

Inter-sexual combat and resource allocation into body parts in the spider, *Stegodyphus lineatus*

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Abstract. 1. Sexual conflict, which results from the divergence of genetic interests between males and females, is predicted to affect multiple behavioural, physiological, and morphological traits.

2. Sexual conflict over mating may interact with population density to produce predictable changes in resource allocation into inter-sexual armament.

3. In the spider *Stegodyphus lineatus*, males fight with females over re-mating. The outcome of the fight is influenced by the cephalothorax size of the contestants. The investment in armament – the cephalothorax, may be traded-off against investment in abdomen, which is a trait that affects survival and fecundity. Pay-offs may depend on population density. Both sexes are expected to adjust resource allocation into different body parts accordingly.

4. Males had increased cephalothorax/body size ratio in low densities where probability of finding another receptive female is low and females had increased cephalothorax/body size ratio in high densities where cumulative costs of multiple mating are high.

5. The results support the theoretical conjecture that population density affects resource allocation into inter-sexual armament and call for further research on the interaction between sexual selection and population density.

Key words. Polyandry, sexual armament, sexual conflict, sexual selection, *Stegodyphus lineatus*, trade-off.

Introduction

Life-history theory predicts trade-offs between sexually and naturally selected traits (Stearns, 1992; Andersson, 1994; Badyaev, 1997). For example, investment in sexual armament may be traded-off against the investment in other body parts related to survival or reproduction (Lopez & Martin, 2002). Inter-locus sexual conflict over mating plays an important part in shaping sexually selected traits (Parker, 1979; Rice, 1996; Arnqvist & Rowe, 2002, 2005; Chapman *et al.*, 2003). Based on the conflicting interests of males and females in reproduction, inter-locus sexual conflict occurs when the outcome of male–female interactions differentially affects fitness of the individual

members of each sex involved in the interaction (Parker, 1979; Holland & Rice, 1998; Chapman *et al.*, 2003; Arnqvist, 2004). Under this scenario, males and females may evolve antagonistic adaptations that bias the outcome of interactions towards their own interests (Holland & Rice, 1998). Such antagonistic coevolution between interacting traits in males and females is suggested to result in a rapid evolution of traits (Gavrilets, 2000) and increased speciation rates (Parker & Partridge, 1998). Several examples of morphological traits that apparently evolved as a direct result of male–female conflict over mating rate are known from the literature (reviewed in Arnqvist & Rowe, 2005). The most famous examples include grasping and antigrasping traits of water striders (Gerridae) (Arnqvist & Rowe, 2002) and diving beetles (Dytiscidae) (Bergsten *et al.*, 2001), as well as the paragenital system (spermatheca) of the human bedbug (*Cimex lectularius*) (e.g. Morrow & Arnqvist, 2003).

Ecological factors, such as population density, may influence the evolution of traits selected via sexually antagonistic

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coevolution (Martin & Hosken, 2003; Tregenza, 2003), as well as via classical sexual selection (Tomkins & Brown, 2004). The population density may potentially affect the development of armament used in inter-sexual conflict, while the pay-offs for each sex may differ in different ecological settings.

The effect of population density on the relative investment in armament used in battles between males and females in a species with overt inter-sexual conflict over mating was explored in this study. The polyandrous spider *Stegodyphus lineatus* exhibits an extreme form of sexual conflict where infanticidal males propagate their genes at a very high cost to females (Schneider & Lubin, 1996). Females are semelparous and extensive maternal care of the offspring ultimately results in matrophagy (Schneider & Lubin, 1998). Males will fight with a female guarding her eggs, and winning males destroy the egg sac and mate with the female. Subsequently, the female produces a second clutch and the infanticidal male benefits by fathering on average half of the offspring from the replacement clutch (Schneider & Lubin, 1996). Field data demonstrate that males in some populations may encounter as few as 1.2–2 females on average during their lifetime, which explains strong selection pressure on males to mate with unreceptive females (Schneider & Lubin, 1998; Maklakov *et al.*, 2005). Such mating behaviour by males is very costly for females because replacement clutches are smaller, reducing female lifetime fecundity and delayed oviposition caused by infanticide decreases the chance of successful reproduction (Schneider, 1999).

Mated females fight aggressively to avoid the costs inflicted by additional males. The outcome of the fight is influenced by the cephalothorax size of the contestants (Schneider & Lubin, 1997a; Maklakov *et al.*, 2004). This investment in armament – the cephalothorax, may be traded-off against the investment in other body parts, in particular the abdomen, which could have negative effects on female fecundity, offspring fitness, and male longevity (Clutton-Brock, 1991; Burpee & Sakaluk, 1993; Marshall & Gittleman, 1994; Andersson, 1994). In *S. lineatus*, female mass positively affects female fecundity (Schneider & Lubin, 1997b; Maklakov *et al.*, 2003), while the size of the cephalothorax does not (Maklakov & Lubin, 2004). Therefore, females with large cephalothoraxes may be more successful in inter-sexual combat but might have fewer resources for egg production. Similarly, a large cephalothorax may facilitate male mating success with unreceptive females (Schneider & Lubin, 1997a; Maklakov *et al.*, 2004), but reduce male survival.

