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Eunuchs as better fighters?

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Abstract Male–male competition for females can significantly affect a male's reproductive success and hence his fitness. Game theory predicts that an individual should avoid fighting when its future reproductive potential is high, but should fight forcefully when its future reproductive potential is insignificant. When mates are scarce, extreme competition and fatal fighting is expected. We recently showed that *Nephilengys malabarensis* eunuchs, i.e. sterile spider males that lost their genitals during copulation, become more aggressive during male–male contests. Here, we add crucial comparative data by exploring eunuch fighting behaviour in *Nephilengys livida* from Madagascar, specifically by testing the 'better fighter hypotheses' in a laboratory setting. Similar to *N. malabarensis*, *N. livida* copulations resulted in total male castration with the severed

palp plugging the female genitals in 70.83% cases, which mostly (63.63%) prevented subsequent copulations. Unexpectedly, however, *N. livida* eunuchs exhibited lower aggressiveness than virgin males. We interpret these results in the light of different mating biology between the so far studied species known for the eunuch phenomenon, which might reflect differing plug effectiveness due to variation in genital anatomy in *N. livida*, *N. malabarensis* and *Herennia multipuncta*. However, detected differences in aggressive behaviour of *N. livida* versus *N. malabarensis* eunuchs might also be explained by the species' ecology, with lower population densities resulting in a relaxed male–male competition making excessive aggression and mate guarding redundant. This study thus questions the generality of overt aggressiveness in mated males with no reproductive value, and highlights the importance of understanding the natural history of species in the question.

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Introduction

Male–male competition over females and related resources can significantly affect a male's reproductive success and hence his fitness (Huntingford and Turner 1987). Yet, costs associated with competition favour the assessment of a resource value relative to the contestant's fighting ability (also termed resource-holding value, e.g. weapons, size) over confronting all rivals indiscriminately (Maynard Smith and Parker 1976; Parker 1970; but see Moore et al. 2008). An important factor is an individual's expected future reproductive value (Enquist and Leimar 1990). When its future reproductive potential is high, an animal should avoid

fighting and hence injury, but should fight forcefully when its future reproductive potential is insignificant (e.g. Fromhage and Schneider 2005a; Innocent et al. 2007). When females are limited, extreme competition and fatal fighting is expected (Bean and Cook 2001; Enquist and Leimar 1990; Maynard Smith and Price 1973).

Male competitive behaviour for females often varies, being dependent on the density of rivals, the availability and value of the contestant resource, as well as the relatedness between competitors (Elias et al. 2010; Enquist and Leimar 1987; Innocent et al. 2011; Kasumovic et al. 2008; Kokko and Rankin 2006; Moore et al. 2008; Murray and Gerrard 1985; Reinhold 2003; West et al. 2001, 2002). Male encounter rates with females depend on female density within a patch, on patch size and on the distance between patches (Schneider and Lubin 1998). When males' chances to encounter more females are high, they are expected to avoid the risk of intensive fighting. On the other hand, if males' chances of encountering more than one female are slim, they are predicted to maximize their reproductive success by investing all of their resources in the first female they encounter (Buskirk et al. 1984). However, the situation also depends on the density of the males, and in the cases where the density of males is as low as that of rare females, there might not be a need for the male to defend his paternity (Fromhage et al. 2005, 2008).

In many sexually dimorphic spider species, males break their copulatory organs, the palps, during copulation to plug up a female (Fromhage and Schneider 2006; Kuntner 2005, 2007; Kuntner et al. 2008; Kuntner et al. 2009a; Uhl et al. 2010). A 'mating plug' hypothesis postulates that these palpal leftovers function as physical barriers to future copulations (Kralj-Fišer et al. 2011a). In most species, the males with damaged or missing palps are functionally sterile and have no further reproductive value. Despite high costs related to mating plugs and sterility, these do not always effectively prevent female remating, and this may depend on both male and/or female genital morphology (Kuntner et al. 2009b; Uhl et al. 2010). Due to incomplete plug effectiveness, those emasculated males that survive copulation commonly practice post-copulatory mate guarding (Fromhage and Schneider 2005b). In accordance with game theory (Enquist and Leimar 1990), *Nephilengys malabarensis* males, which entirely emasculate their palps during copulation (such sterile males are termed 'eunuchs'), commonly escalate fierce fighting and win in contests against rivals—a 'better fighter' phenomenon (Kralj-Fišer et al. 2011a). To elucidate the generality of detected patterns in eunuch behaviour, we here expand our research to include the second *Nephilengys* species.

