# Ventral colour polymorphism correlates with alternative behavioural patterns in female common lizards (*Lacerta vivipara*)

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# Ventral colour polymorphism correlates with alternative behavioural patterns in female common lizards (*Lacerta vivipara*)[1]

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*Abstract*: In the common lizard, female competition for resources is likely to be a strong selective pressure that has enhanced the evolution of conspicuous traits. Female common lizards display a polymorphism in ventral colour correlated with differences in reproduction, dispersal, and susceptibility to resource competition. We tested the hypothesis that this polymorphism is correlated with differences in behaviour in a social context. We studied the agonistic behaviour (aggression and avoidance) and social stress of females of different colours during laboratory-staged encounters with a limiting resource. We found that the behaviour of females was affected by their own colour, or the colour of their opponent, or both. Such alternative behavioural patterns might reflect differences in competitive ability. Orange females were the least aggressive and the most likely to avoid social interactions, and thus could be a weaker competitor. Yellow females were rarely exposed to aggression and often made their opponents flee, and thus might have higher resource-holding potential. Mixed females were aggressive but were also often exposed to aggression, and displayed the highest stress level, which could be characteristic of an intermediate or condition-dependent resource-holding potential. The possibility that ventral colour is used in social interactions to signal resource-holding potential is discussed.
*Keywords*: laboratory-staged encounters, resource holding potential, signals, social competition.

*Résumé* : Chez le lézard vivipare, la compétition pour les ressources entre femelles est probablement une pression de sélection forte, qui pourrait avoir favorisé l'évolution de signaux visibles. Les femelles lézards vivipares présentent un polymorphisme de couleur ventrale, corrélé à des différences au niveau de la reproduction, de la dispersion, et de la sensibilité à la compétition pour les ressources. Nous avons testé l'hypothèse que ce polymorphisme est corrélé à des différences de comportement dans un contexte social. Nous avons étudié le comportement agonistique (agression et évitement) et le stress social de femelles de différentes couleurs au cours de confrontations en laboratoire en présence d'une ressource limitante. Nous avons trouvé que le comportement des femelles était influencé par leur propre couleur, celle de la femelle opposante, ou l'interaction des deux. Une telle variation comportementale pourrait refléter des différences individuelles de potentiel compétitif. L'un des morphes de couleur était le moins agressif et le plus enclin à éviter les interactions sociales, il pourrait donc être le moins compétitif. Au contraire, un autre morphe était rarement agressé et provoquait souvent la fuite de son opposant, il pourrait avoir un fort potentiel compétitif. Enfin, le troisième morphe était agressif, mais également souvent agressé, et montrait le plus haut niveau de stress social, ce qui pourrait être caractéristique d'un potentiel compétitif intermédiaire ou dépendant de la condition. Nous discutons de la possibilité que la couleur ventrale soit utilisée dans les interactions sociales pour signaler le potentiel compétitif des individus.
*Mots-clés* : compétition sociale, confrontations en laboratoire, potentiel compétitif, signaux.

*Nomenclature*: Société Herpétologique de France, 1989.

## Introduction

Although female ornamentation has often been considered a non-functional by-product of sexual selection on males caused by genetic correlation between the sexes (Lande, 1980), recent evidence from comparative studies has challenged this view and suggested that selection has also acted directly on females to favour increased showiness (Rowland, Baube & Horan, 1991; Irwin, 1994; Bleiweiss, 1997; Burns, 1998; Ord & Stuart-Fox, 2006). Indeed, social competition is known to promote the evolution of conspicuous traits in both sexes (West-Eberhard, 1983), and it might be the source of extravagant female traits in many species (Amundsen, 2000). In particular, female contest competition can promote the evolution of signals related to female competitive ability (Langmore, 2000). Female showiness can also be selected by male mate choice, and conspicuous characters can be used as badges of status in mating competition (in pinyon jays: Johnson, 1988) or as indicators of female or offspring quality (in bluethroats: Amundsen, Forsgren & Hansen, 1997; in striped plateau lizards: Weiss, 2006). Social competition can thus lead to variations in social signalling between females, setting the stage for the evolution

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of complex phenotypic alternatives characterized by differences in behaviour (aggressiveness: Johnson, 1988; Trail, 1990), physiology (sexual receptivity: Rowland, Baube & Horan, 1991; LeBas & Marshall, 2000; hormonal levels: Sinervo *et al.,* 2000), and/or life history traits (offspring size and number: Sinervo, Svensson & Comendant, 2000).

