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Exploring the function of red colouration in female spiny-footed lizards (*Acanthodactylus erythrurus*): patterns of seasonal colour change

José J. Cuervo[1,*], Josabel Belliure[2]

Abstract. In spiny-footed lizards (*Acanthodactylus erythrurus*), adult females (but not males) show conspicuous red colouration in the tail and hind legs. To investigate the function of this red colouring and proximal causes of seasonal colour change, we captured adult females before the reproductive season and kept them in captivity in one of the three following situations: with a male and fertilization possible, with a male and fertilization impossible, or with another female (fertilization also impossible). Colour was quantified using spectrophotometry. Red colouration increased shortly before the onset of reproduction, but faded during the breeding season and became whitish (light buff-gray) in all cases. Both fertilized and unfertilized females laid eggs or were gravid after two months of the experiment, but while fertilized females laid mostly fertile eggs, unfertilized females only laid infertile eggs. Both egg formation and colour change might be triggered by abiotic factors, although female characteristics also play a role, since heavier females changed colour and laid eggs earlier. Females interacting freely with a male were darker at the end of the breeding season than females separated from the male, indicating that fertilization or physical contact might also have an effect on colouration. Colour change patterns found in this study suggest that female red colouration might have a mating-related function, but do not support a courtship rejection function for the red colour. However, whitish colouration resulting from red fading might signal gravidity in this species. Future experimental manipulation of female colouration will be needed to test these hypotheses.

Keywords: infertile eggs, Lacertidae, reproduction, sexual dichromatism, spectrophotometry.

Introduction

Many vertebrate species develop conspicuous colouration that frequently works as a signal providing information on the bearer (Butcher and Rowher, 1989; Andersson, 1994). Very often, conspicuous colouration is present in males, while females show a duller version of the male's colour. A traditional explanation for this pattern is that brilliant colouration is selected and functional only in males, while the presence of a similar colour in females is due to genetic correlation between male and female traits (e.g., Muma and Weatherhead, 1989). Many studies, however, indicate that female colouration can evolve independently of the male colour by direct selection on females (Amundsen, Forsgren and Hansen, 1997; Burns, 1998; Amundsen and Forsgren, 2001). In species in which males and females share colouration to some degree it will be difficult to disentangle to what extent female colouration is due to direct selection on females or to a genetically correlated response to selection on males. But a clear example of female colouration evolving as a result of direct selection on females is when this colour is restricted to females. This may happen in species with sex-role reversal, but often also in species with conventional sex roles. Female-restricted conspicuous colouration has been studied in different vertebrate species with conventional sex roles (mammals: Nunn, 1999; fish: Amundsen and Forsgren, 2001; birds: Heinsohn, Legge and Endler, 2005), but appears to be particularly frequent in lizards (Cooper, 1988; Watkins, 1997; Hager, 2001; Weiss, 2002; Baird, 2004; Chan, Stuart-Fox and Jessop, 2009). When conspicuous colouration appears only in females, it is generally expressed during the reproductive

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1 - Departamento de Ecología Evolutiva, Museo Nacional de Ciencias Naturales (CSIC), Calle José Gutiérrez Abascal 2, E-28006 Madrid, Spain
2 - Departamento de Ecología, Edificio de Ciencias, Universidad de Alcalá, E-28871 Alcalá de Henares, Madrid, Spain
*Corresponding author; e-mail: jjcuervo@mncn.csic.es

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season (Hager, 2001; Weiss, 2002; Baird, 2004). The abundance of species with female-restricted colouration and their relatively simple social systems make lizards an ideal subject to study the evolution of female colour ornaments.

Several hypotheses have been postulated regarding the possible function of conspicuous colouration in female lizards (reviews in Cooper and Greenberg, 1992; Baird, 2004). First, colouration might have evolved as a signal for sex recognition during reproduction. In this case, females would be less often the target of the typically aggressive male behaviour towards other males (Cooper, 1984). Second, colouration might be a sexual ornament signalling phenotypic and/or genotypic quality to males (Weiss, 2006; Weiss, Kennedy and Bernhard, 2009; Weiss et al., 2011). Third, colouration might indicate that females are sexually receptive. In this case, bright colours are acquired before mating (Cooper and Crews, 1988). Fourth, colouration might indicate that females are gravid, i.e., not receptive, thus reducing male interest in courtship and aggressive male behaviour associated with mating. This function implies that female colouration is acquired after mating (Cuadrado, 2000; Hager, 2001). The first three hypotheses mentioned above involve mating-related functions and are not mutually exclusive. According to all these previous studies, it seems as if female conspicuous colouration has different functions in different lizard species. However, more studies on female lizard colouration, including species not studied so far, are needed to explore possible common patterns across species.

One lizard species in which adult females show bright colours and adult males do not is the spiny-footed lizard (*Acanthodactylus erythrurus* (Schinz, 1833)). Juveniles of both sexes and adult females (but not adult males) show red colouration on the ventral part of the tail and the rear part of the hind legs. This red colour, particularly on legs, is conspicuous when the lizard is looked at from behind. Information on factors affecting adult female colouration in this species is almost absent, however. Some reviews mention that the tail is red in many adult females (Pérez-Mellado, 1998) and others that the tail is red in sexually receptive females (Belliure, 2009), but none of these comments is based on specific studies. Seasonal colour change and its possible relationship to the reproductive cycle have never been studied in this species, and the function of the red colouring in adult females is currently unknown.

