



Canalization of body size matters for lifetime reproductive success of male predatory mites (Acari: Phytoseiidae)

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The adaptive canalization hypothesis predicts that highly fitness-relevant traits are canalized via past selection, resulting in low phenotypic plasticity and high robustness to environmental stress. Accordingly, we hypothesized that the level of phenotypic plasticity of male body size of the predatory mites *Phytoseiulus persimilis* (low plasticity) and *Neoseiulus californicus* (high plasticity) reflects the effects of body size variation on fitness, especially male lifetime reproductive success (LRS). We first generated small and standard-sized males of *P. persimilis* and *N. californicus* by rearing them to adulthood under limited and ample prey supply, respectively. Then, adult small and standard-sized males were provided with surplus virgin females throughout life to assess their mating and reproductive traits. Small male body size did not affect male longevity or the number of fertilized females but reduced male LRS of *P. persimilis* but not *N. californicus*. Proximately, the lower LRS of small than standard-sized *P. persimilis* males correlated with shorter mating durations, probably decreasing the amount of transferred sperm. Ultimately, we suggest that male body size is more strongly canalized in *P. persimilis* than *N. californicus* because deviation from standard body size has larger detrimental fitness effects in *P. persimilis* than *N. californicus*. © 2014 The Authors. Biological Journal of the Linnean Society published by John Wiley & Sons Ltd on behalf of The Linnean Society of London, *Biological Journal of the Linnean Society*, 2014, **111**, 889–899.

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INTRODUCTION

Adult male body size is shaped by both natural and sexual selection (Blanckenhorn, 2005) and affects nearly all biological phenomena and ecological events during male life. For example, major behavioural and life-history traits such as age at maturity, feeding and mating habits, susceptibility to predation, competitiveness and longevity are related to male body size (Clutton-Brock, 1988; Roff, 1992; Andersson, 1994). Most importantly, in many species the lifetime reproductive success (LRS) of males is closely correlated with male body size (Andersson, 1994; Blanckenhorn, 2005).

Environmental stress triggered by a limited finite, i.e. diminishing, food resource during the juvenile phase commonly decreases body size because selection favours accelerated development enhancing juvenile survival at the expense of smaller body size at maturity (e.g. Abrams *et al.*, 1996). The degree of phenotypic plasticity in response to environmental stress gradients may allow species- and sex-specific predictions of the fitness relevance of adult body size. Potential ultimate explanations for species- and sex-specific plasticities of adult body size can be deduced from the adaptive canalization hypothesis (Waddington, 1942; Schmalhausen, 1949; Stearns & Kawecki, 1994; Stearns, Kaiser & Kawecki, 1995; Stillwell *et al.*, 2010). Traits that are more closely linked to fitness relative to other traits are more

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strongly affected by selection, which in turn should decrease the phenotypic plasticity of these traits. Consequently, traits under strong past selection are less plastic and more robust to environmental stress, whereas traits under low selection pressure have higher plasticities and are more sensitive to environmental changes (Stillwell *et al.*, 2010). In sexually size-dimorphic species, the level of body size plasticity may reflect the relative importance of body size for reproductive success of males and females within a given species or of different species within a given sex. The predictions of the above-mentioned assumptions, however, were exclusively tested in the context of sexual size dimorphism to detect sex-specific selective forces acting on body size, resulting in different optima in males and females, i.e. intra-locus sexual conflict (Fernandez-Montraveta & Moya-Laraño, 2007; Hallsson & Björklund, 2012; Zhang *et al.*, 2012).

The most suitable measure of the fitness relevance of phenotypically plastic traits such as male body size is its effect on male LRS (Grafen, 1982). Measuring male LRS, however, is commonly more laborious and time-consuming than measuring female LRS. Due to widespread polygyny, the former requires the observation of multiple females fertilized during life, whereas the latter requires the observation of only a single female. Additionally, when females are polyandrous, phenomena such as cryptic female choice and sperm competition complicate the exact determination of male LRS. The more difficult determination of male than female LRS is reflected in the strongly female-biased number of topically relevant experimental studies, which is also due to the importance of female LRS as a standard parameter in life table and population growth studies.

Here, we investigated the effects of species-specific phenotypic plasticity of male body size on male LRS in the plant-inhabiting predatory mites *Phytoseiulus persimilis* (low plasticity) and *Neoseiulus californicus* (high plasticity) (Acari: Phytoseiidae). These predators constitute natural guilds in several areas of the Mediterranean Basin (De Moraes *et al.*, 2004), sharing the two-spotted spider mite *Tetranychus urticae* (Acari: Tetranychidae) as prey (Walzer & Schausberger, 2011). Phytoseiid mites are pseudo-arrhenotokous with haploid males arising from originally diploid eggs (Sabelis, Nagelkerke & Breeuwer, 2002). Females are larger than males (Schulten, 1985) and the tertiary sex ratio is female-biased, ranging from a proportion of 0.6 to 0.8 depending on the environmental conditions (Sabelis & Nagelkerke, 1988). The lifetime mating frequency of males is usually > 10 times higher than that of females (Schulten, 1985). The polygynous males of both species are actively searching for receptive females

