



Male terrestrial salamanders demonstrate sequential mate choice based on female gravidity and size



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In many vertebrate mating systems, mate choice evolves when signalling via visual, chemical or auditory traits is an energetically costly process. Selection may favour individuals that can discriminate among potential mates and invest in signalling to mates with particular characteristics. Most commonly, females with costly gametes are thought to be the more selective sex; however, runaway sexual selection can produce elaborate male ornaments and behaviours that are similarly costly to produce, which can lead to male mate choice. In this study, we used behavioural trials to experimentally test male mate choice in a terrestrial salamander, *Plethodon shermani*. We investigated whether males altered the proportion of time they spent performing a potentially costly courtship display, ‘foot dancing’, in the presence of females. Specifically, we explored male mate choice in two experiments: (1) measuring how males modified the time they invested in courtship based solely on female reproductive value, and (2) determining whether males varied the amount of time they invested in courting females of varying sizes but similar reproductive value. In the first experiment, we quantified the duration of male courtship displays when males were paired with females of differing levels of fecundity (nongravid, weakly gravid and strongly gravid). Males displayed longest for females of high reproductive value (strongly gravid females) and less for weakly gravid and nongravid females. In the second experiment, we showed that males paired sequentially with different-sized females of similar reproductive values displayed significantly more often to larger females (i.e. male effort positively correlated with female size). In conclusion, male *P. shermani* are one of the few vertebrates known to modify their display behaviour based on female mate quality, and visual signs, such as size, may provide honest indicators of fitness.

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The coevolution of elaborate male ornaments and female perception is a common phenomenon in reproductive biology, leading to the evolution of diverse male displays in many modalities including visual, auditory and chemical signals (Andersson, 1994). In line with the breadth of displays that have evolved, a hallmark of such ornament/perception systems is rapid coevolution (Wilburn & Swanson, 2015). Early quantitative genetic models by Lande (1981) describe how runaway sexual selection may drive the evolution of increasingly more elaborate male ornaments and female preferences; the extremes of these traits are often bounded by energetic or ecological constraints that impose negative natural

selection (Kokko, Jennions, & Brooks, 2006). Anisogamy between sexes generally results in females having the more costly gametes, and hence mate choice has traditionally been documented in a female-centric manner (Andersson, 1994). However, costly male sexual traits within polygynous species may drive the evolution of male mate choice. For example, in *Drosophila* spp., male seminal fluid contains numerous proteins that have strong effects on female remating and ova maturation, but males strategically allocate the release of these energetically expensive proteins based on perceived sperm competition (Wigby et al., 2009). Similarly, in the house mouse, *Mus musculus*, males are less likely to mate with a female if a male perceives that she has recently mated (and sperm competition risk is greater) (Ramm & Stockley, 2014). And in African buffalo, *Syncerus caffer*, horn size in both males and females is negatively correlated with parasite load, but also positively correlated with female lactation, such that males may select mates based

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on inferred fitness (Ezenwa & Jolles, 2008). While these studies highlight the frequency of male mate choice in diverse taxa, they are among a relatively small number of documented examples (Roff, 2015). In the current study, we explore the influence of male mate choice on a potentially costly display behaviour using a salamander model.

Models predict that male mate choice will evolve in species that meet three criteria: (1) the number of mates available exceeds a male's capacity to mate, (2) females are variable in their reproductive quality and (3) the benefits of choosing females exceeds the cost of assessing them (Edward & Chapman, 2011). Among other factors, limitations on male mating capacity can come from energetically costly or prolonged courtship displays, and this is observed in many species of birds, insects, fish and amphibians (Boduriansky, 2001). Among amphibians, plethodontid salamanders have some of the most complex and prolonged courtships, which involve visual, tactile and olfactory signals (Arnold, 1976). In particular, one of the more elaborate courtship displays is that of the male red-legged salamander, *Plethodon shermani* (Houck & Arnold, 2003). Typically, after a male *P. shermani* orients towards a female, he signals to the female by performing a visual display termed 'foot dancing', which involves the male raising and lowering his legs while his trunk rests on the ground and remains still (Arnold, 1976; Organ, 1958). Males can choose to foot-dance for a female for multiple hours, although foot-dancing displays are intermittent and punctuated by short breaks (Eddy, Kiemnec-Tyburczy, Uyeda, & Houck, 2012). It is hypothesized that females respond to the foot-dancing signal by entering the next stage of courtship, since courtship success is positively correlated with male foot-dancing effort in this species (Eddy et al., 2012). Given a successful foot-dancing display, the male and female will next perform 'tail-straddling walk': during this stage, the female will straddle the male's tail while moving forward in tandem with him (Arnold, 1976; Noble, 1929; Stebbins, 1949). While the pair is in tail-straddling walk, the male typically delivers proteinaceous courtship pheromones to the female by bringing his mental gland in direct contact with the female's nares ('slapping'; Arnold, 1972). A successful tail-straddling walk stage leads to the deposition of a spermatophore (an apical sperm mass on a gelatinous base) and transfer of the sperm mass to the female's cloaca. The overall duration of courtships observed in the laboratory vary greatly between pairs, ranging from 17 min to 4.5 h, with a mean length of 2 h (Eddy et al., 2012). The extensive duration of the courtship in this species and the amount of movement it requires may be energetically costly to males, and thus, males may benefit from greater selectivity in potential mate assessment. In addition, female mate choice is also likely to be important in this system because the female may be assessing male foot-dancing effort and probably choose to complete courtship more quickly with males with particular characteristics. Unlike amphibians that have evolved amplexus, female *P. shermani* are able to terminate courtship at any point (Arnold, 1976; Houck & Arnold, 2003).

