

The role of colour polymorphism in social encounters among female common lizards

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Colour variation in females is expected to play a role in intra-specific communication by signalling for traits that are socially relevant. However, in some cases, the information carried by colour signals is not sufficient and other cues may be used by conspecifics, such as chemosensory cues. In the common lizard, ventral coloration of females can be classified as yellow, orange or mixed. These ventral colours have been shown to predict the outcome of dyad encounters in an experimental context. However, there was no evidence that females really used the colour signal to assess the competitive ability and the social strategy of their opponent. In lacertids, chemical signals are often implicated in intraspecific communication, and could be used by females to acquire information useful for social interactions. We performed dyad encounters in which the ventral colour of the opponent was either visible or not, and studied the response of the focal female. We found that females used the colour of their opponent as a signal to adjust their own behaviour, but they also seem to be able to use other complementary cues, most probably behavioural cues. Females of different colours also differed in their ability to respond to a novel situation, which suggests colour-based differences in the plasticity of social behaviour.

Key words: behavioural plasticity, competitive interactions, *Lacerta vivipara*, multiple signals

INTRODUCTION

Conspicuous traits in general and individual colour in particular are likely to play a role in social interactions, as they convey important information about the individual's phenotype (Amundsen et al., 1997; Sinervo et al., 2000). The role of colour signals in communication has been documented in several species (for mate choice, Beeching et al., 1998; Amundsen & Forsgren, 2001; Jones & Hunter, 1993; LeBas & Marshall, 2000; for sex recognition, Cooper & Burns, 1987). However, in some cases, other cues complement or even replace colour signals as indicators of the individual's phenotype (other visual signals, Zucker 1994; chemosensory signals, Hews & Benard 2001; López & Martín 2001). Indeed, colour signals do not always reflect all the characteristics of an individual that are potentially useful to advertise to its conspecifics (such as age, Amundsen et al., 1997; size, Martín & Forsman, 1999; López et al., 2006; asymmetry, Martín & López, 2000, López et al., 2006; parasitic load, Olsson & Madsen, 1995; immune response, López et al., 2006), and alternative sources of information might be used in social interactions. In addition, different apparently redundant signals may be used at different spatial and temporal scales (e.g. visual signals may be accessible at longer distance than chemical signals, and chemical signals may persist even in the absence of their issuer). Such multiplicity of signals also allows for the construction of more complex messages (López et al., 1998, 2003).

In the common lizard *Lacerta vivipara*, there is consistent variation in female ventral coloration. One way to analyse this variation is to classify females into three dis-

crete colour classes: yellow, orange or mixed. These colour classes have been found to correlate with reproductive traits (clutch size, clutch hatching success, clutch sex-ratio; Vercken et al., 2007) and differences in individual behaviour during social interactions (laboratory trials involving a limited resource; Vercken & Clobert, 2008). When facing another female, female common lizards behave differently depending on their own ventral colour, or their opponent's colour, or both. Ventral colour thus appears to determine the outcome of social interactions in this species. Because ventral colour correlates with alternative strategies, it would be adaptive for females to adjust their own behaviour depending on the strategy of the females they encounter. Game theory predicts that such behavioural plasticity will lower the costs of aggressive interactions during the establishment of dominance relationships (Maynard-Smith, 1982).

However, we could not be sure that females used other females' colour directly as a signal and that they did not use other cues indicative of the strategy of their opponent. In lacertids, several studies have documented the role of chemosensory cues in intraspecific communication (Léna & de Fraipont, 1998; Aragón et al., 2001, 2006b), especially in individual recognition (Aragón et al., 2001; Léna & de Fraipont, 1998). It is known that in other species the presence and relative concentration of pheromonal components from the pre-cloacal and femoral gland secretions vary consistently among individuals (Alberts, 1990, 1992). These specific pheromonal profiles convey information on individual identity that may be used in social interactions (demonstrated so far in female–female and male–male communication; López et al., 2003,

2006). Such chemosensory cues could be used, alone or to complement the colour signal, to assess the competitive ability and behavioural strategy of conspecifics and to adjust behaviour in consequence.

