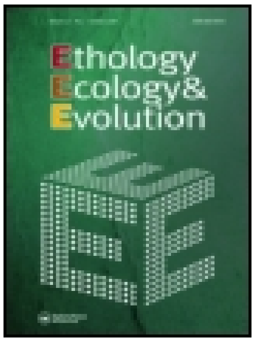

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Absence of visual discrimination by female eastern newts during mate selection

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Male eastern newts (*Notophthalmus viridescens*) exhibit tremendous variation in several characteristics, including the number of dorsal spots, the brightness of those spots, tail depth and tail length. These traits could be used by females for mate selection decisions. We conducted two experiments to determine whether females use visual signals to assess these characteristics in their mate selection decisions by simultaneously exposing a female to males of opposing characteristics. We observed female preference for the number of spots on a male's dorsum, the brightness of male dorsal spots, male body mass, and male tail depth and length. We then recorded the amount of time the female spent in a preference zone adjacent to each of the males. Female newts did not show a significant preference for any of the characteristics observed, spending roughly equal amounts of time in both preference zones. These results, combined with the results of several previous studies, suggest that female eastern newts do not use visual signals to assess these traits in their mate selection decisions. Given that most of these traits are sexually dimorphic, this is likely due to the reproductive advantage created by the intense male–male competition present and their amplexus-based mating system.

KEY WORDS: sexual selection, female choice, eastern newt, male-male competition, secondary sexual characteristics.

INTRODUCTION

Sexual selection is the advantage a certain individual has over other individuals in relation to sex (Darwin 1871). In terms of sexual selection, females, because of the size and energy of their gametes, usually have a greater investment in reproduction than males (Bateman 1948; Fisher 1958; Trivers 1972; Williams 1975). Bateman (1948) linked the discrepancy in gamete investment to mating strategies of males and females: males usually look for quantity over quality in their mates, whereas females typically seek a high-quality mate (Trivers 1972; Williams 1975). Within sexual selection, two processes define the direction of selection on the two sexes (Moore 1990; Hunt et al. 2009). Intrasexual selection, often referred to as "male–male competition", is the

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competition between members of one sex (usually males) for access to the limited sex (usually females) (Halliday 1983; Hunt et al. 2009). Intersexual selection, or "female choice", occurs when the limited sex discriminates between mates during mate selection (Clutton-Brock 2007).

In most species, females are the limited sex (Massey 1990; Clutton-Brock 2007; Miller 2013) due to the energetic costs associated with the production of ova (Bateman 1948). Because females invest more than males, it is understandable that they would express selectivity in their decisions when choosing a mate. Intersexual selection is extremely powerful and can manipulate the characteristics displayed in male traits through preferential selection (e.g. Kirkpatrick 1982; Andersson 1994). By selectively seeking specific traits in males, females are actively showing preference for and choosing males with advantageous qualities such that they can produce a high quantity and/or high quality of offspring (Kirkpatrick 1982; Andersson 1994). There are both direct and indirect benefits that can result from intersexual selection, including the acquisition of nuptial gifts, protection and parental care from a mate, and oviposition sites (direct benefits), and good genes (indirect benefit) (Andersson 1994; Kokko et al. 2003). By exhibiting selective preference for certain secondary sexual characteristics, intersexual selection can drive the expression and occurrence of male sexual traits in a population. Sometimes this preference can be enhanced through male–male competition (intrasexual selection), whereby the female's choice is the winner of the competing males. Since these two selection processes can help facilitate the assessment of high-quality mates, it is unusual for these two processes to occur independently (Wong & Candolin 2005; Hunt et al. 2009).

One species in which the mating system may be comprised of both intersexual and intrasexual selection is eastern newts (*Notophthalmus viridescens*). Eastern newts breed from late winter to early spring (Petranka 1998), during which time females mate 2 or 3 times (Halliday & Verrell 1984). Access to females is limited: both the population sex ratio and the operational sex ratio are male biased in eastern newts (Massey 1988; Clutton-Brock 2007), resulting in intense male–male competition during the breeding season. During the breeding season, male newts patrol the pond in search of females (Verrell 1982). During the mating process, the male can perform one of two types of behaviour depending on the female's responsiveness. If the female is responsive, amplexus may be bypassed and instead, the male will perform a "hula" display, after which he deposits a spermatophore (Verrell 1982). If she is not immediately responsive, the male amplexes the female which is followed by spermatophore deposition (Verrell 1982). Although the female is more responsive to the "hula", sperm transfer is more successful after amplexus than after the "hula" (Verrell 1982).

