THE ROYAL SOCIETY

Balancing sexual selection through opposing mate choice and male competition

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Male–male competition and female mate choice act contemporaneously in the cockroach *Nauphoeta cinerea* and the social pheromone of males influences the outcome of both forms of sexual selection. We therefore examined the joint and separate effects of male–male competition and female mate choice to determine if the selective optima for the pheromone were the same or different. Dominant males in a newly established hierarchy mated more frequently, but not exclusively. Manipulations of the multi-component social pheromone produced by males of *N. cinerea* showed that both long- and close-range attraction of females by males were influenced by the quantity and composition of the pheromone. The most attractive composition, however, differed from that which was most likely to confer high status to males. Since the outcome of male–male competition can conflict with mating preferences exhibited by females, there is balancing sexual selection on the social pheromone of *N. cinerea*. Such balancing selection might act to maintain genetic variation in sexually selected traits. We suggest that the different forms of sexual selection conflict in *N. cinerea* because females prefer a blend different to that which is most effective in male–male competition in order to avoid mating with overly aggressive males.

Keywords: disruptive selection; female mate choice; male–male competition; phenotypic manipulation; sexual conflict; social dominance

1. INTRODUCTION

Darwin (1859, 1871) proposed that sexual selection accounted for the evolution of extravagant characters that appeared to be at a disadvantage under natural selection. Such traits, he suggested, would evolve through either intrasexual (typically male–male) competition or intersexual (typically female) mate choice. He argued that traits providing an advantage in obtaining mates under either mechanism will be selected for and evolve even when disadvantageous to survival. Considerable subsequent research (e.g. Andersson 1994; Houde 1997) has confirmed Darwin's original hypothesized roles for sexual selection and natural selection.

Even though Darwin suggested that different characters might evolve under male–male competition and female mate choice (e.g. weapons and signals, respectively), there is often an assumption that both intersexual and intrasexual selection have similar if not indistinguishable properties. Nonetheless, there is no *a priori* reason why male–male competition and female mate choice should be equivalent or act in concert. Males and females often have conflicts of interest with regard to mating (Berglund *et al*. 1996; Gowaty 1997; Murphy 1998; Parker & Partridge 1998; Qvarnström & Forsgren 1998) and the potential for intrasexual and intersexual forms of sexual selection to be conflicting remains an open empirical question (Moore 1990*b*).

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Species with dominance hierarchies can offer insights into how the different mechanisms of sexual selection act. Both female choice and male–male competition often occur together in species that form hierarchies, and the outcome of male–male competition is often influenced by the same signal used by females to discriminate when among potential males (Berglund *et al*. 1996). There is disagreement, however, over whether females should always prefer dominant males (Berglund *et al*. 1996; Qvarnström & Forsgren 1998). Furthermore, when females do prefer dominant males, it is not clear if mate choice evolved to capitalize on the increased fitness of dominant males (Berglund *et al*. 1996), or if subordinate behaviour evolved to allow males to exploit the attractiveness of a few males and gain access to females (Berglund *et al*. 1996; Moore 1988; Moore *et al*. 1995). To resolve the evolutionary effects of male–male competition and female mate choice in species with social dominance, it is necessary to examine how the cues function in the different social contexts. Ideally, one would identify the selective optima for the cues, comparing the optimum determined by male–male competition versus that determined by female mate choice. Unfortunately, simple observation is rarely sufficient to disentangle the two mechanisms unless they are separated in time or space (Halliday 1983), something that rarely occurs in species with dominance hierarchies.

