THE ROYAL SOCIETY

doi 10.1098/rspb.2000.1399

Sexual conflict and the evolution of female mate choice and male social dominance

Allen J. Moore[1*], Patricia Adair Gowaty[2], William G. Wallin[3] and Patricia J. Moore[1]

[1]*School of Biological Sciences, 3.614 Stopford Building, University of Manchester, Oxford Road, Manchester M13 9PT, UK*
[2]*Institute for Ecology, University of Georgia, Athens, GA 30602-2602, USA*
[3]*Department of Entomology, University of Kentucky, Lexington, KY 40546-0091, USA*

Conflicts between the sexes over control of reproduction are thought to lead to a cost of sexual selection through the evolution of male traits that manipulate female reproductive physiology and behaviour, and female traits that resist this manipulation. Although studies have begun to document negative fitness effects of sexual conflict, studies showing the expected association between sexual conflict and the specific behavioural mechanisms of sexual selection are lacking. Here we experimentally manipulated the opportunity for sexual conflict in the cockroach *Nauphoeta cinerea* and showed that, for this species, odour cues in the social environment influence the behavioural strategies and fitness of males and females during sexual selection. Females provided with the opportunity for discriminating between males but not necessarily mating with preferred males produced fewer male offspring than females mated at random. The number of female offspring produced was not affected, nor was the viability of the offspring. Experimental modification of the composition of the males' pheromone showed that the fecundity effects were caused by exposure to the pheromone component that makes males attractive to females but also makes males less likely to be dominant. Female mate choice therefore carries a demographic cost but functions to avoid male manipulation and aggression. Male–male competition appears to function to circumvent mate choice rather than directly manipulating females, as the mate choice can be cryptic. The dynamic struggle between the sexes for control of mating opportunities and outcomes in *N. cinerea* therefore reveals a unique role for sexual conflict in the evolution of the behavioural components of sexual selection.

Keywords: pheromone; sex ratio; sexual conflict; sexual selection; social dominance

1. INTRODUCTION

Differences in fitness optima between the sexes appear to be prevalent, resulting in discord between the evolutionary interests of males and females or sexual conflict (Parker 1979). Sexual conflict can bring about particularly strong selection, resulting in rapid and antagonistic coevolution of sexual differences (Parker 1979; Gowaty 1996, 1997; Brown *et al.* 1997; Holland & Rice 1998). Thus, sexual conflict is predicted to result in the evolution of male traits that manipulate female behaviour and female traits that resist this manipulation which are often expected to be expressed through the mechanisms of sexual selection—female mate choice and male–male competition (Parker 1979). However, despite the empirical evidence for both sexual selection and sexual conflict, direct evidence for the predicted association between the two is lacking. This deficiency may reflect the difficulty involved in quantifying the costs and benefits of conflict and selection within a single species. Although many studies of sexual selection have shown a fitness benefit for non-random mating (Partridge 1980; Norris 1993; Petrie 1994; Eberhard 1996; Promislow *et al.* 1998; Cunningham & Russell 2000), accumulating evidence for the costs of sexual conflict and, in particular, relating the costs to specific actions of one or the other sex has been more difficult. Even in *Drosophila melanogaster*, where sexual conflict is perhaps best documented (Partridge & Farquhar 1981; Chapman *et al.* 1995; Rice 1996; Holland & Rice 1999) and the expected demographic costs of sexual conflict are supported by artificial selection studies (Rice 1996; Holland & Rice 1999), we cannot always attribute the effects of conflict to specific male or female behaviour. The ubiquity of sexual conflict and its importance in the separate mechanisms of sexual selection therefore remains unknown.

Demonstrating the link between sexual conflict and sexual selection requires experiments that permit an evaluation of the separate roles of the sexes in association with the costs of conflict. An alternative to artificial selection is to manipulate the cues used by individuals in assessing others, but these are not known for most species. An exception is the cockroach *Nauphoeta cinerea*, where the cues that mediate the behavioural mechanisms of sexual selection are known and, therefore, can be manipulated (Moore 1997; Moore *et al.* 1997; Moore & Moore 1999). Furthermore, sexual conflict has been hypothesized for this insect (Moore 1988; Moore *et al.* 1995). Therefore, we used this species in order to investigate how the mechanisms of sexual selection and sexual conflict might be related. We addressed why selective optima differ for male and female *N. cinerea* and investigated the fitness consequences of sexual conflict by manipulating the mating partners and social experiences available to females.

Competition between and within the sexes in *N. cinerea* depends on the composition and quantity of the social pheromone that is produced by males only (Moore 1988, 1990*a*,*b*, 1997; Sreng 1990; Sirugue *et al.* 1992; Moore *et al.* 1995, 1997; Moore & Moore 1999). This pheromone is comprised of three major components (Sreng 1990; Sirugue *et al.* 1992): 3-hydroxy-2-butanone, 2-methylthiazolidine

*Author for correspondence (allen.j.moore@man.ac.uk).

