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Original Article

Male mate choice based on female coloration in a lizard: the role of a juvenile trait

Josabel Belliure,[a] Belén Fresnillo,[a] and José J. Cuervo[b]
[a]Department of Life Sciences, Ecology Section, University of Alcalá, A.P. 20 Campus Universitario, Alcalá de Henares, Madrid, 28871, Spain and [b]Department of Evolutionary Ecology, Museo Nacional de Ciencias Naturales (CSIC), C/ José Gutiérrez Abascal 2, Madrid, 28006, Spain

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Female mate choice for male display traits is widely observed across animal taxa and is a well-established mechanism of evolution. However, males are increasingly seen to exhibit mate choice for female display traits, even in species with traditional sex roles, although this continues to be an understudied aspect of sexual selection. We evaluated the role of female coloration on male mate choice decisions in the spiny-footed lizard (*Acanthodactylus erythrurus*), a species in which adult females show red coloration as a retained juvenile trait. Although both sexes show red tails as juveniles and subadults, only females maintain red colored tails when becoming adult; moreover, this coloration is only present at the beginning of female adulthood and becomes white after ovulation, suggesting a mating-related function. Male courtship preferences were investigated through an experimental approach, where they were offered pairs of females that differed in size (adult/subadult) and tail coloration (red/white). Male lizards preferred adult females using both visual and chemical cues and, when adult female coloration could be chosen, they preferred red females. These results suggest that red coloration is a sexual signal involved in male mate selection. We hypothesize that red coloration in adult females might indicate sexual maturity and a pre-ovulatory reproductive status. Being a juvenile trait retained until the beginning of adulthood, we also suggest that it might indicate reduced risk of sperm competition. This study highlights the role of a juvenile trait for sexual selection and adds to the understanding of the evolution of male mate choice.

Key words: ***Acanthodactylus erythrurus*, female coloration, fertility signaling, male mate choice, reptiles, sexual selection, spiny-footed lizard.**

INTRODUCTION

Mate choice can be defined as the process that occurs whenever the effects of traits expressed in one sex leads to nonrandom mating with members of the opposite sex (Halliday 1983; Kokko et al. 2003; Edward 2015). Corroboration of mate choice and identification of such traits of one sex influencing mate selection in the other sex are 2 challenging areas of investigation for behavioral ecologists, being explored in a diversity of taxa. In species with conventional sex roles, mate selection has been traditionally predicted for females. This is because females typically have a larger a priori investment in reproduction, and therefore, selection should favor careful mate choice by females (Trivers 1972). But males should also show mating preferences whenever the reproductive benefits outweigh the costs of being choosy (Trivers 1972; Parker 1983); for example, if males contribute significant parental care, or are limited in the number and quality of females they can fertilize, selection may favor careful mate choice by males (Dewsbury 1982; Sargent et al. 1986; Schwagmeyer and Parker 1990; Olsson 1993). In support of this, male mating preferences have been observed in several taxa, such as birds (Jones and Hunter 1993; Amundsen 2000), fish (Milinski and Bakker 1990; Amundsen and Forsgren 2001; Baldauf et al. 2011; Wright et al. 2015; Yong et al. 2015), or insects (Bonduriansky 2001; Bateman and Fleming 2006, Assis et al. 2017). However, testing of the phenomenon of male mate choice across taxa and mating systems has been limited compared to the voluminous literature devoted to mate selection by females.

Biological organisms are characterized by myriad different traits, many of which can serve as mating cues. Much of the empirical work investigating sexual selection has focused on visual and acoustic signals, whereas the role of chemical cues for mate choice has been less explored (Johansson and Jones 2007; Thomas 2011). But, our understanding of how phenotypic traits become used in mating decisions is still limited (Thibert-Plante and Gavrilets 2013). When the mate choice strategy is quality-based discrimination, individuals increase their reproductive success by choosing a mate that would produce more and/or higher-quality offspring. In this context, mating cues are expected to be reflecting individual

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Address correspondence to Josabel Belliure. E-mail: josabel.belliure@uah.es

quality. Female choice for male traits indicating quality is widely observed across animals, although the generality of this preferences is in debate as females with arbitrary preferences might also be frequent (Prum 2010). In the case of male choice for female traits, the most common mating preferences are those that tend to maximize a male's expected fertilization success. In this context, mating cues are expected to reflect fecundity and paternity opportunities. In fact, recent theoretical studies suggest that male mate choice is not likely to evolve in polygynous species unless that preference is based on a trait that indicates fecundity in females and thus reproductive opportunity (e.g. readiness to mate or female fecundity; Servedio and Lande 2006; Servedio 2007; Nakahashi 2008; Rowell and Servedio 2008). There are still major gaps in our understanding of how long it takes for the different phenotypic traits to become co-opted for mating decisions (Thibert-Plante and Gavrilets 2013), and more research is necessary to fully comprehend the evolutionary significance of mate choice as a sexual selection mechanism (Andersson 1994; Edward and Chapman 2011; Dougherty and Shuker 2015).