(Amano & Chant, 1978a; Pappas, Broufas & Koveos, 2005) but nothing is known regarding whether *P. persimilis* and *N. californicus* differ in the level of polygyny. Female lifetime mating frequency differs between *P. persimilis* and *N. californicus*. A single mating per lifetime is sufficient for maximum egg production of *P. persimilis*, whereas multiple matings are necessary for *N. californicus* females (Amano & Chant, 1978b; Gotoh & Tsuchiya, 2008). *Phytoseiulus persimilis* females may re-mate shortly after the first copulation (Enigl & Schausberger, 2004) but it is unknown whether second mates have any paternity success. Thus, we dub the female mating system of *P. persimilis* as low-level polyandry and that of *N. californicus* as medium-level polyandry. As a consequence, the number of receptive females per male (operational sex ratio) is lower in *P. persimilis* than *N. californicus*, resulting in fewer lifetime mating opportunities for *P. persimilis* males, assuming similar male longevities.

Based on the adaptive canalization hypothesis and the differing mating systems – low- vs. medium-level polyandry affecting the operational sex ratio – we predicted that male body size has higher fitness relevance in *P. persimilis* than *N. californicus*. Deviations from standard body size should be more costly for *P. persimilis* than *N. californicus* males, resulting in stronger male body size canalization in the former species. To test our prediction we assessed the LRS and related fitness indicators of small and standard-sized males of *P. persimilis* and *N. californicus*.

MATERIALS AND METHODS

SPECIES ORIGIN AND REARING

Specimens of *P. persimilis* and *N. californicus* used to found laboratory-reared populations originated from Sicily (Walzer & Schausberger, 2011). Both species were reared on separate arenas consisting of plastic tiles resting on water-saturated foam cubes in plastic boxes half-filled with water. The predators were fed in 2- to 3-day intervals with spider mites, *T. urticae*, reared on whole common bean plants, *Phaseolus vulgaris*. To obtain predator eggs for generating small and standard-sized males and virgin females used in experiments, ten 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. Each bean leaf arena (5 × 5 cm) consisted of a detached leaf placed upside down on a water-saturated foam cube in a plastic box half-filled with water. Water-saturated cellulose strips (1 cm height) at the edge of the leaf confined the arena and prevented the mites from escaping.

(PRE-)EXPERIMENTAL CAGES

Cages drilled into rectangular acrylic plates (80 × 35 × 3 mm) were used for generating differently sized males and the mating experiment. The cages used to generate small and standard-sized males of *P. persimilis* and *N. californicus* consisted of cylindrical cells of 15 mm diameter and 3 mm height with fine gauze at the bottom and closed on the upper side with a microscope slide (Schausberger, 1997). Cages used for the mating experiment (hereafter termed mating cage) consisted of three interconnected circular cells (two large with 15 mm diameter, one small with 5 mm diameter), closed at the bottom by gauze and covered with a removable microscope slide on the upper side. The two large cells and the small cell were connected by a T-shaped 2-mm-wide aisle (Schausberger & Hoffmann, 2008). The T-shaped arrangement of the mating cage allowed us to release the predatory mites into the cage by opening the small cell while keeping closed the large cells.

GENERATING SMALL AND STANDARD-SIZED MALES

To obtain small and standard-sized males of *P. persimilis* and *N. californicus*, respectively, eggs were randomly taken from the egg production arenas, singly placed into acrylic cells and provided with either limited (ten for *P. persimilis*, eight for *N. californicus*) or ample (> 40) spider mite eggs as prey. Limited prey supply differed between the two predator species because of differing prey needs (Walzer & Schausberger, 2011). The developmental progress of the juveniles was checked every 24 h and their sex determined after reaching adulthood, based on their body size. Virgin males reared under limited and ample prey supply were used as small and standard-sized males, respectively, in the experiment. After the experiment, each male was mounted in a drop of Hoyer's medium on a microscope slide (Krantz & Walter, 2009) and the dorsal shield length, which is a suitable indicator of body size (Croft, Luh & Schausberger, 1999), was measured.

REARING OF VIRGIN FEMALES

Groups of 15–20 eggs (< 24 h old) each of *P. persimilis* and *N. californicus* were taken from the egg production arenas and placed on separate spider mite-infested leaf arenas. The developmental progress of the juvenile predators was observed twice per day in intervals of 8 and 16 h until reaching adulthood. When the predators were in the deutonymphal stage, the males, identifiable by their small body size, were removed to ensure that, in the end, only virgin females remained on the arena.