To test for the role of ventral colour as a direct signal in social interactions, we studied the behaviour of females facing another female whose ventral colour was visible or hidden. If ventral colour is used as a signal during social encounters, then we expect different behavioural responses depending on the ventral colour of the opponent female when it is visible, and only one response when it is hidden. On the contrary, if another signal is involved, we expect the same response for both treatments because females should be able to assess other females' strategies in all cases.

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 four populations we studied 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 May. Mating occurs at female emergence, gestation lasts for two months, and parturition starts in July and lasts for 2–3 weeks. Females lay a clutch of, on average, five soft-shelled eggs (range 1–12). Offspring hatch within 1–2 hours after laying and are immediately independent of their mother. A more detailed description of life history can be found in Clobert et al. (1994). In our populations, the ventral coloration of adult females varies from pale yellow to bright orange, whereas adult males are almost always orange (although different colour patterns are observed in oviparous populations; see Sinervo et al., 2007).

Female colour morphs

Although spectrum components such as chroma and hue vary continuously along the female colour range (Vercken et al., 2007), visual classification of females into three discrete colour classes (yellow, orange and mixed) seems to characterize the heterogeneous nature of mixed coloration better (Vercken et al., 2008). This visual classification is further supported by previous results reporting non-linear differences in reproductive (Vercken et al., 2007) and behavioural strategies (Vercken & Clobert, 2008) between colour classes. Although spectrum components of female colour like chroma and hue have been shown to vary significantly over time in response to several environmental factors (Meylan et al., 2007; Cote et al., 2008), the visual classification was found to be heritable within female lineages, repeatable across time for an individual, and insensitive to the influence of many environmental factors (year, density, colour morph frequency, female feeding rate; Vercken et al., 2007). Therefore, it is most likely that colour classes signal structural phenotypic differences like alternative strategies (under both genetic and environmental determination, but not subject to annual variations), whereas chroma

and hue reflect more transient modifications of the phenotype (e.g. health, stress or motivational state).

Data set

We captured 240 females at the different sites in June 2006 and kept them in the laboratory until parturition (for 2–3 weeks). At capture, females were measured (snout–vent length or SVL) and weighed. Ventral coloration was assessed visually by comparison with a colour reference. Female ventral colour was also measured with a spectrophotometer (Ocean Optics USB2000). Data analysis was handled with the aid of 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, and in particular the hue and the chroma. There was no difference in SVL, weight or body condition (residuals of the regression between weight and SVL) between colour classes, which confirmed previous results on the absence of a relationship between female morphological traits and ventral colour (Vercken et al., 2007, 2008). Females were housed in plastic terraria with damp soil, a shelter and water *ad libitum*, and were fed one *Pyralis farinalis* larva a week. They were exposed to natural daylight and heated by electric bulbs from 0900 to 1200 and from 1400 to 1700. Females were kept in the laboratory until parturition, then participated in behavioural experiments. After all experiments were conducted, females were fed and released with their offspring at the female's capture point. All animals were treated in accordance with the *National Institute of Health Guide for Care and Use of Laboratory Animals*.

Laboratory staged encounters

The subjects of this experiment were 204 females. They encountered other females either the day after parturition or the next day, or both. Females are usually unable to feed during the last days of gestation, thus we expected more competitive behaviours in the first few hours after parturition. However, previous results showed that no interactive behaviours related directly to competition were affected by season (Vercken and Clobert 2008), and thus we assume that most results would be repeatable at another time of year.

Behavioural experiments were conducted during the hours of heating in order to match the natural activity pattern of the species. One female (focal female) encountered two females (opponent females) on two consecutive days. All terraria were cleaned between trials with bleach, and thoroughly rinsed with water. Focal and opponent females were always unfamiliar, either from different populations, or with a minimum distance of 60 m between their respective territories (the average home range size of female common lizards being 25 m). The two opponent females had the same ventral colour, which could be different from the focal female colour, and were involved in only one encounter each.