Received 9 May 2000 *Accepted* 8 November 2000

and 4-ethyl-2-methoxyphenol. While the outcome of both male–male competition and female mate choice depends on assessment of this pheromone (Moore 1988, 1990*b*), the specific functions of individual components within the pheromone differ in intra- and intersexual interactions. The ratio of components but not the overall quantity is important for intrasexual competition as the different components have additive effects (Moore 1997; Moore *et al*. 1997). Males with high levels of 2-methylthiazolidine and 4-ethyl-2-methoxyphenol are more likely to be socially dominant in contests with other males while males with higher levels of 3-hydroxy-2-butanone are subordinate, but increasing all three components cancels the effects of each on male social status. In contrast, female choice is only based on 3-hydroxy-2-butanone and the ratio of pheromone components is unimportant—the amount of 3-hydroxy-2-butanone determines attractiveness both from a distance and during courtship regardless of the presence or quantities of other components (Moore & Moore 1999). 3-hydroxy-2-butanone is genetically and developmentally independent from the other pheromone components while 2-methylthiazolidine and 4-ethyl-2-methoxyphenol are genetically and developmentally correlated (Moore *et al*. 1995; Moore 1997). Consequently, although there is balancing selection resulting from the opposing forces of male–male competition and female mate choice (Moore & Moore 1999), there are no constraints on the evolution of the components with different functions (Moore 1997). However, the question remains as to why male and female *N. cinerea* differ in their use of the same pheromonal cues.

2. MATERIAL AND METHODS

(a) *Insect rearing*

General husbandry followed our previous studies (e.g. Moore *et al*. 1995; Moore 1997; Moore & Moore 1999). All individuals used in our experiments were derived from large mass colonies of several thousand individuals maintained at 27 °C in incubators in the laboratory under a 12 L:12 D photocycle. Offspring of randomly mated females were reared in single-family groups of nymphs. Last-instar individuals were then isolated in 11 cm × 11 cm × 3.5 cm plastic containers and provided with fresh food (rat chow) and water daily. This ensured that individuals used in this study had no prior exposure to other adults or the male pheromone, i.e. that they were socially naive and virgins. Individuals were randomly assigned to treatments. Four sisters were used (one per treatment) in order to minimize the genetic variation contributed by females. Family membership was not a significant effect in any of the analyses and was therefore dropped so that analyses where one family was not represented in a treatment could be included. The males used in the treatments were 12–14 days post-adult moult and the females were ten days post-adult moult in order to ensure full sexual maturity and similar development (Moore *et al*. 1995).

(b) *Experiment 1: manipulation of the social environment*

We undertook four treatments in the first experiment: females mating with a preferred male, females mating with a non-preferred male, females mating in a population and females mating at random. Male–male competition was eliminated as a factor in mating interactions in the first two treatments and the ability of females to exert mating preferences was varied. For these treatments we used an olfactometer, which is a device whereby females could perceive the odour of males but males could not interact with or perceive females (Moore 1988; Moore & Moore 1999). The use of an olfactometer in these treatments ensured that the females discriminated between males using just odour cues and prevented direct interactions between males and females or the perception of the female by either male. Females were presented with two males held in separate chambers in the olfactometer with filtered air gently blown over them (which stimulates calling behaviour by males; A. J. Moore, personal observation). A single female was presented into an entry chamber downwind and allowed to indicate a preference between the two males by approaching upwind of the odour of one or the other. Females typically orientated towards one or the other odour in less than 1 min and within minutes walked towards the odour of the preferred male. After indicating a preference, the female was allowed to mate with either the male she had approached in the olfactometer ('preferred' mating treatment) ($n = 56$) or the other male ('non-preferred' mating treatment) ($n = 56$). Males were never used in more than one replicate or experiment.

The third treatment permitted both male–male competition and female mating preferences and did not determine which sex would control mating opportunities. In this 'population' mating treatment ($n = 56$), four virgin males were allowed to form a dominance hierarchy (e.g. Moore & Breed 1986; Moore 1988, 1990*a*, 1997). Hierarchies of males consisted of four 12- or 14-day-old males who had previously been socially isolated since moult to adult. These males were individually marked and placed together in a 17 cm × 12 cm × 6.5 cm container and allowed to interact until a stable dominance hierarchy formed. When the hierarchies were stable but the intensity and duration of interactions between males was still high, two socially naive females were introduced into the group. Matings were allowed to occur without interference. New hierarchies were formed for each replicate. Matings were not completely monopolized by the most dominant male although only the top two ranking males (alpha and beta) ever mated. One male mated with both females in 14 of the groups. In half of these matings the alpha male mated with both females while in the other half the beta male mated with both females. In the remainder of the trials, both the alpha and beta males each mated with a single female.

