Lack of evidence for mate choice in a neotropical lizard, Liolaemus quilmes (Iguania: Liolaemidae): weight, colour and familiarity

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Abstract. Choosing a mate is based on a complex process in which one or more attributes of the opposite sex may indicate its condition and potential for reproductive success. Determining which traits may be relevant has not been easy and may depend on the history of the species and/or ecological factors. Body size, colouration and familiarity are three characteristics that have been proposed in the literature with differing results. Here we investigate whether any of these traits may be important in mate selection in a neotropical lizard, *Liolaemus quilmes*, from northwestern Argentina. Lizards were captured at the site Los Cardones, Tucumán, Argentina, during two reproductive and two post-reproductive seasons. Choice experiments were conducted using a quadrangular terrarium of $70 \times 70 \times 25$ cm with three partitions. Each male and each female were offered a choice between two lizards of the opposite sex that varied in weight, or colouration, or familiarity. The responses were filmed in 30-minute sessions. No significant differences were obtained for any of the three parameters combined or separately. This suggests that the lizards might not be using this information to choose a mate and may instead rely on other signals (such as chemical or behavioural) and, in the case of females, on resources defended by a potential mate as well.

Key words. sexual selection, reproductive success, neotropical lizards, Liolaemus quilmes.

Introduction

An animal may enhance its reproductive success by selecting mates with certain traits rather than others (AN-DERSSON 1994). When a male encounters two different females, being able to distinguish between them and choose the female with greater fitness, i.e., who will leave him with the greatest number of viable offspring, would be adaptive (WHITING & BATEMAN 1999). Females, on the other hand, may favour males with conspicuous traits as a sign of good genes. Which characteristics and how males and females select these is still being debated, the evolutionary mechanisms involved being very complex (ANDERSSON 1994, AN-DERSSON & SIMMONS 2006, CLUTTON-BROCK 2008). It is therefore important to continue looking for patterns in different species as we try to interpret the results in the context of sexual selection.

Here we investigate which of three possible attributes or combination thereof may be important in mate selection by males and females of the neotropical lizard, *Liolaemus quilmes*. We considered weight, colour and familiarity.

Considering which characteristic may influence the choice of an animal, one that is often mentioned is body

size (e.g., KRAAK & BAKKER 1998, DOSEN & MONTGOMERIE 2004). In many lizard species, there may be some degree of sexual dimorphism with respect to size, males being larger than females (e.g., COOPER & VITT 1988, ANDERSON & VITT 1990). It has generally been suggested that in males, body size could be an indicator of fitness since it can be an advantage when fighting other males to access females (OLSSON 1992, ANDERSSON 1994, STAMPS & KRISHNAN 1998) and in females an indicator of fecundity since a larger body size has been shown to be correlated with egg size or number of offspring (e.g. OLSSON 1993, COOPER & VITT 1997, WHITING & BATEMAN 1999, SHANBHAG et al. 2000, WYMANN & WHITING 2003).

Furthermore, larger males could provide more resources than smaller males (ANDERSSON 1994, CENSKI 1997). Bigger males have higher quality territories, more females, and copulate more frequently than smaller males (DU-GAN 1982, ANDREWS 1985). Although some studies support this (e.g., RODDA 1992, COOPER & VITT 1993, SALVADOR & VEIGA 2001), others were unable to show it (ANDREWS 1985, OLSSON 2002, HAMILTON & SULLIVAN 2005). As for females, because male lizards do not offer them food or parental care, quality of resources within the territory of

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the male may be important (Andrews 1985, Ruby 1986, Calsbeek & Sinervo 2002).

Chromatic sexual dimorphism is well distributed among diurnal lizards, generally more conspicuous in males and absent or weakly expressed in females (COOPER & GREEN-BERG 1992), being a potentially important attribute in mate choice. Colours are usually more brilliant during the reproductive season. Females may prefer more colourful mates as an indicator of his condition of being free of parasites, as has been suggested by HAMILTON & ZUK (1982). However, other studies have shown that colouration in males could serve as a threat sign, suggesting that conspicuous colours in males could be related to intrasexual and not intersexual selection (COOPER & VITT 1988, THOMPSON & MOORE 1991; HAMILTON & SULLIVAN 2005).