Coloration has been often associated with mate quality in a wide number of species, including both vertebrates and invertebrates (e.g. Weiss 2006; Rutowski et al. 2010; Kemp and Rutowski 2011; Olsson et al. 2011). Indeed, one of the functions of animal coloration most commonly addressed has been the role as sexual ornament involved in mate choice (e.g. Andersson 1994; Espmark et al. 2000; Waitt et al. 2003; Hutter et al. 2011; Kemp and Rutowski 2011; Richards-Zawacki et al. 2012; Flamarique et al. 2013; Molnár et al. 2016). In female-controlled mating systems, males with the most conspicuous coloration have been demonstrated to be actively selected in many species, and these males have been proved to be high quality individuals. As a consequence, it has been argued that male coloration may experience direct selection (Richards-Zawacki et al. 2012; Selz et al. 2016). Nevertheless, conspicuous coloration has also been found in females of species with conventional sex roles (Montgomerie and Thornhill 1989; Cooper and Greenberg 1992; Watkins 1997; Nunn 1999; Cuadrado 2000; Amundsen and Forsgren 2001; Baird 2004; Heinsohn et al. 2005; Weiss 2006; Chan et al. 2009; Stuart-Fox and Goode 2014), but the significance of color in females has been less commonly addressed relative to the attention given to males.

Female coloration could be a sexual ornament signaling phenotypic and/or genotypic quality to males (Amundsen and Forsgren 2001; Bonduriansky 2001; Weiss 2006; Weiss et al. 2009, 2011; South and Arnqvist 2011), but what might drive the evolution of female ornamentation is still an unknown. Although there is growing evidence that males prefer to mate with ornamented females, it has been suggested that the production of costly ornaments may reduce female fecundity, hence favoring males with a preference for females with average ornamentation (Fitzpatrick et al. 1995; Kokko 1998). Moreover, theoretical models support that, even in a "best case scenario" where high quality males with a preference for ornamented females are able to mate disproportionately more often with them, the evolution of female traits by sexual selection may be relatively weak (Fitzpatrick and Servendio 2017). Therefore, the association of female ornaments such as conspicuous coloration with male mate decisions remains poorly understood.

Species in which females show conspicuous coloration that is not present in males provide perfect study cases to investigate male mate selection and the possible role of female ornamentation. One species in which adult females show bright colors while adult males do not is the spiny-footed lizard (*Acanthodactylus erythrurus*, Schinz 1833). In this species, females show red coloration in the tail and hind limbs at the beginning of their adulthood that becomes white later on in the season, whereas this coloration is absent in adult males that are white during their whole adulthood. This red coloration, particularly on limbs, is conspicuous when females are looked at from behind. The red color does not appear de novo in adult females, because it is also present in juveniles and subadults of both sexes. Although both sexes show red tails as juveniles and red tails and hind limbs as subadults, only females maintain red colored tails and hind limbs as adults. Therefore, adult females show red coloration as a retained juvenile trait. Recent studies support a "decoy" function of coloration in juveniles (Fresnillo et al. 2015a) and an age-signaling function in subadults (Fresnillo et al. 2015b). However, the possible function of adult female coloration remains unknown. Information on factors affecting adult female coloration in this species is scarce, but it is known that red coloration is present when adult females emerge after winter hibernation, increases in intensity at the beginning of the reproductive season, possibly reaching a peak around ovulation, and fades to become pallid yellow, nearly white, when they are gravid (Cuervo and Belliure 2013). This pattern of seasonal color change suggests that red coloration in adult females of this species might have a mating-related function (Cuervo and Belliure 2013), but this hypothesis has not been tested so far.

Our aim in this study was to evaluate the role of red female coloration on male mate selection in the spiny-footed lizard. The influence of female coloration on male mate choice could shed some light on this sexual dichromatism that does not appear until maturity and that involves a loss of color in males and retain of color in females until they become gravid. We explored the effect of female coloration in male mate preference for 2 simultaneously available females in a series of experiments in captivity. The mating system of the species is unknown, but promiscuity and multiple mating has been suggested for most lacertid species (Olsson and Madsen 2001; Laloi et al. 2004; Salvador et al. 2008). If male mate choice for female color occurs in this group, we hypothesize it may be due to differential fertilization or paternity opportunities.

