P)/ survival rate (Φ)	P(fixed)	P(time)	P(colour)
Φ fixed	2443.06 (2)	2445.39 (14)	2445.88 (4)
Φ(time)	2449.45 (14)	2446.26 (25)	2452.45 (16)
Φ(colour)	2446.49 (4)	2448.97 (16)	2449.52 (6)
Φ(fdens)	4255.43 (3)	3732.33 (15)	4258.84 (5)
Φ(fo)	2444.47 (3)	2447.24 (15)	2447.33 (5)
Φ(fy)	**2436.66** (3)	2439.72 (15)	2439.53 (5)
Φ(time + colour)	2452.96 (16)	2449.97 (27)	2456.13 (18)
Φ(time*colour)	2476.68 (40)	2474.75 (51)	2480.18 (42)
Φ(fdens + colour)	4259.46 (5)	3736.42 (17)	4262.88 (7)
Φ(fdens*colour)	4141.91 (7)	4141.91 (7)	2881.29 (9)
Φ(fo + colour)	2447.91 (5)	2450.64 (17)	2450.98 (7)
Φ(fo*colour)	2449.37 (7)	2451.89 (19)	2452.55 (9)
Φ(fy + colour)	2440.14 (5)	2443.34 (17)	2443.163 (7)
Φ(fy*colour)	2440.36 (7)	2444.26 (19)	2443.49 (9)

Fdens, female density; Fo, orange females frequency; Fy, yellow females frequency.
Value shown in bold is the lowest AIC value.

suggests the existence of a genetic determinism to ventral colouration, which might be associated with phenotypic plasticity or epistatic interactions with other genetic factors. As mixed colour females display a distinct reproductive strategy from yellow or orange individuals, which is clearly not intermediate to the strategies of these extreme phenotypes, the hypothesis of the continuity of colour variation is poorly supported. A discrete polymorphism seems more likely, and mixed colour individuals could be heterozygotes expressing more or less of the yellow and orange alleles depending on their own environment: internal (genetic and physiological) or external (biotic and abiotic).

Comparison of the heritability of colour in the common lizard ($h^2 = 0.48$) is salient with early estimates of the heritability of colour in the side-blotched lizard ($h^2 = 0.48$, Sinervo *et al.*, 2000). Since these early estimates, heritability estimates based on sire–progeny regression from controlled laboratory crosses in the side-blotched lizard indicate colour has a heritability approaching 1.0 ($h^2 = 0.96$, Sinervo *et al.*, 2001). Heritability estimates from mother–progeny correlations are always significantly lower, presumably due to very strong maternal effects associated with the reproductive traits that interact with measured biases in colour transmission arising from natural selection, which cull progeny before maturity owing to strong frequency-dependent selection (see Appendix in Sinervo *et al.*, 2001). Genetic mapping studies of free-ranging lizards indicate that colour in the side-blotched lizard maps to a single major genetic factor. As controlled crosses become available in the common lizard it thus seems likely that these initial impressions will be revised by incorporating, models of more complex maternal-effects and the distorting effects of selection on heritable variation.

Zone effect

In the study population the habitat is heterogeneous, with a zone of high structural diversity and high lizard densities (high quality zone), and a zone of low structural diversity, and of poor habitat quality (low-density zone, Clobert *et al.*, 1994). This population thus displays a coupling between habitat structure and processes of density-dependent regulation (Massot *et al.*, 1992; Clobert *et al.*, 1994; Lecomte *et al.*, 1994), which are known to increase the dimensionality of the environment (Heino *et al.*, 1998). In this system, the environment is likely to be at least two-dimensional, which allows for the evolution and maintenance of a stable polymorphism (Heino *et al.*, 1997). In two of our analyses, we found colour effects to be significant only in a specific area of the population, the low-density zone. It is possible that these effects of colour are essentially relevant at a very local scale (in the case of interactions between close neighbours for example, as found in the side-blotched lizard, see Sinervo *et al.*, 2000), and thus are more obvious in the low-density zone. This would mean that these effects are present in the high-density zone, but not visible at the spatial scale of our study. Alternatively, selective pressures could be different between zones (level of intraspecific competition and relatedness) and therefore adaptive responses to these pressures would also differ.