The aim of this study was to look for patterns of red colour change in adult female spiny-footed lizards as a necessary first step to investigate possible functions and causes of this colouration. Using an experimental approach in captivity and simultaneous field observations, we were able to describe the timing of female colour change during the reproductive season and determine the effects of a sexual stimulus (presence of a male) and fertilization on female colouration. This information allowed us to hypothesize proximal and ultimate mechanisms affecting red colouration in females of this species. It also allowed us to determine the effect of captivity on colouration. Regarding ultimate causes of colouration, at least three mechanisms are possible: (1) Red colouration has a mating-related function. This is typically the case when colouration is acquired shortly before mating (e.g., Cooper and Crews, 1988; Weiss, 2006). We know that red colour does not appear de novo in adult females of this species because it is also present in juveniles. However, female red colouration might still have a mating-related function if it is increased shortly before mating. (2) Red colouration has a courtship rejection function. Red colouration indicates that females are gravid and, consequently, the colour is acquired after mating (Watkins, 1997; Hager, 2001). As explained above, red colour is present in juveniles and also in adult females before mating, but a courtship rejection function might be possible if fertilized females have their red colouration increased after mating. (3) Red colouration has a non-reproductive function. This would be the case if red colouring does not change shortly before or during the reproductive season.

Regarding proximal causes of colour change, at least three mechanisms are possible: (1) A sexual stimulus (e.g., presence of a male) is the only requisite for female colour change to happen, and mating would not be required. As far as we know, this mechanism has never been explicitly investigated in lizards. (2) Fertilization (or copulation) triggers the physiological mechanism producing colour change and therefore this change will only happen after mating (Hager, 2001). (3) Abiotic factors such as temperature or photoperiod determine the onset of reproduction (Duval, Guillette and Jones, 1982) and also the timing of colour change. In this case, neither mating nor sexual stimuli would be required to elicit colour change.

Materials and methods

Study species

Spiny-footed lizards are medium-sized lacertids living in sandy, open habitats of Northern Africa and the Iberian Peninsula (Pérez-Mellado, 1998). The phenology of the reproductive cycle varies among populations, but in southern Spain, most spiny-footed lizards hibernate during November-February, emerge from hibernation in March, and begin to mate in April, females lay eggs during May-July, and most hatchings take place in August and September (Busack and Jaksić, 1982; Seva, 1982; Busack and Klosterman, 1987). There is no evidence of multiple clutches in populations in southern Spain (Busack and Klosterman, 1987), but a second clutch might be possible in other populations (Castilla, Barbadillo and Bauwens, 1992). Average clutch size is 4.4 eggs (range 1-8; Belliure, 2009). The species only lives for about two years (Busack and Jaksić, 1982) and reaches sexual maturity at the age of one year and a half (Belliure, 2009). This means that spiny-footed lizards have a single breeding season, and females probably produce only one clutch, in their lifetime. The mating system of the species is unknown, but most lacertids studied so far are promiscuous and mate multiply (Olsson and Madsen, 2001; Laloi et al., 2004; Salvador et al., 2008).

Field procedures

The study was carried out during February-May 2009 in Almería, south-eastern Spain. All individuals were captured in Cabo de Gata-Níjar Natural Park (36°49′08″-36°50′13″N, 2°16′59″-2°18′36″W), in open coastal shrubland with sandy soils and Mediterranean semi-arid climate conditions (average annual rainfall less than 200 mm). Lizards were captured with a noose at the end of a 2-m-long fishing pole and placed in individual cloth bags inside a cooler to avoid overheating. All animals were taken to the lab, where they were measured (snout-vent length (SVL) and total length with a ruler to the nearest 0.1 cm) and weighed (with an electronic balance to the nearest 0.1 g). For field observations, 37 females were caught during April and May (fig. 1), tail and hind-leg colour was quantified (see Colour Measurement below) immediately after the other measurements were taken, and the individuals were released less than 24 h after capture in exactly the same places where they had been captured. Lizards were not individually marked, so to decrease the risk of catching the same individual twice, during April and May we always looked for lizards in areas where none had previously been released. These areas were at least 200 m away from previous release points. Recaptures were highly improbable because home ranges of adult females are usually 500-600 m^2 (Seva, 1982). For the experimental study, individuals (31 males and 47 females) were caught during February and March, and were kept in captivity for at least two months (see Experiment in Captivity below). All females were more than 60 mm SVL (range 61-71 mm) and all males more than 70 mm SVL (range 71-77 mm), so they were considered to be adults. These thresholds strongly reduce the chance of considering immature individuals as mature, at least in

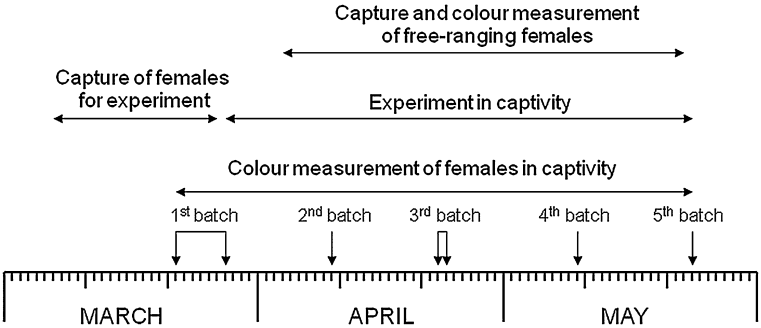

Figure 1. Dates of capture and colour measurement of the two groups of spiny-footed lizards investigated in this study: free-ranging females and females involved in the experiment in captivity.

spiny-footed lizard populations in southern Spain, where females reach sexual maturity at around 57-58 mm and males at around 60-61 mm (Busack and Jaksić, 1982; Seva, 1982). Males were easily distinguishable from females because the base of the tail is much wider in the male (Blasco, 1975).