In some cases, female lizards also develop brilliant colours during the reproductive season. There is considerable discussion with respect to the function of colour in females (review in COOPER & GREENBERG 1992). It has been suggested that colour could be an indication of phenotypic quality, related to the reproductive success of the individual (WEISS 2006). It may also help synchronize sexual behaviour or attract males during periods of sexual receptivity (e.g., WATKINS 1997).

Males of L. quilmes are brightly coloured with yellowish, brick reddish and light blue spots scattered along their body (ETHERIDGE 1993). Females are more cryptic, exhibiting a similar pattern but in beige to brownish tones. During the reproductive season, male colouration becomes more intense, especially the head, tending to become more yellowish to orange. Females, for their part, develop a colour patch on the side of the head, that goes from light yellow to intense orange. SALICA & HALLOY (2009a) have shown that these colour variations are related to the female's reproductive state, as has been shown in other lizard species (COOPER & GREENBERG 1992). Nevertheless, it is not clear whether males use these signals to determine when the female would be the most receptive. Moreover, although colours become more intense during the reproductive season, variation in colour morphs occur in both this season and the post-reproductive season (SALICA 2008). Because these changes in colouration possibly imply an energy cost and may increase the predation risk, it is suggested they may provide some adaptive advantage by being an indicator of an individual's reproductive quality (COOPER & GREEN-BERG 1992, BAIRD 2004, CLUTTON-BROCK 2008).

Considering familiarity, some studies have shown that males prefer non-familiar females (e.g., DEWSBURY 1981, COOPER 1985, TOKARZ 1992, 2008, ORRELL & JENS-SEN 2002). In species that exhibit promiscuous or polygynous mating systems, a male should avoid females with whom they have been in contact in order to distribute his sperm in as many females as possible and thus maximize the number of eggs that he fertilizes (TRIVERS 1972). According to COOPER (1985), to maximize the number of offspring, a territorial male should mate with females that reside in his territory and attempt to attract non residential females to get established in his territory to also mate with them. OLSSON & SHINE (1998) showed that in the lizard *Niveoscincus microlepidotus*, males preferred to associate with known/familiar females, which implies some capacity for individual recognition. Conspecific recognition has a central role in social behaviour, lizards using visual and chemical signals to recognize mates and possibly using these to determine body size and condition, and reproductive state (MARTINS et al. 2004, CARAZO et al. 2007, LABRA 2008).

In insectivorous and territorial lizard species, females have few opportunities to evaluate different males as mates during the reproductive season since males tend to organize their territories so as to include female home ranges, excluding other males (STAMPS 1983). HEWS (1993) found in Uta palmeri that the majority of territorial males mate with resident females. In a DNA analysis of female offspring of Sceloporus virgatus, ABELL (1997) recorded that the fathers were the males found spatially closest to the mothers. In previous studies on L. quilmes (e.g., HALLOY & ROBLES 2002, ROBLES & HALLOY 2009, 2010, ROBLES 2010), the authors reported that males and females maintain relatively stable territories and that these overlap. During the reproductive season, males get involved in agonistic encounters (visual displays, persecutions, even wrestling occasionally, HALLOY 1996), limiting entrance to other males. In this context, it is suggested that the lizards may show preference for mates with whom they overlap territories.