Alternative strategies

There was no simple colour-dependent difference in morphological characters, but we found differences in clutch size and clutch hatching success. Yellow females lay smaller clutches than mixed and orange females, whereas mixed females have the highest clutch hatching success. These differences in mean reproductive value of females of different colours are balanced by other interactions between colour classes and individual or environmental variables on reproductive parameters, which are characteristics of a variation in phenotypic plasticity between colour variants. Such a variation in reaction norms could result from different constraints or of different strategies, depending on the adaptive value of that response.

We found colour effects on the response of clutch hatching success to various environmental parameters. Orange and yellow females tended to lay smaller clutches when yellow females were frequent in the population. Orange females also laid smaller clutches when female density was high. Orange females thus seem sensitive to intraspecific competition, and more specifically to colour-specific competition, which has likewise been observed in the side-blotched lizard for reproduction (Sinervo *et al.*, 2000) immune function (Svensson *et al.*, 2001, 2002) and corticosterone secretion (Comendant *et al.*, 2003). Orange females reduced their clutch when density was high, or when surrounded by many yellow competitors. This could be compatible with a specific strategy of energy saving for survival and future reproduction events, which is indicative of a cost of reproduction, or a strategy of energy allocation by redistributing energy among the surviving juveniles, which is indicative of a potential trade-off between progeny size and number and the survival costs of reproduction (reviewed in Sinervo & Svensson, 1998). Juveniles from small clutches tend to be larger ($F_{1,502} = 15.66$, $P < 0.0001$, $n = 504$), so if the female reduces her clutch, it will affect the corpulence of juveniles at birth and therefore their future survival in a context of high competition.

Yellow females had a lower clutch hatching success when ageing. This effect is likely to be a physiological constraint because if a small clutch was beneficial for an old female, it would be less costly to adjust initial clutch size directly, as female age is a parameter already assessable at the beginning of gestation. Yellow females may thus be more physiologically sensitive to ageing and senescence than orange and mixed females. Moreover, yellow female frequency correlates with a higher female survival, and a larger clutch size in the low-density zone. It is possible that yellow females are more sensitive to environmental conditions, and that their abundance is strongly influenced by environment quality. Therefore, yellow females would be more frequent in good years, where survival is high and reproduction relatively easy.

Reproduction of mixed-colour females was the least sensitive to female density and female age, and not affected at all by yellow female frequency. Mixed females are thus clearly different from yellow and orange females, and their reproduction seems to be less sensitive to female competition and colour-specific competition. Under a simple genetic model where the intermediate females possess copies of yellow and orange alleles, one might expect that these females can adopt the best responses of either the orange or the yellow, a form of overdominance (discussed in greater detail below).

Clutch sex-ratio was affected by maternal corpulence and SVL. Clutch sex-ratio is known to respond to different internal (female age, hormonal level) and external (population density) factors in order to maximize the fitness of offspring (Ronce *et al.*, 1998; Le Galliard *et al.*, 2003). Corpulence may be an indicator of female body condition or health, and thus be related to the female's probability of survival. On the other hand, SVL is thought to correlate with female age in this species and could also be a predictor of females' survival prospects (Meylan *et al.*, 2002, 2004). Orange females in poor condition, with a low probability of survival, produced more daughters. Mother-daughter competition is a strong evolutionary force in the common lizard (Léna *et al.*, 1998; Ronce *et al.*, 1998; Le Galliard *et al.*, 2003), and this competition is expected to decrease with the probability of survival of the mother. In that case, we expect an increase in the production of daughters when the female prospects of survival are low, because kin competition is reduced and female offspring may benefit from the territory of their mother. Large orange females also produced more daughters, which supports the hypothesis of kin competition avoidance. Mixed females also produced more daughters when getting larger, and could thus be sensitive to kin competition too, though in a lesser extent.

On the other hand, yellow females produced more sons when in poor condition or old, which is not expected under the hypothesis of kin competition avoidance. In the common lizard, juveniles born from older females are larger at the age of 2 years than juveniles born to younger females. This size advantage is likely to affect mostly male reproductive success, because if almost all females reproduce at the age of 2 years, only the largest males can do so (Leturque, 2002). Differences in social behaviours or life-history strategies between colour variants might modulate the benefits from an early reproduction, so that male offspring of yellow females would take more advantage of a size advantage than those of other females. Yellow females may thus benefit more than other females from producing male offspring that will reproduce earlier, supporting the hypothesis of an intrasexual competition for access to reproduction.