Nephilengys livida is a highly sexually size dimorphic and synanthropic species (Kuntner 2007; Kuntner and Agnarsson 2011), which exhibits a combination of inviting

sexual traits such as complex genitalia, male genital damage resulting in plugging and eunuchs, as well as sexual cannibalism and post-copulatory mate guarding (Kralj-Fišer et al. 2011b; Kuntner 2007; Kuntner et al. 2009c). The interaction between current resource value, future resource value, investment in sperm plugs and male–male competition for a female, make this species an interesting system for testing the predictions of game theory models. We explored male fighting behaviour in *N. livida*, by conducting a series of laboratory male–male contests on female webs. We compared contests between two virgin rivals with those between a virgin male and a eunuch. Since plug efficiency likely affects male fighting behaviour, e.g. effective plugs reduce sperm competition, we staged laboratory mating trials to test if plugged female genitalia could be reused by another male. In accordance with the better fighter hypothesis (Kralj-Fišer et al. 2011a), we predicted that eunuchs would escalate fighting intensity to outcompete virgin rivals and that eunuchs would be more aggressive in a species with lower plug efficiency.

Materials and methods

Study animals

We collected *N. livida* (formerly known as *Nephilengys borbonica*, Kuntner 2007) spiders in Andasibe-Mantadia (Toamasina Province) and Ranomafana (Fianarantsoa Province) in Madagascar, between 24 February 2010 and 4 April 2010. To examine remating, we collected subadults and reared them to adulthood in the laboratory (females=19, males=33). We housed females in glass frames (50×50×10 cm), and males in smaller plastic cups (250 ml). We provided water to spiders daily and fed them fruit flies, crickets and mealworms twice a week. As previously, we define eunuchs as those adult males lacking both palps, and half-eunuchs as those lacking one palp (Kralj-Fišer et al. 2011a). We compared *N. livida* with *N. malabarensis* from Southeast Asia (for details see Kralj-Fišer et al. 2011a).

Experimental protocol

We tested the 'better fighter' and the 'mating plug' hypotheses in series of laboratory tests. The spiders reached maturation at various times, thus we had to continuously adapt our ongoing experiments to the available spiders (see work flow table in [ESM](#)). Due to the small number of wild-caught spiders, several spiders were reused (*N* reused males=24; *N* reused females=19; see also [ESM](#)), however, we considered this in our analyses.

Better fighter hypothesis

To establish if palpal severance during copulation triggers mate guarding, particularly fighting as known in *N. malabarensis* (Kralj-Fišer et al. 2011a), eunuchs were placed on a random female web, immediately followed by the introduction of the second, virgin male ($N=12$ trials). The control group staged contests between two virgin males ($N=12$ trials). During male–male contests, we noted the frequencies of guarding behaviours, i.e. walking towards female, touching female and exploring (walking back and forth), and estimated the distance between males and a female every five minutes. Male–male fighting behaviour was scored as frequencies of walking towards another male (score=1), web shaking (score=2), chasing (score=3) and attacking (score=4). Aggressiveness intensity levels were estimated as sums of scores (Kralj-Fišer et al. 2011a, b). We also noted frequencies of escaping and web plucking (defined as male tapping on web threads). We noted whether copulations took place. Trials lasted 60 min. After a trial the spiders were given at least a 24-h rest.