Although intrasexual selection appears intense in eastern newts, the opportunity for "choosiness" by females also exists. Males exhibit multiple sexually dimorphic traits that have the potential to be correlated with fitness. For example, some males are substantially larger and have longer and deeper tails than other males. Body mass is a common trait for which females exhibit preference in other species (Lank & Smith 1992; Morrison et al. 2001; Moya-Laraño et al. 2002), and tail length and depth are correlated with swimming performance in newts (Gabor et al. 1999). Both tail length and tail depth are sexually dimorphic, with males possessing deeper and longer tails then females, whereas there does not appear to be sexual size dimorphism in our population of newts (authors' unpub. data). Eastern newts possess a powerful neurotoxin (tetrodotoxin) in their skin and individuals within a population vary dramatically in toxicity (Yotsu-Yamashita et al.

2012; authors' unpub. data). In addition to size and toxicity, eastern newts also possess colour variation that females could utilise in mate selection. Both male and female newts possess red spots on the dorsum; these spots vary in both size and hue, with some males being relatively dull (few dark spots) while others possess many bright red spots. The purpose of these red spots is unknown. However, many other amphibian species exhibit sexually dimorphic pigmentation (Wells 1980; Buchanan 1994), and it is possible that they impact reproductive success. Since the spots are red, they are energetically expensive to produce, affecting the number of dorsal spots that appear on the animal (male or female) (Davis & Grayson 2008). The brightness of these spots is sexually dimorphic with males' spots being redder and brighter than females (Davis & Grayson 2008). Because of this, the formation of the males' spots is likely more costly than that of females. With these spots being energetically expensive, it is reasonable to hypothesise that both the number of these dorsal spots and their brightness could play a role in females' sexual selection preferences. The abundance of variation in physical characteristics, and the presence of sexual dimorphism associated with many of these traits, provides an optimal system to test the role of intersexual and intrasexual selection in driving the evolution of these traits in newts.

Despite the variability in physical traits possessed by males, females appear less involved in sexual selection than males, and several previous studies have found no evidence of intersexual selection in newts with regard to several secondary sexual characteristics (Dawley 1984; Gabor et al. 1999; Davis & Grayson 2008; Takahashi et al. 2010). Nevertheless, in many species both intrasexual and intersexual processes occur and it is rare for the two processes to occur independently (Wong & Candolin 2005; Hunt et al. 2009). By eliminating the option for male–male competition to influence a female's mate selection decisions, we sought to determine whether female preference is present in eastern newts. Specifically, we examined female preference in response to a variety of physical characteristics present in males. Since these newts exhibit tremendous variation in the number and brightness of red spots on the dorsum (Davis & Grayson 2008), we believed these spots could be used by females for mate selection decisions. In addition to testing the influences of spot number and spot brightness on female preference, we also tested the influences of body mass, tail length and tail depth.

METHODS

Animal collection and maintenance

Eastern newts were collected from a fishless pond (0.16 ha) in Switzerland County, Indiana between 27 January and 2 February 2016. A total of 48 females and 87 males were collected and transported back to Hanover College. The newts were then sorted by sex based on secondary sex characteristics: males were identified as having a swollen, round cloaca and females were identified as having a cone-shaped cloaca (Petranka 1998). Newts were housed in small groups in 37-L aquaria and sexes were kept separate. After the sexes were separated, the males were further subdivided by the number of red spots they contained on their dorsum: 0–10 red spots, 11–19 red spots, and 20 + red spots. Each of the tanks was filled with approximately 3.0 cm of water. These tanks were then moved to an environmental chamber (17.0 °C; light/dark cycle 12:12 hr). Male and female tanks were kept on different shelves as to avoid pre-exposure and preference prior to the trials. Newts were fed California blackworms (*Lumbriculus variegatus*) twice per week.