EXPERIMENTAL PROCEDURE

To start the experiment, one small or one standard-sized male of *P. persimilis* or *N. californicus* was placed into a mating cage previously loaded with mixed spider mite life stages serving as prey. For five consecutive days the male was daily provided with four conspecific virgin females. Each set of four females was daily replaced by a new set of four virgin females. To make the four females of a set discernible, they were marked with small water colour dots on their dorsal shields before the experiment. This marking method was successfully used before and did not affect the behaviour of the females (Walzer & Schausberger, 2013). After 5 days of mating, the males were transferred to a cage without conspecific females but with spider mite prey for a 2-day rest period. Then, the males were again placed in a mating cage and daily provided with four virgin females for five consecutive days followed by a 2-day rest period. This 5 days of mating plus 2-day rest procedure was repeated until the males died of natural causes. Male mating behaviour was observed every 30 min within the first 6 h of each day after a set of four virgin females had been added to the mating cage. Males and females were considered mating (copulating *sensu stricto*) when the male was underneath the female in the venter-to-venter position (Amano & Chant, 1978b). The duration of each mating, occurring during the 6-h observation periods, was recorded. Each species and male body size treatment was replicated ten times. To calculate the LRS of each male, each female was singly placed on a detached spider mite-infested bean leaf arena. Females not laying eggs within 3 days after being caged with a male were considered unfertilized. Eggs daily produced by fertilized females were counted until oviposition ceased. To determine the sex-ratio of offspring sired by each male, the eggs of each female were placed in groups of up to 20 individuals on spider mite-infested leaf arenas and their developmental progress was observed daily. After reaching adulthood the offspring sex was visually determined.

STATISTICAL ANALYSES

SPSS 18.0.1 (SPSS Inc., 2006) was used for all statistical analyses. The data are available as Supporting Information (Table S1). Generalized linear models (GLMs) were used to analyse the lifetime traits whereas generalized estimating equations (GEEs) were used to analyse repeatedly measured traits. A generalized linear model (GLM) was used to determine the effects of species and prey availability (limited, ample) on the juvenile survival probabilities (binomial distribution, identity link function) and body size (normal distribution, identity link function) of the

males used in the experiments. To detail the effects of prey availability on male body size within and between species, pairs of the estimated marginal means were compared by least significant difference (LSD) tests. Similarly, GLMs (normal distribution, identity link function) were used to analyse the effect of species (*P. persimilis*, *N. californicus*) and male body size (small, standard-sized) on adult longevity of the males, total number of fertilized females and fertilized eggs (LRS) by each male, total number of eggs laid by each female (female LRS) and the sex ratio (females/females + males) of offspring sired by each male. GEEs (normal distribution with identity link function, autocorrelation structure between observation days indicating male age) were used to compare the influence of species (*P. persimilis*, *N. californicus*), male body size (small, standard-sized) and male age (used as nested within-subject variable) on daily male fertilization success (i.e. the proportion of successfully fertilized females out of the number of females observed mating), daily male reproductive success (number of daily fertilized eggs), daily latency to first mating after presenting the virgin females and daily mean mating duration. The time-dependent parameters were analysed only for the first 3 weeks of the experiment because of the low number of surviving males in the fourth week. To select the most parsimonious GEE model for each parameter, we started with a full model and then stepwise removed non-significant interaction terms. The model with the smallest quasi information criterion value was chosen for analysis (Cui, 2007). All proportional parameters (sex ratio and fertilization success) were arcsin square-root transformed before analyses. Results are given as mean \pm SE.

RESULTS

MALE BODY SIZE PLASTICITY, JUVENILE SURVIVAL AND ADULT MALE LONGEVITY

GLM revealed that species (Wald $\chi^2_1 = 10.129$, $P = 0.001$), prey availability (Wald $\chi^2_1 = 192.300$, $P < 0.001$) and their interaction (Wald $\chi^2_1 = 5.168$, $P = 0.023$) affected male body size. *Phytoseiulus persimilis* and *N. californicus* males provided with ample prey had similar body sizes (*P. persimilis*: $275.88 \pm 1.22 \mu\text{m}$; *N. californicus*: $274.56 \pm 1.46 \mu\text{m}$; LSD: $P = 0.520$). In contrast, under limited prey *N. californicus* males ($251.13 \pm 0.77 \mu\text{m}$) grew smaller than *P. persimilis* males ($259.05 \pm 2.27 \mu\text{m}$), indicating higher body size plasticity in *N. californicus* than *P. persimilis* males (LSD: $P < 0.001$). Male juvenile survival probabilities were not affected by species (GLM: Wald $\chi^2_1 = 0.361$, $P = 0.548$), prey availability (Wald $\chi^2_1 = 0.009$, $P = 0.924$) or their interaction (Wald $\chi^2_1 = 1.417$, $P = 0.234$). Similarly, the longevities of