Mating plug hypothesis

To test for genital reuse, our aim was to document at least two successful insertions in the same copulatory opening (CO). We took 11 females that received plugs and males that could only insert their palp(s) in the plugged CO (insertions were always ipsilateral; $N=13$, see *ESM*). If mating into the used CO was attempted but was unsuccessful in two subsequent mating trials, we assumed that plugging prevented successful access to the previously used CO (Kralj-Fišer et al. 2011a). Observations lasted for 60 min. After a trial the spiders were given at least a 24-h rest. In the analysis, we considered also rematings into the used CO that occurred during male–male contests.

Morphological examination

At the end of all trials, the females were euthanized and preserved in 70% ethanol. The epigyna of 17 females (two females escaped) were excised and macerated in concentrated KOH for 24 h, cleaned in distilled water, then further treated with methyl salicylate (Kuntner et al. 2009b). Examinations of epigynal microscopic preparations were done under a Leica MZ16 stereomicroscope.

Statistical analyses

We compared plugging efficiency between *N. livida* and *N. malabarensis* using a chi square test. To detect the effect of emasculation on fighting and guarding behaviours of *N. livida* eunuchs, we employed generalized

linear mixed models (GLMMs). The fixed factors were male's and rival's reproductive status (1=eunuch, 2=virgin). We introduced male identities as random factors, because some males were reused. Response variables were behavioural scores. We sequentially deleted fixed terms in order of decreasing significance; only terms with $P \leq 0.1$ remained in the final model. Excluded terms were re-entered one by one into the final model to confirm that they did not explain a significant part of the variation (Poesel et al. 2006). We present Wald statistics for final models including fixed terms with $P \leq 0.1$ only. The differences of behavioural measures—where $P \leq 0.1$ —were interpreted using the graphs. The analyses were done in PASW version 18.