Plethodon shermani meet all of the aforementioned criteria for male mate choice to evolve. In addition to the protracted mating display that may be costly, this species lives at high densities often greater than 2.5 salamanders/m² (Connette & Semlitsch, 2013). Second, female salamanders are of variable reproductive quality: as with most salamanders, larger females have higher fecundity among the *Plethodon* and thus have more reproductive value to males (Kaplan & Salthe, 1979). In addition to the variation in body size, female *Plethodon* may only come into reproductive condition every other year (Highton, 1962; Saylor, 1966). The multimonth period that a female must spend defending her eggs prevents her from foraging extensively (Petranka, 1998). Therefore, at the beginning of the mating season, some large females will not have

any reproductive value to a male (nongravid), while others will only have a few or poorly developed ova (weakly gravid), and still others will have a high reproductive value to a male (strongly gravid). Female reproductive state also varies later in the season because females are only estimated to produce sufficient yolk in their eggs every other year, and thus, some individuals never develop mature ova within a reproductive season (Petranka, 1998). This variation in gravidity could place additional evolutionary pressure on males to be selective in investing time and energy into courting particular females. Finally, males must be able to assess females, and the benefit of choosing females with high reproductive value should be greater than the cost of assessing female quality if male mate choice is to evolve. In many oviparous species, the most common indicator of a female's fitness is her size, which is often correlated with fecundity (Servidio & Lande, 2006). In several salamander species, males distinguish among conspecifics by the visual cue of size (Verrell, 1985, 1986). Some species can also detect differences between gravid and nongravid females through olfaction (Dantzer & Jaeger, 2007; Marco, Chivers, Kiesecker, & Blaustein, 1998). This size assessment has not been documented for *P. shermani*; however, *P. shermani* males can identify the sex and species of an individual based on substrate-borne chemicals (Palmer & Houck, 2005). Hence, finding and assessing mates is unlikely to be highly costly for *P. shermani* males during the breeding season.

We hypothesize that foot dancing represents an example of a costly male ornament whose evolution is balanced by positive sexual selection (increased male mating success) and negative natural selection (expensive with regard to both time and energy), and therefore, males should selectively allocate foot-dancing effort based on female quality. In the present study, we tested for male mate choice in *P. shermani* by experimentally staging courtship trials and measuring the length of time that males invested in foot dancing when presented with females of varying gravidity (nongravid, weakly gravid or strongly gravid). We chose foot dancing as a proxy for male investment as it is easily quantified and is directly correlated with courtship success (Eddy et al., 2012). We also investigated whether males used cues other than gravidity (such as body size) to assess female reproductive condition by quantifying foot-dancing effort when each male was sequentially paired with strongly gravid females of different sizes.

METHODS

Animal Collection and Maintenance

We collected 60 adult male and 100 adult female *P. shermani* in Macon County, North Carolina, U.S.A. (035°10'48"N 083°33'38"W) during early August 2011 with the appropriate permits from the North Carolina Wildlife Resources Commission (permit no. 13-SC00345). Animals were housed in individual boxes when not being used in behavioural trials. In most cases, animals were fed two waxworms (*Galleria mellonella*) weekly, with one exception: females used in experiment 1 were not fed for the duration of the experiment to prevent their condition from changing between trials with different males. Females were fed at the end of the experiment (approximately 2 weeks after collection). Because these animals are only fed weekly in the laboratory (Eddy et al., 2012; Houck et al., 2008; Wilburn et al., 2015), withholding food for one extra week was likely to be within the normal variation in feeding for this ectothermic species and should not have negatively impacted their body condition. In both laboratory locations (described below), each animal was housed individually in a clear plastic box (17 × 9 × 13 cm) with a substrate of moist paper towels and crumpled damp towels for refugia when not being used in courtship trials. All animal care and experimental protocols used in

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