Experiment 1: female preference for number of spots and spot brightness

The experimental trials were conducted in February 2016 in the environmental chamber; this is the peak mating period for this population of newts and mating behaviour is routinely observed both in the wild and in the lab at this time. Our methods were modified from a previous experiment observing the mating preference of *Euproctus asper* (Poschadel et al. 2007). For each trial, three separate aquaria (33.0 × 18.5 × 24.0 cm deep) were aligned horizontally and used to observe the newts: the central tank housed the female newt and the outer tanks each held one male newt. Each tank contained approximately 2–3 cm of gravel at the bottom and approximately 3.0–3.5 cm of water; this water depth was chosen to ease breathing by the newts during the experiment. Dorsal colouration occurs above the midline and below a shallow vertebral ridge on top of the animal; therefore, females are able to visually assess the characteristics tested under these shallow conditions. The outside walls of the tanks were covered with black paper to reduce external visual stimuli. The central tank was visually subdivided into three equal sections, each 11.0 cm long. There were two outer preference zones, and one neutral preference zone between the outer preference zones. The outer tanks housing the males were reduced in size by inserting a glass barrier to create a limited space (11.0 × 18.5 cm) immediately adjacent to the female tank (Fig. 1).

After the tanks had been properly arranged, two male newts (one with a high spot count and one with a low spot count) were randomly placed on either side of the central tank. A small, white acclimation cylinder (4.0 cm diameter) was placed in the centre of the middle tank to acclimate the female. A female was haphazardly selected, and was placed inside the acclimation cylinder. After all newts were in their respective tanks, a 15-min acclimation began.

At the end of the acclimation period, the observation period began and was conducted for 30 min. The amount of time the female spent in each preference zone and how often she moved between zones were recorded. The location of the female was determined by the position of her head; if her head crossed into a different zone, she was considered to be in that new preference zone.

At the completion of the experiment, the newts were removed from the experimental tanks and were placed in individual containers (15.5 × 15.5 × 8.0 cm deep; 4.0 cm of water). The glass dividers were removed and cleaned with de-ionised water, as were the tanks. The gravel was not changed between trials, but was thoroughly rinsed with de-ionised water. The experimental procedure was then repeated (n = 27). Female newts were never reused in any experiment after testing. Male newts were not reused within an experiment but may have been used more than once across the two experiments. At the completion of all trials, all newts were anesthetised with Tricaine mesylate (MS222), and the newts' mass, tail length, tail width, number of spots, and spot brightness (qualitatively measured on a scale of 1–5, 1 being the dullest and 5 being the brightest) were recorded. We used a paired t-test to compare the amount of time the females spent in each preference zone in response to males with many or few spots. Although we did not factor spot brightness into the original experiment, we also conducted a paired t-test on the amount of

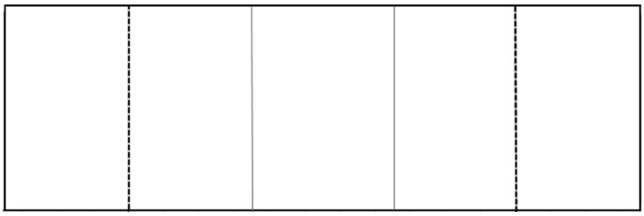

Fig. 1. — Experimental layout to test female preference for male visual characteristics (number of dorsal spots, spot brightness, tail depth, and tail length). A female was placed in the centre of the central tank, henceforth referred to as the "neutral zone". To the right and left of the neutral zone were the preference zones. The males were located in the two compartments at either end of the experimental set-up.

time females spent near the bright male and dull male (ignoring the number of dorsal spots). Because some males were equally dull/bright, we removed these (n = 6) from the analysis. Finally, we conducted linear regressions to determine whether there were any relationships between the number of spots and spot brightness, spot brightness and body mass, and number of spots and body mass.

