



## Male mate preference is influenced by both female behaviour and morphology



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Males of many species prefer females that are more fecund, novel and/or sexually receptive. Males assess the desirability of potential mates using female morphological traits, including size and sexual coloration, or olfactory cues. However, few studies have directly examined how female behaviour influences male mate choice, which is surprising because males often respond strongly to female behaviours. We examined factors influencing male preference using the eastern fence lizard, *Sceloporus undulatus*, a species with a large repertoire of behavioural displays. Males were presented with two tethered females in a paired choice test, and we measured the time that males spent associating with and courting (shuddering to) each female. We recorded female behaviour, including approach to and retreat from the male, sidle-hopping (a rejection behaviour) and pushups. Males associated more with females that (1) approached and retreated from them, (2) did not sidlehop and (3) had relatively higher body condition. Likewise, males shuddered more to females that approached and retreated from them. Approach and retreat behaviours may advertise a female's readiness to mate, as these behaviours can heighten male interest, suggesting that males may be most likely to invest in courtship once females indicate their willingness to mate. Neither the female's pushup behaviour nor her snout–vent length influenced a male's tendency to associate with or court her. These results provide evidence that female behaviour has an important influence on male courtship behaviour. Incorporating measures of female behaviour into future studies on male mate choice may be illuminating and provide a greater ability to predict male preference.

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Male choice of mates is thought to be less common than female choice because of sexual differences in reproductive investment: females are choosier due to their higher reproductive costs; males are indiscriminate due to their presumed lower investment (Bateman 1948; Andersson 1994). However, male reproductive costs may also be significant, for instance when reproduction involves male paternal care, lengthy courtship or mate defence, sperm depletion, time limitations, or even male mortality (Bonduriansky 2001; Wedell et al. 2002). Evaluating females before engaging in reproductive attempts may maximize male fitness benefits, helping to offset energetic and survival costs of mating by primarily focusing a male's efforts on high-value females (Byrne & Rice 2006; Edward & Chapman 2011). In a wide variety of species, males prefer females that are more fertile (e.g. Deschner & Boesch 2007; Gesquiere et al. 2007), have higher potential reproductive output (e.g. Jones et al. 2001; Werner & Lotem 2003; Barry et al.

2010) and are virgin (e.g. Carazo et al. 2004; Guevara-Fiore et al. 2009; Baruffaldi & Costa 2010) or novel (e.g. Sæther et al. 2001; Tokarz 2006). Making mate choice decisions based on these parameters has been shown to enhance male reproductive success (e.g. Byrne & Rice 2006; Chen et al. 2012).

Males assess a female's phenotypic cues and signals to estimate her value as a reproductive partner. Males routinely prefer higher-quality females and oftentimes more fecund females by selecting those that are larger (Verrell 1989; Ptacek & Travis 1997; Bateman & Fleming 2006; Reading & Backwell 2007), have better body condition (Maxwell 1999; Jones et al. 2001; Barry et al. 2010), or are more colourful (Amundsen et al. 1997) than other females. Male preference can be discouraged by the presence of a female's dependent offspring (Craig et al. 2002; Ruscio & Adkins-Regan 2003) or lack of sexual advertisement (Deschner & Boesch 2007; Gesquiere et al. 2007), both of which may indicate female infertility. Males of some species use the extent (Baird 2004; Baldauf et al. 2011) or intensity (Watkins 1997; Weiss 2002) of female body coloration to inform their mate choice decisions, as female-specific coloration can correlate with female receptivity or fecundity. A female's olfactory cues may also communicate her fertility

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(Guevara-Fiore et al. 2010; Chen et al. 2012; Schlechter-Helas et al. 2012), mated status (virgin or nonvirgin; Carazo et al. 2004; Guevara-Fiore et al. 2009) or fecundity (Lemaster & Mason 2002; Poschadel et al. 2006), making these cues important determinants of male choice in a variety of species (see above references).

Females have mate preferences that may conflict with those of males (e.g. Parker 1979), as females attempt to secure their own reproductive benefits by discriminating between males differing in phenotypic or genotypic quality (Kokko et al. 2006; Clutton-Brock & McAuliffe 2009). A female's behaviour, especially receptive (i.e. nonrejection; Beach 1976), proceptive (intending to initiate sexual interactions; Beach 1976) and rejection behaviours, can alter a male's expected payoff when entering into a reproductive attempt with a female. For instance, continued rejection by a female should escalate the energetic and time costs of reproduction if a male perseveres in an attempt, whereas engaging with more receptive females should reduce those costs (Adkins-Regan 1995; Haulenbeek & Katz 2011). Counterintuitively, some proceptive female behaviours may actually increase male reproductive costs: female encouragement can cause males to perform more intense or complex courtship behaviours, which in turn may increase male energy expenditure or predation risk (Balsby & Dabelsteen 2002; Akre & Ryan 2011).