Several predictions can be made regarding the relative investment in inter-sexual armament by males and females of *S. lineatus* under high and low population densities. Female spiders are predicted to increase their investment in cephalothorax under high population density (HD), due to the high probability of encountering additional males, which would result in cumulative detrimental effects of multiple mating. Male spiders may be predicted to respond by increased investment in their armament in a coevolutionary arms race. In HD populations, however, males can encounter a number of receptive females during their lifetime, because the costs of mate search are reduced when the nests are densely located, while mated

females are less aggressive shortly after their first mating (Maklakov, 2004). Female maturation extends over a period of 2 months (Schneider, 1997) and males that survive longer will encounter more receptive females. Males may thus adopt different mating tactics especially as males can be injured or killed when fighting with unreceptive females (Schneider & Lubin, 1997a). Therefore, male fighting ability may be traded-off against male survival in HD populations. Males in low-density (LD) populations are unlikely to find many receptive females due to high costs of mate search. Therefore, males may increase their investment into cephalothorax relative to total body size under low population density, due to the low probability of encountering a receptive female if rejected. Both sexes are expected to adjust resource allocation into different body parts accordingly. These predictions should generate a population by sex interaction when comparing relative cephalothorax size in males and females from two populations of different densities. This scenario is based on the assumption that population density is constant over multiple generations, allowing for selection to act on resource allocation into body parts. Alternatively, differential resource allocation to body parts may be a phenotypically plastic response to different population densities during juvenile growth. This study compares the pattern of sex-specific differences in body parts in two genetically distinct populations of *S. lineatus* of high and low population densities respectively.

Materials and methods

Subadult *Stegodyphus lineatus* Latreille (1817) spiders were collected in March 1999 from one population in the Negev desert (Sede Boqer, Israel) and one population from the Judean desert (Kfar Adumim, Israel). The collection sites were about 160 km away from each other. The Negev and Judean desert populations are genetically distinct and represent vicariant lineages with different evolutionary history (Johannessen *et al.*, 2005). The Negev population is characterised by a very low density of spiders (Ward & Lubin, 1993) and ranges between 0.00006 and 0.008 spiders m⁻². Long-term monitoring of this population confirms these results (Y. Lubin, unpubl. data). By contrast, the Judean population was of high density estimated as 0.25 spider m⁻².

The cephalothorax width and total body length of adult individuals was measured at hatching using digital (± 0.02 mm) callipers, while live spiders were fixed on soft foam against transparent plastic wrap (Schneider, 1997). Thirty-three females and 18 males from the LD population and 87 females and 44 males from the HD population were measured. The relative investment in armament was calculated as the cephalothorax/body length ratio.

Cephalothorax/body length ratio was analysed as the dependent variable and population density (LD and HD), sex, and the interaction term as explanatory variables using general linear models (SYSTAT 10). Ratios were arcsine square root transformed to normalise the data. Within-model contrasts were used to test the changes in relative cephalothorax size in males and females from the two populations.

Results

There were significant effects of sex ($F_{1,178} = 375.253$, $P < 0.001$) and population by sex interaction ($F_{1,178} = 20.442$, $P < 0.001$) on cephalothorax/body size ratio. The significant effect of sex was due to males having relatively larger cephalothoraxes than females (Fig. 1). The interaction resulted from a significant increase in relative cephalothorax size in LD males in comparison with HD males (contrasts: $F_{1,178} = 6.106$, $P < 0.001$) and a significant decrease in relative cephalothorax size in LD females relative to HD females (contrasts: $F_{1,178} = 14.395$, $P = 0.014$) (Fig. 1). Therefore, overall there was no significant difference between populations in cephalothorax/body size ratio ($F_{1,178} = 2.578$, $P = 0.11$). The results are qualitatively identical if we use cephalothorax width as dependent variable, and total body size as additional explanatory variable (sex: $F_{1,177} = 60.831$, $P < 0.001$; population: $F_{1,177} = 0.344$, $P = 0.564$; size – $F_{1,177} = 120.58$, $P < 0.001$; population by sex: $F_{1,177} = 11.397$, $P = 0.001$; between-population contrast for males: $F_{1,177} = 6.03$, $P = 0.015$; between-population contrast for females: $F_{1,177} = 5.64$, $P = 0.019$).