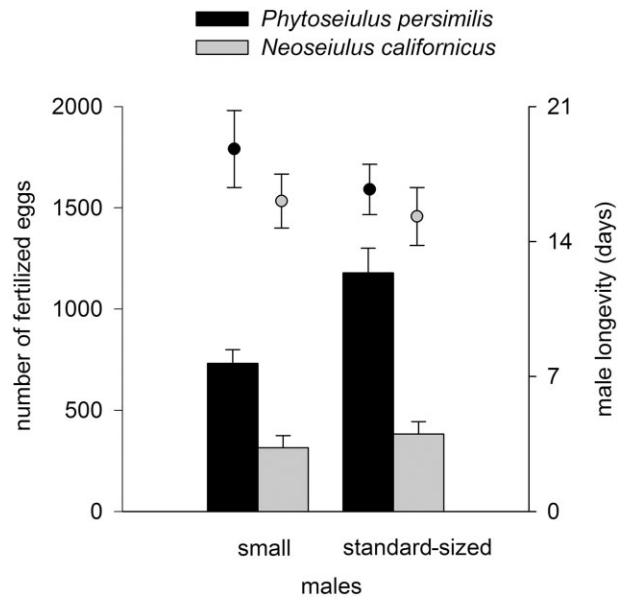


Figure 1. The influence of species and male body size on LRS, i.e. the lifetime number of fertilized eggs (bars), and longevity (symbols) of *P. persimilis* and *N. californicus* males (mean \pm SE).

adult *P. persimilis* and *N. californicus* males were not influenced by species (GLM: Wald $\chi^2_1 = 0.847$, $P = 0.357$), body size (Wald $\chi^2_1 = 1.550$, $P = 0.213$) or their interaction (Wald $\chi^2_1 = 0.237$, $P = 0.626$) (Fig. 1).

MALE AND FEMALE REPRODUCTIVE SUCCESS

The total number of fertilized females by each male was affected by species (GLM: Wald $\chi^2_1 = 15.193$, $P < 0.001$) but not male body size (Wald $\chi^2_1 = 0.184$, $P = 0.668$) or the interaction of species and male body size (Wald $\chi^2_1 = 0.354$, $P = 0.552$) (Table 1). The daily number of fertilized females was affected by species and male age, but not male body size or the interaction of species and male body size. The effect of species on the daily number of fertilized females depended on male age (Table 2, Fig. 2A, B). Male *P. persimilis* fertilized more females per day (2.69 ± 0.09) than *N. californicus* males (1.93 ± 0.09). Older males fertilized fewer females than younger males. Pooled over male body size, the number of females fertilized by *N. californicus* males decreased continuously with increasing male age, whereas the number of females fertilized by *P. persimilis* males remained constant until a male age of 5 days and decreased afterwards (Fig. 2A, B). The daily fertilization success of the males was influenced by species and male age, but not male body size or the interaction of male body size and species (Table 2). *Phytoseiulus persimilis* males had a higher daily

Table 1. The influence of species and male body size on the total number of females fertilized by each male, the female LRS (eggs/female/lifetime) and the sex-ratio of the offspring sired by each male (mean \pm SE)

Parameter	Male body size	Species	
		<i>P. persimilis</i>	<i>N. californicus</i>
Fertilized females	Small	32.60 \pm 2.30	22.60 \pm 3.84
	Standard-sized	35.70 \pm 2.87	22.10 \pm 3.53
Female LRS	Small	21.50 \pm 1.85	13.80 \pm 1.32
	Standard-sized	31.66 \pm 1.91	15.45 \pm 1.64
Sex-ratio	Small	0.66 \pm 0.05	0.58 \pm 0.05
	Standard-sized	0.72 \pm 0.05	0.66 \pm 0.02

Table 2. Generalized estimating equations for the influence of species (*P. persimilis*, *N. californicus*), male body size (small, standard-sized) and male age (used as nested within-subject variable) on the daily number of fertilized females and eggs (DRS), the fertilization success, the latency to first mating after presenting the virgin females and the daily mean mating duration of each male

Parameter	Factor	Wald χ^2	d.f.	<i>P</i>
Fertilized females	Species	17.369	1	< 0.001
	Size	0.895	1	0.344
	Age	730.242	14	< 0.001
	Species \times size	0.557	1	0.456
	Species (age)	42.924	14	< 0.001
Fertilization success	Species	16.817	1	< 0.001
	Size	0.022	1	0.881
	Age	164.616	14	< 0.001
	Species \times size	2.061	1	0.151
DRS	Species	82.126	1	< 0.001
	Size	16.464	1	< 0.001
	Age	1079.326	14	< 0.001
	Species \times size	8.565	1	0.003
	Species \times size (age)	355 107.069	36	< 0.001
Mating latency	Species	36.781	1	< 0.001
	Size	0.357	1	0.550
	Age	744.721	14	< 0.001
	Species \times size	3.838	1	0.050
	Species \times size (age)	2.427E12	38	< 0.001
Mating duration	Species	84.153	1	< 0.001
	Size	6.154	1	0.013
	Age	394.658	14	< 0.001
	Species \times size	0.004	1	0.947
	Species \times size (age)	1.266E12	37	< 0.001

fertilization success than *N. californicus* males and older males had a lower fertilization success than younger males (Fig. 2C, D).