Results

Better fighter hypothesis

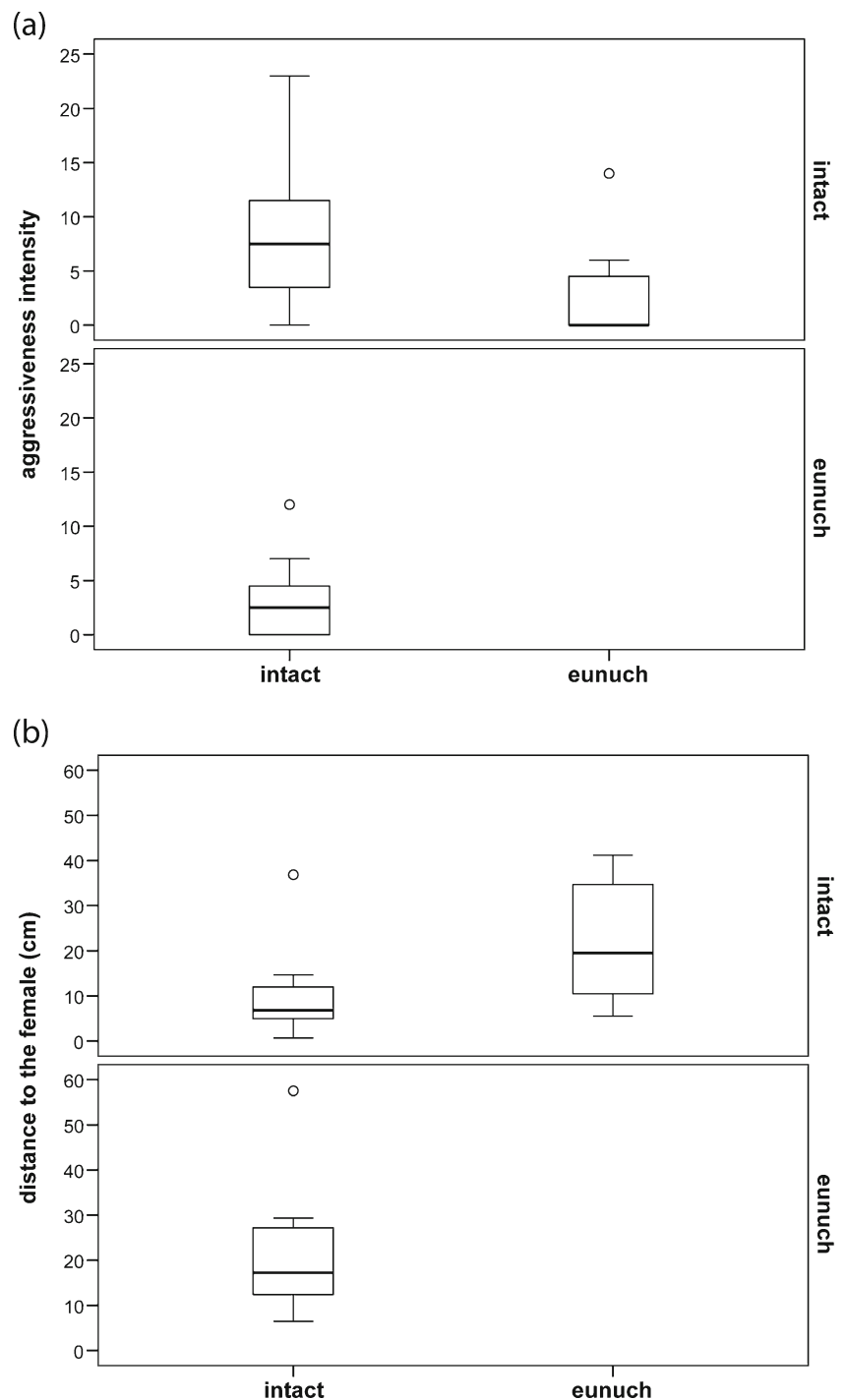
Virgin males were generally more aggressive than eunuchs in male–male contests: virgin males shook the web more often, walked more frequently towards a rival and had higher general aggressiveness intensity than eunuch males (for probabilities see Table 1; Fig. 1a). Virgin males were more aggressive when confronted with another virgin male than when opposed with a eunuch (frequency of walking towards a rival, aggressiveness intensity; Table 1). Interestingly, virgin males exhibited escape behaviour more frequently than eunuchs (Table 1). Virgin males signalled (web plucking) more frequently than eunuchs, again more often so when confronted with

Table 1 Statistical results of the final GLMM model

	State of ♂ 1	State of ♂ 2
Signal (pluck web)	0.037	0.006
Touch female	>0.1	>0.1
Explore web	>0.1	>0.1
Walk towards female	<i>0.064</i>	>0.1
Distance to female	0.003	0.004
Shake	0.034	>0.1
Walk towards rival	0.002	0.01
Attack	>0.1	>0.1
Chase	>0.1	>0.1
Intensity of aggressiveness	0.009	0.015
Escape	<i>0.1</i>	>0.1

Probabilities that fixed factors, e.g. number of palps in male 1, number of palps in the rival male (male 2) affect the occurrences of behaviours in male 1. Statistical probabilities $P < 0.05$ bolded, $0.05 < P < 0.1$ italicized. $N=24$ contests, N of trials virgin vs virgin=12; N of trials virgin vs eunuch=12

Fig. 1 Male behaviours during male–male contests. **a** aggressiveness intensity; **b** average distance to the female (cm) of the male 1 in the contest with male 2



another virgin rival (Table 1). Eunuchs did not employ guarding behaviour: eunuchs and virgin males did not differ in frequencies of touching a female and exploring a web; however, virgin males more often walked towards a female and stayed closer to her than eunuchs (Table 1; Fig. 1b). Again, virgin males stayed closer to a female when opposed with a virgin rival than when opposed with a eunuch male (Table 1, Fig. 1b).