In the common lizard, *Lacerta vivipara*, both correlative and experimental data suggest that female contest competition is a strong selective pressure, at least at high densities (Massot *et al.,* 1992; Lecomte *et al.,* 1994), and affects female reproductive success (Vercken *et al.,* 2007). Recent evidence supports the hypothesis that female common lizards are involved in active mate choice (Laloi *et al.,* 2004; Richard *et al.,* 2005), and female mating competition is likely to take place since males are a limiting resource in this species (Richard *et al.,* 2005; Fitze *et al.,* 2005). However, competition for access to mates should affect females only during the mating season, which is notably short in this species (a few days: Massot *et al.,* 1992; Laloi *et al.,* 2004; Richard *et al.,* 2005). Competition for other resources (food, heating sites) is likely to generate prolonged social stress during gestation, as demonstrated by its consequences on clutch size, offspring size, and survival (Massot *et al.,* 1992; Meylan, Clobert & Sinervo, 2007; Vercken *et al.,* 2007).

Female common lizards display a polymorphism in ventral coloration (yellow, orange, or mixed) associated with alternative strategies in reproduction (different responses of clutch size, clutch hatching success, and clutch sex-ratio to several individual or environmental parameters: Vercken *et al.,* 2007) and offspring dispersal (different responses to environmental parameters: E. Vercken, M. Massot, B. Sinervo and J. Clobert, unpubl. data). In particular, females of different colours seem to differ in their sensitivity to intrasexual competition (negative effect of female density on reproductive success of orange females: Vercken *et al.,* 2007), and to morph-specific competition (negative effect of yellow female frequency on reproductive success of yellow and orange females: Vercken *et al.*, 2007). Such differences in the fitness costs of competition might result from colour-related differences in resource-holding potential and competitive ability. Indeed, major differences in competitive ability (*e.g.,* related to alternative strategies) should be signalled by conspicuous traits such as ventral colour. Competitive ability and social behaviour could thus be part of larger phenotypic syndromes correlated with ventral colour, including differences in reproduction and dispersal.

In order to identify a correlation between female ventral colour and behavioural patterns, we studied the behaviour (stress, aggressiveness and submission) of females during laboratory-staged encounters at different periods in the activity season. In particular, we tested if the colour and the morphology of females interacting with each other affected their behaviour, in order to identify alternative behavioural patterns potentially implicated in social interactions in female common lizards.

## Methods

### THE SPECIES

*Lacerta vivipara* is a small (adult snout–vent length from 50 to 70 mm), live-bearing lacertid lizard that is found throughout Europe and Asia. The 4 study populations are located on Mont Lozère (in southern France, altitude 1455 m). In these populations, males emerge from hibernation in mid-April, followed by yearlings and females in mid-May. Mating occurs at female emergence, and up to 5 different males can sire young from a single clutch (Richard *et al.,* 2005). Gestation lasts for 2 months, and parturition starts in July and lasts 2–3 weeks. Females lay a clutch of, on average, 5 soft-shelled eggs (range 1–12). Offspring hatch within 2 h of being laid and are immediately independent of their mother. A more detailed description of life history can be found in Clobert *et al.* (1994). In these populations, adult females display ventral coloration varying from pale yellow to bright orange, whereas adult males are almost always orange (with a low proportion of yellow males, between 0 and 2% depending on populations). Juveniles start by being melanic, and slowly turn to a pale green ventral coloration when yearlings. Stability of ventral colour arises with sexual maturity (around 2 y), and no further modifications of the colour signal (hue and chroma) appears to be age-dependent thereafter (Vercken *et al.,* 2007). In addition, heritability of ventral coloration was found to be significantly different from zero (0.48 for maternal heritability), with no effect of the pre- and post-natal environments (Vercken *et al.,* 2007).