The cockroach *Nauphoeta cinerea* has been a useful model system to investigate the details of sexual selection acting in a species with social dominance and mate choice (Moore 1990*a*, 1997). Because this species is amenable to

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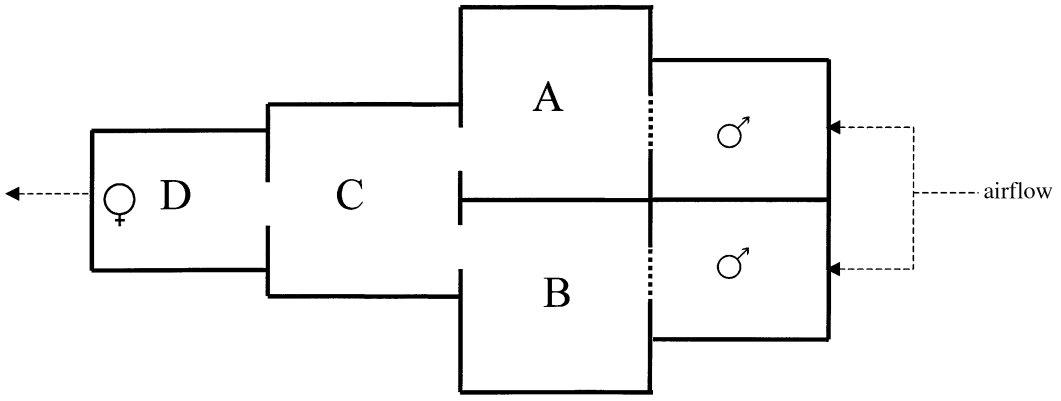

Figure 1. Diagram of the olfactometer. Chambers A, B and C are 10 cm × 10 cm. Chamber D and the chambers holding the males are 6.5 cm × 7 cm. Trials are run under photographic red light to prevent females from using visual cues. Filtered air passes over both males, towards the female, and exits through the holding chamber (D). Areas where air can pass are indicated with a stippled line (holes in the wall) or broken lines (openings between chambers). Solid lines indicate intact walls. In each trial a female was placed into chamber D, then moved to the common chamber (C) where odours from both males could be detected. The female then chose by entering chamber A or B where only one odour was present.

manipulations and laboratory studies, we now know that both male–male competition and female mate choice are mediated by the same social (sex) pheromone (Sreng 1990; Sirugue *et al*. 1992; Moore 1997), a pheromone that plays no role outside that of influencing adult social interactions. The social pheromone of *N. cinerea* is produced only by males and is primarily composed of three components: the heritable, genetically correlated and developmentally integrated 2-methylthiazolidine and 4-ethyl-2-methoxyphenol, plus the heritable but genetically and developmentally independent 3-hydroxy-2-butanone (Sreng 1990; Sirugue *et al*. 1992; Moore 1997). Males vary tremendously in the composition of this pheromone and much of this variation is genetically based (Moore 1997). Experimentally manipulating the social pheromone has shown that different components play different roles in male–male competition and that the pheromone acts as a badge of status (Moore 1997; Moore *et al*. 1997). Other researchers have shown that the long-range attraction of females is influenced by this pheromone (Sreng 1990; Sirugue *et al*. 1992), but have not investigated the consequences of variation in the pheromone blend.

We conducted three experiments designed to investigate if the selective optimum for the pheromone resulting from female mate choice is similar to or different from the optimum determined by male–male competition. First, we documented the behaviour of individuals when multiple virgin females were introduced into newly formed hierarchies. This allowed us to relate our individual investigations of male–male competition and female mate choice to more natural social contexts, when both may occur simultaneously. We then manipulated the pheromone, as in the previous study (Moore *et al*. 1997), adding single or combinations of pheromone components to males. We then investigated how this engineering influenced the long-range attractiveness of males to females, measured in an olfactometer (figure 1), and close-range interactions, measured as courtship speed. Both have been implicated in mate choice in this species, as the males preferred by females attract more of them, and mate faster (Moore 1988, 1990*a*,*c*; Clark *et al*. 1997). Our goal was to determine the optima for different components of the social pheromone under mate choice or male–male competition. This allows us to determine whether the individual mechanisms of sexual selection have complementary or conflicting effects, and how these may be resolved in social contexts.