Mating plug hypothesis

In total we observed 31 copulations (N females=19; N males=21). A palp insertion always ended with total emasculation, resulting in whole-palpal mating plug in the used CO. Mating plugs remained in the used female CO after copulation termination, but were usually absent (externally) several hours thereafter. In two cases, a plug was observed

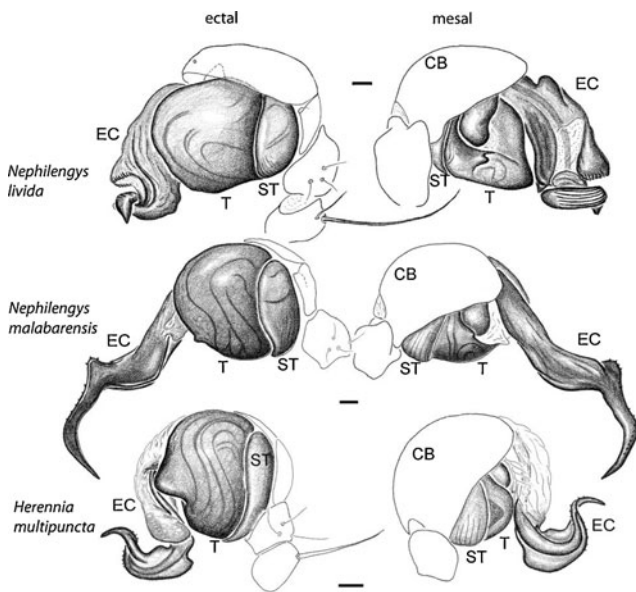


Fig. 2 Morphological comparison in palpal structure between *N. livida* (short, wide and broad tip), *N. malabarensis* (long and thin tip) and *H. multipuncta* (long and thin tip). Redrawn from Kuntner (2005, 2007). Scale lines=0.1 mm. CB cymbium, EC embolic conductor, ST subtegulum, T tegulum

externally even a day after copulation. We observed four females removing their plugs using the third pair of legs.

Plugging mostly prevented subsequent copulation into the used female CO: in seven out of 11 females with a plugged CO (63.63%) no further copulations occurred, whereas in 36.36% (four out of eleven) of cases a subsequent male used the already plugged CO and produced the second plug seen externally. Plugging efficiency by means of unsuccessful insertion attempts in *N. livida* did not significantly differ from plugging efficiency in *N. malabarensis* ($\chi^2=0.21$, $df=1$, $p=0.647$, $N=22$).

Our morphological examination revealed broken parts of embolic conductor (EC) within the internal female genital tract (within copulatory duct and/or spermathecae) in 17 out of 24 cases (70.83%, N females=17). Eleven females were subjected to males that could only copulate in the used CO. We found a double plug in one such female, i.e. two parts of EC in the remated organ. The other remated female had no internal plug despite the previous occurrence of two external palpal plugs. In seven females that did not remate, we found parts of EC in the used genitals.

Discussion

Our study found significantly different results to those predicted by theory, where mated (and functionally sterile) males with no residual reproductive value (eunuchs) are predicted to fight with maximal force when facing an

intruder (e.g. Fromhage and Schneider 2005a; Kralj-Fišer et al. 2011a). Unexpectedly, eunuch behaviour in *N. livida* differed strikingly from that in *N. malabarensis*, despite these species being congeneric and exhibiting a similar sexual biology (Kralj-Fišer et al. 2011a). In both species, copulation leads to total emasculation of the used palp and plugging of the female copulatory opening; about 70% of males fall victim to sexual cannibalism, and about 30% of females can remate using the same CO (this study; Kralj-Fišer et al. 2011a). Contrary to the theory predicting that surviving males with no reproductive value will escalate fatal fighting (Enquist and Leimar 1990; Maynard Smith and Price 1973), this was never observed in *N. livida* and only rarely in *N. malabarensis* (this study; Kralj-Fišer et al. 2011a). Nevertheless, *N. malabarensis* eunuchs exhibited higher aggressiveness levels than their virgin rivals in the male–male contests on the female webs as predicted by game theory (Kralj-Fišer et al. 2011a), while *N. livida* eunuchs behaved rather meekly in comparison with virgin males. A study on parasitoid wasps *Mellittobia* similarly found mated and virgin males exhibiting similar levels of aggression (Innocent et al. 2011). The contrasting results between the studies suggest that a male fighting behaviour depends on additional factors, not only future reproductive value. Potential benefits of fighting may vary with plug efficiency, sperm precedence, ability to assess resource value, and/or resource density (e.g. Innocent et al. 2011; Reinhold 2003).