Experiment 2: female preference for body mass, tail depth and tail length

The experimental procedure was the same as described previously except one large (> 3.61 g) and one small (< 3.17 g) male were selected and randomly placed in each end tank. A haphazardly selected female was placed inside the acclimation cylinder, and was acclimated for 15 min. The amount of time the female spent in each preference zone and how often she moved between zones were again recorded. After all trials had been performed (n = 27), a paired t-test was used to compare the amount of time the female spent near the large or small male. We also used a paired t-test to compare the amount of time the females spent near males with deep vs shallow tails and males with long vs short tails. As with experiment 1, any trials consisting of males with similar tail depth/length were removed from the analysis (tail depth = 10 removed; tail length = 2 removed). Finally, we ran linear regressions to determine whether relationships existed between body mass and tail length, body mass and tail depth, and tail depth and tail length.

RESULTS

Experiment 1: female preference for number of spots and spot brightness

A paired t-test found no significant difference between the amount of time female newts spent in the preference zone adjacent to the high-spot male and the zone next to the low-spot male (t = 0.299, df = 26, P = 0.767, Fig. 2A). A paired t-test also found no difference between the amount of time female newts spent near males with bright spots vs males with dull spots (t = 1.67, df = 20, P = 0.11, Fig. 2B).

A linear regression found a significant, positive relationship between the number of spots on males and the brightness of their spots (R^2 = 0.199, P < 0.001, Fig. 3). In this case, individuals with more spots tend (weakly) to also have brighter spots (Fig. 3). A linear regression also yielded no significant relationship between spot brightness and body mass (R^2 = 0.041, P = 0.143) or the number of spots and body mass (R^2 = 0.023, P = 0.273).

Experiment 2: female preference for body mass, tail depth and tail length

A paired t-test found no significant difference between the mean number of seconds female newts spent in the large-male preference zone and the mean number of seconds spent in the small-male preference zone (t = – 0.69, df = 26, P = 0.49, Fig. 4A). Similarly, paired t-tests also found no difference between the time females spent near deep/shallow- and long/short-tailed males (tail depth: t = 1.1, df = 16, P = 0.29, Fig. 4B; tail length: t = – 1.66, df = 24, P = 0.11, Fig. 4C).

A linear regression found a significant, positive relationship between male body mass and tail depth (R^2 = 0.183, P = 0.001, Fig. 5A). There was also a significant positive relationship between male body mass and tail length (R^2 = 0.218, P < 0.001, Fig. 5B). These data (weakly) indicate that larger males have deeper and longer tails than smaller