2. MATERIALS AND METHODS

(a) Nauphoeta cinerea *husbandry*

Individuals used in all of our experiments were generated from randomly mated *N. cinerea* females isolated as virgins from mass colonies. Offspring from these females were reared from birth in family groups at 27 °C and a 12L:12D photocycle. All groups were provided with water and dry rat chow. Prior to being used in experiments, nymphs were isolated from their families on the day of emergence to adulthood. Individual males were housed in 11 cm × 11 cm × 3.2 cm plastic containers with food and water. Males were socially isolated in these containers for 12–14 days prior to treatment. This isolation ensures that all individuals were sexually mature at the time of treatment (Moore *et al*. 1995) and controls for the effects of learning (Manning & Johnstone 1970; Moore *et al*. 1988) because the males had never experienced another adult prior to our experiments.

As the females nymphs became older they were grouped into separate containers. On the day of emergence to adulthood, females were either placed into individual 11 cm × 11 cm × 3.2 cm containers (for mating) or placed into a 17 cm × 12 cm × 6.5 cm container of five females that emerged the same day.

(b) *Manipulation of pheromone components.*

This study focused on the three components of the *N. cinerea* social pheromone that are most abundant and are known to have a role in attracting females (Sreng 1990; Sirugue *et al*. 1992) and influencing male–male interactions (Moore 1997; Moore *et al*. 1997): 2-methylthiazolidine, 3-hydroxy-2-butanone, and 4-ethyl-2-methoxyphenol. 3-hydroxy-2-butanone was purchased from Aldrich, 4-ethyl-2-methoxyphenol was purchased from Pfaltz and Bauer, and 2-methylthiazolidine was synthesized using the methods of Yasuhara & Shibamoto (1989). Gas

chromatography indicated a purity of >95%, 93% and 95%, respectively.

Pheromonal profiles of males were manipulated, as in our previous study (Moore *et al*. 1997). 10 µl of compound in solution (acetone) was applied to a filter paper disk (type D, Matheson Scientific, Inc.; 6 mm diameter). Males were treated 12–14 days post-emergence with either the control (acetone) or a pheromone solution. There were three different solutions: the genetically and developmentally independent components of the pheromone alone (i.e. 3 hydroxy-2-butanone or a combination of 2-methylthiazolidine and 4-ethyl-2-methoxyphenol), or a blend of all three pheromone components. The quantity of each of the three components in the pheromone blend to be applied was based on the mean quantity of pheromone isolated from the sternites of dominant males (Moore 1997). Thus, the concentration of the 2-methylthiazolidine was 400 ng μl^{-1}, 3-hydroxy-2-butanone was 300 ng μl^{-1}, and 4-ethyl-2-methoxyphenol was 100 ng μl^{-1}. The concentration of the individual components remained at these levels in both of the mixtures of pheromone components. All experiments were performed blind with respect to the manipulation.

(c) *Experiment 1: mating outcomes in newly formed hierarchies*

Previous studies of mating outcomes in *N. cinerea* dominance hierarchies focused on the mating success of males for considerable time after dominance was established (Breed *et al*. 1980; Schal & Bell 1983). Here we examined male mating success while male social interactions and dominance were established, but social interactions were still intense. Interactions among males in long-established hierarchies are often less frequent and not as prolonged (A. J. Moore, unpublished data).

The males had no social experiences with adult males prior to our experiments because they were raised in family groups only made up of nymphs. As last-instar nymphs, each male was placed into individual 11 cm × 11 cm × 3.2 cm plastic containers with food and water. The males were allowed to moult to adulthood (usually within a few days) and then mature in their individual containers for 12 days. This period is sufficient to ensure complete development and maturation of the pheromone (Moore *et al*. 1995).

After the maturation period, we placed four identically aged males into a 27 cm × 19 cm × 10 cm plastic arena. Males were individually marked with liquid paper the day prior to being placed together. These males were allowed to interact for 20 min; in all cases a clearly identifiable hierarchy based on previously defined behaviour (Bell & Gorton 1978) was established. Dominant males initiate interactions and are aggressive; subordinate males avoid and retreat from interactions and are rarely aggressive.