Perhaps unexpectedly, this study invalidates the generality of eunuch-enhanced fighting abilities in spiders, but it may provide some new insights into the *N. livida* mating system in particular and into the eunuch biology in general. In both studied *Nephilengys* species and in *Herennia*, eunuch contests were observed at least 1 day after copulation: after the male had lost a palp(s), it was separated from the female for a day, then placed on a random female web for a male–male contest (Kralj-Fišer et al. 2011a; Kuntner et al. 2009b). Despite a time lag and an unfamiliar female, *N. malabarensis* or *Herennia* eunuchs aggressively fought a virgin rival off, while the *N. livida* eunuchs in this study did not. A possible explanation is that in nature, *N. livida* eunuchs guard their mates only shortly after copulation, but leave the female web, or even offer themselves as prey to the female thereafter. Such strategy is known in other orbweaving spiders, e.g. *Argiope keyserlingi* (Herberstein et al. 2005), and hints at a pronounced first sperm priority, where mate guarding is only adaptive until the female fertilizes the eggs. That *N. malabarensis* and *Herennia* eunuchs are more persistent in mate-guarding might suggest a fiercer sperm competition and perhaps longer sperm storage.

A possible reason for discrepancies between both *Nephilengys* studies may also be a difference in efficiency of sperm plugs to prevent paternity of subsequent suitors. This is because a mere reuse of a plugged CO does not necessarily

imply paternity. Although the ultimate test of this would be paternity analysis, which was beyond our scope here, genital morphology suggests plug efficiency by means of protecting paternity (Kuntner et al. 2009b). *N. malabarensis* and *Herennia multipuncta* males have longer, thinner and more hooked embolic conductors compared with short, wide and broad-tipped ones in *N. livida* (Kuntner 2005; 2007; Fig. 2). We speculate that broader embolic plugs better shield the female CO and thus prevent subsequent sperm transfer into spermathecae than thinner plugs. Although the shift to more complex and wider palps (*N. livida*) may have coevolved with corresponding counter adaptations in females (Kuntner et al. 2009b), we find it nevertheless plausible that plug efficiency is higher in *N. livida* with more complex palps than in *N. malabarensis* and *H. multipuncta* with relatively simpler ones. If true, more aggressive behaviour of *N. malabarensis* and *H. multipuncta* compared to *N. livida* eunuchs might be means of compensating for plug inefficiency.

Our results might also imply that in contrast to *N. malabarensis* and *Herennia*, *N. livida* males might be able to assess whether a given female has in fact been their mate. Furthermore, *N. livida* males might also be able to assess their rivals' status, i.e. virgin versus sterile male, in the female web. Virgin males signalled, tried to approach the female and engaged in agonistic interactions more often when confronted with another virgin male than when opposed by a eunuch. Such behaviour of virgin males might be enhanced by females, which significantly more often cannibalized non-aggressive than aggressive males (Kralj-Fišer et al. 2011b; e.g. Stoltz et al. 2008). Such female choice strategy might explain the differences in aggressiveness in *N. livida* and *N. malabarensis* virgin males. Interestingly, despite their higher aggressiveness, virgin males nevertheless retreated more often than eunuchs. Such higher risk aversion in virgin males compared with mated ones is in accordance with game theory (Fromhage and Schneider 2005a; Kralj-Fišer et al. 2011a).