In the final 'random' mating treatment ($n = 53$), a randomly selected male and a randomly selected female were placed together and allowed to mate. For this treatment, males and females were held in social isolation from moult to adult. When males reached 12 days post-moult and females reached ten days post-moult, they were then placed together in an 11 cm × 11 cm × 3.2 cm plastic cage and allowed to mate. Thus, neither had any prior social interactions with adults or exposure to adult male odours. The male was removed immediately after mating in all treatments.

(c) *Experiment 2: manipulation of the pheromone*

In the second set of experiments, we manipulated the pheromone profiles of individual males as in previous studies (Moore *et al*. 1997; Moore & Moore 1999) by topical application of individual pheromone components or combinations of pheromone components. The pheromone was applied to a filter paper disc glued to the pronotum of the male. Four manipulations were performed: increasing the components that are functionally and genetically independent (3-hydroxy-2-butanone or a combination

of 2-methylthiazolidine and 4-ethyl-2-methoxyphenol) (Moore 1997), increasing all three components combined in the average proportions in the population (Moore 1997), or treatment with the solvent alone (acetone). Treatments were assigned at random and experiments conducted blind with respect to treatment. The quantity applied reflected the average total pheromone contents of a gland in the population and, therefore, masked the inherent odour of an individual (Moore *et al.* 1997; Moore & Moore 1999). Five minutes after males were treated they were placed with an individual female in an 11 cm × 11 cm × 3.2 cm plastic cage and allowed to mate. The male was removed once they had mated. Individuals treated with excess pheromone have normal levels of behaviour (Moore *et al.* 1997; Moore & Moore 1999). Males were never used in more than one replicate or treatment.

After mating, all females were placed in a 27 °C incubator in their individual cages under a 12 L:12 D photocycle and allowed to give birth. Mothers remained with their offspring for two weeks and were then removed to another container in a different incubator and allowed to give birth to a second clutch. *Nauphoeta cinerea* is ovoviviparous; females were checked daily for the birth of a clutch. The number of offspring born was scored within 24 h of birth for both experiments. Thereafter, family groups in experiment 1 were observed daily and the number of offspring alive each day was scored. Survivorship was scored until all nymphs emerged to adulthood (*ca.* 125 days after parturition for males and 130 days after parturition for females; Moore 1994). The number and sex of the adults was recorded for each family.

3. RESULTS

(a) *Experiment 1: manipulation of the social environment*

Female fertility was high in each mating treatment with all but one (preferred, non-preferred and random treatments) or four (population treatment) females producing offspring. Although fertility was not different, fecundity varied between mating treatments (figure 1). The social environment encountered by a female but not the female's mating partner had a significant effect on the fecundity of the female for the first clutch she produced (figure 1*a*). Mating without exposure to multiple males (random treatment) resulted in significantly more offspring being produced than mating after encountering multiple males (population treatment) or after being exposed to males in an olfactometer regardless of the mate choice (preferred or non-preferred) treatments ($F = 4.144$, d.f. = 3,210 and $p = 0.007$). Random mating produced significantly more offspring in pairwise comparisons than did mating with a preferred male ($p = 0.05$) or mating in a population ($p = 0.0007$). Significantly more offspring were produced by non-preferred matings than by population matings ($p = 0.020$). The effect of social environment on fecundity was transitory; the number of offspring produced in the second clutch was not significantly different between treatments (figure 1*b*) ($F = 1.312$, d.f. = 3,180 and $p = 0.272$).

There were no effects of social environment or mother's mating partner on offspring fitness. Although offspring viability was slightly higher in the first clutch in the random treatment (79%) than any other treatment (76% for each), the difference did not approach significance ($F = 0.663$, d.f. = 3,210 and $p = 0.576$). The viability of offspring from the second clutch, although slightly lower (68–74%), was likewise unaffected by treatment ($F = 0.664$, d.f. = 3,166 and $p = 0.575$).