Despite the fact that female behaviour can exert a strong influence on a male's mating behaviour and his reproductive costs, female behaviour has been largely ignored in the context of male mate selection. Female morphological cues are widely accepted as influencing male mate preference, but few studies also quantify and examine the influence of female behavioural cues (but see Bukowski & Christenson 2000; Dunn et al. 2001; Orrell & Jenssen 2002; Rowland et al. 2002; Ruscio & Adkins-Regan 2003; Werner & Lotem 2003; Fernandez et al. 2008). This is surprising, as a female's behaviour may also convey reliable information regarding her reproductive value (e.g. de Jonge et al. 1994; Rowland et al. 2002; Kolm 2004). For example, male seaweed flies, *Gluma musgravei*, prefer more active females, and activity in females is correlated with postmating survivorship in this species (Dunn et al. 2001). Males may prefer females that show behaviours that indicate receptivity (swordtails, *Xiphophorus cortezi*; Fernandez et al. 2008; sticklebacks, *Gasterosteus aculeatus*; Rowland et al. 2002) or a lack of dependent offspring (Japanese quail, *Coturnix japonica*; Ruscio & Adkins-Regan 2003). Male preference for certain female behaviours can also help minimize male reproductive costs; for example, because of the propensity of female spiders to cannibalize their mates, male *Micrathena gracilis* attend closely to female foraging behaviour when selecting a mate (Bukowski & Christenson 2000), and courting a more receptive female may reduce energetic costs and predation risk. The importance of female behaviour for male mate choice decisions may therefore be greatly underestimated.

Male mate selection has been well documented in lizards. Sperm production (Olsson & Madsen 1997), display behaviour (Brandt 2003) and the act of mating itself (Olsson et al. 2004) all incur high energetic costs for male lizards. When deciding whether to engage in a reproductive attempt, male lizards attend to many cues that are informative of a potential mate's value, including female body size (Olsson 1993; Cuadrado 1998a; Whiting & Bateman 1999; Fritzsche & Weiss 2012), coloration (Weiss 2002), ornament size (Weiss et al. 2009), familiarity (Tokarz 1992, 2007, 2008; Orrell & Jenssen 2002) and advertisements of sexual receptivity (Cuadrado 1998b, 2000; Head et al. 2005). Self-referential cues are also used, as males of some lizard species prefer females possessing complementary major histocompatibility complexes (Olsson et al. 2003), or females of the same colour patterns as their own (Rosenblum 2008). However, as is true for most taxa, little is known about how female behaviour influences male mate choice decisions

in lizards. This may be explained in part by the fact that female behaviour during reproductive events is difficult to quantify or is largely invariable between individuals (see Ruiz et al. 2008, 2010) for some species. However, male anoles (*Anolis carolinensis*) tend to be deterred from further courtship of females that perform proceptive or rejection behaviour (Jenssen & Nunez 1998), and male lesser earless lizards, *Holbrookia maculata*, preferentially court females that perform longer displays (Rosenblum 2008), although female display length and residency status were confounded in this study. This provides some evidence that female behaviour could influence male mate choice in lizards.

Here, we examined whether male eastern fence lizards, *Sceloporus undulatus*, use both a female's behaviour and morphology when deciding whether to attempt to mate with her. Fence lizards are medium-sized (~65 mm snout–vent length) iguanid lizards found in the eastern United States (Conant & Collins 1998), and males and females both possess a large repertoire of behavioural signals (e.g. Carpenter 1962; Haenel et al. 2003). The two primary male displays include pushups (using forelegs to raise and lower the head and upper body, implicated in territory assertion and challenge displays; Carpenter 1962; Purdue & Carpenter 1972; Rothblum & Jenssen 1978) and shudders (very rapid head nods performed by males when they court females or engage in aggressive male–male encounters; Carpenter 1962; Vinegar 1975; Rothblum & Jenssen 1978). Males have blue colour badges on either side of their throat and abdomen that function in sex recognition (Noble 1934; Cooper & Burns 1987) and can be seen by other lizards during displays (Quinn & Hews 2010). When courting a female, males typically perform a ritualized series of behaviours, including shuddering at and following a female, followed by biting the female's neck, mounting and intromission of their hemipenis (Carpenter 1962; Haenel et al. 2003). During encounters with males, females may perform pushups and a stereotyped mate rejection behaviour called sidledding (quick, 'jerky' hops accompanied by arching the back; Carpenter 1962).

We predicted that males would prefer females of larger size and higher body condition, as these measurements are correlated with female fecundity in *S. undulatus* (Tinkle & Ballinger 1972; Ballinger et al. 1981; Angilletta et al. 2001). Furthermore, female behaviour should influence male preferences: males should prefer females that show receptive or proceptive behaviours (i.e. approaching a male), and be disinclined to associate with or court females that show rejection behaviours (i.e. retreating from a male and/or sidledding). They may also favour females that pushup for longer, as this may signal higher quality (e.g. endurance; Brandt 2003).

## METHODS

### Study Animals

We captured gravid female fence lizards from Marianna, Arkansas (34°43'50"N, 90°42'18"W,  $N = 12$ ) and Dixie, Alabama (31°09'49"N, 86°42'10"W,  $N = 13$ ), U.S.A., in May 2008, and housed them in the laboratory until they oviposited (May–June). We reared hatchlings from these clutches in plastic terraria (55-litre, 56 × 40 × 30 cm, L × W × H), each containing six hatchlings of the same sex. Hatchling lizards were fed crickets (*Acheta domesticus*) daily, and provided with water ad libitum. Each terrarium was lined with paper towels, furnished with a log for basking and shelter, and a heat lamp (40 W incandescent light bulbs on a 10:14 h light:dark cycle) placed at one end to allow lizards to thermoregulate. Overhead fluorescent lights provided an LD 10:14 h cycle, and room temperature was maintained at ~25 °C. To prepare lizards for reproductive activity the following year, we induced hibernation in juvenile lizards according to the methods of Ferguson & Talent

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