



Interdependent effects of male and female body size plasticity on mating behaviour of predatory mites



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The adaptive canalization hypothesis predicts that traits with low phenotypic plasticity are more fitness relevant, because they have been canalized via strong past selection, than traits with high phenotypic plasticity. Based on differing male body size plasticities of the predatory mites *Phytoseiulus persimilis* (low plasticity) and *Neoseiulus californicus* (high plasticity), we accordingly hypothesized that small male body size entails higher costs in female choice and male–male competition in *P. persimilis* than *N. californicus*. Males of both species are highly polygynous but females differ in the level of polyandry (low level in *P. persimilis*; medium level in *N. californicus*). We videotaped the mating interactions in triplets of either *P. persimilis* or *N. californicus*, consisting of a virgin female (small or standard-sized) and a small and a standard-sized male. Mating by both small and standard-sized *P. persimilis* females was biased towards standard-sized males, resulting from the interplay between female preference for standard-sized males and the inferiority of small males in male–male competition. In contrast, mating by *N. californicus* females was equally balanced between small and standard-sized males. Small *N. californicus* males were more aggressive ('Napoleon complex') in male–male competition, reducing the likelihood of encounter between the standard-sized male and the female, and thus counterbalancing female preference for standard-sized males. Our results support the hypothesis that male body size is more important to fitness in the low-level polyandrous *P. persimilis* than in the medium-level polyandrous *N. californicus* and provide a key example of the implications of sexually selected body size plasticity on mating behaviour.

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Male body size is a decisive factor for the outcome of male–male competition and female choice in numerous animals (Andersson, 1994; Blanckenhorn, 2005). Commonly, the competitively inferior males are smaller than their rivals, which are also more often selected by the females as mates (Wong & Candolin, 2005). In some species, however, small males have evolved alternative mating tactics such as sneakers, satellites or patrollers, to circumvent direct male–male competition and increase their mating success (Gross, 1996; Taborsky, Oliveira & Brockman, 2008). Small males may also act hyperaggressively against larger rivals ('Napoleon complex') and frequently initiate fights (Jenssen, DeCourcy, & Congdon, 2005; Moretz, 2003). Hyperaggressive behaviour of small males may be adaptive if the probability of winning male–male competition is higher for the initiating than reacting male (Morrell, Lindström, & Ruxton, 2005).

Large dominant males do not always guarantee the highest net benefit for females willing to mate. For example, the direct costs of interacting with dominant, large males arising from harassing may lead to female preference for small males (Qvarnström & Forsgren, 1998). Harassment costs should vary with female phenotype such as body size. Small females have a higher risk of injury by male harassment and may thus prefer small over large mates (Crespi, 1989). Size-assortative female choice may balance the mating success of small and large males. Indirect costs may arise when large males are comparatively poor food providers of offspring (Forsgren, 1997), resulting in female preference for small males (Hakkarainen et al., 1996).

Regarding sexual selection, male body size should be less important to fitness in species in which the costs of being small are counterbalanced by male or female strategies than in species without such compensating mechanisms. The fitness relevance of male body size should in turn be reflected in its plasticity. Strong past sexual selection on male body size should reduce plasticity, according to the adaptive canalization hypothesis. Robustness of male body size against environmental disturbances, preventing

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large deviations from the optimum male size, is considered an adaptive consequence of canalization (Schmalhausen, 1949; Stearns & Kawecki, 1994; Stillwell, Blanckenhorn, Teder, & Davidowitz, 2010; Waddington, 1942). Strikingly, the predictions of the adaptive canalization hypothesis have primarily been used to explain the evolution of body size plasticity in the context of sexual size dimorphism within species (Stillwell et al., 2010). We argue that species- and sex-specific variation in canalization of body size plasticity may also reflect species-specific strengths in past sexual selection arising from different mating systems (Walzer & Schausberger, 2011, 2014).