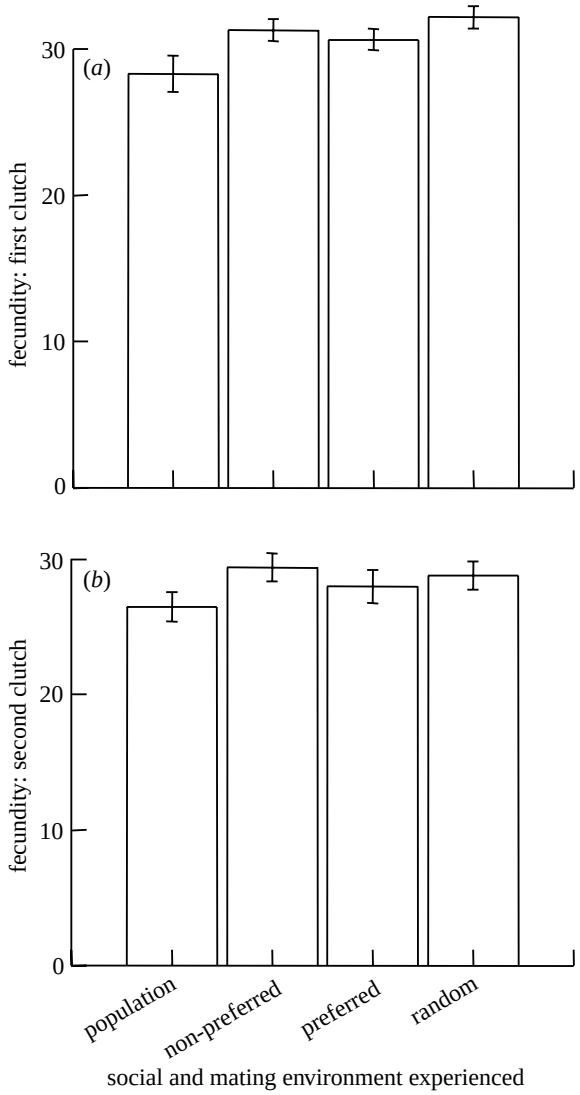

Figure 1. The effect of exposure to different social environments on female fecundity. (*a*) The average number (± 1 s.e.) of offspring in the first clutch born. (*b*) The average number (± 1 s.e.) of offspring in the second clutch born. There is a significant effect of treatment in the first clutch and significantly different pairwise comparisons between random and preferred trials, random and population trials, and non-preferred and population trials. There is no significant effect of treatment on the number of offspring born in the second clutch. Sample sizes in the first clutch in parentheses: population ($n = 52$), preferred ($n = 55$), non-preferred ($n = 55$) and random ($n = 53$) treatments. Sample sizes for the second clutch in parentheses: population ($n = 47$), preferred ($n = 49$), non-preferred ($n = 44$) and random ($n = 44$) treatments.

As in stalk-eyed flies (Wilkinson *et al.* 1998), the indicator trait used by *N. cinerea* females during mate choice is also associated with sex ratio variation. However, unlike stalk-eyed flies, meiotic drive is not involved as the sex ratios among adult offspring depended on the social environment but not the mating partner experienced by the female (figure 2). Differences in the sex ratio reflected

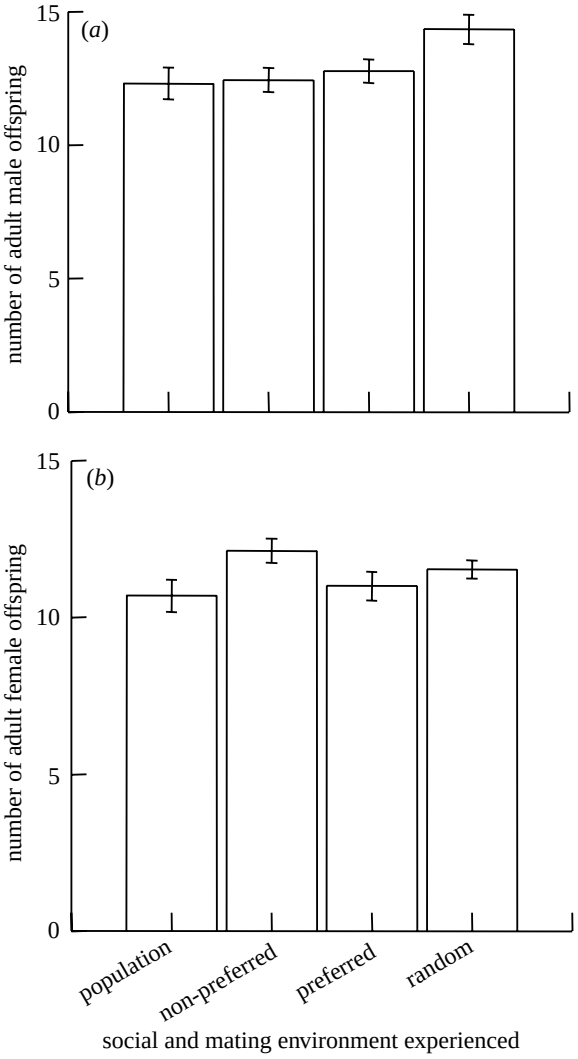

Figure 2. The effect of exposure of mothers to different social environments on the offspring sex ratio. (*a*) The number of adult males produced. (*b*) The number of adult females produced. There were significantly more males produced by females mated to random males than any other treatment. There were no significant differences in the number of females produced and, thus, the sex ratio was significantly different between treatments. *Wolbachia* was not present in our population of *N. cinerea* and antibiotics did not affect the sex ratio. The sample sizes are as in figure 1.