METHODS

Study species

Spiny-footed lizards are medium-sized lacertids living in open habitats of Northern Africa and the Iberian Peninsula (Seva Román 1982; Carretero and Llorente 1995; Pérez-Mellado 1998). The species reaches sexual maturity at the age of 1 year and a half, during their second spring (Belliure 2009). The mating period occurs around June (Pollo and Pérez-Mellado 1990; Castilla et al. 1992), and in some populations females seem to be able to lay 2 clutches in the same season (Escarré and Vericad 1981; Seva Román 1982; Barbadillo et al. 1987; Castilla et al. 1992; Carretero and Llorente 1995). Average clutch size is 4.4 eggs (range = 1–8; Belliure 2009). In this species, both sexes show conspicuously red tails as juveniles and red tails and hind limbs as subadults, that become white in adults except in the case of females (Seva Román 1982; Carretero and Llorente 1995; Belliure 2009; Cuervo and Belliure 2013; Fresnillo et al. 2015a, 2015b, 2016). Females retain the red color of tails and hind limbs at the beginning of adulthood, and later, when they become gravid, the red coloration disappears and becomes pallid yellow, nearly white (Cuervo and Belliure 2013).

Captures and captivity conditions

A total of 46 lizards (16 males and 30 females) were captured by noosing between May and June 2009 in Chapinería, south-western Madrid Region, central Spain (N40°22'; W4°13'). Lizards were transported to the Alcalá University Animal Research Centre, Madrid, where they were weighed (with an electronic balance to the nearest 0.1 g) and measured (with a ruler to the nearest 0.1 cm). All males were adult (mean SVL ± SE = 7.96 ± 0.06 cm; range = 7.60–8.40 cm, *N* = 16), and from the 30 females, 16 were adult (7.86 ± 0.08 cm; range = 7.20–8.60 cm) and 14 were subadult (6.49 ± 0.11 cm; range = 5.90–7.00 cm). All females in the study reached the minimal size described for sexual maturity (Bauwens and Díaz-Uriarte 1997). At the time of capture, all subadult females showed their characteristic red coloration; whereas all adult females had already lost their red coloration and showed the nearly white color already described for the species (Cuervo and Belliure 2013), thus they were apparently mated.

Lizards were placed in individual terraria (42 × 26 cm and 19 cm high) with a thin layer of sand on the bottom and available shelter, and maintained with a light cycle of 12:12 h light:dark. Room temperature was 25 °C and a bulb hanging over the edge of each individual terrarium provided a temperature gradient for thermoregulation. Lizards were supplied with food (*Tenebrio molitor*) dusted with vitamins once a day and water ad libitum, and were kept in their individual terraria at least 3 days before trials for acclimatization.

Experimental design

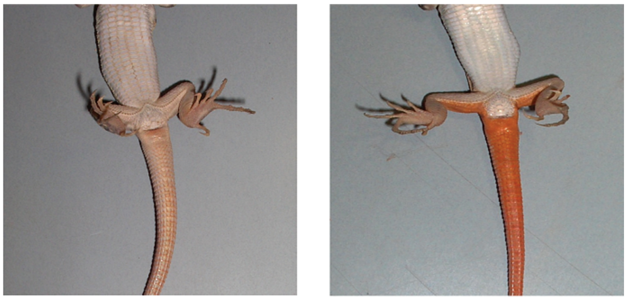
Male mate preference was studied using dichotomous choice trials, where focal males were given a choice between 2 stimuli in a series of different experiments. Dougherty and Shuker (2015) have raised that, for species in which mates are rarely encountered simultaneously, choice tests may overestimate the strength of the preference. We do not know if that is the case for this species, but expressing a consistent response to different stimuli in repeated choice trials may support discrimination in mate choice studies (Ritchie 1996; Lynch et al. 2005; Fresnillo and Belliure 2011; Edward 2015). In general, male mate choice is not selected for when the interval between encounters with receptive females is long compared to the time until a male is able to mate again (e.g. replenish sperm) because choosiness sharply reduces a male's mating rate (Jennions and Kokko 2010). In contrast, when several mates are simultaneously available, being choosy does not lower a male's mating rate, and male mate choice is readily favored if females vary in their value as mates (Barry and Kokko 2010). Studies that offer males a simultaneous choice of females can, therefore, address how males assess the relative value of potential mates (Callander et al. 2012).

We designed a series of 4 experiments to accurately focus on the role of the retained red coloration showed by the adult females. Decoupling the natural associations between size and color present in the females of the species was necessary to understand how size and coloration are prioritized by males. We also explored the role of chemical cues in male selection, as chemical cues are also important for intraspecific communication of lizards (Mason 1992; Cooper 1994; Martín and López 2000; López and Martín 2001, 2005) but which possible signaling of female reproductive status to males has been poorly addressed.