Experiment in captivity

Individuals involved in the experiment were mostly captured during March (from the 6th to the 26th (fig. 1), although one male was captured on February 26th), because at this time of the year spiny-footed lizards in this area are already active after hibernation but have not begun mating (Seva, 1982; Busack and Klosterman, 1987). Females were randomly assigned to one of three experimental groups. Sixteen females were assigned to a group in which one female and one male shared a terrarium where they could freely interact. Fifteen females were assigned to another group consisting of one female and one male in the same terrarium, but separated by a transparent methacrylate wall with holes, so that females could see and smell the male but physical contact, and thus copulation, was impossible. Holes in the methacrylate wall were made because chemical intraspecific communication might be important in this species (López and Martín, 2005). Finally, 16 females were assigned to a group consisting of two females sharing a terrarium in which they could freely interact. Females in the eight two-female pairs were individually identified by measuring their total length, which differed, on average, by 2.1 mm within pairs. Long and short females within pairs, however, did not differ significantly in SVL (mean (SE) SVL of short females = 66.3 (0.7) mm; mean (SE) SVL of long females = 65.9 (0.9) mm; paired Student's t-test; $t_7 = 0.89$, $P = 0.40$). Females in different experimental groups did not differ significantly in SVL, total length, body weight, weight relative to body size (an estimate of underlying energy reserves expressed as the residuals of weight regressed on SVL; hereafter condition) or capture date (ANOVAs; $F_{2,44} \leqslant 2.29$, $P \geqslant 0.11$ in the five tests).

The experiment took place in outdoor terraria located at the Finca Experimental La Hoya, a facility of the Estación Experimental de Zonas Áridas (CSIC) in Almería city (36°50′38″N, 2°28′22″W), about 20 km from the area where lizards were captured. Weather conditions in both areas are very similar. All terraria were made of opaque white high-density polyethylene, were the same size (80 cm long × 60 cm wide × 42 cm high) and were placed in an open area, thus receiving direct sunlight most of the day. Although the area appeared to have identical conditions, terraria containing females from different experimental groups were intermixed to avoid any microclimatic differences among groups. The bottoms of the terraria were covered with a 3-5-cm-thick layer of sand, and every terrarium also contained hollow bricks and pieces of wood for refuge and thermoregulation. Lizards were fed live crickets dusted with calcium and vitamins three times per week and water was provided ad libitum. Colouration of all experimental lizards (males and females) was quantified (see Colour Measurement below) on March 21st-27th (fig. 1). In addition, female colour was measured about every two weeks on April 9th, April 22nd-23rd, May 9th, and May 23rd (i.e., five measurement batches in total; fig. 1). Experimental lizards were released May 24th-28th in exactly the same places where they had been captured. Females at the time of release had already laid eggs or were close to lay. Fecundity (number of eggs), egg characteristics (colour: white or yellowish; turgidity: turgid or flaccid), and laying date were determined by checking females every second day during the egg-laying period. In the case of females that had not laid eggs at the time of release ($n = 15$; female and male together: $n = 8$; female and male separated: $n = 4$; two females together: $n = 3$), the number of eggs was estimated by gently palpating the abdomen, and laying date was considered the day after the release date. When the eggs did not seem to have been laid the same day they were found because they looked dry ($n = 7$ clutches; female and male together: $n = 2$; female and male separated: $n = 3$; two females together: $n = 2$), laying date was considered the day before the finding date. Number of eggs could not be determined for one female because eggs were not found. A sample of 38 eggs from 16 females from the 3 experimental groups (female and male together: 4 females, 14 eggs; female and male separated: 6 females, 12 eggs; two females together: 6 females, 12 eggs) was carefully examined by candling to look for the blastodisc, a circular spot with a reddish border (due to vascularisation) typically visible through the shell in fertilized eggs (Olsson and Shine, 1997).

Colour measurement

Colour was quantified in terms of reflectance, i.e., the ratio of the total amount of radiation reflected by a surface to the total amount of radiation incident on the surface. Reflectance spectra (325-700 nm) were recorded with an Ocean Optics USB2000 spectrophotometer (Ocean Optics, Inc., Dunedin, FL, USA) connected to a deuterium tungsten halogen light source (DT-MINI-2-GS) by a coaxial reflection probe (QR400-7-UV/BX), using SpectraSuite (Ocean Optics, Inc., Dunedin, FL, USA) software. Reflectance was always measured with the probe placed at a constant distance from the object at a 45° angle. The measurements were referenced to standard white (WS-1) and dark, which were calibrated before measuring each lizard. Reflectance was measured 12 times for each individual and batch of measurements, three on the rear part of the right hind leg, three on the rear part of the left hind leg, three on the ventral part of the tail around 1 cm from the cloaca, and three around 2.5 cm from the cloaca. The three measurements of each body part were taken in a row, and the probe was repositioned after each measurement. To our knowledge, this is the first time spiny-footed lizard colouration is studied using spectrophotometry.