### DATA SET

Females were captured from 4 different populations and brought to the laboratory in individual terraria. At each capture, females were measured (snout–vent length or SVL) and weighed. Ventral coloration was assessed visually by comparison to a homemade colour reference used from the initiation of a long-term study in 1988. Female ventral colour fell into one of 3 categories: pale yellow, bright orange, or mixed coloration (mixture of yellow and orange). This classification reflects differences in chroma and hue, and alternative strategies in reproduction (Vercken *et al.,* 2007) and offspring dispersal (E. Vercken, M. Massot, B. Sinervo & J. Clobert, unpubl. data). In particular, the responses of mixed females in reproduction and dispersal were never intermediate between the responses of yellow females and orange females, which suggests that the apparent continuity of colour variation is better described functionally as 3 discrete colour morphs. Therefore, the 3 colour classes were assumed to represent 3 distinct colour morphs, correlated with discrete alternative strategies.

Females were housed in plastic terraria with damp soil, a shelter, and water *ad libitum*. They were exposed to natural daylight and heated by electric bulbs (25 W) from 0900 to 1200 and from 1400 to 1700 to match the natural activity cycle, in which females hide in shelters during the hottest hours of the day. Because social interactions might differ in nature and strength through the course of the season, we studied female behaviour in the lab both in spring (early gestation period, from May 15th until June 4th, $n = 434$) and in summer (post-gestation period, from July 8th until July 20th, $n = 274$) to account for seasonal effects. The behaviour of females captured in spring was studied on the day after capture; they were then fed a *Pyralis farinalis* larva and released at their capture point. Females captured in summer were kept in the laboratory until parturition, and their behaviour was studied on the day after parturition. For 90% of the females captured in summer, the average time spent in captivity was 25 d (range 20–30). Length of captivity had no effect on any of the behavioural variables studied here (all *P*-values > 0.7).

At the end of their captivity, the females were fed and released with their offspring at the mother's capture point. Female behaviour was studied after parturition to avoid perturbation during gestation, and because females reduce their activity when approaching parturition (Bauwens & Thoen, 1981; Lecomte, Clobert & Massot, 1993).

### LABORATORY-STAGED ENCOUNTERS

Behavioural experiments ($n = 354$) were conducted during the heating hours in order to match the natural activity pattern of the species. A female common lizard (focal female) was introduced in a plastic terrarium (25 × 15 × 17 cm) containing a small heating wire (allowing basking for 1 female only) and left for 10 min so it could explore the terrarium and find the heating source (the limiting resource). Then another female was introduced in the opposite side of the terrarium (opponent female), and the behaviour of both females was monitored for 10 min. The design was balanced for the different colour combinations, and each female was used only once to avoid individual effects.

Several components of behaviour were analyzed: time spent scratching the terrarium walls, number of biting attempts, and number of "moves-away" (when a female moved away in reaction to the other female's approach). The 2 females were always unfamiliar, either because they came from different populations or because they had non-overlapping home ranges in the same population. Even though the experimental enclosure is smaller than a female home range (30 m in diameter on average: Massot, 1992), females are likely to interact at close range when competing for access to discrete resources in nature, and the behaviours displayed in this setting should be representative of real-life competitive interactions. In particular, the time spent scratching the walls can be interpreted as an indicator of level of stress (de Fraipont *et al.,* 2000), the number of biting attempts is likely to be an indicator of level of aggressiveness, and the number of moves-away is likely to reflect the tendency of a female to avoid competitive interactions and thus should be interpreted as a submissive behaviour. This kind of experimental design has been used successfully for this species in other contexts and the observed behaviours were found to relate to specific differences in behavioural decisions or life history traits in the field (de Fraipont *et al.,* 2000; Léna, de Fraipont & Clobert, 2000; Belliure, Meylan & Clobert, 2004; Aragon, Meylan & Clobert, 2006; Cote & Clobert, 2007). Analysis of colour-specific behavioural patterns is thus likely to give reliable information about the social relationships that connect the different colour morphs in nature.

### STATISTICAL ANALYSIS

For each trial, we analyzed only the behaviour of the focal female (the first introduced into the terrarium). Behaviour of the opponent female was used only as a covariate because it was not independent. To analyze the time spent scratching, we used a general linear model (GLM procedure, SAS Institute, Cary, North Carolina, USA). Variables that followed a Poisson distribution (numbers of biting attempts or moves-away) were analyzed using log-linear regressions (GENMOD procedure, SAS Institute). *F* statistics and likelihood ratio tests ($\chi^2$ 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 3-way interactions): population of origin, season, focal female colour, focal female size (correlated with age for females under 4 y), opponent female colour, opponent female size, the absolute size difference between focal female and opponent female, and opponent female behaviour (scratching time, number of biting attempts, and number of moves-away). We then dropped the non-significant effects (backward selection), starting with the most complex interaction terms. The same final model was obtained using the alternative information-theoretic approach (using AIC). Only the results of the final model are reported.