In one encounter, the belly of the opponent female was covered with green paint (Snazaroo Face Paint, Grass Green 444) so that the original ventral colour was not visible anymore. We chose to use green paint because it was

the colour closest in wavelength to the natural ventral colours of females, with enough contrast to avoid any confusion of signals. The green paint was thus experienced as a novel signal, with no apparent relation to any of the naturally occurring phenotypes. However, we are confident in assuming that green-painted females were still recognised as conspecifics by focal females. Indeed, in several cases, female behaviour was affected by the interaction between the colour of the opponent and the painting treatment, which would not be expected if the green colour was perceived as a heterospecific signal only. It is more likely that other species-specific signals are used for species recognition, such as behaviour and dorsal patterns (Lepetz et al., 2009), that are easier to recognize at a distance than ventral coloration.

In the other encounter, the belly of the opponent female was slightly stained with diluted white paint (Snazaroo Face Paint, White 000) so that the original ventral colour was still visible, but the smell of paint was present in both trials. Such manipulation could have affected the normal behaviour of females, but since the smell was present in both experimental treatments, it should not affect the comparisons made between treatments. In addition, the general behavioural trends we found were quite conservative in comparison with previous experiments without painting treatments (see Discussion), which gave us confidence that the painting treatment (either green or white) did not modify female behaviour significantly.

The effect of the manipulation on colour spectrum was tested on 20 females for each group with paired *t*-tests. Colour spectrum was significantly different after the green-painting treatment (*t*-test for chroma = -23.87, $P < 0.0001$; *t*-test for hue = -15.09, $P < 0.0001$), whereas it was not different from the natural spectrum after the white-painting treatment (*t*-test for chroma = 0.42, $P = 0.679$; *t*-test for hue = -0.86, $P = 0.39$). The same results were found for brightness, though with a stronger relative effect of the white-painting treatment (green-painting treatment, $t = 12.44$, $P < 0.0001$; white-painting treatment, $t = 1.74$, $P = 0.098$). However, because brightness is the most variable spectrum component, with strong variations in relation to sloughing in particular, we assumed that female ventral colour was still easily recognisable in the white-painting treatment.

For each focal female, the sequence of presentation of green- and white-painted opponent females (first or second day) was determined randomly. We chose not to mimic a natural signal (e.g. painting a yellow female orange), because after several tests with a spectrophotometer we were not able to mimic correctly the natural colours of lizard skin (especially for brightness and chroma). In this experiment, focal females are thus confronted with a novel signal (green colour) that is likely to be inconsistent with other information they can acquire from the phenotype of opponent females (e.g. chemical cues).

The focal female was introduced in a plastic terrarium (25 × 15 × 15 cm) containing a small heating wire (allowing basking for one female only) and left for 10 minutes, so that she could explore the terrarium and find the heat

source. Then the opponent female was introduced in the opposite side of the terrarium and the behaviour of both females was monitored for 15 minutes. Such asymmetry in the experimental design is expected to affect female relationships: indeed, focal females were shown to behave like residents and opponent females like intruders in a previous study (Vercken & Clobert 2008; see also Aragón et al., 2006a). However, as only the behaviour of the focal female was analysed, this asymmetry should not have affected our interpretation of the results.

Several components of the behaviour were analysed: time spent walking, time spent scratching the terrarium walls, time spent basking on the heating wire, number of biting attempts, number of “moves-away” (when a female moved away in reaction to the other female’s approach), number of non-aggressive contacts (when a female moved towards the other female in a direct way, and stayed close to her). Individual behaviours such as walking, basking or scratching the walls give information about the individual’s level of stress (exploration, escape or resource exploitation; Clobert et al., 1994; de Fraipont et al., 2000; Belliure et al., 2004). On the other hand, the number of biting attempts, moves-away or non-aggressive contacts characterise the dominance status or the social strategy (Aragón et al., 2006a; Vercken & Clobert, 2008).