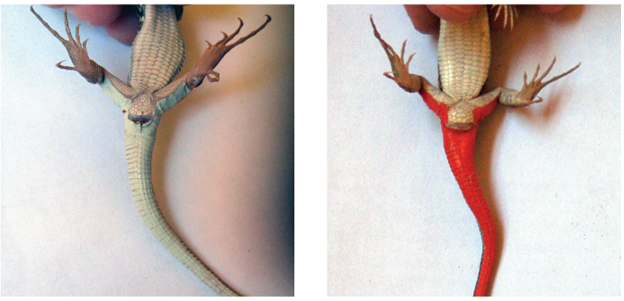
Experiments 1 and 2 aimed decoupling the natural associations between size and color present in the females of the species, to clarify how size and coloration are prioritized by males. Therefore, males were offered either a white adult versus a red subadult female (Experiment 1), or the reversed situation of a white subadult versus a red adult female (Experiment 2). Given that such reversed size/color combination does not exist in nature, we experimentally generated a red-painted adult female versus a white-painted subadult female in Experiment 2. For color manipulations, the rear part of the hind limbs and the ventrolateral part of the tail were painted with nontoxic paint (Satin Paint, La Pajarita, Manises, Spain) that mimic natural white and natural reddest coloration showed by the species (Figure 1). Through spectrophotometer measurements, we checked that experimental white and red coloration were within the natural color range showed by the species (Fresnillo et al. 2015b).

Experiment 3 aimed to explore whether males exhibit mate choice based on chemosensory cues. For that, we tested the possible role of chemical cues in male discrimination of adult and subadult females of the species. Therefore, the pair of stimuli corresponded to odor from a naturally white adult female versus odor from a naturally red subadult female. To obtain female odors, a blotting paper piece (16 × 10 cm) was left in contact with the focal individual to get impregnated by female secretions during the 24 h previous to the experiment.

Experiment 4 aimed to explore male preferences for adult female coloration. Males had to choose between 2 adult females, size-matched, showing the characteristic retained red coloration of the beginning of adulthood versus the later acquired white coloration (Cuervo and Belliure 2013). Because seasonal color change from red to white occurs almost simultaneously in all females (Cuervo and Belliure 2013), we were not able to find both types of adult females in nature but only white ones; thus, we experimentally (following the same procedure than in Experiment 2) generated red-painted adult females, that were showed to males versus white-painted ones.



Natural individuals



Painted individuals

Figure 1
Detail of natural and experimentally painted females of the spiny-footed lizard used in the study.

Mate choice trials

Trials were conducted in an experimental terrarium (77 × 55 cm and 43 cm high) where a focal male freely moved, explored and approached a pair of stimuli during 45 min. Both options for selection were offered at one end of the terrarium, one at the right side and the other at the left side, separated by an opaque cardboard wall. This wall was long enough to define a selection area of 15 × 20 cm, where the presence of the male was interpreted as a willingness to select that particular stimulus. The focal male was introduced at the other end of the terrarium, at a distance of approximately 50 cm from both options, which were simultaneously visible for the male from this position.

We considered proximity to the stimulus as a measure to assess male choosiness. In free-ranging animals, male–female proximity is a reliable predictor of offspring paternity (Abell 1997), and proximity has already been considered an indicator of mate preference in other lizard studies (e.g. Weiss 2002). Therefore, for all experiments, male choosiness was assessed as time in seconds (out of the first 30 min of valid time in each video) spent close (<15 cm) to the stimulus offered in the different experiments (a transparent compartment containing a female or an odorful piece of paper), and we considered the direct contact with the stimulus (0 cm) as a measure of strong preference.

In Experiments 1, 2, and 4, both females were placed into identical transparent plastic compartments (20 × 12 cm and 14 cm high) at the right and left sides of the experimental terrarium. The transparent walls of the plastic compartments prevented any physical contact between the females, and the opaque cardboard wall prevented visual contact between them. Physical contact between the male lizard and the stimulus (females) was not possible, but the male could contact the transparent wall of the plastic compartment containing the female.

In Experiment 3, both blotting paper pieces containing odor from an adult and a subadult female were placed at the experimental terrarium, in the middle of both selection areas defined by the opaque cardboard at both right and left sides of the terrarium. In this experiment, physical contact between the male lizard and the stimulus (the piece of paper) was possible.

Two trials were performed per male in every experiment in order to offer each stimulus at both right and left sides of the terrarium, thus controlling any male preference for one side of the terrarium independent of the stimulus offered. Disposition of stimuli in the first trial alternated among males. Results of both trials per male and experiment were averaged for subsequent analyses. Males randomly passed through the 8 trials, with no order established among experiments, and a same female was encountered by a male twice as a maximum along the study. Male behavior was videotaped (JVC GZ-MG680 camera), so there was no human disturbance during the trial. All males spent a variable time (from 2 to 10 min) motionless at the beginning of the trial, time that was discarded for the analyses.

Trials were performed from 10 to 17 h local time, within the species activity period (Busack 1976; Belliure 2009). Temperature at the laboratory during the trials was always around 25 °C, but a bulb hanging over the trial terrarium provided light and heat in the middle of the terrarium, allowing a temperature of around 32 °C in the trial terrarium, within the activity range for the species (Belliure et al. 1996). No lizard was involved in more than 1 trial per day, and each pair of female stimuli was used only once in the study, that is, no pair was ever the same for any trial. Trials were discarded if the male did not move or did not visit each of both options at least once during their initial exploration of the cage.