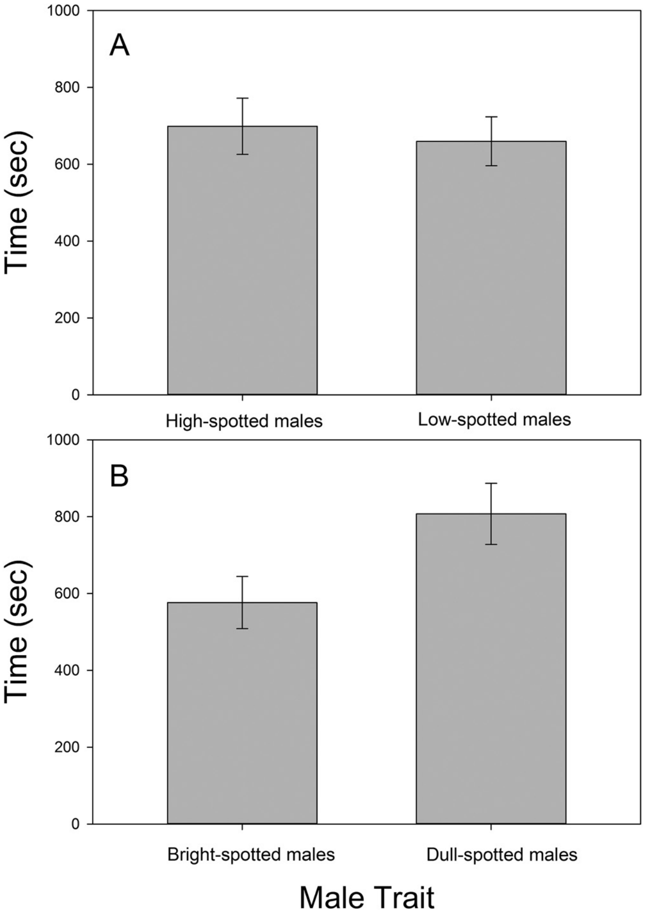

Fig. 2. — Mean (± SE) amount of time female eastern newts (*Notophthalmus viridescens*) spent near A: high-spotted and low-spotted male newts and B: bright-spotted and dull-spotted male newts. No significant difference was found in the amount of time females spent near each male (spot number: $t = 0.299$, df = 26, $P = 0.767$; spot brightness: $t = 1.67$, df = 20, $P = 0.11$).

males (Fig. 5). Finally, no significant relationship was found between male tail depth and tail length ($R^2 = 0.050$, $P = 0.103$).

DISCUSSION

We found that female newts did not spend a significantly different amount of time near or away from conspecific males with variable secondary sexual traits. This included a lack of preference for males with more or less spots, brighter or duller spots, larger or smaller mass, longer or shorter tails, or deeper or shallower tails. These results indicate that female eastern newts do not show a preference for these secondary sexual characteristics in their mate selection process, and suggest that

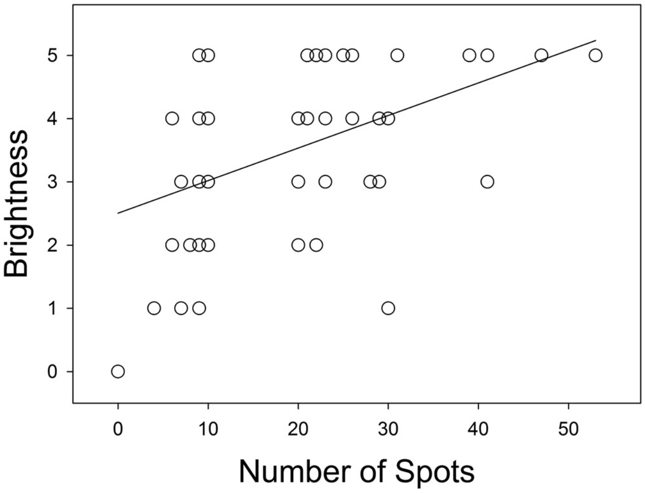

Fig. 3. — Relationship between the number of male dorsal spots and the brightness of those spots. A weak, positive relationship between these two male traits exists ($R^2 = 0.199$, $P < 0.001$).