Once a hierarchy was established, two virgin females which were ten days past the moult to adulthood were introduced into the hierarchy. Interactions between males and females were scored, and the females were left with the males until both females had completed mating. The time spent interacting, as well as specific acts, were recorded for all males and females. Courtship speed (i.e. the time spent courting a female), is a useful indication of mate choice because females control how quickly males mate (Moore & Breed 1986). In *N. cinerea*, once females have accepted a mate, mating occurs end-to-end with the male attaching himself to the female with a phallomere (a hook-like structure). Only males can terminate copulation (see Moore & Breed 1986; Clark *et al*. 1997).

(d) *Experiment 2: phenotypically engineered pheromone and long-range attraction*

In the first experiment, a pair of males was presented in an olfactometer (figure 1; Moore 1988). In this apparatus, filtered air (8 l min^{-1}) was passed over each male in each arm of the olfactometer. Because all trials were run under photographic red light, the only information available to the female was odour. Females were introduced into the apparatus then allowed to approach the male which was travelling down one or the other arm of the olfactometer. Females typically sampled air from the opening between the common chamber and both individual chambers, moving back and forth, before making a choice. A female was scored as having made a choice once her entire body entered the area of the olfactometer where only one male odour could be detected (chambers A and B, figure 1). Choices were only scored after females remained in a chamber for over 30 s. Females rarely left a chamber once they entered it completely and typically continued their approach until they reached the barrier preventing contact with the male. Contact between the female and male was not possible, although females antennated the openings where air passed or sat quietly next to the barrier.

Two different trials were run for each pair of males. Females were first allowed to orientate to a male until a choice was scored. We then placed a treated filter paper disk (acetone control or pheromone component) in each arm of the olfactometer with the male. Females were then allowed to orientate and choose a second time after the manipulation. Preferences, along with switches in preferences were scored. We tested for non-random preferences using a *G*-test with William's correction and non-random switches using Fisher's exact test.

(e) *Experiment 3: phenotypically engineered pheromone and courtship*

In this experiment, between day three and day eight post-emergence to adulthood, a filter paper disk was attached to each male's pronotum with rubber cement. Males were then returned to their individual containers. On the day of the experiment, males were treated with a pheromone solution or the acetone control then placed into a 17 cm × 12 cm × 6.5 cm arena. After a 15 min recovery period a single female was introduced into the arena at the opposite end from the male. Courtship speed, which indicates female preferences (Moore & Moore 1988; Moore 1990*a*,*c*; Clark *et al*. 1997), was scored. Data were log-transformed and analysed using analysis of variance and Fisher's least significant difference test.

3. RESULTS

(a) *Experiment 1: mating outcomes in newly formed hierarchies*

In all of the hierarchies examined, both females mated. Furthermore, these females mated with either the most dominant (alpha) or the next most dominant male (beta). The two most subordinate males never mated.

Beta males mated in 15 out of the 26 hierarchies. In three hierarchies, the beta male mated with both females. In three other hierarchies, the beta male mated first. In contrast, alpha males mated both females in 11 hierarchies. In the remaining nine hierarchies, where both the beta and alpha male mated, the alpha male mated first.

Females interacted with all four males in all of the hierarchies. The first mating occurred, on average, in just over 2 min after introducing the females into the

hierarchy ($\bar{x} = 137.7$ s; s.d. $= 221.6$ s) with the longest delay to the first mating of 16 min 30 s and the shortest 5 s. When two different males mated the two females, the second mating began before the first ended in ten out of 12 instances. In all of these cases the first mating ended prior to the end of the second mating.

When a single male mated both females, time between mating was highly variable but was on average delayed by over 34 min ($\bar{x} = 2054.5$ s, s.d. $= 1882.4$ s). The longest interval was 95 min and the shortest was 7 min 20 s. The males spent most of the time between mating re-establishing and maintaining their social positions by chasing and directing aggression towards other males.