Statistical Analyses

A total of 128 trials were recorded, 32 (2 per male) per experiment, but 24 trials were discarded because the male did not move or did not visit each of both options at least once, or because a female escaped from its compartment during the trial. Therefore, the trials used in the study were 32 for Experiment 1, 22 for Experiment 2, 30 for Experiment 3, and 20 for Experiment 4, and after averaging results from both trials of the same male and experiment, samples sizes were 16, 11, 15, and 10, respectively.

Paired *t*-tests were used to analyze within-males differences in the time spent close or in contact to each stimulus of the pair offered in each experiment. Time was $\log_{10}(x+1)$ transformed to approach normality. All statistical analyses were carried out using STATISTICA v. 8.0. (StatSoft Inc. 2007).

RESULTS

Results from Experiment 1 showed that males spent a similar time close to both types of females ($t_{15} = 0.95$, $P = 0.359$), but spent more time in contact with adult than with subadult females ($t_{15} = 2.13$, $P = 0.0497$; Figure 2a). When coloration was experimentally reversed between adult and subadult females in Experiment 2, males spent more time close to red adult than to white subadult females ($t_{10} = -3.07$, $P = 0.012$; Figure 2b), and a similar time in contact with both types of females ($t_{10} = -0.19$, $P = 0.855$). When odors of adult and subadult females were offered to males in Experiment 3, males spent a similar time close to both types of female odors ($t_{14} = 1.61$, $P = 0.129$), but preferred to spend more time in contact with the adult than with the subadult female odor ($t_{14} = 2.41$, $P = 0.030$; Figure 2c). Finally, when female adults with different coloration were offered to males in Experiment 4, males spent more time close to red than to white adult females ($t_9 = -2.65$, $P = 0.027$; Figure 2d), and similar time in contact with both types of females ($t_9 = -0.71$, $P = 0.498$).

DISCUSSION

The results of this study demonstrate that male spiny-footed lizards exhibit mate preferences. Specifically, our study suggests that males prefer females that are displaying the red ventrolateral breeding color over females that display the white color (or lack of red) that is characteristic in this species of being gravid. In addition to the effect of color on male behavior, our study suggests that males base mate preferences on age or sexual maturity; males preferred adult over subadult females and this preference was based on both visual and olfactory cues. Thus, our study adds to the growing body of literature that demonstrates male mate choice even in species that are not sex-role reversed (Bonduriansky 2001; Edward and Chapman 2011).

In the following sections, we will discuss (1) the possible factors determining the existence of male mate choice in the spiny-footed lizard, (2) the correlates of signaling from a retained juvenile trait, and (3) the possible benefits of red coloration for females.

Male mate choice and possible factors driving male mate selection

Our aim was to test whether red coloration in adult females was an attractive trait for males, thus providing insights into the possible