This kind of experimental design has been used successfully for this species in other contexts and the behaviours observed in laboratory conditions were found to reflect individual differences in behavioural decisions such as dispersal in the field (de Fraipont et al., 2000; Léna et al., 2000; Belliure et al., 2004; Aragón et al., 2006c; Cote & Clobert, 2007a). Such repeatable behaviours also seem to reflect competitive relationships in natural conditions (Clobert et al., 1994). Stereotyped behaviours that can be observed in controlled laboratory conditions, although not always directly interpretable in terms of adaptive responses to the environment, are, however, likely to be indicative of dominance relationships and space use behaviours that are expressed in more natural conditions.

Statistical analysis

For each encounter, we analysed only the behaviour of the focal female. The behaviour of the opponent female was not considered as an independent variable, and was only included as a covariate whenever relevant. As the focal female was used in two trials, we used mixed models that included a random female effect. Continuous variables (time spent walking, scratching or basking) were analysed using mixed general linear models (MIXED procedure, SAS Institute), whereas variables that followed a Poisson distribution (number of interactions) were analysed using mixed log-linear regressions analysis (GLIMMIX procedure, SAS Institute). We tested the effects of focal female colour, opponent female colour, painting treatment, focal female SVL, difference in SVL between females and population of origin of each female. Estimations and test statistics were calculated with restricted maximum likelihood approach. *F*-tests were used to assess significance of fixed effects. Random female ef-

Table 1. Significant effects on female behaviour (FF SVL: snout–vent length of the focal female; FF colour: colour of the focal female; OF colour: colour of the opponent female; painting: painting treatment)

| Behavioural variable | Explanatory variables | Comparisons between colour classes | | |
|-----------------------------------|--|------------------------------------|--------------------------|--------------------------|
| | | Yellow vs mixed | Yellow vs orange | Orange vs mixed |
| Time spent walking | FFSVL $F_{1,65}=8.84, P=0.004$ | – | – | – |
| | OF colour $F_{2,65}=4.21, P=0.015$ | $F_{1,37}=6.72, P=0.014$ | $F_{1,45}=5.43, P=0.024$ | $F_{1,40}=0.74, P=0.69$ |
| | FF colour*painting $F_{2,65}=3.5, P=0.036$ | $F_{1,46}=1.17, P=0.28$ | $F_{1,44}=3.26, P=0.08$ | $F_{1,37}=5.75, P=0.022$ |
| Number of biting attempts | OF colour $F_{2,65}=4.85, P=0.01$ | $F_{1,40}=3.17, P=0.082$ | $F_{1,47}=1.91, P=0.17$ | $F_{1,43}=9.33, P=0.004$ |
| | painting $F_{1,65}=7.14, P=0.0095$ | – | – | – |
| Number of non-aggressive contacts | FF colour*OF colour*painting $F_{4,56}=2.48, P=0.054$ | $F_{2,40}=4.52, P=0.017$ | $F_{2,38}=4.34, P=0.020$ | $F_{2,31}=0.01, P=0.99$ |

fects always accounted for a significant part of the variance (all $P < 0.0005$), and thus were always included in models. 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-factor interactions. We selected the fittest model with lowest AIC criterion. Only the results of the selected model are reported.

Colour effects were interpreted by comparing the three different colour pairs alternately (either for the effect of focal female colour or opponent colour). In this case, we used a Bonferroni correction to assess significance of effects (the significance threshold for the critical probability being lowered to 0.017).

RESULTS

Time spent scratching the terrarium walls, time spent basking on the heating wire and number of “moves-away” never responded to focal or opponent females’ colours (alone or in interaction) or to painting treatment (all $P > 0.15$). However, we found that both female colour and painting treatment affected the other three behavioural variables (time spent walking, number of bite attempts, number of searches for physical contacts), either as a main effect or in interaction (Table 1). The visibility of the ventral colour of the opponent female thus affects both the individual and social behaviour of the focal female in the components that are influenced by ventral colour.