Colour parameters were determined using a principal component analysis (PCA) on raw spectral values (Cuthill, 1999; Cuervo and Shine, 2007). This method is not free from criticism (e.g., Grill and Rush, 2000; Endler and Mielke, 2005), but was chosen because it makes no a priori assumptions about which aspects of the spectrum might be important. Only one PCA was done for both captive

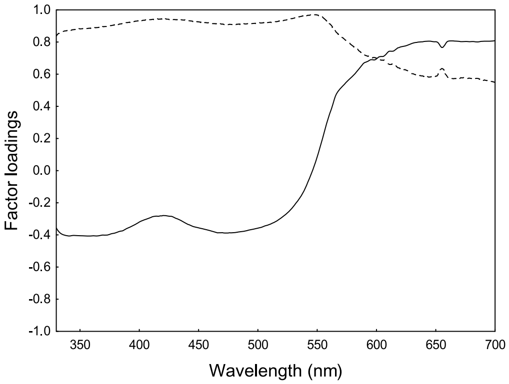

Figure 2. Loadings of the first two factors from a principal component analysis on reflectances measured at 1-nm intervals between 325 and 700 nm on the tail and hindlegs of spiny-footed lizards (*Acanthodactylus erythrurus*). The first factor (broken line) represents mainly variation in brightness and the second factor (solid line) in red colouration. Both loading and factor values were multiplied by -1 to render positive relationships between factors and colour traits (see the text).

and wild females. The first two factors from the PCA explained 69.1% and 27.2% of the variance (96.3% in total) and were retained for subsequent analyses. The first factor (PC1) represented variation in brightness and the second factor (PC2) represented mainly variation in orange-red colouration (fig. 2). PC values were multiplied by -1 to render positive relationships between PC1 and brightness, and between PC2 and redness (Cuthill et al., 1999). Measurement error of the two PCs was small for the four body parts (repeatability according to Lessells and Boag, 1987; PC1: $0.595 \leqslant r \leqslant 0.786$, $P < 0.0001$; PC2: $0.769 \leqslant r \leqslant 0.825$, $P < 0.0001$), thus justifying the use of means for each body part and measurement batch. We admit, however, that repeatability estimates might have been lower if measurements had not been taken in a row but at longer intervals (e.g., hours). Colour estimates of different body parts were strongly and significantly correlated (Pearson correlations; when all measurement batches for the 84 females are included: PC1, $0.560 \leqslant r \leqslant 0.715$, PC2, $0.643 \leqslant r \leqslant 0.784$, $n = 272$, $P < 0.0001$ in the six tests; when only one measurement is included for each female: PC1, $0.502 \leqslant r \leqslant 0.702$, PC2, $0.576 \leqslant r \leqslant 0.728$, $n = 84$, $P < 0.0001$ in the six tests), so we calculated a single PC1 value and a single PC2 value for each individual and measurement batch (the mean of the four body parts) and used these in later analyses.

Statistical analyses

Most variables were approximately normally distributed (Kolmogorov-Smirnov tests; $P \geqslant 0.10$) and, consequently, parametric tests were used in these cases. The only exception was number of eggs, which we considered a discrete variable and was analyzed using non-parametric statistics (Kruskal-Wallis tests and Spearman correlations). Differences in PC1 and PC2 among measurement batches (i.e., temporal variation) and among experimental groups, and the relationships between colour parameters (PC1 and PC2) and body size and weight were tested using two-way ANCOVAs with repeated measures in one factor (measurement batch) followed by Tukey post-hoc tests, ANCOVAs or Pearson correlations. All variables and the interactions time × experiment, time × SVL, and time × weight were included in initial models, but terms that did not explain a significant amount of the variance ($P \geqslant 0.10$) were removed from final models following a backward stepwise procedure. Females captured in the wild during April and May were compared with females kept in captivity using ANOVAs and Tukey post-hoc tests as follows: colouration of captive females in the second measurement batch (April 9^{th}) was compared to wild females captured on April 3^{rd}-14^{th} ($n = 12$), colouration in the third measurement batch (April 22^{nd}-23^{rd}) was compared to females captured on April 20^{th}-29^{th} ($n = 11$), colouration in the fourth measurement batch (May 9^{th}) was compared to females captured on May 8^{th}-13^{th} ($n = 7$) and colouration in the fifth measurement batch (May 23^{rd}) was compared to females captured on May 19^{th}-22^{nd} ($n = 7$). In the experimental treatment consisting of two females sharing a terrarium, the change in colour of the two females of the same pair might not be completely independent if the terrarium per se had any influence on colour change. Consequently, to avoid any problem of pseudo-replication, one female of each pair was chosen randomly and only these eight females were included in subsequent analyses for this treatment. All statistical analyses were two-tailed with a significance level of 0.05, and performed with the Statistica (StatSoft, 2011) programme.

Results

Female colour change in captivity

Sexual dichromatism before the onset of reproduction was obvious to a human observer, as adult females had red tails and hind legs but adult males did not (fig. 3a and b). Females kept in captivity underwent a noticeable colour change during the breeding season, and in all cases, by the time of egg-laying, red had become light buff-grey (fig. 3c). Redness differed significantly among measurement batches (table 1), and was particularly reduced between late April and early May (fig. 4b), possibly coinciding with the beginning of egg formation. In fact, redness differed significantly among all measurement batches (Tukey post-hoc tests; $P \leqslant 0.035$ in the nine tests) with the exception of the comparison between early and late