Materials and methods

The genus *Liolaemus* (Liolaemidae) belongs to an iguanian group of lizards from South America (FROST et al. 2001). Already 223 species have been described and more are being discovered (LOBO et al 2010). They range from Peru and Bolivia in the North to Tierra del Fuego in Southern Argentina (CEI 1986, ETHERIDGE & DE QUEIROZ 1988). The species *L. quilmes* is found in northwestern Argentina between 1600 and almost 3000 m, in arid to semi arid regions of the phytogeographic province of the Monte (CEI 1993, ETHERIDGE 1993) and the Prepuna (HALLOY et al. 1998; for phytogeographic provinces, see CABRERA & WILLINK 1980). It is a diurnal, oviparous and insectivorous species (RAMIREZ PINILLA 1992, HALLOY et al. 2006). Studies related to home ranges and core area are reported in HALLOY & ROBLES (2002) and ROBLES & HALLOY (2009, 2010).

Lizards were captured at the study site Los Cardones (26°40'1.5" S, 65°49'5.1" W, datum: WGS84, 2700 m), Amaicha del Valle, Tucumán, Argentina. In the first year of the study, nine males and nine females were captured during the austral reproductive season (October 2005) and another nine males and nine females during the post-reproductive season (February 2006). The lizards were marked from previous studies and their home ranges were known (HALLOY & ROBLES 2002, ROBLES & HALLOY 2009, 2010). During the second year, we captured thirteen males and nine females during the reproductive season (October 2005) and another females during the reproductive season (October 2006).

productive season (February 2007). Lizards were brought to the Instituto de Herpetología, Fundación Miguel Lillo, Tucumán. They were measured and weighed after which they were placed in individual glass terraria of 24 \times 13 \times 24 cm, with partitions between them that visually isolated each lizard from its immediate neighbours. They were kept in a room with large open windows through which sunlight entered diagonally, coinciding with natural conditions of light and temperature for the season for this species. The terraria had a layer of 2 to 3 cm sand substrate, similar to that found at the study site. The lizards had access to a refuge and water was provided at all times. Tenebrionid larvae were provided every two to three days. Once the experiments were completed, after about two weeks, the lizards were taken back to the study site and released at the point of capture with a follow-up of their activities.

The experimental design followed methodology used in similar studies (e.g., ANDREWS 1985, HAMILTON & SUL-LIVAN 2005, STUART-SMITH et al. 2007). We determined categories according to the following criteria. For weight, we compared light (6 to 7 gr) and heavy (> 8. 5 gr) males, and light (4.5 to 5.5 gr) and heavy (> 7 gr) females. Considering colour, we selected males that were not brightly coloured versus males with a more intensified colour pattern, particularly the head area. For females, we selected females that did not present a colour patch on the side of their neck versus females which varied between yellow and an intense orange (following colour categories from SALI-CA & HALLOY 2009a). Finally, with respect to familiarity, individuals were considered to be familiar with each other (sensu TOKARZ 1992) or "neighbours" if their home ranges overlapped and unfamiliar or "non-neighbours" when their home ranges were more than 50 m from their closest border.

The experiments were conducted in the same room in which the lizards were kept, maintaining the same temperature and light conditions in both areas. For the experiments, lizards were placed in a quadrangular glass terrarium of $70 \times 70 \times 25$ cm. It was divided in half by a glass partition, one of the halves again subdivided in two. Substrate was a thin layer of sand that was mixed before each new experiment. Beige coloured paper was placed on all the external walls and on the smallest partition to visually isolate the lizards from the outside and the two choice lizards placed in the smaller sections. The test lizard was placed in the non-partitioned half and had visual access to the two choice lizards.

An example of a typical experiment consisted in a test male being placed in the non-partitioned half under a plastic cover for about two minutes in order for him to settle down. The cover was then slowly lifted and the lizard could see two females in front of him that varied in weight but not in colour or familiarity (i.e., females of similar colouration and that were non-neighbours). In an other experiment, performed on another day, two females that differed in colouration but were of similar weights and were non-neighbours were placed before a male. Finally, two females, one being a neighbour and the other a non-neighbour (both of similar weights and colour) were offered to the male for selection. The same protocol was used for each female with respect to males.