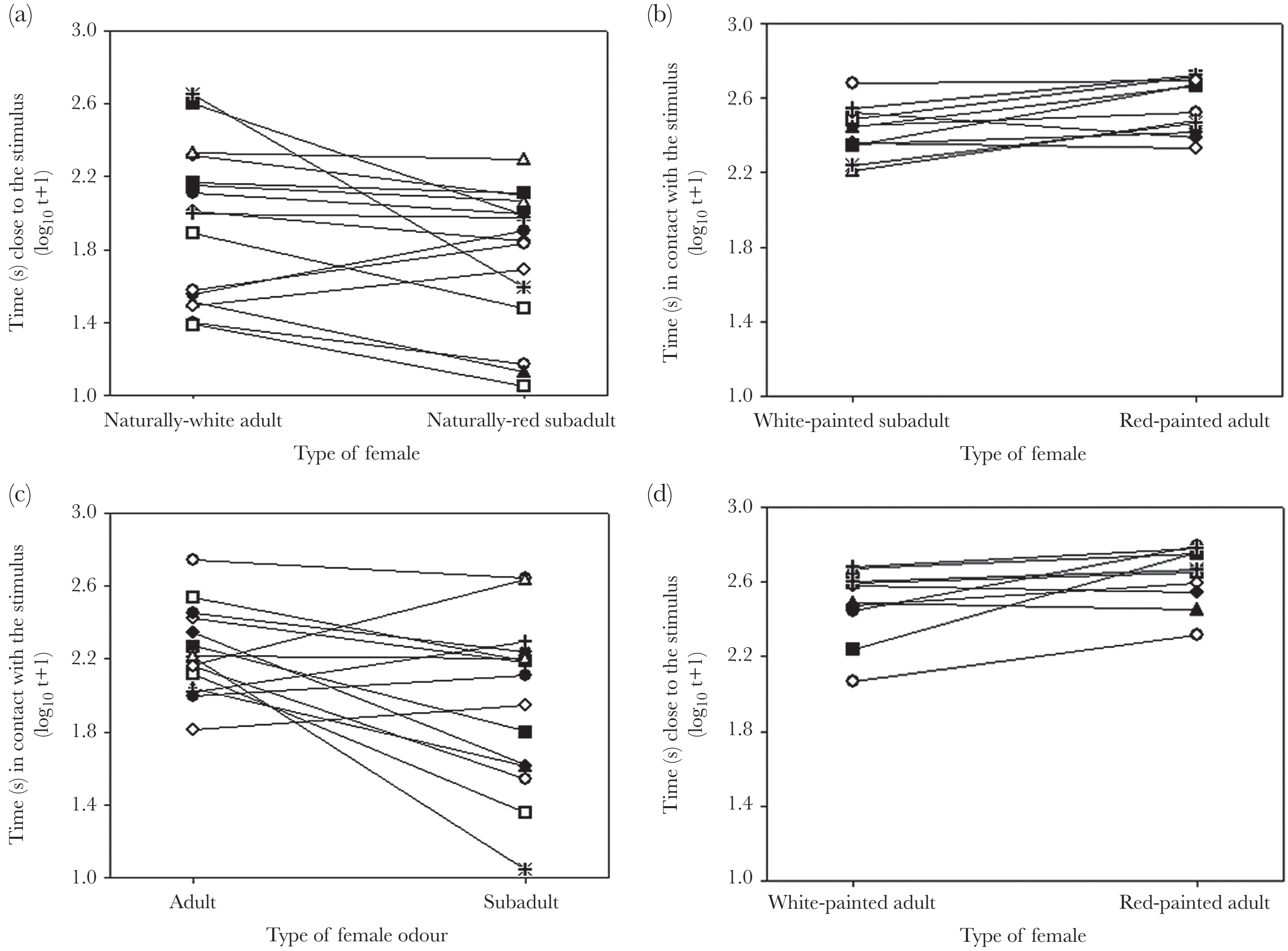


Figure 2

Paired results for time (s) spent by males (a) in contact with the transparent compartments containing adult and subadult unpainted females (Experiment 1); (b) in the selection area of white-painted subadult and red-painted adult females (Experiment 2); (c) in contact with the piece of paper containing adult and subadult female odors (Experiment 3); and (d) in the selection area of white-painted and red-painted adult females (Experiment 4).

role of this trait in male mate selection. Through a sequence of 4 experiments in which males were offered 4 different pairs of female stimuli, we found that male mate choice is present in the spiny-footed lizard, and that at least 2 female traits influence male preferences in this species: size and coloration. Males of the spiny-footed lizards preferred adult to subadult females regardless of female coloration. This preference agrees with the fact that female size may determine fecundity in lizards (Andrews 1985; Qualls and Shine 1995; Qualls and Andrews 1999; Du et al. 2005; Luo et al. 2012), and thus influence male mate choice (Olsson 1993; Whiting and Batema 1999). When males were offered adult females showing white or red coloration, they selected red adult females; therefore, suggesting that female coloration adds relevant information about the reproductive status or the phenotypic quality of the females to males and that this information is used for mate selection, as it occurs in other lizard species (Weiss 2002; Stuart-Fox and Goode 2014). Adult females were selected using both visual and chemosensory stimulus. The evidence of odor-based male mate preference adds to the ability by males to detect female reproductive status through chemical cues (Marco et al. 1998; Chen et al. 2012; Assis et al. 2017). Interestingly, males of the spiny-footed lizards showed preferences by direct contact with the stimulus when it was not experimentally painted (experiments with natural colors or odors), and proximity to the stimulus (less than 15 cm) when it was experimentally painted (experiments with painted females). These results suggest a possible effect of paint on male willingness to come into contact with the selected stimulus, to be considered in similar designed studies.

Since females are generally a limiting resource for males (Bateman 1948), it is not obvious why males should exhibit mate choice. Males in conventional mating systems are expected to mate indiscriminately to maximize the number of fertilizations they obtain and thus their reproductive success (Anderson 1994; Bonduriansky 2001). Therefore, the existence of male mate choice is better understood when mating involves costs for males, and males may discriminate between potential mates by preferring the ones that provide the largest increase in male fitness (Amundsen 2000; Bonduriansky 2001; Parker and Pizzari 2010). Examples of mating costs include the so-called “opportunity costs” of mating with one female over another of potentially higher quality (Kokko and Monaghan 2001), or the physiological cost of sperm production, which may limit the number of females that a male can successfully inseminate over a set period of time (Reinhold et al. 2002). Although most of these aspects have not been studied in the spiny-footed lizard, we consider that mating can be costly for male lizards. For example, sperm has been demonstrated to be energetically costly to produce in large quantities, in high quality, or with particular morphologies (Olsson et al. 1997; Kahrl and Cox 2015). Moreover, courtship is also costly, because it requires considerable time and energy (e.g. Shine and Mason 2005; Sozou and Seymour 2005) and exposes males to higher predation risk (e.g. Daly 1978; Pruden and Uetz 2004).