Male LRS (lifetime number of fertilized eggs) was influenced by species (GLM: Wald $\chi^2_1 = 60.150$, $P < 0.001$), male body size (Wald $\chi^2_1 = 10.847$, $P = 0.001$) and their interaction (Wald $\chi^2_1 = 5.915$, $P = 0.015$). Pooled over male body size, *P. persimilis*

males (954.65 \pm 85.31) had a higher LRS than *N. californicus* males (348.75 \pm 42.88). Within species, small body size resulted in lower LRS of *P. persimilis* but not *N. californicus* (Fig. 1). Male daily reproductive success (DRS) was affected by species, age, body size, and the interaction of species and body size (Fig. 2E, F). Additionally, the species-specific male body size effects changed differently with male age

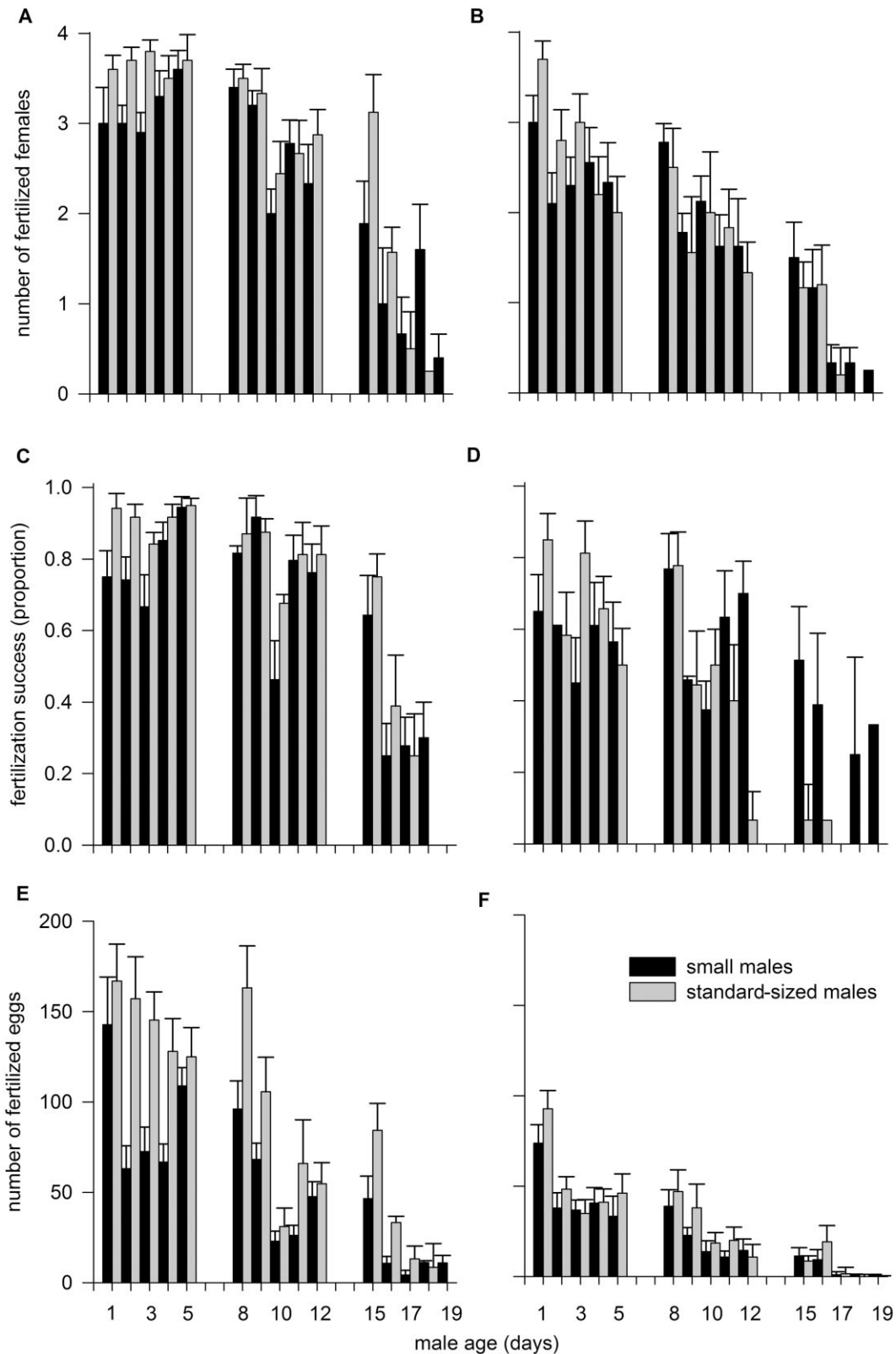


Figure 2. The influence of species (*P. persimilis*: A, C, E; *N. californicus*: B, D, F), male body size and male age on the daily number of fertilized females, daily reproductive success (i.e. number of fertilized eggs) and daily fertilization success (i.e. the proportion of fertilized females out of those mated with) of *P. persimilis* and *N. californicus* males (mean \pm SE).