Time spent walking depended on focal female SVL, opponent female’s colour, and the interaction between focal female’s colour and the painting treatment. Focal females spent more time walking when facing a yellow opponent than a mixed opponent, and more time walking when facing a yellow opponent than an orange opponent. Orange females tended to increase their activity when facing an opponent whose colour was hidden (Fig. 1), whereas the opposite trend was found for mixed females.

Number of biting attempts depended on opponent female’s colour and painting treatment. Focal females were more aggressive towards orange opponents (mean number of biting attempts = 0.74) than towards yellow (0.30) or mixed opponents (0.15). Focal females tended to bite their opponent more often when they could see her colour (mean number of biting attempts when the opponent’s colour was visible = 0.48; mean number of biting attempts when the opponent’s colour was hidden = 0.25).

Number of non-aggressive contacts was affected marginally by the interaction between focal female’s colour, opponent female’s colour, and painting treatment. The responses of yellow females are opposite in the two painting treatments (Fig. 2): yellow females are more likely to approach mixed and orange opponents when their colour

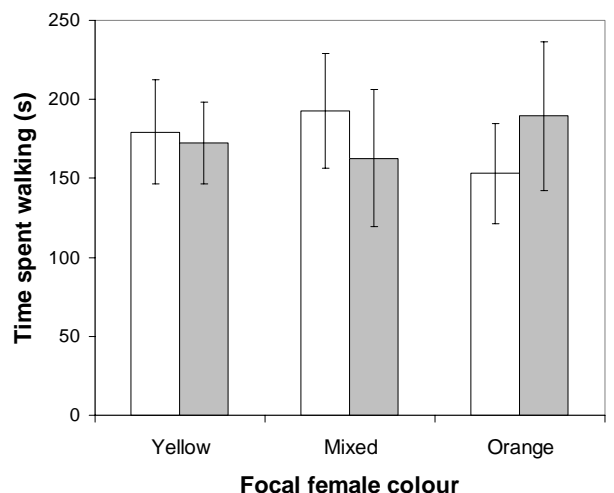


Fig. 1. Time spent walking as a function of the colour of the focal female in the white-painting (white bars) or green-painting treatment (grey bars). Error bars are 95% CI.