Colour effects were interpreted by comparing alternately the 3 different colour pairs, using a Bonferroni correction to assess significance of effects. As we performed 3 tests in each case, the significance threshold for the critical probability was lowered to 0.017 (0.05 divided by 3).

## Results

Scratching time depended on season ($F_{1,\,349} = 7.68$, $P < 0.0001$), time spent scratching by the opponent female ($F_{1,\,349} = 4.66$, $P = 0.032$), and focal female colour ($F_{2,\,349} = 4.52$, $P = 0.012$). Focal females tended to scratch longer in summer (71 ± 5.44, mean ± SE) than in spring (38.6 s ± 3.06), and when the opponent female scratched longer. Mixed females tended to scratch longer on average than yellow or orange females (difference between yellow and mixed females $F_{1,\,220} = 4.52$, $P = 0.0347$, $n = 225$; between yellow and orange females $F_{1,\,233} = 0.16$, $P = 0.68$, $n = 238$; between orange and mixed females $F_{1,\,240} = 8.62$, $P = 0.0037$, $n = 245$; Figure 1).

The number of biting attempts depended on the number of biting attempts by the opponent female ($\chi^2_1 = 45.35$, $P < 0.0001$, $n = 354$) and the interaction between focal

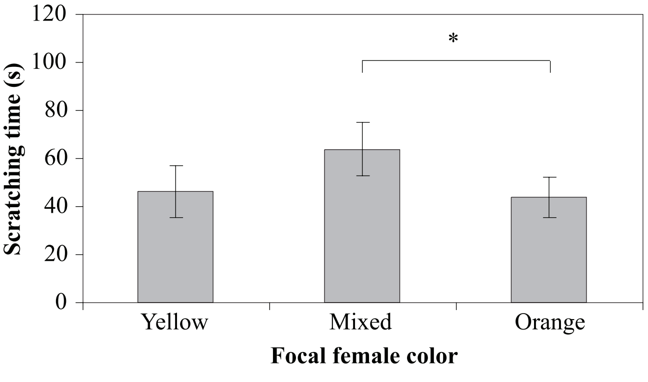

FIGURE 1. Time spent scratching depending on the colour of the focal female. Error bars are 95% confidence intervals. *: $P < 0.01$.

female colour and opponent female colour ($\chi^2_4 = 15.15$, $P = 0.0044$). All focal females attempted to bite more often when their opponent was aggressive. Yellow and orange focal females attempted to bite yellow opponent females less often than other opponent females, whereas the opposite pattern was found for mixed females (difference between yellow and mixed focal females $\chi^2_2 = 7.31$, $P = 0.026$, $n = 225$; between yellow and orange focal females $\chi^2_2 = 3.95$, $P = 0.14$, $n = 238$; between orange and mixed focal females $\chi^2_2 = 8.54$, $P = 0.014$, $n = 245$; Figure 2)

The number of moves-away depended on season ($\chi^2_1 = 17.37$, $P < 0.0001$, $n = 347$), the size difference between the focal female and her opponent ($\chi^2_1 = 10.94$, $P = 0.0009$), the number of biting attempts by the opponent female ($\chi^2_1 = 66.39$, $P < 0.0001$), and opponent colour ($\chi^2_2 = 26.40$, $P < 0.0001$). Focal females tended to flee more often when facing an opponent larger than themselves, more often in spring (1.24 ± 0.129 move-away) than in summer (0.93 ± 0.125), and more often when their opponent was aggressive. Focal females also tended to flee more often when facing a yellow or a mixed opponent than an orange opponent (difference between yellow and mixed opponent females $\chi^2_1 = 1.18$, $P = 0.28$, $n = 235$; between yellow and orange opponent females $\chi^2_1 = 16.18$, $P < 0.0001$, $n = 231$; between orange and mixed opponent females $\chi^2_1 = 22.52$, $P < 0.0001$, $n = 228$; Figure 3).