(Table 2). Male DRS was higher in *P. persimilis* (79.20 ± 4.40) than *N. californicus* (31.55 ± 2.19) and decreased with male age. Pooled over male age and species, small males had a lower DRS than standard-sized males. However, the interaction terms indicate that male body size affected the DRS of only *P. persimilis* but not *N. californicus*. Moreover, the DRS of standard-sized *P. persimilis* males decreased much more strongly with male age than the DRS of standard-sized *N. californicus*.

Female LRS (number of eggs per female per lifetime) was affected by species (GLM: Wald $\chi^2_1 = 55.176$, $P < 0.001$), male body size (Wald $\chi^2_1 = 13.464$, $P = 0.001$) and their interaction (Wald $\chi^2_1 = 6.980$, $P = 0.008$). Pooled over male body size, female LRS of *N. californicus* was lower than that of *P. persimilis*. Small male body size reduced the LRS of *P. persimilis* but not *N. californicus* females (Table 1).

Offspring sex ratio was affected by species (GLM: Wald $\chi^2_1 = 19.321$, $P < 0.001$) and body size (Wald $\chi^2_1 = 21.868$, $P < 0.001$) but not their interaction (Wald $\chi^2_1 = 0.242$, $P = 0.623$). Pooled over body size, the sex ratio of *P. persimilis* offspring was more female biased than that of *N. californicus*. In both species, the sex ratio of offspring from small males was less female-biased than that of standard-sized males (Table 1).

MALE MATING BEHAVIOUR

Species and male age, but not male body size, influenced the latency to first mating after presenting the virgin females. The interaction term of species and male body size was also significant but this interaction changed with male age (Table 2). *Phytoseiulus persimilis* males mated earlier than *N. californicus* males and older males mated later than younger males. Pooled over male age, standard-sized males of *P. persimilis* but not *N. californicus* mated later than small males. The differences between standard-sized and small *P. persimilis* males were mainly caused by the delayed first mating of standard-sized males at the end of the 2nd and 3rd week, respectively. Such a pattern was not observed in *N. californicus* (Fig. 3A, B).

Species, male body size and male age affected the daily mean male mating duration. Additionally, the interaction of species and male body size depended on male age (Table 2). *Neoseiulus californicus* males mated for longer (124.94 ± 5.39 min) than *P. persimilis* males (76.20 ± 1.63 min). Mating duration was negatively correlated with male body size and male age, being shorter in small and old males, respectively. The mating duration of *P. persimilis* males was almost constant over time but shorter in the small young males up to an age of 8 days. By

contrast, the mating duration of young *N. californicus* males was not affected by body size until an age of 5 days; however, with proceeding age the mating duration of the small males decreased and became shorter than that of standard-sized males (Fig. 3C, D).

DISCUSSION

Our study confirms that male body size plasticity is higher in *N. californicus* than *P. persimilis* (Walzer & Schausberger, 2011). Accordingly, prey limitation during juvenile development induced a larger deviation from standard male body size in *N. californicus* than *P. persimilis*. Both limited and ample prey regimes allowed similarly high juvenile survival probabilities, excluding any inadvertent bias in body sizes due to size-dependent mortality. If mortality had depended on size, genetically predetermined large individuals could have had lower survival chances under limited prey availability than genetically predetermined small individuals. The observed fitness implications of deviations from standard male body size suggest that the difference in male body size plasticities of *P. persimilis* and *N. californicus* is adaptive. Consistent with the predictions of the adaptive canalization hypothesis, deviations from standard male body size were linked to high fitness costs in *P. persimilis* (low plasticity) but not *N. californicus* males (high plasticity), resulting in lower LRS of small than standard-sized males of *P. persimilis* but not *N. californicus*. We suggest that lower male body size plasticity in *P. persimilis* than *N. californicus* is the result of stronger past sexual selection, making this highly fitness-relevant trait more robust to environmental disturbance (Stearns & Kawecki, 1994; Walzer & Schausberger, 2011).

SPECIES-SPECIFIC MALE REPRODUCTIVE SUCCESS

Pooled over male body sizes, male LRS of *P. persimilis* was about three times higher than that of *N. californicus*. As in most sexually reproducing animals, paternal investment in offspring by *P. persimilis* and *N. californicus* is insignificant relative to maternal investment. Male reproductive success is mainly a function of the number of matings (e.g. Trivers, 1972). Indeed, the fertilization success (number of fertilized females out of the number of mated females) and the total number of fertilized females were significantly higher in *P. persimilis* than *N. californicus* males. Sperm quality, which is a decisive factor for the fertilization success in single pair matings (Levitan, 2000; Kime *et al.*, 2001), could have been higher in *P. persimilis* than *N. californicus* males. Alternatively or additionally, lower male LRS of *N. californicus* could have been due to a lower quantity of sperm