On the other hand, recent theoretical models predict that male mate choice can be selected for when (1) there is substantial male effort in terms of searching, courtship, mating, or mate guarding (Pomiankowski 1987); (2) females are scarce due to a biased operational sex ratio (van den Berghe and Warner 1989); (3) individual quality varies among females (Johnstone et al. 1996); (4) males invest in parental care (Sargent et al.1986); and (5) male fertilization success varies among females (Nakatsuru and Kramer 1982; Verrell 1985; Bonduriansky 2001; Edward and Chapman 2011). Given that promiscuity and multiple mating has been found in most lacertids studied so far (Olsson and Madsen 2001; Laloi et al. 2004; Salvador et al. 2008), we consider that male spiny-footed lizards may exert mate choice in a context of ensuring paternity. Three aspects may affect the probability of paternity when males mate with adult females: (1) fertility conditions of females according to the specific moment of their reproductive cycle, (2) risk of sperm competition according to previous encounters of females with other males, and (3) phenotypic quality of the female, which, in turn, will determine quantity and/or quality of offspring. From these aspects, fertility and risk of sperm competition play the major role ensuring paternity. Males would benefit from female phenotypes associated with fertility and reduced sperm competition, as has been observed in other species (Wedell et al. 2002; Friberg 2006; Cornwallis and Birkhead 2007) and is supported by theoretical models (Servedio and Lande 2006; Servedio 2007; Nakahashi 2008; Rowell and Servedio 2008).Therefore, male spiny-footed lizards should be able to assess both fertility condition and probability of previous encounters with other males. Whether a phenotypic trait in adult female spiny-footed lizards could advertise both aspects to males, it could become a mating cue for male selection.

Correlates of signaling from a retained juvenile trait

As it was mentioned above, red coloration of adult females does not appear de novo because it is also present in juveniles and subadults of both sexes. Adult females retain the red coloration in the tail and hind limbs through the beginning of their adulthood, that is, at the beginning of the reproductive season; red coloration increases around ovulation and becomes white later on in the season (Cuervo and Belliure 2013). Thus, red color in adult females might function as a sexual ornament signaling that they are in the fertile period, when probability of fertilization after mating is high. In contrast, when red coloration fades and becomes white, females are probably already gravid, when fertilization is no longer possible (Whittier and Tokarz 1992), and mating would imply costs of sperm depletion to males. Regarding previous encounters of the female with other males, the probability will be lower early in the season than late. As adult females show red color early in the reproductive cycle and white color late in the reproductive cycle, red color might indicate that females are in the early phases of their cycle and thus with less probabilities of having met other males. Although we think that the intensity of the red coloration is indicating mainly the fertility status of the female (Cuervo and Belliure 2013), we cannot rule out the possibility that it is also indicating to some degree the probability of previous encounters with other males, that is, of sperm competition.

Another relevant aspect of ornaments that may influence mate preference is the cost of production and maintenance of the signal. It has been suggested that the production and maintenance of costly ornaments may reduce female fecundity, hence favoring males with a preference for females with average ornamentation (Fitzpatrick et al. 1995; Kokko 1998). The nature of red coloration in adult female spiny-footed lizards a priori excludes high costs related to the signal production, as the trait is already present in subadult females. Costs related to maintenance or to the increment of coloration around ovulation are unknown, but probably lower than the costs of producing a new signal. In case that female fecundity is reduced to some extent, disadvantages for males would be probably outweighed by the benefits of an ornament that indicates fertility and low probability of sperm competition. This reasoning is valid at least at the beginning of female adulthood, that is, in the first reproductive event. Whether females change from white to red coloration during a second ovulation, either in the same or in the following year, has not been clarified for the species yet. The development of red coloration in a second ovulation during the same reproductive season would imply that the putative function of coloration indicating low sperm competition risk is not possible in this second reproductive event, and red coloration would signal female fertility exclusively.

In another context of information, recent studies suggest that drosopterin is the pigment responsible for red coloration in the spiny-footed lizard (Cuervo et al. 2016). Pterins seem to be involved in oxidative processes (McGraw 2005) and might play a role in immunocompetence and detoxification (Huber et al. 1984; Ziegler and Schwuléra 1989; Gieseg et al. 2001). The specific physiological functions of drosopterin have never been studied, but this pigment might also have antioxidant and immunological properties. If this is the case, then drosopterin-based coloration might entail physiological costs (the amount of pigment devoted to coloration would not be used for other physiological functions) and could potentially signal phenotypic condition. In fact, pterin-based coloration has been shown to reflect phenotypic quality in some fish and lizard species (Weiss 2006; Johnson and Fuller 2015). If more intense red coloration reflects condition or quality in adult females, and phenotypic quality determines the number and/or quality of offspring (e.g. Weiss et al. 2009, 2011), males will obtain fitness advantages by choosing to mate with females showing the most intense red colors. Female coloration changes throughout the reproductive cycle from red to white (Cuervo and Belliure 2013), thus probably signaling fertility status, but the possibility that it also signals phenotypic or genotypic quality remains to be tested, so it cannot be completely ruled out. The possibility of being an indicator of sexual maturity is less supported for this trait to our view, given that juveniles and subadults of the species also show red coloration, and once demonstrated that female adult size is actively selected by males regardless coloration.