In the three instances where only beta males mated, the alpha males were aggressive towards females. The longest delays before mating began occurred in a hierarchy where the females repeatedly tried to approach the alpha male, but were rebuffed. Both females eventually mated with the beta male. When the alpha male mated second or the alpha male finished mating first, or when only beta males mated, the alpha male was highly aggressive towards the mating pair in nearly all cases. Alpha males chased mating pairs around the arena, attempting to bite or butt the pair. Aggression was directed equally towards females and males, and generally the female ran from the aggressive male dragging the male behind her. The beta male attempted to disrupt the mating attempts and copulation of the alpha male in only two hierarchies.

(b) *Experiment 2: phenotypically engineered pheromone and long-range attraction*

Female preferences for males depended on their pheromone blend (figure 2). Females preferred to approach manipulated males compared to control males when they were manipulated to have an excess of 3-hydroxy-2-butanone ($G_{adj} = 7.484$, d.f. $= 1$, $p < 0.01$) or excess of the full blend ($G_{adj} = 4.619$, d.f. $= 1$, $p < 0.05$). In contrast, when males were manipulated to have excess of the two components that cannot change independently (2-methylthiazolidine + 4-ethyl-2-methoxyphenol), there was no preference towards manipulated males over control males ($G_{adj} = 0.317$, d.f. $= 1$, $p > 0.5$).

The likelihood of a female switching her preference depended on the pheromone component manipulated. Females were more likely to switch preferences if 3-hydroxy-2-butanone was increased ($p = 0.045$) or the full blend was increased ($p = 0.019$). Increasing the coupled components did not result in a significant number of switches from non-preferred to preferred males ($p = 0.767$).

(c) *Experiment 3: phenotypically engineered pheromone and courtship*

Similar results were obtained in the measure of close-range attractiveness of males and manipulated pheromones (figure 3). Pheromone manipulation had a significant effect on the length of time males courted before females mated ($F_{3,99} = 2.976$, $p = 0.035$). In this experiment there was no significant difference between the amount of time spent courting between control males and males that had increased levels of 3-hydroxy-2-butanone ($p = 0.984$), or between control and increased full-blend males ($p = 0.314$). Nor was there a significant difference in courtship speed between males with increased 3-hydroxy-2-butanone and increased full-blend males ($p = 0.383$). However, when males were manipulated to have increased levels of the coupled components, their courtship was significantly longer than that of the control males ($p = 0.057$), the males with increased 3-hydroxy-2-butanone ($p = 0.044$) and also the males with increased levels of the full-blend pheromone ($p = 0.005$).

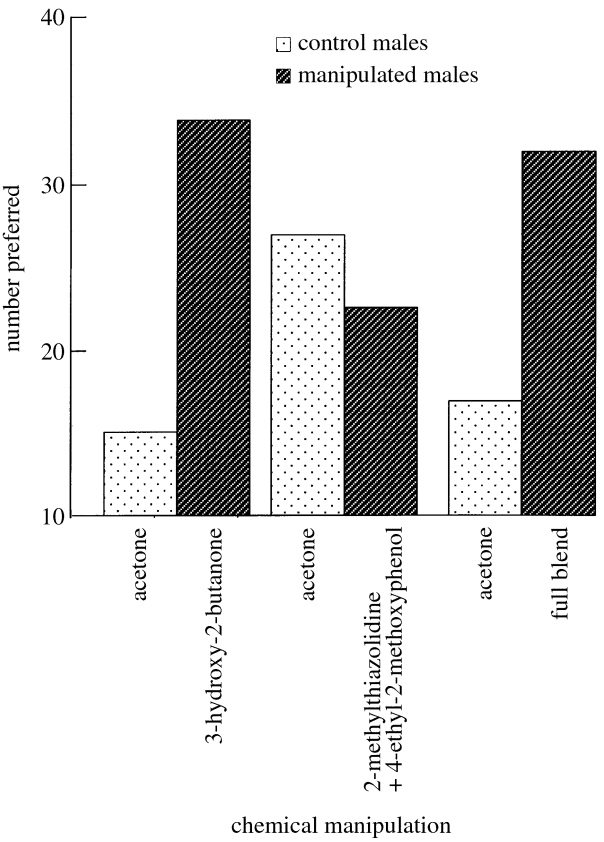

Figure 2. Female preferences for males manipulated to have increased levels of the genetically independent pheromone component, a combination of genetically integrated pheromone components, or the complete pheromone blend. Quantities and combinations of pheromone components are based on studies showing integration and levels in this population (Moore 1997; Moore *et al.* 1997).