Our study system consisted of the plant-inhabiting predatory mite species *Phytoseiulus persimilis* and *Neoseiulus californicus*, which constitute a natural predator guild in several regions in the Mediterranean Basin (De Moraes, McMurtry, Denmark & Campos, 2004), sharing the two-spotted spider mite, *Tetranychus urticae*, as prey (Walzer & Schausberger, 2011). In both species, both females and males develop from fertilized eggs but the male genome is eliminated during egg development resulting in haploid males (Sabelis, Nagelkerke, & Breeuwer, 2002). Adult males are about one-third smaller than adult females (e.g. Walzer & Schausberger, 2011). The female-biased tertiary sex ratio ranges from 0.6 to 0.8 under optimal conditions and can shift to equality, when the population density increases or prey availability decreases (Sabelis et al., 2002). Both species are highly aggregated at the leaf scale (Walzer, Moder, & Schausberger, 2009), but patchily distributed among leaves within plants (Zhang & Sanderson, 1993). Males actively search for mates, orienting themselves on pheromones released by the females (Amano & Chant, 1978a; Pappas, Broufas, & Koveos, 2005). Male–male fighting has been observed in *P. persimilis* (Enigl & Schausberger, 2004). It is unknown whether *N. californicus* males also engage in contest mate competition. After the mates encounter each other, the female decides whether or not mating takes place. Female choice may manifest as the female readily accepting the potential mate, delaying the mating or completely avoiding the potential mate by running away (personal observation), with the latter indicating female resistance and/or sexual conflict (Gosden & Svensson, 2009). In both species the average mating duration is 2–4 h (Amano & Chant, 1978b; Enigl & Schausberger, 2004; Gotoh & Tsuchiya, 2008). The mates do not stay together after mating, indicating the absence of male postcopulatory guarding behaviour (Amano & Chant, 1978b). Males of both *P. persimilis* and *N. californicus* are highly polygynous but the female mating system differs between the two species (Schausberger et al., 2014; Walzer & Schausberger, 2014). A single mating is sufficient for *P. persimilis* females to reach the maximum lifetime reproductive success (LRS) but females do remate occasionally (Schausberger et al., 2014). In contrast, *N. californicus* females need multiple matings to reach the maximum LRS (Gotoh & Tsuchiya, 2008; Schausberger et al., 2014). Thus, we defined the female mating systems of *P. persimilis* and *N. californicus* as low-level and medium-level polyandry, respectively (Schausberger et al., 2014; Walzer & Schausberger, 2014). Food shortage during juvenile development induces species- and sex-specific adult body size plasticity. In both species female body size is similarly plastic and more plastic than male body size. However, male body size is more plastic in *N. californicus* than *P. persimilis* (Walzer & Schausberger, 2011, 2014). Consistent with the adaptive canalization hypothesis, small deviations from standard male body size reduce male LRS of *P. persimilis* but not *N. californicus* (Walzer & Schausberger, 2014).

Here, we tested the predictions that (1) the fitness relevance of male body size plasticity is also reflected in male–male competition and female choice of *P. persimilis* and *N. californicus*, and (2)

the costs of small male body size are more effectively counterbalanced in *N. californicus* than *P. persimilis*. To this end, we conducted mating experiments using triplets consisting of a single small and standard-sized male and a small or standard-sized female and characterized the mating behaviour (mate choice, mating latency, duration and frequency) and the intensity and direction of male–male competition and female choice within the triplets.

METHODS

Species Origin and Rearing

Specimens of *P. persimilis* and *N. californicus* used to found laboratory-reared populations originated from Sicily (Walzer & Schausberger, 2011). The species were reared on separate arenas consisting of plastic tiles resting on water-saturated foam cubes in plastic boxes half-filled with water (for details see Walzer & Schausberger, 2014). To obtain predator eggs for generating small and standard-sized females and males used in experiments, 10 females each of *N. californicus* and *P. persimilis* were randomly taken from the rearing units and placed on separate spider mite-infested bean leaf arenas for egg production (for details see Walzer & Schausberger, 2014).

Experimental Cages and Arenas

Cages drilled into rectangular acrylic plates were used for generating virgin females and males with different body sizes. Each cage consisted of a cylindrical cell 15 mm in diameter and 3 mm high closed at the bottom by fine gauze and on the upper side by a microscope slide (Schausberger, 1997). White plastic discs (diameter 14 mm) were used as experimental arenas. The chosen disc size provided sufficient space for free movement of the predators (body length ca. 0.3–0.5 mm), but at the same time increased the likelihood of encounter (Walzer & Schausberger, 2013a, b). Additionally, the disc size fitted the requirements of the video-tracking software we used, EthoVision XT 8, to distinguish the individuals from system noise without identification errors (Noldus Information Technology b.v., 2010). Each plastic disc was fixed on a metallic cylinder (height 20 mm, diameter 10 mm), which was centrally placed in a cubic plastic box (side length 25 mm) filled with tap water up to the margin of the disc to confine the mites to the arena. Forty spider mite eggs serving as prey for the predators were placed on each disc using a moistened camel's hair brush.

Generating Small and Standard-sized Females and Males

To get small and standard-sized females and males of *P. persimilis* and *N. californicus*, respectively, eggs were randomly taken from the egg production arenas, placed singly into acrylic cages and provided with either limited (10 for *P. persimilis*, eight for *N. californicus*) or ample (40 for either predator) spider mite eggs as prey. Limited prey supply differed between the two predators because of species-specific prey demands (Walzer & Schausberger, 2011). The developmental progress of the predators was checked daily. Sex-specific body size differences were used to determine their sex after reaching adulthood. Virgin females and males reared under limited and ample prey supply were termed small and standard-sized females and males, respectively. After the experiment, each female and male was mounted in a drop of Hoyer's medium on a microscope slide (Krantz & Walter, 2009) to measure the dorsal shield length, which is a suitable body size indicator (Croft, Luh, & Schausberger, 1999).

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