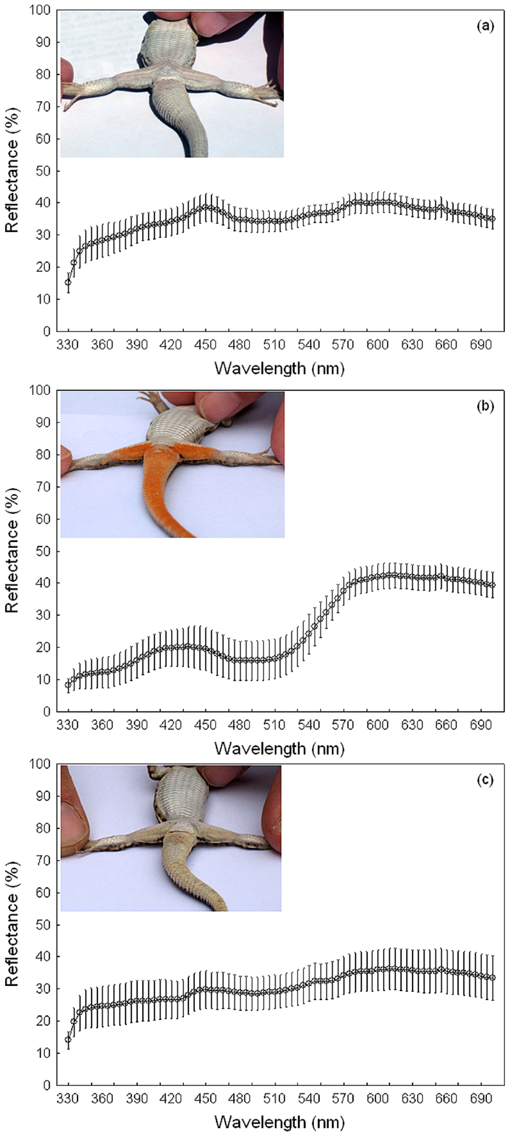

Figure 3. Average (SD) reflectance spectra of ventral tail and hind legs of spiny-footed lizards (*Acanthodactylus erythrurus*): (a) adult males ($n = 31$) and (b) adult females ($n = 47$) before the onset of reproduction (March 21st-27th), (c) adult females around egg-laying time ($n = 47$, May 23rd). Reflectances for each individual are means of tail and hind leg measurements. This figure is published in colour in the online version.

May ($P = 0.35$). This also means that redness temporarily increased between March and early April (fig. 4b). However, redness did not differ significantly among experimental groups, and all groups showed similar temporal variation in this colour (table 1, fig. 4b).

Brightness differed significantly among measurement batches and among experimental treatments, but measurement batch effect depended on the treatment (table 1). Specifically, brightness increased along the breeding season to reach a peak in early May (Tukey post-hoc tests; $P < 0.001$ in the three treatments when comparing March and early May), but the subsequent decrease between early and late May was only statistically significant in females sharing the terrarium with a male and with no restriction for copulation ($P = 0.0033$; in the other two treatments $P \geqslant 0.70$; fig. 4a). Differences among experimental groups were significant only in May, but exclusively between the two groups in which females shared the terrarium with a male (Tukey post-hoc tests; $P = 0.0054$ in early May, $P < 0.001$ in late May, $P \geqslant 0.52$ in all other comparisons). Females sharing the terrarium with a male and interacting freely showed lower brightness than females separated from males by a methacrylate wall (fig. 4a).

All females in the three experimental groups laid eggs or were unequivocally gravid at the end of May. The first eggs in captivity were laid on May 22nd, and laying date did not differ significantly among experimental groups, either considering the 39 females (ANOVA; $F_{2,36} = 0.56$, $P = 0.57$) or only females that laid eggs before the time of release ($F_{2,24} = 0.31$, $P = 0.74$). All eggs ($n = 25$) laid by females that had shared the terrarium with a male and interacted freely were white and turgid. Blastodiscs were found in 13 of 14 eggs (from 4 females) examined (93%). On the contrary, all eggs ($n = 89$) laid by females in the other two groups were yellowish and flaccid, indicating they were unfertilized. No blastodiscs were found in any of the 24 eggs (from 12 females) examined. The number of eggs did not differ significantly among experimental groups, either considering all females for which clutch size was estimated (mean (SE) clutch size; female

Table 1. Two-way ANCOVAs with repeated measures in one factor (measurement batch) testing for temporal effects (differences among five measurement batches, the first one at the end of March, the last one at the end of May) and experimental treatment effects (differences among three experimental groups: female with a male, fertilization possible; female with a male, fertilization impossible; and two females) on PC1 (representing brightness) and PC2 (representing redness) in tail and hind legs of adult female spiny-footed lizards (*Acanthodactylus erythrurus*) while simultaneously controlling for body weight at the time of capture (March).

	PC1				PC2			
	Mean square	df	F	P	Mean square	df	F	P
Experiment effects	4.443	2	6.81	0.0032	–	–	–	–
Weight	0.086	1	0.13	0.72	2.505	1	4.17	0.048
Error	0.653	35			0.601	37		
Temporal effects	0.955	4	5.83	<0.001	1.638	4	11.90	<0.001
Interaction time × experiment	0.655	8	4.00	<0.001	–	–	–	–
Interaction time × weight	0.725	4	4.42	0.0021	0.831	4	6.04	<0.001
Error	0.164	140			0.1438	148		

Note: Body size (SVL) and the interaction between measurement batch and body size were removed from final models because they did not explain a significant portion of the variance ($P \geqslant 0.10$). For the same reason, experimental treatment and the interaction between measurement batch and treatment were removed from PC2 final model. Exclusion of experimental treatment turned PC2 final model into a one-way repeated measures ANCOVA.

and male together: 3.87 (0.19), $n = 15$; female and male separated: 4.07 (0.30), $n = 15$; two females together: 3.50 (0.42), $n = 8$; Kruskal-Wallis test; $H_2 = 2.02$, $n = 38$, $P = 0.36$) or only females that laid eggs before the time of release (female and male together: 3.57 (0.20), $n = 7$; female and male separated: 4.09 (0.34), $n = 11$; two females together: 3.50 (0.42), $n = 8$; $H_2 = 2.41$, $n = 26$, $P = 0.30$).