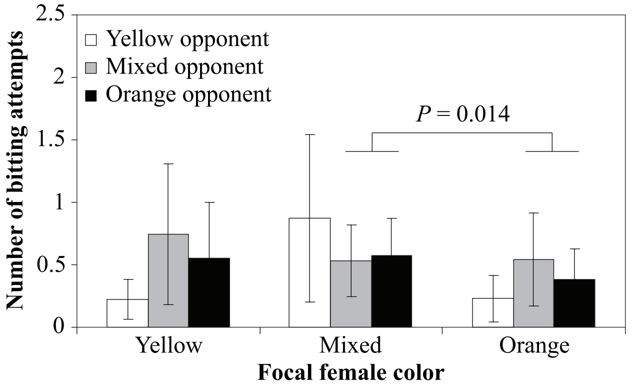

FIGURE 2. Mean number of biting attempts depending on the colour of the focal female and the colour of the opponent female. Error bars are 95% confidence intervals.

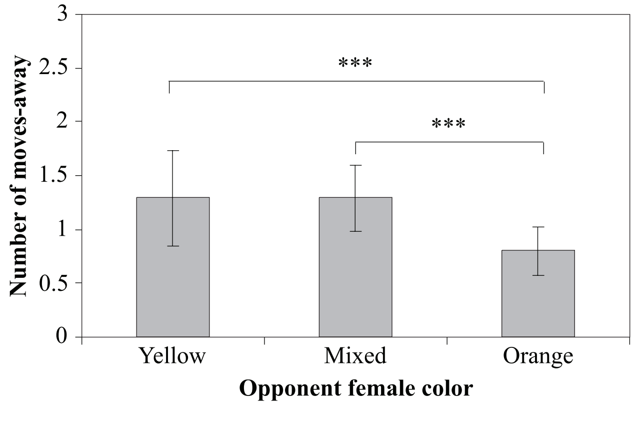

FIGURE 3. Mean number of moves-away depending on the colour of the opponent female. Error bars are 95% confidence intervals. ***: $P < 0.0001$.

## Discussion

In our experiment, females differed in their stress level and in their agonistic behaviour when facing other females, depending on their own colour, the colour of their opponent, or both. The population of origin never influenced female behaviour, which supports the generality and reliability of ventral colour as a correlate of social behaviour. As female ventral colour appears to influence strongly the outcome of social interactions, it might act as a social marker signalling resource-holding potential.

### PRIOR RESIDENCY ADVANTAGE

In our experiment, the focal female was introduced first in the terrarium and left alone to explore it for 10 min. The purpose of this design was to allow the focal female to find the heating source and reveal its presence to the opponent female by basking on it. However, the sequence of female introduction might have generated an asymmetry in the competitive encounter. The time the focal female spent alone in the terrarium, though short, might have nevertheless allowed the focal female to establish residency, thus gaining a competitive advantage over the opponent female. However, this competitive asymmetry should not have affected our results, because in all trials we analyzed the behaviour of the focal female only. Therefore, we analyzed the colour-related differences in territorial behaviour with respect to intruders, instead of plain social behaviour. In all cases, this should not restrict the range of our conclusions regarding the correlation of ventral coloration with behavioural patterns.

### SEASONAL EFFECT

In this study, 2 out of the 3 behavioural variables depended on season, which could result from seasonal variations in the levels of hormones implicated in behaviour (Dauphin-Villemant *et al.,* 1990; Woodley & Moore, 1999), as well as from behavioural responses to captivity (longer for females captured in summer). However, seasonal effects never interacted with colour effects, meaning that although season (or extended captivity) affects the overall pattern of activity, it does not modify the nature of social interactions. This result suggests that the selective pressures acting on female social behaviour do not change significantly during the reproductive season, *i.e.,* that competition for resources is far more likely to shape females' social relationships than competition for mates, and that female ventral colour might correlate with stable individual differences in resource-holding potential.

### ALTERNATIVE BEHAVIOURAL PATTERNS AND COMPETITIVE ABILITY

Orange females tended to avoid agonistic interactions more often than other females. Orange females might thus be the least competitive females, as they also appeared to be the most sensitive to social competition in a previous study (Vercken *et al.,* 2007). On the other hand, yellow females tended to make their opponents flee more than orange females and were rarely exposed to aggression by yellow or orange females, which might reflect a high competitive ability and/or a dominant status. Mixed females showed a more unusual behavioural pattern: although these females seemed especially aggressive towards yellow females (stronger competitors or dominant females), they were exposed to aggression by all females, and they spent more time scratching the terrarium walls, showing a higher stress level than other females. Such behaviour could be related to an intermediate or condition-dependent competitive ability, and these females might play the role of social challengers.