4. DISCUSSION

The behaviour of *N. cinerea* males and females when females are receptive and males have recently formed dominance hierarchies supports the notion of different optima for the social pheromone in different social contexts. In about half of the social groups, the dominant male mated with both receptive females. Indeed, in all of the groups only the alpha or beta male mated. However, in a nearly equal number of groups both the alpha and beta males mated. In three groups both females mated with the beta male and the alpha male never mated. Behaviour of both males and females suggest that conflicts of interest over mating are not uncommon in *N. cinerea*.

Manipulating the pheromone indicates that females prefer males with higher levels of all three pheromone

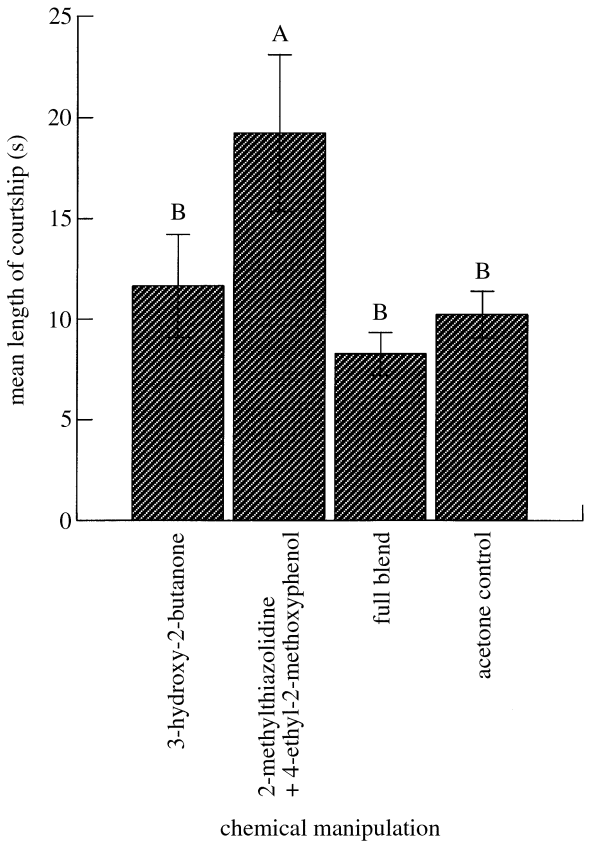

Figure 3. Female preferences measured as courtship speed (length of courtship; Moore & Moore 1988; Clark *et al*. 1997) for males manipulated to have increased levels of the independent pheromone component, the integrated pheromone components, the complete pheromone blend, or the acetone control. Different letters indicate significant differences. Quantities and combinations of pheromone components are based on studies showing integration and levels in this population (Moore 1997; Moore *et al*. 1997).

components. Importantly, increasing the two components that are genetically correlated and developmentally integrated, 2-methylthiazolidine and 4-ethyl-2-methoxyphenol (Moore 1997), does not make males attractive. This is true for long-distance attraction but especially true for close-range interactions where increasing these two components decreases the attractiveness of males to females. Increasing just the third genetically and developmentally independent component, 3-hydroxy-2-butanone, makes males more attractive from a distance but not at close range. Increasing all three components leads to increased attractiveness both at a distance and during contact.