Colour parameters measured in five batches from late March to late May were not significantly related to body size (SVL) at the time of capture (March), but we found significant interactions between measurement batch and weight at the time of capture for both brightness and redness (table 1). Regarding brightness, although the interaction between measurement batch and weight was statistically significant (table 1), analyses within each measurement batch showed non-significant relationships between brightness and weight in all five batches (ANCOVAs with experimental treatment as a factor; $F_{1,35} \leqslant 3.74$, $P \geqslant 0.061$). Redness, however, was negatively related to weight in early and late April (Pearson correlations; $r \leqslant -0.367$, $n = 39$, $P \leqslant 0.022$ in the two tests), but the relationship was not statistically significant in the other three batches ($-0.064 \leqslant r \leqslant 0.010$, $n = 39$, $P \geqslant 0.70$). These results suggest that female body weight before reproduction (March) predicted the timing of change in red colouration, even though weight was not significantly related to initial (late March) or final (late May) redness. Specifically, red colouration faded earlier in heavy females. Female body size, weight and condition before reproduction were negatively correlated with laying date when all 39 females were considered (Pearson correlations; $r \leqslant -0.325$, $n = 39$, $P \leqslant 0.043$ in the three cases), but female body size was no longer significantly correlated to laying date when only females that laid eggs before the time of release were included in the analyses ($r = -0.234$, $n = 27$, $P = 0.24$; for the other two variables $r \leqslant -0.422$, $n = 27$, $P \leqslant 0.028$). Female body size, weight and condition before reproduction were not significantly correlated with clutch size, either considering all females for which clutch size was estimated (Spearman correlations; $0.044 \leqslant r \leqslant 0.201$, $n = 38$, $P \geqslant 0.23$ in the three tests) or only females that laid eggs before the time of release ($-0.081 \leqslant r \leqslant -0.036$, $n = 26$, $P \geqslant 0.69$ in the three tests).

The time (number of days) elapsed between colour measurement and laying date was corre-

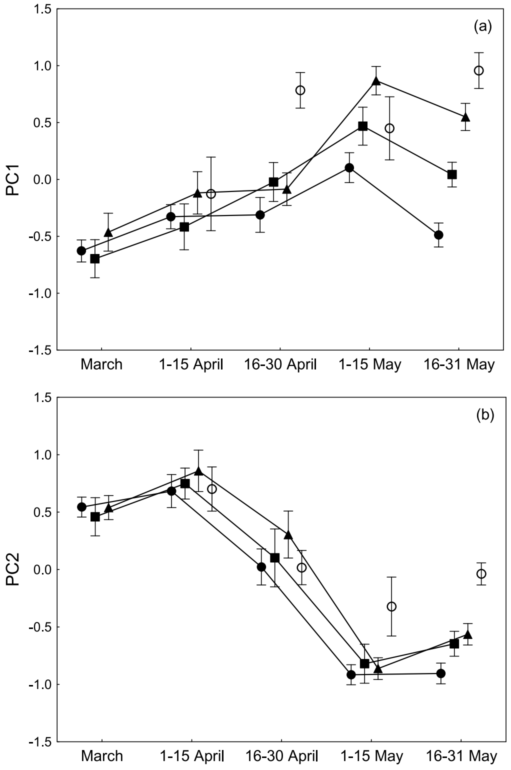

Figure 4. Mean (SE) (a) PC1 (representing brightness) and (b) PC2 (representing redness) in ventral tail and hind legs of female spiny-footed lizards (*Acanthodactylus erythrurus*) in five measurements from late March to late May. Solid symbols: females kept in captivity in the experiment (circles ●: with a male and fertilization possible ($n = 16$); triangles ▲: with a male but fertilization impossible ($n = 15$); squares ■: with a female ($n = 8$)). Open circles ○: free-ranging females (these individuals were measured only once). Colouration was measured on March 21st-27th, April 9th, April 22nd-23rd, May 9th, and May 23rd in captive females and on April 3rd-14th ($n = 12$), April 20th-29th ($n = 11$), May 8th-13th ($n = 7$) and May 19th-22nd ($n = 7$) in free-ranging females. The first copulation was observed on April 3rd. Females began to lay eggs around May 8th in the wild and May 22nd in captivity (see the text for more details).

lated with colour parameters in late April, either considering the 39 females (Pearson correlations; brightness: $r = -0.357$, $n = 39$, $P = 0.026$; redness: $r = 0.563$, $n = 39$, $P < 0.001$) or only females that laid eggs before the time of release (brightness: $r = -0.439$, $n = 27$, $P = 0.022$; redness: $r = 0.686$, $n = 27$, $P < 0.001$). In contrast, these correlations were not statistically significant in the other measurement batches (all females: $-0.223 \leqslant r \leqslant 0.227$, $n = 39$, $P \geqslant 0.16$ in the eight tests; females that laid eggs before release: $-0.278 \leqslant r \leqslant 0.379$, $n = 27$, $P \geqslant 0.051$ in the eight tests). Specifically, at the time of red colour fading (late April), brighter/less red females were closer to egg-laying (i.e., more advanced in the reproductive cycle) than less bright/redder females. This suggests that colour changes occurred at certain phases of the female reproductive cycle.

Colour parameters before the onset of reproduction (March) were related to colour parameters at the time of egg-laying (late May) (Pearson correlations; brightness: $r = 0.403$, $n = 39$, $P = 0.011$; redness: $r = 0.363$, $n = 39$, $P = 0.023$), suggesting high intra-individual consistency of female colouration through time.