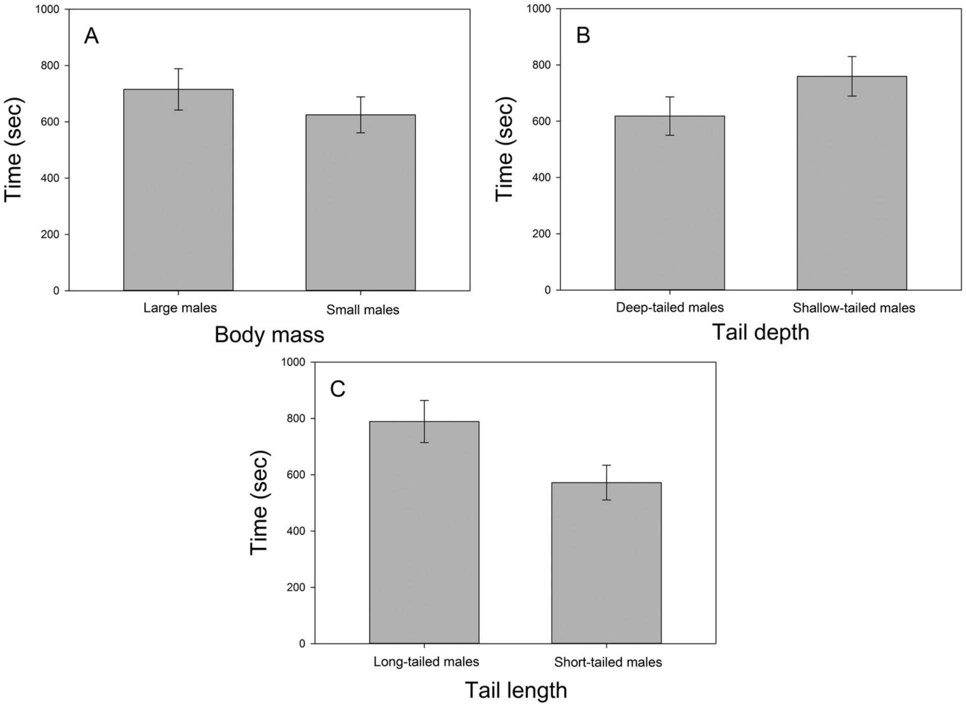

Fig. 4. — Mean (± SE) amount of time female eastern newts (*Notophthalmus viridescens*) spent near A: large and small male newts, B: deep-tailed and shallow-tailed male newts, and C: long-tailed and short-tailed male newts. No significant difference was found in the amount of time females spent near each male (body mass: $t = -0.69$, df = 26, $P = 0.49$; tail depth: $t = 1.1$, df = 16, $P = 0.29$; tail length: $t = -1.66$, df = 24, $P = 0.11$).

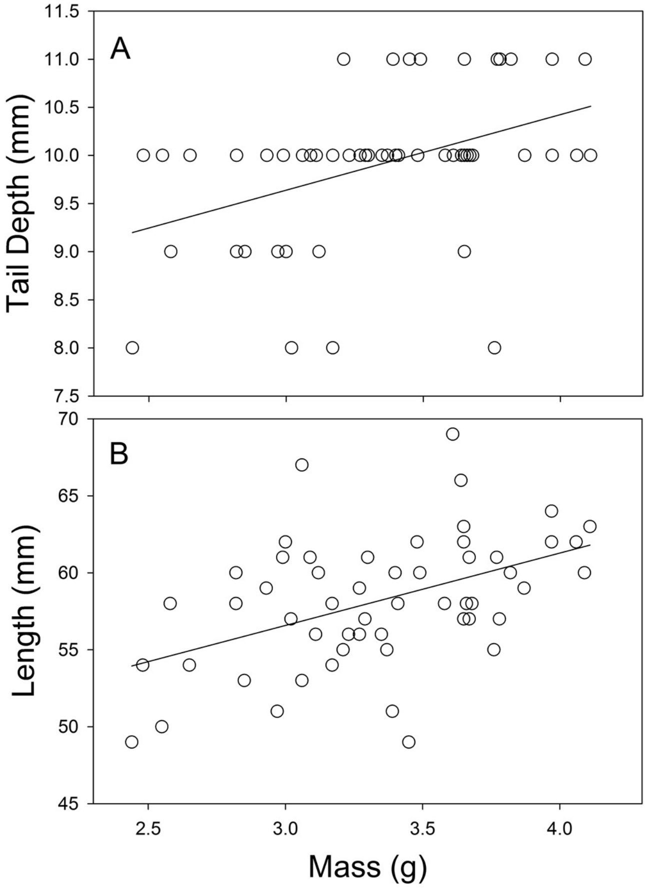

Fig. 5. — Relationships between A: male body mass and tail depth and B: male body mass and tail length. Positive, significant (weak) relationships were found in both A and B (tail depth: $R^2 = 0.183$, $P = 0.001$; tail length: $R^2 = 0.218$, $P < 0.001$).

females of this species may not be inherently "choosy". These results are surprising given the large amount of variation in these physical characteristics between males of this species (Davis & Grayson 2008), as well as the many species in which females are choosy (e.g. Halliday 1983; Miller 2013). Nevertheless, several previous studies have also failed to find evidence of female choice related to these secondary sexual characteristics. For example, Davis and Grayson (2008) tested female preference for spot brightness in *N. viridescens* and found no significant preference for males with brighter or duller spots (despite being sexually dimorphic). Also congruent with our results, Takahashi et al. (2010) found no significant female preference for males with a larger or smaller body mass. In addition to testing preference for body mass, they tested female preference for conspecific and heterospecific males (*N. viridescens* and *N. dorsalis*). They again found no female preference exhibited for one species over the other (Takahashi et al. 2010). Gabor et al. (1999) performed several experiments, all of which produced results that support the absence of female choice in this species. In their studies, females did not exhibit preferences related to tail length (long or short) or tail depth (deep or shallow) (Gabor et al. 1999). Gabor et al. (1999) also studied cryptic female choice by observing their spermatophore selection, and, again, no significant preference was observed. In addition to physical characteristics, female newts also appear to lack a preference for sex-specific water-borne chemical stimuli, whereas males show strong preferences for female scent over male or odorless situations (Dawley 1984). Each of the previous studies, regardless of the secondary sexual characteristic observed, failed to produce results identifying female preference in eastern newts.