significant differences in the number of male offspring produced (figure 2*a*) ($F=3.384$, d.f. $=3,209$ and $p=0.019$). Significantly more male offspring were produced when females were randomly mated than when mated to non-preferred males ($p=0.008$), mated in a population ($p=0.006$) or mated to preferred males ($p=0.03$). There were no significant differences between treatments in the number of female offspring produced (figure 2*b*) ($F=1.977$, d.f. $=3,209$ and $p=0.118$). The sex ratio was therefore more male biased in the random treatment than in the other treatments, but these differences were not statistically significantly different ($F=2.420$, d.f. $=3,209$ and $p=0.067$). Thus, the reduction in fecundity when females have social experiences is reflected in production of fewer male offspring.

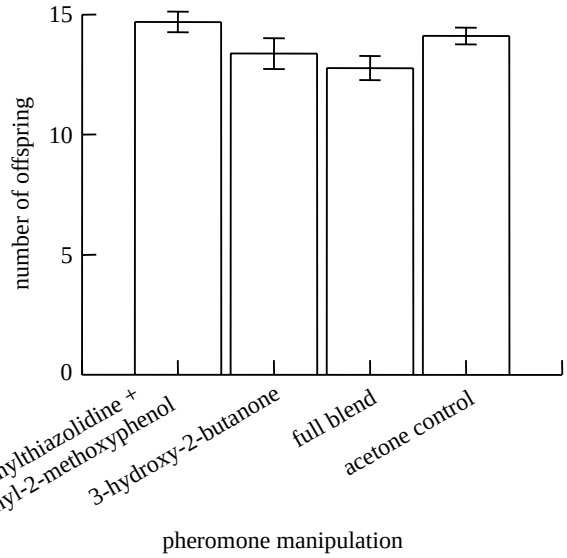

Figure 3. The effect of manipulating the pheromone blend or components on female fecundity. Pheromone components were added singly (3-hydroxy-2-butanone alone) ($n=24$) or in combination (2-methylthiazolidine combined with 4-ethyl-2-methoxyphenol) ($n=23$) or a full blend of all three components ($n=22$)) to a filter paper disc glued to the pronotum of a randomly selected male who was then mated to a randomly selected female. Acetone, the solvent used for the pheromone components, was used as a control ($n=27$). All females reproduced, but the addition of 3-hydroxy-2-butanone both by itself and contained within the full blend resulted in the production of significantly fewer offspring.

(b) *Experiment 2: manipulation of the pheromone*

Experimentally altering the pheromone environment experienced by a female while mating with a randomly selected male confirmed that it is the odour environment rather than the mating partner *per se* that causes differences in female fecundity (figure 3) ($F=2.996$, d.f. $=3,92$ and $p=0.035$). Furthermore, a specific component of the pheromone had the greatest negative effect on fecundity. Females exposed to an excess of 3-hydroxy-2 butanone, the component of the male pheromone that increases attractiveness of males, produced significantly fewer offspring than females exposed to the components important in male–male competition (2-methylthiazolidine and 4-ethyl-2-methoxyphenol) ($p=0.05$). Females exposed to an excess of the full three-component blend produced significantly fewer offspring than did females exposed just the two components that function in male–male competition ($p=0.007$) or the acetone control ($p=0.05$). Thus, exposure to 3-hydroxy-2-butanone lowers fecundity and this effect occurs regardless of the presence of other pheromone components.

4. DISCUSSION

It is often assumed that female mate choice and male–male competition are complementary (see, for example, Andersson 1994; Berglund *et al.* 1996). However, sexual conflict theory predicts the evolution of antagonistic mechanisms of sexual selection (Parker 1979; Gowaty 1996, 1997; Brown *et al.* 1997; Holland & Rice 1998).

When traits that lower the fitness of females evolve in males, females are predicted to evolve resistance mechanisms that in turn determine the mechanisms of reproductive competition available to males (Gowaty 1997). For many species, this will result in sexual conflict driving the evolution of costly mechanisms of sexual selection because, although sexual selection can and does enhance fitness (Partridge 1980; Norris 1993; Petrie 1994; Eberhard 1996; Promislow *et al.* 1998; Cunningham & Russell 2000), there can be negative fitness effects as well as when mating exposes females to harmful substances or behaviour (Partridge & Farquhar 1981; Chapman *et al.* 1995; Clutton-Brock & Parker 1995; Eberhard 1996; Rice 1996; Holland & Rice 1999). Sexual conflict in *N. cinerea* is expressed through both female mate choice and male–male competition and results in demographic costs of sexual selection and effects on the sex ratio resulting from exposure to 3-hydroxy-2-butanone. The behavioural mechanisms of sexual selection are not always complementary and their evolution can reflect a reproductive conflict between the sexes.