Finally, competitive and mating behaviours may depend on ecological factors. Males may adapt their mating strategies according to female density, levels of male competition, patch size, etc. (Innocent et al. 2011; Kasumovic et al. 2008; Kokko and Rankin 2006; Reece et al. 2007). Population density, in particular, is important for mate guarding behaviour; if population densities intensify male–male competition through male-biased operational sex ratio, the intensity of mate guarding is expected to increase (Davis and Brown 1999; Hardling 2004; Jormalainen 1998). According to our observations in nature, *N. livida* occur at lower local abundances compared to *N. malabarensis*. In populations with lower densities, male survival during mate searching might be lower than in populations with high densities, resulting in further reduced numbers of rival males. If so, sperm competition in *N. livida* is reduced, which makes paternity protection additional to sperm plugs unnecessary (Fromhage et al. 2005, 2008).

In conclusion, our study found no support for the better fighter hypothesis in *N. livida* eunuchs. Differing mating biology between the so-far-studied species known for the eunuch phenomenon may account for this result. However, non-aggressive behaviour of *N. livida* eunuchs might also be explained by population ecology, with lower population densities perhaps resulting in relaxed male–male competition, which makes excessive aggression and mate guarding redundant.

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References

- Bean D, Cook JM (2001) Male mating tactics and lethal combat in the nonpollinating fig wasp *Sycoscapter australis*. *Anim Behav* 62:535–542
- Buskirk RE, Frohlich C, Ross KE (1984) The natural selection of sexual cannibalism. *Am Nat* 123:612–625
- Elias DO, Botero CA, Andrade MCB, Mason AC, Kasumovic MM (2010) High resource valuation fuels “desperado” fighting tactics in female jumping spiders. *Behav Ecol* 21:868–875
- Davis JA, Brown CR (1999) Costs of coloniality and the effect of colony size on reproductive success in purple martins. *Condor* 101:737–745
- Enquist M, Leimar O (1987) Evolution of fighting behavior—the effect of variation in resource value. *J Theor Biol* 127:187–205
- Enquist M, Leimar O (1990) The evolution of fatal fighting. *Anim Behav* 39:1–9
- Fromhage L, Schneider JM (2005a) Virgin doves and mated hawks: contest behaviour in a spider. *Anim Behav* 70:1099–1104
- Fromhage L, Schneider JM (2005b) Safer sex with feeding females: sexual conflict in a cannibalistic spider. *Behav Ecol* 16:377–382
- Fromhage L, Schneider JM (2006) Emasculation to plug up females: the significance of pedipalp damage in *Nephila fenestrata*. *Behav Ecol* 17:353–357
- Fromhage L, Elgar MA, Schneider JM (2005) Faithful without care: the evolution of monogyny. *Evolution* 59:1400–1405
- Fromhage L, Houston AI, McNamara JM (2008) A model for the evolutionary maintenance of monogyny in spiders. *J Theor Biol* 250:524–531
- Hardling KA (2004) Male brood care without paternity increases mating success. *Behav Ecol* 15:715–772
- Herberstein ME, Barry KL, Turoczy MA, Wills E, Youssef C, Elgar MA (2005) Post-copulation mate guarding in the sexually cannibalistic St Andrew's Cross spider (Araneae Araneidae). *Ethol Ecol Evol* 17:17–26
- Huntingford FA, Turner AK (1987) *Animal Conflict*. Chapman and Hall, London
- Innocent TM, Savage J, West SA, Reece SE (2007) Lethal combat and sex ratio evolution in a parasitoid wasp. *Behav Ecol* 8:709–715