Discussion

The results support the idea of a sex by population density interaction in relative cephalothorax size in *S. lineatus*. Interestingly, the direction of change in body morphology in each sex corroborates the predictions that may be derived from sexual conflict theory. Males in the LD population have larger cephalothoraxes than males in the HD population, while females exhibit the opposite trend. The size of the cephalothorax is important in male–female combat (Schneider & Lubin, 1996). The investment in inter-sexual armament (cephalothorax) may be traded against the investment in the abdomen. If so, males are

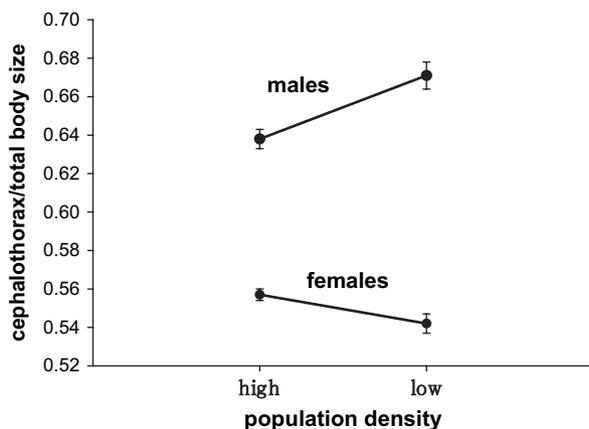


Fig. 1. The differences in body morphology in males and females from two populations: low-density population from Negev (LD) and high-density population from Judean desert (HD). The y-axis is arcsine square-root transformed cephalothorax width divided by total body size (dots represent least squares means from general linear model and whiskers represent \pm SEs).

likely to be selected to increase their weaponry relative to the total body size in LD populations, when their ability to impose copulation upon unreceptive females may prove crucial to their lifetime reproductive success. In HD populations, a rejected male is likely to be able to find another receptive female in the near vicinity or later in the season. On the other hand, females in HD populations are expected to experience higher male encounter rate, which should select for increased resistance to remating. Interestingly, Wigby and Chapman (2004) found that females evolved increased resistance to male-induced harm under experimentally male-biased sex ratio. This finding is in line with increased cephalothorax/body size ratio in females from the HD population in our study. We acknowledge, however, that other ecological factors, such as predation levels, could potentially contribute to the observed pattern. Finally, non-adaptive explanations, such as genetic drift, may account for the morphological differences observed in these two populations.

Males generally have larger cephalothorax/body size ratio than females, which suggests that in males the trade-off between the investments in cephalothorax and in abdomen is biased towards an increase in cephalothorax dimensions compared with females. Apart from inter-sexual combat, *S. lineatus* males also engage in direct male–male competition and the size of the male cephalothorax is a predictor of male winning success (Maklakov *et al.*, 2004). Consequently, males may experience additional selective pressures on the size of their cephalothoraxes. This finding is in line with a comparative study on eublepharid geckos, which indicates that male-biased dimorphic heads are weapons used in aggressive encounters (Kratovichil & Frynta, 2002).

While evolutionary conflicts of interest between males and females are widely recognised (Chapman *et al.*, 2003; Arnqvist & Rowe, 2005), the effect of sexually antagonistic coevolution on traits is intrinsically difficult to show. Both sexes are expected to increase their investment in arms in proportion to the investment by the opposite sex (Chapman & Partridge, 1996). Therefore, our ability to reveal the evolution of sexually antagonistic interactions may be limited. One way to circumvent this problem is to use multispecies comparative analysis of the effect of the change in relative development of armament used in male–female combat on critical elements of the mating system, such as mating rate (Arnqvist & Rowe, 2002). It may also be possible to demonstrate antagonistic coevolution by comparing different populations, which are subject to different environmental conditions. This idea is based on the assumption that sexually antagonistically evolved traits are likely to affect other traits, which would result in a trade-off between them. Ecological factors, such as population density may alter the fitness returns of the build-up of arms differently for each sex. The pay-offs are expected to differ between sexes due to inherently different life histories of males and females (Trivers, 1972; Andersson, 1994). These results provide preliminary data in support of this hypothesis and call for further research on the effect of population density on sexually selected traits. More data involving a full density gradient is needed from different taxa; also other techniques, such as artificial selection, may prove particularly useful in elucidating the general pattern of the interaction between population density and sexual conflict.

Acknowledgements

We thank Ofer Eitan for help in collecting and maintaining spiders. We thank Jutta Schneider and Martin Edvardsson for commenting on the manuscript. A.A.M. was supported by Department of Life Sciences, BGU; the Swedish Royal Academy of Sciences and Marie Curie fellowship MEIF-CT-2003-505891; T.B. by the Danish Natural Science Foundation and Y.L. by US-Israel Bi-national Science Foundation grant 2000259.

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Accepted 13 January 2006

First published online 13 October 2006