These differences in social behaviour are not related to female condition since there is no difference in morphology between colour morphs (Vercken *et al.,* 2007), and in our experiment, morphological variables never interacted with colour effects. The observed behavioural patterns are thus more likely to result from genetically based differences in resource-holding potential, leading to differences in competitive ability. Indeed, in a previous study, yellow females seemed to display stronger senescence (Vercken *et al.,* 2007), which can result from the immunosuppressive effects of elevated testosterone levels often associated with high competitive ability (immunocompetence handicap hypothesis: Folstad & Karter, 1992). In addition, other hormones such as progesterone or corticosterone could also be implicated in the development of different competitive profiles and alternative behavioural patterns.

### Is ventral colour a signal in social interactions?

If female behaviour during laboratory-staged encounters is a reliable indicator of social behaviour in nature, then ventral colour could reflect relevant genetically or physiologically based differences in resource-holding potential. This information could be used by individuals to limit the costs of agonistic interactions with unfamiliar conspecifics of superior (or inferior) competitive ability (status signalling hypothesis: Rohwer, 1975). Ventral colour could also be used to rapidly recognize familiar individuals whose competitive ability has already been challenged (individual recognition hypothesis: Collias, 1943). Indeed, as adult common lizards are sedentary (Massot *et al.,* 1992; Clobert *et al.,* 1994), groups of individuals that are spatially associated are likely to be temporally stable. In such stable social groups, signals allowing rapid individual recognition are expected to evolve (Maynard-Smith & Parker, 1976; Barnard & Burk, 1979). Honest signals of resource-holding potential, such as ventral colour in the common lizard, thus should benefit both weaker and stronger competitors in stable groups as well as unfamiliar individuals that come into contact for the first time, as they reduce the costs of escalated contests (Rohwer & Ewald, 1981; Ydenberg, Giraldeau & Falls, 1988; Höjesjö *et al.,* 1998).

Female common lizards do not perform conspicuous displays of their ventral colour. However, ventral coloration extends up to the throat, where the signal can be visible in many occasions of everyday life, for instance when a female is raising her head, walking, or climbing over substrate. Furthermore, as ventral colour is correlated with many aspects of the phenotype (reproductive traits: Vercken *et al.,* 2007; dispersal behaviour: E. Vercken, M. Massot, B. Sinervo & J. Clobert, unpubl. data), it could also correlate with chemosensory signals that females would assess at close range (Alberts, 1990; Alberts, 1992). In addition, this study showed that ventral colour is correlated with individual behaviour; thus, behaviour could also be used as an indicator of ventral colour during social interactions. Ventral colour is therefore likely to be an ecologically relevant signal of both the owner's individual phenotype (Vercken *et al.,* 2007) and its competitive ability and could be used to take adaptive decisions in competitive interactions. However, the specific role of ventral colour as a signal used in social interactions remains to be tested.

## Conclusion

Female colour polymorphism in the common lizard correlates with alternative behavioural patterns that might reflect differences in competitive ability. Such differences in resource-holding potential and social behaviour would thus be part of larger adaptive syndromes, including various life history traits, such as reproductive or dispersal strategies as already found in another lizard species (Sinervo, Svensson & Comendant, 2000; Sinervo & Clobert, 2003; Sinervo *et al.,* 2006).

Such alternative strategies are likely to structure the social environment, and the spatial association of females in nature might not be random with respect to this structure. In this study, we showed that the outcome of social interactions between unfamiliar females was colour dependent. These outcomes could affect female fitness through the establishment of relations of social dominance. Settlement decisions are thus likely to be based on the colour of the social environment alone or in interaction with local relatedness. We used confrontations between unfamiliar and most probably unrelated females to avoid kin interaction effects and to isolate the role of ventral colour in shaping behavioural patterns. However, spatial studies on the distribution of females with regard to relatedness and ventral colour would help clarify how the social landscape affects female spacing behaviour and fitness. In particular, adaptive spacing strategies could allow the maintenance of several phenotypic alternatives associated with unequal competitive abilities. In addition, to better understand the role of ventral colour in competitive interactions and in the establishment of territories in nature, experimental studies of space use and resource exploitation are still needed.

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