Female colour change in the wild

Intensive field observations begun at the beginning of March, but the first copulation in the wild was not observed until April 3rd. The first female with evident signs of having laid eggs (loose folds of lateral and ventral skin) was observed on May 8th. Brightness of adult females captured in the wild during April and May differed significantly in the four periods considered (ANOVA; $F_{3,33} = 3.72$, $P = 0.021$), although differences were statistically significant only between early and late April (Tukey post-hoc test; $P = 0.045$) and between early April and late May ($P = 0.034$; in the other four tests $P \geqslant 0.43$). This means that brightness increased during April and remained unchanged during the rest of the breeding season (fig. 4a). Redness also differed significantly in the four periods (ANOVA; $F_{3,33} = 5.90$, $P = 0.0024$), but differences were statistically significant only between early April and later periods (Tukey post-hoc tests; $P \leqslant 0.045$ in the three tests; in the other three tests $P \geqslant 0.60$). In other words, redness decreased during April and remained unchanged until the end of May (fig. 4b).

Colour change during the breeding season in wild and captive female lizards showed similarities because in general both became lighter and less red (see fig. 4). When brightness was compared among the four groups of females (three experimental treatments in captivity and wild females), differences between wild females and experimental groups were significant only in late April (ANOVA; $F_{3,46} = 8.95$, $P < 0.001$; Tukey post-hoc tests; $P \leqslant 0.016$ in the three comparisons) and late May (ANOVA; $F_{3,42} = 25.69$, $P < 0.001$; Tukey post-hoc tests; $P = 0.16$ when wild females were compared to captive females sharing the terrarium with a male but separated by a methacrylate wall, $P < 0.001$ in the other two comparisons). In these two periods, captive females generally showed lower brightness, indicating that colour lightening was more pronounced and happened earlier in wild females. Redness did not differ significantly among the three groups in captivity (table 1), so they were pooled together and compared to wild females. Captive females showed lower redness in early and late May (ANOVA; $F_{1,44} \geqslant 9.81$, $P < 0.001$ in the two tests), but not in early or late April ($F_{1,44} \leqslant 0.33$, $P \geqslant 0.57$ in the two tests), implying that reduction of redness was less pronounced in wild females.

Discussion

In the current study, adult female spiny-footed lizards in the population in southern Spain underwent a colour change during the breeding season that was noticeable to a human observer. Although females' tails and hind legs were red before and at the beginning of breeding, they became light buff-gray when gravid. This colour change was not instantaneous but gradual, taking several days or even weeks, thus making it difficult to determine the exact moment when redness began to fade. In any case, red colouration was still strong at the time of first copulations. In addition to this obvious colour change, spectrophotometry revealed other important changes in female colouration, such as an increase in redness between late March and early April, probably immediately before the onset of reproduction. This increase in redness prior to mating does not support the courtship rejection function (Watkins, 1997; Hager, 2001) for red colouration in females of this species but is consistent with a mating-related function. Unfortunately, this study does not allow us to distinguish between different mating-related functions, so female red colouration might be a sexual ornament (signalling individual quality; e.g., Weiss, 2006), a courtship stimulus (signalling sexual receptiveness; e.g., Cooper and Crews, 1988) and/or even a sex indicator (signalling the sex of the individual; e.g., Cooper and Burns, 1987). Although the sex recognition function cannot be completely ruled out, we do not think it is probable, because juvenile males also have red tail and hind legs.

This study has focused exclusively on investigating female red colouration, but the red colour disappeared shortly after the beginning of reproduction, becoming light buff-grey on tail and hind legs. This whitish colouration might indicate that females are gravid and, if this is the case, might have a courtship rejection function. Gravid females might be showing they are no longer sexually receptive to avoid male harassment. It should be noted, however, that unfertilized females also became gravid and laid eggs, and showed the same reduction in redness as fertilized females. Therefore, the whitish colouration would provide information exclusively about gravidity, but would not be informative in relation to the fertilization status of the female. The distinction between fertilization and gravidity might however be irrelevant for males, because following ovulation, the eggs (fertile or not) cannot be fertilized (Whittier and Tokarz, 1992). In any case, we should not only think of red colouration but also of light buff-grey colouration (i.e., lack of red colouring) as possible signals in intraspecific communication in this species.

As stated above, redness reduction during the breeding season was very similar in fertilized and unfertilized females. This implies that mating or fertilization itself was not the cause of colour change. The exposure to a sexual stimulus (presence of a male in the terrarium) did not affect female red colouration either. We cannot completely rule out the possibility that female experience prior to capture, for example interactions with males before the start of reproduction, had a subsequent effect on colouration, but our experiment shows that exposure to a male, at least during the breeding season, did not affect colouration significantly. All females kept in captivity, regardless of their exposure to a male or their fertilization status, laid eggs. However, while unfertilized females only laid infertile eggs, fertilized females (the ones allowed to interact freely with a male) laid mostly (93%) fertile eggs. All these findings suggest that male spiny-footed lizards might contribute little to triggering female reproductive cycle or female change in redness. However, they are consistent with a scenario in which external abiotic factors would induce physiological changes responsible for both breeding and colour change (Duval, Guillette and Jones, 1982). Abiotic factors triggering the physiological (and colour) changes in this species are unknown, but we can speculate that temperature and/or photoperiod might play a role, as suggested for other lizard species (e.g., Ramírez-Sandoval, Ramírez-Bautista and Vitt, 2006). The physiological mechanisms causing colour changes are probably hormone-mediated (e.g., hormones involved in gravidity; Cooper and McGuire, 1993), but identifying these hormones was beyond the scope of this study. Our results, mainly the association between colour parameters and the stage of the reproductive cycle (time to egg-laying), suggest a link between reproduction and colouration, but we do not know the specific moments of the reproductive cycle in which colour changes occurred. In other lizard species, colour changes have been suggested to occur during the vitellogenic stage (e.g., Cooper, Adams and Dobie, 1983; Salica and Halloy, 2009). Our experiment in captivity also suggests that female spiny-footed lizards ovulate spontaneously even in the absence of males, as it is the case in other lizard species (Bleu et al., 2011). Spontaneous ovulation implies strong selection on females to have their eggs fertilized, what might affect the mating system of the species, for example making female multiple mating more advantageous (Uller and Olsson, 2005).