Fifty-one experimental sets were performed during the two years of the study (25 for male choice and 26 for female choice). For weight and colour, there were two to three repetitions for each set. For example, the nine males captured during the first reproductive season were tested for preferences in weight three times, on different days, with different pairs of females, one being heavy and the other light. With each repetition, position of the female was changed (if in the left sector, she was placed in the right sector, and vice-versa). With respect to neighbours, there was only one set of experiments for each season, due to the low number of individuals considered to be neighbours. During some of the experiments, some individuals remained inactive the whole time. Those were excluded from the analysis. Each set lasted 30 minutes. The response of the animal being tested was filmed with a Minolta K-500S camera. Approximately 207 hours of film were obtained.

In order to quantify male and female responses, the portion where the test animal was placed was subdivided into three approximate parallel sections (no actual partitions existed), the furthest from the choice lizards was arbitrarily assigned "zero" indicating no interest on the part of the experimental lizard, the middle portion was given a value of 0.5, indicating some interest, and finally the closest portion, next to the individuals to be chosen, was given a "one" indicating interest for one or the other animal. Position of the test lizard was recorded every 15 seconds. The total frequency was then used in the final analyses. Data for the two reproductive and two post-reproductive seasons were pooled since we did not find significant differences between years. Data were analysed using the Friedman two-way analysis of variance and the Wilcoxon signed ranks Test (SPSS 17.0 software, SIEGEL & CASTELLAN 1988).

Results

An analysis of variance was performed taking into account the three variables, weight, colour and familiarity, in order to determine if there was a preference for one of these or a combination. No significant differences were obtained neither in males nor females ($F_r = 1.5$, n = 4, p = 0.50; $F_r = 0.5$, n = 4, p = 0.80, respectively) indicating no preference for any of the three parameters in the opposite sex. Performing analyses for each parameter the following was obtained:

Weight

During the reproductive season of the first and second year, about 36% of males chose the heavier female meaning that 64% chose the lighter female (Table 1). This difference was not significant. During the post-reproductive season of both years, 45% of males chose the heavier female, showing no real tendency for one size or the other.

Table 1. Number of lizards relative to total number of lizards tested (NL), percent of individuals making a choice (%) for heavier (W+), more colourful (C+) and neighbour (N+), and the number of significant sets relative to the total number of sets performed (p, Wilcoxon signed ranks test), of choices made by males and females of *Liolaemus quilmes* during two reproductive seasons (RS) and two post-reproductive seasons (PRS).

	Weight			Colour			Neighbour		
	NL	W (+) %	р	NL	C (+) %	р	NL	N (+) %	р
Males									
RS	14 / 39	35.9	0/5	36 / 66	54.5	1/6	7 / 16	43.7	1/2
PRS	15 / 33	45.4	0/4	24 / 52	46.1	2/6	5 / 17	29.4	0/2
Females									
RS	32 / 54	59.2	0/6	26 / 53	49.0	0/6	4 / 15	26.7	1/2
PRS	24 / 50	48.0	0/6	23 / 35	65.7	0/4	10 / 15	66.7	1/2

As for females, during the reproductive seasons, 59% chose the heavier male, 41% choosing the lighter male. Differences were not significant. During the post-reproductive seasons, 48% of females chose the heavier male, indicating no preference for one or the other type of male (Table 1).

Colour

During the reproductive seasons, 54% of males elected the coloured female. The difference was not significant, except for one set when males chose significantly more coloured females ($W_x = 70$, p = 0.05, n = 13, Table 1). During the post-reproductive seasons, 46% of males chose the coloured female, showing overall no clear tendency, except in two of six sets. In one set, the males chose significantly more the coloured females ($W_x = 32$, p < 0.05, n = 8), whereas in the other set, males chose significantly more the non-coloured females ($W_x = 37$, p < 0.05, n = 9, Table 1). As for females, during the reproductive seasons, close to half (49%) chose the more coloured males whereas during the post-reproductive seasons, 66% of them chose the more coloured males. Differences were not significant.