Therefore, the two contemporaneous mechanisms of sexual selection acting on the male social pheromone in *N. cinerea* have conflicting effects. Male *N. cinerea* are more likely to be dominant if they have higher levels of 2-methylthiazolidine and 4-ethyl-2-methoxyphenol, while increasing 3-hydroxy-2-butanone increases the likelihood of being subordinate (Moore *et al*. 1997). By increasing all three, there is neither a positive nor negative effect on male social status. Thus, for male social status, it is the composition rather than the quantity of the pheromone that is important. Here we show that to be successful in female mate choice, males must have 3-hydroxy-2-butanone. Furthermore, for females, it appears that both composition and quantity are important, and the attractive composition differs from the dominant composition. The conflicting functions of the male pheromone in the sexual selection of *N. cinerea* explain why the outcome of male–male competition is not a perfect predictor of male attractiveness for this species (Moore 1988). Furthermore, when male–male competition and female mate choice work in concert in *N. cinerea*, there is not complete overlap in a single 'successful' pheromone blend. Since the mechanisms are spatially but not temporally separate, and these two different mechanisms of sexual selection have conflicting effects on the evolution of the pheromone, selection results in advantages for both extremes and therefore creates a balance.

Although our study focused on the outcomes rather than the causes of selection, our results do raise the question of why female mate choice should have a different selective optimum than male–male competition. Why is it that high status is not equivalent to high male quality, as is generally supposed (Berglund *et al*. 1996)? We suggest that status and fitness are not always equivalent and females should not always prefer the most dominant male (see also Qvarnström & Forsgren 1998). Even though in *N. cinerea* dominance can be influenced by heritable components because the badge is heritable (Moore 1997), so offspring of dominant males are themselves dominant (Moore 1990*a*,*c*), females and their offspring do receive other fitness benefits from mate choice (Moore 1994). Thus dominance is only one component of fitness for the females' offspring. Furthermore, dominance is frequency dependent, so choosing a less-than-dominant male does not mean that their offspring will not be dominant. We suggest that females prefer males that are not overly aggressive. In this way, females avoid injury and have sons that will be dominant under some conditions. This hypothesis is supported by the observation in the current study that females avoided excessively aggressive males, presumably avoiding injury.

Many characters that are presumed to be under strong directional selection as a result of sexual selection, including the pheromone of *N. cinerea* (Moore 1997), are highly genetically variable (Bakker & Pomiankowski 1997). Why this should be is not clear, but our results suggest one mechanism for maintaining variation. It is possible that the different mechanisms of sexual selection may themselves be responsible for balancing selection that maintains variation. Balancing selection can occur when populations are spatially subdivided; under such conditions balancing selection results in either no total selection or apparent disruptive selection (Via & Lande 1985). If we consider social interactions that result in subdivision of the population, we can treat this as a genotype by environment problem, with the environment being determined by social conditions. In such spatially subdivided populations, when there are different optima for the same character (i.e. the genetic correlation is valued at one across environments) simultaneously experiencing both male–male competition and female mate choice, genetic variation will be maintained by this form of balancing selection.

There is value in recognizing the complexity of sexual selection. Fisher (1958), in the preface to his seminal work, wrote, 'natural selection is not evolution'. With apologies to Fisher and his advocates and paraphrasing this: mate choice is not sexual selection. While one-dimensional studies can document the existence of the separate mechanisms of sexual selection, especially mate choice (Halliday 1983), we need to carefully consider how all of the mechanisms of sexual selection interact before we presume to have described sexual selection in a species. Mate choice and male–male competition may occur contemporaneously or consecutively, resulting in spatial or temporal variation in selection, and the outcomes of sexual selection will vary under these different scenarios. As we show here, one form of sexual selection can even act in opposition to balance the effects of another, resulting in a more variable sexually selected character than might otherwise be expected.

The power of our study derives from our ability to experimentally separate male–male competition and female mate choice in *N. cinerea*. Furthermore, we are able to manipulate the pheromonal signal that influences the outcome of both of these mechanisms of sexual selection. Although not all species of interest will be so amenable for studying sexual selection, our results strongly suggest that studying mate choice (or male–male competition) by itself can give a misleading picture of sexual selection. When evolutionary outcomes of sexual selection are of interest, more balanced approaches should be adopted. Such studies are not necessarily difficult; correlative studies, such as statistical or graphical measures of sexual selection in the wild (Brodie *et al*. 1995), can also suggest opposing aspects of sexual selection (e.g. Moore 1990*b*).

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