- Innocent TM, West SA, Sanderson JL, Hyrkkänen N, Reece SE (2011) Lethal combat over limited resources: testing the importance of competitors and kin. *Behav Ecol* 22:923–931
- Jormalainen V (1998) Precopulatory mate guarding in crustaceans: male competitive strategy and intersexual conflict. *Q Rev Biol* 73:275–304
- Kasumovic MM, Bruce MB, Andrade MCB, Herberstein ME (2008) Spatial and temporal demographic variation drives within-season fluctuations in sexual selection. *Evolution* 62:2316–2325
- Kokko H, Rankin DJ (2006) Lonely hearts or sex in the city? Density-dependent effects in mating systems. *Phil Trans R Soc B* 1466:319–334
- Kralj-Fišer S, Gregorič M, Zhang SC, Li D, Kuntner M (2011a) Eunuchs are better fighters. *Anim Behav* 81:933–939
- Kralj-Fišer S, Schneider JM, Justinek Ž, Kalin S, Gregorič M, Kuntner M (2011b) Mate quality, not aggressive spillover, explains sexual cannibalism in a size dimorphic spider. *Behav Ecol Sociobiol* doi:10.1007/s00265-011-1262-7
- Kuntner M (2005) A revision of *Herennia* (Araneae: Nephilidae: Nephilinae), the Australasian 'coin spiders'. *Invertebr Syst* 19:391–436
- Kuntner M (2007) A monograph of *Nephilengys*, the pantropical 'hermit spiders' (Araneae, Nephilidae, Nephilinae). *Syst Entomol* 32:95–135
- Kuntner M, Coddington JA, Hormiga G (2008) Phylogeny of extant nephilid orb-weaving spiders (Araneae, Nephilidae): testing morphological and ethological homologies. *Cladistics* 24:147–217
- Kuntner M, Kralj-Fišer S, Schneider JM, Li D (2009a) Mate plugging via genital mutilation in nephilid spiders: an evolutionary hypothesis. *J Zool* 277:257–266
- Kuntner M, Coddington JA, Schneider JM (2009b) Intersexual arms race? Genital coevolution in nephilid spiders (Araneae, Nephilidae). *Evolution* 63:1451–1463
- Kuntner M, Agnarsson I, Gregorič M (2009c) Nephilid spider eunuch phenomenon induced by female or rival male aggressiveness. *J Arachnol* 37:266–271
- Kuntner M, Agnarsson I (2011) Biogeography and diversification of hermit spiders on Indian Ocean islands (Nephilidae: *Nephilengys*). *Mol Phylogenet Evol* 59:477–488
- Maynard Smith J, Price GR (1973) Logic of animal conflict. *Nature* 246:15–18
- Maynard Smith J, Parker GA (1976) The logic of asymmetric contests. *Anim Behav* 24:159–175
- Moore JC, Obbard DJ, Reuter C, West SA, Cook JM (2008) Fighting strategies in two species of fig wasp. *Anim Behav* 76:315–322
- Murray MG, Gerrard R (1985) Putting the challenge into resource exploitation—a model of contest competition. *J Theor Biol* 115:367–389
- Parker GA (1970) Sperm competition and its evolutionary consequences in insects. *Biol Rev Camb Philos Soc* 45:525
- Poesel A, Kunc HP, Foerster K, Johnsen A, Kempenaers B (2006) Early birds are sexy: male age, dawn song and extrapair paternity in blue tits, *Cyanistes* (formerly *Parus*) *caeruleus*. *Anim Behav* 72:531–538
- Reece SE, Innocent TM, West SA (2007) Lethal male–male combat in the parasitoid *Melittobia acasta*: are size and competitive environment important? *Anim Behav* 74:1163–1169
- Reinhold K (2003) Influence of male relatedness on lethal combat in fig wasps: a theoretical analysis. *Proc R Soc Lond Ser B Biol Sci* 270:1171–1175
- Schneider JM, Lubin Y (1998) Intersexual conflict in spider. *Oikos* 83:496–506
- Stoltz JA, Elias DO, Andrade MCB (2008) Females reward courtship by competing males in a cannibalistic spider. *Behav Ecol* 62:689–697
- Uhl G, Nessler S, Schneider J (2010) Securing paternity in spiders? A review on occurrence and effects of mating plugs and male genital mutilation. *Genetica* 138:75–104
- West SA, Murray MG, Machado CA, Griffin AS, Herre EA (2001) Testing Hamilton's rule with competition between relatives. *Nature* 409:510–513
- West SA, Pen I, Griffin AS (2002) Conflict and cooperation—cooperation and competition between relatives. *Science* 296:72–75