The combination of these results and the results of the previously mentioned studies (Dawley 1984; Gabor et al. 1999; Davis & Grayson 2008; Takahashi et al. 2010) suggest that sexual selection is driven intrasexually by male–male competition in eastern newts, rather than by female choice (intersexual selection). While there are numerous physical traits evident in newts that are likely correlated with fitness (e.g. tail depth), female eastern newts may not have to search for the best-quality male because they are indirectly mating with these males as a consequence of the nature of the mating system. In many other species, male–male competition occurs to gain the attention and interest of a female (e.g. elk, leaf-footed cactus bugs, bighorn sheep, etc.; Miller 2013), after which she selects a particular male with high quality or viability (Halliday 1983). However, in eastern newts, male–male competition occurs to gain access to the female (Massey 1988). In *N. viridescens* there is limited access to females due to the higher proportion of males in the population (Halliday & Verrell 1984). Eastern newts are fully aquatic, and during the breeding season males actively search for females. If they detect a female's presence, they will rapidly swim towards her and attempt to mate (Verrell 1982). Because of the limited access to females and increased male activity (males constantly patrol the pond), male–male competition is intense in this species (Gabor et al. 1999). Usually when two males engage in competition, a female will swim away, thus causing the male with the more advantageous traits for swimming (e.g. longer tail, deeper tail, smaller body mass, etc.) to gain access to the female (Massey 1988). Although it is unknown whether swimming speed and performance are correlated with other traits, this competition would eliminate the need for female choice, as the male with the more fit characteristics will access the female first. This explanation is supported by Able (1999) and Gabor et al. (1999), who found that males of *N. viridescens* with deeper tails had greater success capturing females in both pond and in laboratory environments.

Another explanation for the lack of female choice present in eastern newts could be that females are unable to detect the differences among males or that these differences are not correlated with quality (Gabor et al. 1999). For the evolution of a female preference to occur, a reproductive advantage must be gained by exhibiting a preference (Kirkpatrick 1982). If females are unable to assess male quality or the physical traits are uncorrelated with quality, females exhibiting a preference would not achieve a reproductive advantage and thus female choice would not evolve. However, these conditions would expose females to the risk of mating with a poor-quality male. To compensate for this risk females could mate with multiple males, and indeed female newts mate 2–3 times each breeding season. Mating with multiple males could be a form of "genetic bet-hedging" which reduces the risk of producing offspring of low genetic quality, thus allowing females to compensate for the inability to assess male quality based on secondary sex characteristics (Gabor et al. 1999). The amplexus-based mating system combined with the male–male competition present in eastern newts may form a reproductive advantage without requiring female selection. Because of this, the females may not benefit from being choosy, and thus do not exhibit preference for certain sexual characteristics.

The role of male–male competition limiting the need for female choice may be common in species with similar reproductive pressures. For example, in the strawberry poison frog, females mated with the closest male and were not selective regarding the acoustics of the male's call, territory size, or various physical traits including body length or mass (Meuche et al. 2013). The authors hypothesised that strong male–male competition prevents low-quality males from maintaining territories and accessing reproductively receptive females (Meuche et al. 2013). Another species with an amplexus-based mating system and intense male–male competition, the wood frog (*Rana sylvatica*), also lacks female choosiness in its sexual selection process (Berven 1981). The results of our experiment, combined with other studies, suggest that the particular mating system used in these species creates a reproductive advantage for females, thus eliminating the need for female selection.

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DISCLOSURE STATEMENT

No potential conflict of interest was reported by the authors.

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