We proposed here several hypotheses explaining the differences in sex allocation strategy between female morphs, but there could be others. Clutch sex-ratio is known to affect natal dispersal (Massot & Clobert, 2000), which is also under maternal control (Meylan *et al.*, 2002). Females could thus act at different levels (clutch size, sex-ratio, dispersal and even differential energy allocation) and integrate various internal and external factors, in order to produce a specific type of offspring whose fitness should be maximized considering their mother's phenotype.

Maintenance of colour variation

If colour variation in these populations of common lizard is at least partly genetically determined, then this variation must be maintained by natural selection.

We showed that the reproduction of females of the different colours was affected differently by several environmental factors (density, yellow female frequency, habitat structure). As these environmental factors vary temporally and spatially in this population, all three of the colour variants might achieve equal geometric mean fitness, which would allow for the persistence of colour variation (Calsbeek *et al.*, 2001; Mazer & Damuth, 2001). Moreover, we showed that mixed females had a higher mean clutch size than yellow females, and a higher mean clutch hatching success than both yellow and orange females. Under the hypothesis of a discrete polymorphism, mixed females would be heterozygotes, and the observed differences in mean reproductive parameters could be indicative of the overdominance of heterozygous genotypes relative to homozygous genotypes, which is known to maintain polymorphisms in nature. On the other hand, we found frequency-dependent effects on clutch hatching success of yellow and orange females. Yellow female frequency had a negative impact on clutch hatching success of both female types. Yellow females could thus be subject to negative frequency-dependent selection, and orange females to frequency-dependent competition. If orange females have a competitive disadvantage towards yellow females, which are more aggressive and territorial (E. Vercken and J. Clobert, unpublished data), then their higher clutch size could balance this disadvantage and allow for the persistence of colour variants in this population. Finally, all these mechanisms are likely to interact in nature to maintain colour variation, and might also be complemented by other colour-specific effects on fitness (differences in dispersal, mating strategies, behaviour and physiology). This would also be the case, even if the heritability of colour were due to a polygenic form of inheritance.

Comparison to the side-blotched lizard system

The existence of colour variants in females associated with differences in reproductive strategies in the common lizard is extremely similar to that observed in the side-blotched lizard system (*Uta stansburiana*). In that North American species, a colour polymorphism supported by a single locus with three alleles (the OBY locus, Sinervo *et al.*, 2001, 2006a,b; Sinervo & Zamudio, 2001) is associated with a rock-paper-scissors game in males (with three colour morphs, Sinervo & Lively, 1996), and with *r* and *K* reproductive strategies in females (with two colour morphs, Sinervo *et al.*, 2000). The patterns of density-dependent and frequency-dependent progeny allocation in colour variants of the common lizard we described here are remarkably analogous to those observed in the side-blotched lizard (clutch and egg size, Sinervo *et al.*, 2001, costs of reproduction, Svensson *et al.*, 2001, 2002). There also appears to be a common mechanism of overdominance in fitness traits associated with heterozygous genotypes (Sinervo and Calsbeek, unpublished data) and striking parallels in progeny dispersal (E. Vercken, M. Massot, B. Sinervo and J. Clobert, unpublished data, Sinervo *et al.*, 2006a). Intriguingly, the colours are also conserved in the form of orange and yellow female morphs in the side-blotched lizard.

However, several specific features demarcate the two systems. Indeed, in the side-blotched lizard, colour variation is expressed as a true discrete polymorphism, also present in males, which makes the heritability of colour much higher (0.96 in sire–offspring regression, Sinervo *et al.*, 2001, and 0.48 in dam–offspring regression, Sinervo *et al.*, 2000). In the common lizard, phenotypic plasticity and epigenetic mechanisms are likely to play a stronger role in colour determinism. Moreover, female strategies in the common lizard differ less in their mean values of reproductive parameters than in their reaction norms to several environmental and internal factors.

The common lizard and the side-blotched lizard, although they display some specific characteristics, nevertheless possess similar density-dependent life-history syndromes. Given that *Uta* and *Lacerta* are phylogenetically divergent, having last shared a common ancestor 175 Ma (Estes, 1983), either the OBY locus is extremely conserved phylogenetically and is homologous in the common lizard, or such colour-related life-history polymorphisms evolved independently in a highly coordinated and replicated fashion. Either of these possibilities is of considerable interest for general life history theory and mating system theory. Future comparisons of these two social systems with respect to density regulation (Sinervo and Calsbeek, unpublished data), dispersal (Sinervo *et al.*, 2006a) and kin competition (Sinervo & Clobert, 2003) will be most informative for general theory on the evolution of alternative life-history strategies, and the genetic causes of density regulation.

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