(a) *Female mate choice as a mechanism for avoiding male manipulation*

Female *N. cinerea* increase their exposure to 3-hydroxy-2-butanone by expressing mating preferences (Moore & Moore 1999). Initially, these mating preferences appear to be maladaptive as exposure to this component of the pheromone results in fewer offspring being produced. However, this immediate cost in terms of the number of offspring may be overcome by longer-term benefits of reducing personal risk and potentially producing higher-quality offspring. By exercising pre-copulatory mate choice, females avoid dominant males that have very low levels of 3-hydroxy-2-butanone and are therefore unusually aggressive (Moore & Moore 1999). Although aggressive behaviour is not always directed towards females, dominance interactions and male aggression can result in injury to females. However, mate choice based on 3-hydroxy-2-butanone has the potential cost of producing sons that may be more likely to be less dominant because the components of the pheromone are heritable (Moore 1997) and sons resemble their fathers in social status (Moore 1990*a*,*b*). Thus, attractive males may also be less likely to be dominant (Moore 1988).

Because mating is non-random and not all males mate, reducing the number of offspring produced could be adaptive. Eberhard (1996) suggested that this can be a form of cryptic mate choice and reviewed other research showing a reduction in the number of offspring produced as a result of female behaviour. Further, *N. cinerea* females do not decrease the number of female offspring produced, just male offspring. The relative value of different-sex offspring depends on the quality as well as quantity produced (Leimar 1996) and increasing the relative value of those sons produced can lower the potential cost of these males being more likely to be subordinate. The production of fewer males in the next generation may help minimize potential disadvantages in male–male competition for more attractive but more subordinate sons by reducing the likelihood of encountering other males and reducing or maintaining the density of males so that male control of mating opportunities is also minimized. An alternative is that females avoid aggressive males where possible but, when unavoidable and mating with aggressive males occurs, produce more male offspring. A similar association between an altered sex ratio and variation in social status has been seen in paradise fish (Francis 1984). Lines selected for high dominance were found to have a more male-biased sex ratio than control or low-dominance lines and different social environments exacerbated these differences in sex ratio (Francis 1984).

(b) *Male response to female mate choice: male–male competition*

Males do not accept female manipulation passively. Dominance status influences but does not determine mating success (Moore & Breed 1986; Moore 1988, 1990*a*,*b*; Moore & Moore 1999) because *N. cinerea* males cannot force copulations (Moore & Breed 1986; Moore 1990*a*). Nonetheless, dominant males attempt to inhibit the release of pheromone by subordinate males who have more 3-hydroxy-2-butanone (Moore *et al.* 1995). Dominant males also attempt to keep subordinate males from females through physical coercion (Moore *et al.* 1995).

Because females appear to be exercising post-copulatory cryptic female choice as well as pre-copulatory female choice, male options for responding to or manipulating females may be limited. Reducing the number of offspring produced may be a particularly effective mechanism of cryptic female choice (Eberhard 1996) because it is difficult for males to circumvent. Thus, it may be that male *N. cinerea* are forced to adopt male–male competition in an effort to influence the success of other males in order to compensate for female mate choice. The hypothesis that male–male competition has evolved as a response to female mate choice in *N. cinerea* has been presented previously (Moore 1988; Moore *et al.* 1995), although it was not originally presented in the context of sexual conflict.

(c) *Conclusions*

Even though females appear to be able to behave in such a way as to avoid male manipulation, we think it is premature to conclude that females are winning. It is always difficult to determine which sex controls sexual conflict (Parker 1979) and we have not studied all of the contexts where conflict can be played out. While the forms of mate choice expressed by female *N. cinerea* clearly limit the responses of males prior to mating, there are likely to be additional circumstances where sexual conflict is driving the evolution of sex differences in *N. cinerea*. We suspect that, at a minimum, 3-hydroxy-2-butanone has effects on other aspects of *N. cinerea* reproduction. Areas where sexual conflict is expected to be important, such as sperm competition (Parker 1979; Eberhard 1996; Gowaty 1996, 1997) and immunocomplementarity (Gowaty 1996, 1997; Penn & Potts 1998, 1999) should also be investigated in this species. Our studies only investigated a single mating and the effects of remating should be examined. We also need to examine how males influence or respond to cryptic mate choice. For example, males appear to control female remating in *N. cinerea* and we suspect that 3-hydroxy-2-butanone plays a role in the likelihood of remating by female *N. cinerea*. Receptivity in