Possible benefits of red coloration for females

From a female's perspective, red coloration should have evolved and been maintained only if this signal provides benefits that outweigh the probable costs of the signal (Maynard Smith and Harper 2003; Fitzpatrick 2015; Hosken et al. 2016). Would female spiny-footed lizards benefit from signaling fertility, phenotypic quality, and/or low probability of previous encounters with males? We know that females can increase their reproductive success by producing more and/or higher-quality offspring, and becoming more sexually attractive might provide benefits in both aspects. First, an attractive trait like red coloration might make that females mate with more males, and this can increase the number of offspring, for example by a higher fertility insurance (Krokene et al. 1998; Byrne and Whiting 2008). Mating with more males might also increase competition among males and thus benefit offspring quality, as high competition among males might allow the female to mate with (and/or choose sperm from) the highest quality male ("indirect female choice" from Wiley and Poston 1996, but see Fitzpatrick and Servedio 2017). Second, showing fertility as soon as possible after hibernation implies higher probability of laying eggs early in the season, increasing the probability of a second clutch, and thus of the total number of offspring; moreover, early clutches have been demonstrated to be larger and have higher survival rates in other lizard species (the sand lizard, *Lacerta agilis*; Olsson and Shine 1997), with benefits for offspring number and quality. And third, signaling fertility with certain coloration implies that a different coloration will signal that the female is not fertile, and the coloration signaling the nonfertile period may have a courtship rejection function (Cooper 1988; Cooper and Greenberg 1992; Cuadrado 2000; Hager 2001; Chan et al. 2009), preventing male aggression related to courtship and copulation.

CONCLUSIONS AND FINAL CONSIDERATIONS

The present study demonstrates male mate choice in the spiny-footed lizard, who preferred adult females that showed red coloration. Therefore, at least 2 female traits influence male preferences in this species: size and coloration. Our results also suggest that males can discriminate, both visually and chemically, between adult and subadult females, preferring always the former regardless of their color. This preference for adult size points to the benefit of higher fecundity of larger females. Red coloration is probably indicating sexual maturity and a pre-ovulatory reproductive status, but we cannot rule out the possibility that it is also indicating reduced sperm competition risk or phenotypic quality. We hypothesize that males would benefit from an increased probability of fertilizing the females and siring their offspring. Females might also benefit from exhibiting the red coloration leading to male mate choice because it might favor mating with higher-quality males or reproducing earlier.

This information adds to the growing body of literature about male mate choice in species that are not sex-role reversed. This phenomenon happens across a wide range of taxa and as empirical evidence of its prevalence has accumulated, it has often been cast as simply the mirror image process—even if less common—of sexual selection through female mate choice. The mating system of the species is unknown, what difficult inferring sexual selection from evidence of male mate choice. But recently, studies have started to make the point that, in fact, male mate choice might differ (i.e. be more or less constrained) in important ways from female mate choice and, likewise, that we might not be justified in assuming that female ornaments arise from the same processes and function just like male ornaments do.

Future directions

In general, this study makes an important contribution to the understanding of male mate choice and female ornamentation. Results suggest that red coloration in adult female spiny-footed lizards is a sexual ornament that is involved in male mate selection. Therefore, the study supports that red coloration serves 3 different purposes in the life of this species: "decoy" for juveniles (Fresnillo et al. 2015a), age signaling for subadults (Fresnillo et al. 2015b) and a mating function in adult females (this study). But this study points follow-up questions relating this or other taxa, that are necessary to improve our general understanding of nonrandom mating through mate choice and the evolutionary patterns and processes it originates. Future studies should address, for example: 1) whether female coloration in this species is a sexual ornament that therefore might signal individual quality, a pre-ovulatory status, decreased sperm competition risk, or all this reproductive values to males; this aspects would imply assessing female reproductive fitness linked to the red coloration; 2) to study the evolution of red coloration of the species during the season in relation to possible second clutches, necessary to better understand the signaling of the trait; 3) to assess benefits for females from exhibiting the red coloration, such as mating with higher-quality males or reproducing earlier; 4) the possible role of female coloration in this species for female–female competition, and thus functioning as a threat signal; the extent to which female ornamentation may evolve as an indicator of quality through male choice, female–female competition, or both, would be key to understand the evolution of such sexual-signaling; f) address in this and other taxa whether male choice leads to sexual selection processes. All these questions would add to the general knowledge about male mate choice, a surprisingly understudied aspect of sexual selection.

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