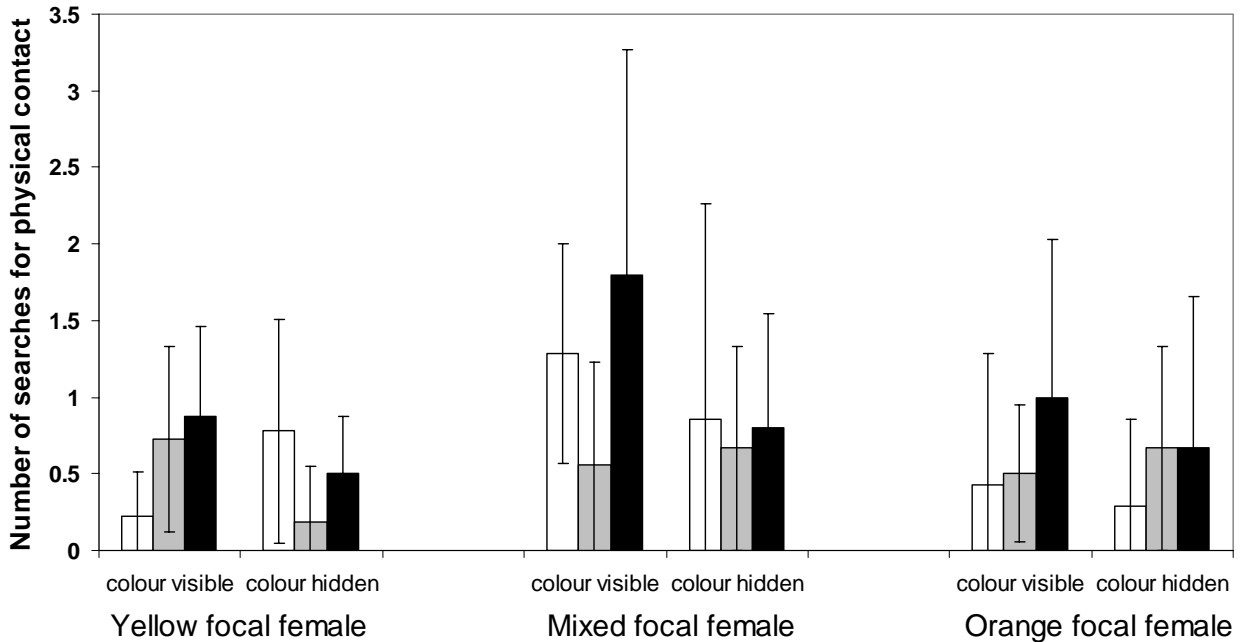


Fig. 2. Number of non-aggressive contacts displayed by the focal females of different ventral colours for the two painting treatments as a function of the colour of the opponent female (yellow, white bars; mixed, grey bars; orange, black bars). Error bars are 95% CI.

is visible, and yellow opponents when their colour is hidden. On the other hand, the responses of mixed and orange females, although modified in intensity, are similar between treatments: mixed females are less likely to approach mixed opponents than yellow or orange opponents, whereas orange females are less likely to approach yellow opponents than mixed or orange ones.

DISCUSSION

Effect of signal visibility on female behaviour

In all variables that responded to at least one of the females' colour, we found an effect of the painting treatment. This means that the focal female was influenced by the colour signal of her opponent, and when this signal was not available, her behaviour was modified. If we hypothesize that ventral colour is the only signal available to females to assess other females' strategy and adjust their behaviour in consequence, the focal female's behaviour should depend on the opponent female's colour when only this information can be assessed. Therefore, the opponent female's colour should affect the behaviour of the focal female in the white-painting treatment only, and we should observe a significant interaction between the colour of the opponent female and the painting treatment. This is not what we found. Although we found such an interaction in one case (for the number of non-aggressive contacts), for the other variables, the treatment effect was significant either alone (number of biting attempts) or in interaction with the colour of the focal female (time spent walking). This implies

that the social signal that gives information about the opponent female's strategy is not entirely blurred by the painting treatment, but still partly accessible. Most behavioural encounters (whether the colour of the opponent female was visible or not) began with a few minutes of "reciprocal assessment": during this short period, females displayed low activity and did not come into close contact with one another. Our hypothesis is that females used these first moments to gather information about their opponent (e.g. strategy, condition, motivation), which they then used to adjust their own behaviour. It is most likely that during this period, focal females perceived several cues that gave them information about their opponent's phenotype. Therefore, even in the case where the colour of the opponent female was not visible, the focal female had the opportunity to assess her strategy through other cues, which could explain why we found a continuing effect of opponent female's ventral colour on the behaviour of the focal female.

Several alternative sources of information can be accessible to females when ventral colour is not visible. For instance, individual behaviour is known to be a source of information for conspecifics in this species (Aragón et al., 2006a; Cote & Clobert, 2007b), and female behaviour correlates with her colour-based strategy (this study; Vercken & Clobert, 2008). Focal females could thus use the behaviour of opponent females (e.g. time spent walking or scratching or more subtle behaviours like head movements or tongue-flicking rate, which were not tested in this study) as an indicator of their colour class and strategy, which would explain why the colour of the opponent still affects focal female behaviour even when it is

covered with green paint. On the other hand, different chemical signatures could also allow other females to identify potential competitors even in their absence. In many species, dominance relationships between males are mediated by status-specific pheromones (e.g. Everaerts et al., 1997; Moore & Bergman, 2005; Barata et al., 2007). The same kind of communication is quite likely to take place between females when female social interactions reflect alternative strategies potentially related to dominance status (Vercken & Clobert, 2008). Indeed, preliminary analyses have shown that the plasma level of testosterone differs between females of different colour classes (E. Vercken, unpubl. data), so it is likely that other steroid molecules also differ qualitatively and/or quantitatively between colour classes.