Female characteristics such as body weight also contributed to modulating the timing of breeding (e.g., laying date) and red colour change. Heavier females experienced red reduction earlier and were able to breed also earlier, perhaps allowing their offspring to grow faster and increase their probability of survival (Warner and Shine, 2007). The fact that weight, but not skeletal size, was related to timing of colour change suggests that body condition, but not size per se, was responsible for this relationship. Therefore, both abiotic and biotic (female characteristics) factors might be important in determining the onset of reproduction and red colour change in females of this species. A minimum body size and/or weight might be required for reproduction to occur (e.g., Bauwens and Verheyen, 1987; Galán, 1996), but all females included in this study would fulfil these requirements, since they were clearly adults (SVL > 60 mm) and seemed to be in good condition (i.e., looked healthy and behaved normally). The fact that female weight was related to both laying date and timing of red colour change emphasizes the link between reproduction and colouration.

Spectrophotometric data also showed that during the breeding season, and simultaneously with redness fading, tail and hind legs were increasing in brightness as colouration became whiter. A subsequent decrease in brightness was also observed shortly before egg-laying in the group of females sharing the terrarium with a male and interacting freely. These temporal changes in brightness resulted in significant differences between two of the experimental groups of females late in the breeding season. Specifically, females interacting freely with a male showed darker tail and hind legs than females separated from a male by a methacrylate wall. We can think of at least two explanations for this finding. First, fertilization might have contributed substantially to darkening, but in this case we would also expect darker colours in females interacting freely with a male than in females sharing the terrarium with another female, and this did not happen. It should be noted, however, that sample size in the two-females treatment was considerably reduced, thus decreasing the power of the statistical test. Second, physical contact between individuals might have an effect on brightness. This effect could be either direct, e.g., bites might produce scars and darken the skin, or indirect, e.g., physical contact might affect hormone levels (e.g., epinephrine; Matt et al., 1997) which in turn would affect colouration (Vaughan and Greenberg, 1987). Physical contact between lizards sharing the same terrarium might be exacerbated with increased competition for resources. However, competition in our experiment was at most weak, because food was abundant and there was a surplus of basking and refuge sites in all terraria.

Females in the captivity experiment experienced an overall decrease in red colouration and increase in brightness over the breeding season. A similar colour change was also observed in females in the wild, thus implying that colour change in our experiment was not a mere artefact due to conditions in captivity. However, some differences between captive and free-ranging females were evident. Specifically, redness reduction was less pronounced, and brightness increase more pronounced, in wild than in captive females. In addition, the increase in brightness happened earlier in wild females. It should be emphasized that both the increase in brightness and laying of eggs happened earlier in wild females, suggesting again a link between reproduction and colouration. We do not know why captive and wild females differed in colouration, but can think of at least three differences between the two groups of females that might affect their colour. First, microclimatic conditions that lizards faced in outdoor terraria were probably different to those experienced by females in the field. Although weather conditions were almost identical in both areas, free-ranging females could make use of some behaviour not available to captive females, for example, moving to another patch or digging deeper into the ground. Given that abiotic factors possibly play a role in the reproductive cycle and seasonal colour change (Duval, Guillette and Jones, 1982), different conditions experienced by captive and free-ranging females might result in different colourations. Second, the diet of lizards in the wild is probably more varied than in captivity, and would include plant material (Busack and Jaksić, 1982) not available to captive females. Pterins are probably the pigments responsible for red colouration in spiny-footed lizards (J.J. Cuervo, J. Belliure and J.J. Negro, unpublished data), and these pigments are not obtained directly through the diet but synthesized within the cells (Ziegler, 1965). However, diet might still have an effect on pterin-based colouration, as it happens with other endogenously produced pigments such as melanin (McGraw, 2007). Third, captivity-associated stress might affect hormone levels (e.g., corticosterone), which in turn could influence lizard colouration (Fitze et al., 2009).

As stated in the Introduction, red colouration in female spiny-footed lizards might also have a non-reproductive function. It might be the case, for example, that red colouring has the same function as in juveniles. Unfortunately, the function of red colouration in juveniles of this species has never been investigated, but studies in other *Acanthodactylus* species suggest that conspicuously coloured tails in juveniles have an anti-predatory function (Hawlena, 2009). Specifically, conspicuous colours would attract attention on the expendable tail, thus increasing the probability of surviving a predator attack. Therefore, differences in the degree of exposure to predators would underlie colour differences between juveniles and adults. In a similar way, adult females might develop a more conspicuous tail if they are more exposed to predators than adult males. For example, gravidity generally impairs locomotion in lizards (e.g., Shine, 2003), thus probably increasing predation risk. Our study, however, does not support the link between gravidity, predation risk and conspicuous coloration, because red colour faded when females became gravid. In any case, further studies are needed before the anti-predatory function for red colouration in adult females can be completely ruled out.

To summarize, seasonal colour change in female spiny-footed lizards consisted of an increase in brightness and a decrease in redness, and was associated with reproduction. Colour change was probably triggered by abiotic factors, although female characteristics such as weight, and maybe also fertilization status or social interactions, contributed to modulating both timing and final colour. The results of this study are consistent with a mating-related function for red colouration, with red colour probably signalling individual quality and/or sexual receptiveness. The results are not consistent however with a courtship rejection function for red colouration, although whitish colours resulting from red fading might signal gravidity. Future experiments manipulating female colouration will be needed to test these hypotheses.

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