females immediately after mating is inhibited by the presence of a spermataphore in the female bursa (Roth 1962, 1964*a*). Female *N. cinerea* are ovoviviparous and cannot remate while pregnant (Roth 1964*b*) and, thus, males that mate are assured of fertilizing at least one clutch. However, after parturition females can remate but not all do (Roth 1962, 1964*b*). The male pheromone of may affect this as the rate of offspring development (gestation) influences the likelihood of female remating after parturition (Roth 1964*b*) and the attractiveness of a male and the rate that his offspring develop are correlated in *N. cinerea* (Moore 1994). However, a direct link between the male pheromone and the rate of offspring development remains to be demonstrated. Thus, sexual conflict may have effects on multiple levels, at multiple life-history stages and across generations. Our current interpretations are speculative, but our ability to manipulate the cue that influences mate choice, male–male competition and reproduction in *N. cinerea* will allow us to investigate further the developmental, physiological and morphological arenas where sexual conflict may be played out in this species.

Our results are consistent with other studies that have shown that sexual conflict can carry a demographic cost (Partridge & Farquhar 1981; Chapman *et al.* 1995; Eberhard 1996; Rice 1996; Holland & Rice 1999), perhaps because of the operation of sexual selection. These results also confirm the need for investigating the multiple components of fitness effects, as the effects of sexual conflict are subtle and often involve multiple steps. A unique and important conclusion though is that we need information on the cues or signals used by individuals in order to mediate sexual conflict. By having this information and manipulating the signal, we gain valuable insight into the ways sexual conflict influences evolution. In particular, like most studies of sexual selection (Andersson 1994), it is important to be able to manipulate these cues to be able to control for the separate effects of male–male competition and female mate choice fully. Only such manipulative studies can determine whether these separate mechanisms of sexual selection are contradictory or complementary. We suspect that, as more systems that can be used to study sexual conflict in an experimental arena are developed, mate choice and male–male competition will often be found to oppose each other and reflect evolutionary and behavioural responses to sexual conflict.

Ken Haynes again provided expert advice and essential help regarding pheromones. We thank Nilla Rosenqvist, Lee Drickamer, Cindy Blum and Wyatt Anderson for critical input into the design and analysis of these experiments and Sarah Joseph, Jen Sadowski and Richard Preziosi for discussions and comments on the manuscript. Randy Nelson recognized the value of collaborative research and, therefore, the US National Science Foundation supported this research (IBN-9616203 to A.J.M. and IBN-9631801 to P.A.G.).

REFERENCES

Andersson, M. 1994 *Sexual selection*. Princeton University Press.

Berglund, A., Bisazza, A. & Pilastro, A. 1996 Armaments and ornaments: an evolutionary explanation of traits of dual utility. *Biol. J. Linn. Soc.* **58**, 385–399.

Brown, W. D., Crespi, B. J. & Choe, J. C. 1997 Sexual conflict and the evolution of mating systems. In *The evolution of mating systems in insects and arachnids* (ed. J. C. Choe & B. J. Crespi), pp. 352–377. Cambridge University Press.

Chapman, T. L., Liddle, F., Kalb, J. M., Wolfner, M. F. & Partridge, L. 1995 Cost of mating in *Drosophila melanogaster* females is mediated by male accessory gland proteins. *Nature* **373**, 241–244.

Clutton-Brock, T. H. & Parker, G. A. 1995 Sexual coercion in animal societies. *Anim. Behav.* **49**, 1345–1365.

Cunningham, E. J. A. & Russell, A. F. 2000 Egg investment is influenced by male attractiveness in the mallard. *Nature* **404**, 74–77.

Eberhard, W. G. 1996 *Female control: sexual selection by cryptic female choice*. Princeton University Press.

Francis, R. C. 1984 The effects of bidirectional selection for social dominance on agonistic behavior and sex ratios in the paradise fish (*Macropodus opercularis*). *Behaviour* **90**, 25–45.

Gowaty, P. A. 1996 Battles of the sexes and origins of monogamy. In *Partnerships in birds* (ed. J. M. Black), pp. 21–52. Oxford University Press.

Gowaty, P. A. 1997 Sexual dialectics, sexual selection, and variation in reproductive behavior. In *Feminism and evolutionary biology* (ed. P. A. Gowaty), pp. 351–384. New York: Chapman & Hall.

Holland, B. & Rice, W. R. 1998 Chase-away sexual selection: antagonistic seduction versus resistance. *Evolution* **52**, 1–7.