The absence of a strict interaction between opponent female colour and painting treatment thus suggests the existence of another signal affecting the behaviour of the focal female. Such a signal, either behavioural or chemical, would belong to the phenotypic syndrome associated with ventral colour (because it allows the identification of the colour of the opponent female when it is not visible), and thus would be indicative of female strategy. However, this signal does not convey the same information as ventral colour, because it does not trigger the same behavioural responses in the focal female. It might reflect other components of the phenotype that are useful for potential competitors (e.g. for behaviour: dispersal status, Aragón et al., 2006a; motivational state, Elwood et al., 2006; for chemical cues: age, López et al., 2003; relatedness, Léna & de Fraipont 1998; immune status, López et al., 2006, etc).

Female behavioural patterns and dominance relationships

A first study of the behaviour of female common lizards suggested that yellow females were likely to be stronger competitors and thus to hold a dominant position over other females, whereas orange females were weaker competitors and would use a submissive behavioural strategy. The strategy of mixed females appeared more complex, and it was proposed that they played the role of social challengers (Vercken & Clobert, 2008). This general classification of female dominance relationships is now strongly supported by the results of the present study. Indeed, we found here that orange opponents suffered more aggression from the focal females than yellow or mixed opponents, which is consistent with orange females being dominated by other females. We also found that opponent females were more often recipients of aggression when their colour was visible than when it was hidden: it seems that green-painted females were assessed as strong competitors by the focal females. The same pattern was found again in the analysis of time spent walking: focal females spent more time walking when facing yellow or green-painted opponents (strong competitors) than when facing orange or white-painted opponents. Although this behaviour observed in laboratory conditions may be difficult to interpret in terms of adaptive strategies, it appears that the time spent walking

responds positively to the level of competition experienced by the focal female, and thus could be an indirect indicator of the level of social stress in this species.

Different reactions towards novel situations

In our experiment, it seems that focal females chose to behave towards green-painted females quite similarly to how they behave towards stronger competitors (i.e. yellow females). This could be interpreted as a "precautionary strategy": in the absence of other information about their dominance status, it is probably safer not to challenge these females aggressively. However, the significant interaction between opponent female's colour and painting treatment for several behaviours showed that females were still able to assess part of their opponent's strategy correctly in the absence of the colour signal they would have expected. Females were thus confronted with an apparent contradiction, and displayed different reactions to this situation, depending on their own ventral colour.

Orange and mixed females reacted directly to the presence of an unknown stimulus, and spent more time walking when the belly of the opponent female was painted green, whereas the painting treatment did not affect time spent walking by yellow females. In addition, females differed in their propensity to modify their behaviour in response to the strategy of the opponent female in the absence of the colour signal. For orange and mixed females, the number of non-aggressive contacts was influenced by the colour of the opponent female in a similar way whether the colour was visible or not, whereas yellow females displayed different responses to the colour of the opponent female depending on the presence of the visual signal. It is possible that females with alternative strategies differ in their sensitivity to other cues (chemical or behavioural) that allow them to assess their opponent's strategy or resource holding potential correctly: in this case, only mixed and orange focal females were able to correctly identify the strategy of green-painted females. Another explanation would be that because yellow females are dominant, they do not benefit from adaptive behavioural plasticity during competitive encounters.

CONCLUSION

This experiment demonstrates that the visual signal of ventral colour plays a direct role in social interactions, by allowing females to adjust their behaviour to the strategy and dominance status of other female competitors. Such plasticity is likely to be adaptive as it would lower the costs of direct agonistic interactions for the establishment of dominance relationships. In addition, although the colour signal is likely to be complemented with other cues (behavioural or chemical), it appears necessary for the reliable identification of female strategies. Colour polymorphism in this species would thus be selected as an advertizing signal for female alternative strategies. However, further information is needed to assess more precisely the importance of multiple signals and the nature of competitive interactions between alternative female strategies in this species.

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