Familiarity

During the reproductive seasons, 44% of males chose a female neighbour. This was not a significant difference except for the set in the second year, when males significantly chose a non-neighbour female ($W_x = 20$, p < 0.05, n = 6; Table 1). During the post-reproductive seasons, only 29% of males chose a female neighbour. The difference was not significant. Considering females, during the reproductive seasons, 73% chose a non-neighbour male, significantly choosing non-neighbour males in one of the two sets ($W_x = 36$, P < 0.05, n = 8; Table 1). During the post-reproductive seasons, the reverse occurred with 67% of females choosing a neighbour male, significantly choosing these in one of two sets ($W_x = 24$, P < 0.05, n = 7; Table 1).

Discussion

Predictions related to choice of an individual of greater size (e.g., Anderson & Vitt 1990, Cooper & Vitt 1993, Whiting & Bateman 1999, Calsbeek & Sinervo 2002), colouration (e.g., COOPER & VITT 1988, COOPER & GREEN-BERG 1992, LEBAS & MARSHALL 2000, HAMILTON & SUL-LIVAN 2005), and familiarity (e.g., COOPER 1985, HEWS 1993, OLSSON & SHINE 1998) were not fulfilled in Liolaemus quilmes. Neither males nor females showed significant preferences for any of the variables under study. Individual differences (e.g., KIRKPATRICK 1982, ANDREWS 1985, ORRELL & JENSEN 2002, CLUTTON-BROCK 2008) may have been a factor complicating any interpretation. Nevertheless other authors have found that weight might not be a determinant in female choice (e.g., ANDREWS 1985, OLS-SON 2002, HAMILTON & SULLIVAN 2005, STUART-SMITH et al. 2007), and that females might be choosing resources (food, refuges) more than phenotypic characteristics of the male (TOKARZ 1998, HEWS 1993, CALSBEEK & SINERVO 2002). On the other hand, that males did not choose the heavier female has been reported in other lizard studies (e.g., STUART-SMITH et al. 2007) in which no relationship was found between female size and her reproductive success.

Liolaemus quilmes males did not show a preference for more coloured females as might have been expected (LE-BAS & MARSHALL 2000, CLUTTON-BROCK 2008). SALICA (2008) reported that in *L. quilmes* there was no clear relationship between nuptial colouration of females and the courtship response of males, i.e., males did not seem to differentiate between females of different colouration or it may not have been enough information for them to make a choice. Thus, it may be that the colour patch in females, although possibly related to gonadal hormonal activity (e.g., COOPER & GREENBERG 1992, WHITTIER & TOKARZ 1992, WEISS 2002), may not necessarily be a signal to males. Moreover, SALICA & HALLOY (2009b) indicated that there was no significant relationship between nuptial colouration and body condition. Females, for their part, did not choose more coloured males either (e.g., OLSSON & MADSEN 1995, SMITH & ZUCK-ER 1997). Conspicuous colours in males may be favoured in intrasexual competition as has been shown for other lizard species (e.g., CREWS 1975, THOMPSON & MOORE 1991). Males of *L. quilmes* have often been seen to engage in agonistic encounters (HALLOY 1996).

It is expected that males would prefer to mate with new non-familiar females (e.g., DEWSBURY 1981, TOKARZ 1992, 2008, COOPER 1985) although in some cases they may prefer familiar females (CLUTTON-BROCK 2008). Neither male nor female *L. quilmes* showed preferences for neighbours or non-neighbours, females even showing opposite choices in two different sets (Table 1).

Mate choice is possibly based on an ensemble of signals. Interaction among them may obscure preferences for unique signals (CANDOLIN 2003, HAMILTON & SULLI-VAN 2005). The experimental conditions in this study may have favoured only visual cues not allowing the lizards to consider other signals such as chemical. It will therefore be important to evaluate other variables such as chemical signals (LABRA 2008, AGUILAR et al. 2009) but also behavioural signals and other phenotypic traits (ANDREWS 1985), as well as information on resources that may indicate quality of a territory (RUBY 1986, HEWS 1993).

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