Holland, B. & Rice, W. R. 1999 Experimental removal of sexual selection reverses intersexual antagonistic coevolution and removes a reproductive load. *Proc. Natl Acad. Sci. USA* **96**, 5083–5088.

Leimar, O. 1996 Life history analysis of the Trivers and Willard sex-ratio problem. *Behav. Ecol.* **7**, 316–325.

Moore, A. J. 1988 Female preferences, male social status, and sexual selection in *Nauphoeta cinerea*. *Anim. Behav.* **36**, 303–305.

Moore, A. J. 1990*a* The inheritance of social dominance, mating behaviour, and attractiveness to mates in *Nauphoeta cinerea*. *Anim. Behav.* **39**, 388–397.

Moore, A. J. 1990*b* Sexual selection and the genetics of pheromonally mediated behaviour in *Nauphoeta cinerea* (Dictyoptera: Blaberidae). *Entomol. Gen.* **15**, 133–147.

Moore, A. J. 1994 Genetic evidence for the 'good genes' process of sexual selection. *Behav. Ecol. Sociobiol.* **35**, 235–241.

Moore, A. J. 1997 The evolution of social signals: morphological, functional and genetic integration of the sex pheromone in *Nauphoeta cinerea*. *Evolution* **51**, 1920–1928.

Moore, A. J. & Breed, M. D. 1986 Mate assessment in a cockroach, *Nauphoeta cinerea*. *Anim. Behav.* **34**, 1160–1165.

Moore, A. J. & Moore, P. J. 1999 Balancing sexual selection through opposing mate choice and male competition. *Proc. R. Soc. Lond.* B **266**, 711–716.

Moore, A. J., Reagan, N. L. & Haynes, K. F. 1995 Conditional signalling strategies: effects of ontogeny, social experience and social status on the pheromonal signal of male *Nauphoeta cinerea*. *Anim. Behav.* **50**, 191–202.

Moore, P. J., Haynes, K. F., Reagan-Wallin, N. L. & Moore, A. J. 1997 Odour conveys status on cockroaches. *Nature* **389**, 25.

Norris, K. 1993 Heritable variation in a plumage indicator of viability in male great tits *Parus major*. *Nature* **362**, 537–539.

Parker, G. A. 1979 Sexual selection and sexual conflict. In *Sexual selection and reproductive competition in insects* (ed. M. S. Blum & N. A. Blum), pp. 123–166. New York: Academic Press.

Partridge, L. 1980 Mate choice increases a component of fitness in fruit flies. *Nature* **283**, 290–291.

Partridge, L. & Farquhar, M. 1981 Sexual activity reduces lifespan of male fruitflies. *Nature* **294**, 580–582.

Penn, D. & Potts, W. K. 1998 Chemical signals and parasite-mediated sexual selection. *Trends Ecol. Evol.* **13**, 391–396.

Penn, D. J. & Potts, W. K. 1999 The evolution of mating preferences and major histocompatibility genes. *Am. Nat.* **153**, 145–164.

Petrie, M. 1994 Improved growth and survival of offspring of peacocks with more elaborate trains. *Nature* **371**, 598–599.

Promislow, D. E. L., Smith, E. A. & Pearse, L. 1998 Adult fitness consequences of sexual selection in *Drosophila melanogaster*. *Proc. Natl Acad. Sci. USA* **95**, 10 687–10 692.

Rice, W. R. 1996 Sexually antagonistic male adaptation triggered by experimental arrest of female evolution. *Nature* **381**, 232–234.

Roth, L. M. 1962 Hypersexual activity induced in females of the cockroach *Nauphoeta cinerea*. *Science* **138**, 1267–1269.

Roth, L. M. 1964*a* Control of reproduction in female cockroaches with special reference to *Nauphoeta cinerea*. I. First pre-oviposition period. *J. Insect Physiol.* **10**, 915–945.

Roth, L. M. 1964*b* Control of reproduction in female cockroaches with special reference to *Nauphoeta cinerea*. II. Gestation and postparturition. *Psyche* **71**, 198–244.

Sirugue, D., Bonnard, O., Le Quere, J.-L., Farine, J.-P. & Brossut, R. 1992 Methylthiazolidine and 4-ethylguaiacol, male sex pheromone components of the cockroach *Nauphoeta cinerea* (Dictyoptera, Blaberidae): a reinvestigation. *J. Chem. Ecol.* **18**, 2261–2276.

Sreng, L. 1990 Seducin, male sex pheromone of the cockroach *Nauphoeta cinerea*: isolation, identification, and bioassay. *J. Chem. Ecol.* **16**, 2899–2912.

Wilkinson, G. S., Presgraves, D. C. & Crymes, L. 1998 Male eye span in stalk-eyed flies indicates genetic quality by meiotic drive suppression. *Nature* **391**, 276–279.

As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.