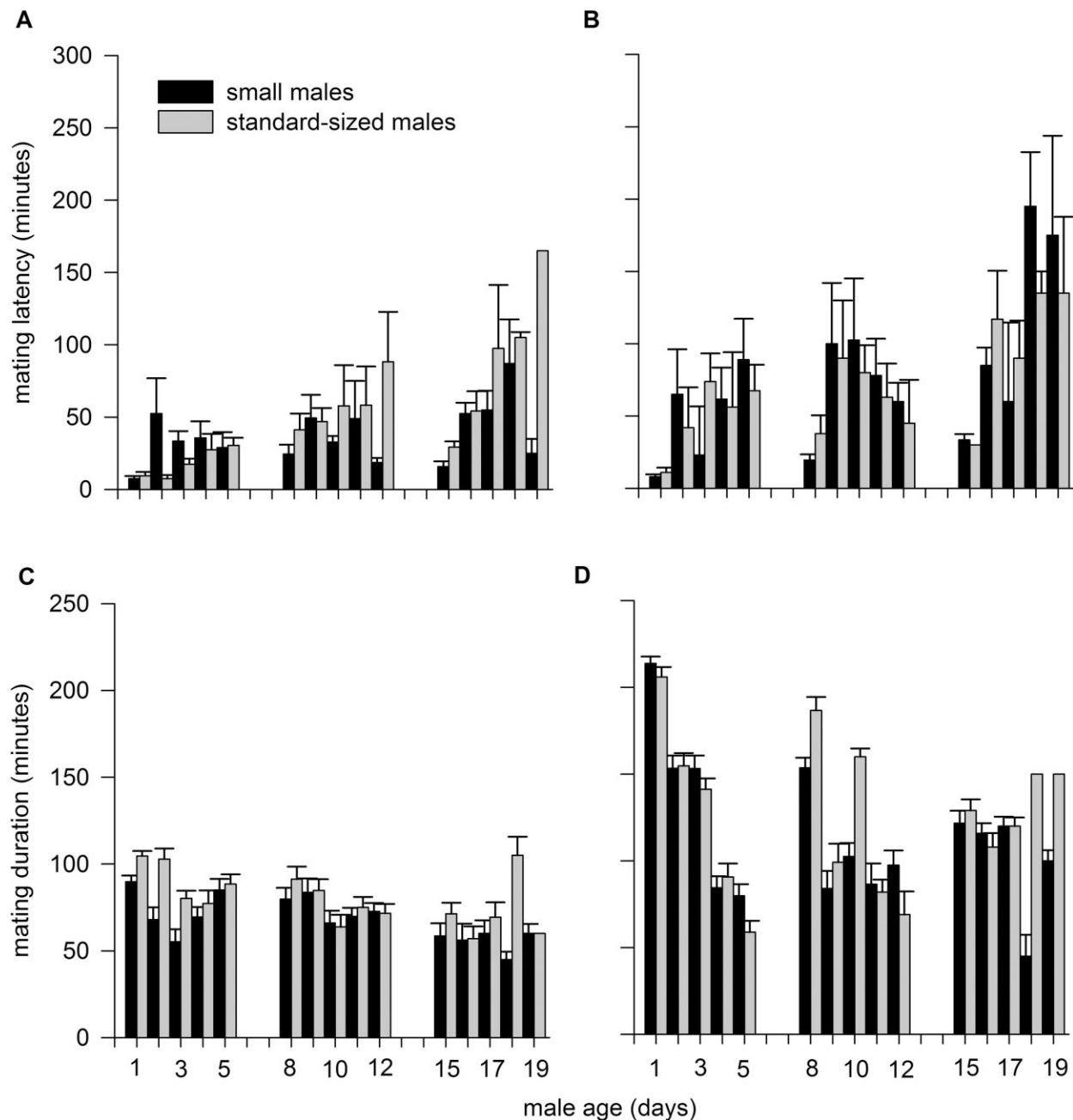


Figure 3. The influence of species (*P. persimilis*: A, C; *N. californicus*: B, D), male body size and male age on the daily mating latency and daily mean mating duration of *P. persimilis* and *N. californicus* males (mean \pm SE).

transferred per mating, as indicated by the lower number of fertilized eggs per single mating in *N. californicus* than *P. persimilis*.

SPECIES-SPECIFIC MALE BODY SIZE EFFECTS ON REPRODUCTIVE SUCCESS

Proximately, various physiological and/or behavioural constraints may have caused the body size-dependent

LRS of *P. persimilis* males, as compared with the body size-independent LRS of *N. californicus* males. In general, being smaller than standard may reduce male reproductive lifespan (Jennions, Moller & Petrie, 2001), which in turn often results in lower LRS of small males (Clutton-Brock, 1988). In our experiments, however, the longevities of small and standard-sized *P. persimilis* males were similar and independent of their body size.

The mating latency of standard-sized *P. persimilis* males was longer than that of small males, which may indicate either that sperm regeneration depended on body size (Sato *et al.*, 2005), taking longer in standard-sized males, or that females were more reluctant to mate with standard-sized than small males, or that standard-sized males needed longer than small males to locate receptive females. However, prolonged mating latency falls short as an explanation for male body size effects on LRS because the fertilization success (number of fertilized females out of the number of mated females) of *P. persimilis* males did not depend on their body size.

Sperm quantity is considered to be a function of male body size (Fox, McLennan & Mousseau, 1995; Schlüns *et al.*, 2003), and mating duration is an appropriate indicator of the amount of transferred sperm in several species (e.g. Arnqvist & Danielsson, 1999; Wilder & Rypstra, 2007), including *P. persimilis* and *N. californicus* (Amano & Chant, 1978a; Gotoh & Tsuchiya, 2008). In contrast to *N. californicus*, the mating duration of young small *P. persimilis* males was significantly shorter than that of young standard-sized males within the first week, where more than half of all offspring were sired by the *P. persimilis* males. The number of descendants of small *P. persimilis* males was about 40% lower than that of standard-sized males during this time period, indicating that short mating duration correlated with a low amount of transferred sperm. Three non-exclusive reasons may have shortened the mating duration of small *P. persimilis* males. First, small males may have finished mating earlier than standard-sized males because they were exhausted sooner or had a lower amount of sperm material available. If so, the size of the spermatophores transferred to females in single pairings should be positively correlated with male body size, as documented for bush crickets, seed beetles and leaf beetles (Wedell, 1997; French & Hammack, 2012). This needs further investigation for *P. persimilis*. Second, large male body size is a common indicator of high male quality (Andersson, 1994). Females may have finished mating with smaller males earlier than with standard-sized males, allowing re-mating and thus opening the chance for sperm competition. Third, mating events involving small males could have been disturbed more strongly by the other females than matings involving standard-sized males. Irrespective of male body size, the mating couples were frequently surrounded by the other females, apparently shortening the mating duration compared with matings in the absence of other females (Enigl & Schausberger, 2004; Gotoh & Tsuchiya, 2008). If small males were less vigorous than standard-sized males, interference by the other females could have been more severe in mating

couples involving small males, shortening their mating duration.

MALE BODY SIZE EFFECTS ON OFFSPRING SEX-RATIO

In both *P. persimilis* and *N. californicus* small male body size reduced the proportion of female offspring. Proximately, sex-specific offspring mortality may have lowered the proportion of daughters among offspring fathered by small males. Daughters are larger than sons and the larger sex is often more strongly affected by adverse parental effects (Nylin & Gotthard, 1998; Walzer & Schausberger, 2013). Paternal effects may have negative sex-specific effects on offspring survival. For example, in male *Plodia interpunctella* moths, food limitation during development resulted in reduced sex-specific offspring immunity: sons had a lower immune reaction than daughters in resource-rich environments, whereas the reverse was true in resource-poor environments (Triggs & Knell, 2012). The proportion of daughters is also positively correlated with total oviposition in phytoseiid mites (Sabelis & Nagelkerke, 1988; Sabelis *et al.*, 2002). Mating with small males reduced the total number of eggs produced by *P. persimilis* but not *N. californicus* females. Possibly, female eggs of *P. persimilis* were disproportionately negatively affected by oviposition reduction because they are more costly to produce than male eggs (Nagelkerke & Sabelis, 1998). *Phytoseiulus persimilis* females are able to precisely adjust the offspring sex-ratio to environmental conditions (Sabelis & Nagelkerke, 1988; Nagelkerke & Sabelis, 1998). More favourable conditions such as ample food supply correlate with higher female proportions among offspring (Friese & Gilstrap, 1982). If male body size of *P. persimilis* and *N. californicus* is an indicator of mate quality, a maternally decreased proportion of daughters could reduce the transfer of paternally induced detrimental effects such as epigenetic marks to the filial generation because only diploid daughters carry the paternal genome.

CONCLUSIONS

Our results correspond to observations of life-history plasticity in other arthropods such as water striders (Fairbairn, 2005), fruit flies (Stearns *et al.*, 1995) and spiders (Fernandez-Montraveta & Moya-Laraño, 2007): the lower the phenotypic plasticity of a given trait, the higher its fitness relevance. Such canalization is considered adaptive because it buffers fitness-relevant traits against environmental perturbations, preventing large deviations from trait optimum (Stillwell *et al.*, 2010). Most studies, however, evaluated sex-specific effects on plasticity of life-history traits to explain the evolution of sexual

size dimorphism (Stillwell *et al.*, 2010). Our study provides a key example of possible linkages between body size plasticity and species-specific mating systems (low- versus medium-level polyandry). Male body size had higher fitness relevance in the low-level polyandrous *P. persimilis*, resulting in stronger canalization of male body size, than in the medium-level polyandrous *N. californicus*. It is likely, but needs yet to be shown, that male body size is also more important in male competition and female choice in *P. persimilis* than *N. californicus*.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table S1. Data from the experiments presented in separate working sheets. Working sheet (WS) 1: GLM (data analysed with generalized linear models): male body size, juvenile survival, adult survival, male LRS, female LRS, offspring sex-ratio; WS 2: GEE (data analysed with generalized estimating equations): DRS, mating latency, fertilization success, fertilized females, mating duration.