Female agreement over male attractiveness is not affected by cost of mating with experienced males

Martin Edvardsson, John Hunt, Patricia J. Moore, and Allen J. Moore
Centre for Ecology and Conservation, School of Biosciences, University of Exeter, Cornwall Campus, Penryn, TR10 9EZ, UK

The extent to which females differ in their mating preferences has important consequences for the evolution of male sexual traits; yet, the way in which female mating preferences vary remains largely unexplored in most animal taxa. Even less is known about the implications of this variation to female fitness. Here, we examine the degree of between-female agreement in the mating preferences of the cockroach, *Nauphoeta cinerea*, and relate this variation to differences in female reproduction. Using a repeated-measures design, we mated a series of males sequentially to 5 different females. We found that females were largely in agreement in their mating preferences with a significant, albeit low (0.094 ± 0.061), repeatability of male attractiveness as assessed by different females. This is surprising given that females experienced a consistent reduction in offspring production when mating to more experienced males and suggests that females have a limited ability to detect male mating history. This cost may, in part, be offset by a longer gestation time when mating with more experienced males, which is known to extend female longevity in this species. There appears to be good reason for females to agree in their mate choice in this species. Across males, we found a significant negative correlation between male attractiveness and gestation time, suggesting that females actively discriminate against males that accelerate gestation. We discuss the implications of our findings to the operation of sexual selection in *N. cinerea*. *Key words:* agreement, cockroach, female reproduction, male attractiveness, male mating history, mate choice, *Nauphoeta cinerea*. *[Behav Ecol 19:854–859 (2008)]*

Female mate choice is a potent driving force behind the evolution of male sexual traits (Andersson 1994; Andersson and Simmons 2006). However, sexual selection is generated by variation among males in mating success, and this variation can change over space and time (Shuster and Wade 2003). The extent to which females of a species vary in their mating preferences will have important effects on the strength of sexual selection (Shuster and Wade 2003). For example, if females consistently differ in their mating preferences, the variance in male mating success will decrease and the strength of sexual selection can be considerably weaker (Shuster and Wade 2003). Furthermore, differences in mating preferences between females can also alter population dynamics through the effects that variance in male mating success has on effective population size (Anthony and Blumstein 2000; Shuster and Wade 2003; Quader 2005).

There are a number of reasons why females may differ in their mating preferences (Jennions and Petrie 1997; Widemo and Sæther 1999). First, intrinsic differences among females may alter their mating preferences. For example, female age (e.g., Gray 1999; Moore PJ and Moore AJ 2001), mating experience (e.g., Bateman et al. 2000; Pitcher et al. 2003) and condition (e.g., Hunt et al. 2005; Fisher and Rosenthal 2006) are known to influence mating preferences in a number of species, most likely by altering the time and energy costs associated with expressing choice (Jennions and Petrie 1997). Furthermore, mating preferences may differ with female phenotype due to constraints associated with the detection and

processing of male sexual signals (Jennions and Petrie 1997; Widemo and Sæther 1999). For example, frequency tuning in the cricket frog (*Acris crepitans*) is negatively correlated with female body size leading to size-assortative mating in this species (Ryan et al. 1992).

Second, females may differ in their underlying reason for choosing a mate. For example, if females are seeking males that are most compatible with their own genotype (Tregenza and Wedell 2000; Mays and Hill 2004), male attractiveness will be specific to the assessor and there should be a low level of agreement across females in their mating preferences (Forstmeier and Birkhead 2004). Conversely, if females are seeking males that possess "good genes," all females in the population should prefer the same males resulting in strong between-female agreement in mating preferences (Forstmeier and Birkhead 2004).

Finally, female preferences for individual males may vary if male attractiveness changes over time and/or across matings. It is well documented that a male's attractiveness can vary over his lifespan (reviewed by Brooks and Kemp 2001). However, male attractiveness can also vary on a much shorter timescale. For example, mating with a large number of females can make males sperm depleted (e.g., Preston et al. 2001; Harris and Moore 2005), decrease the quality of their nuptial gifts (e.g., Wedell and Ritchie 2004; Torres-Vila and Jennions 2005), or increase the risk of carrying sexually transmitted diseases (e.g., Knell 1999; Thrall et al. 2000). Conversely, males of some species include manipulative substances in their ejaculates that are harmful to females (Fowler and Partridge 1989; Chapman et al. 1995), and depletion of these substances may make mating with experienced males less costly for females. If females are able to evaluate male mating history and adjust their mate choice decisions accordingly (Harris and Moore 2005; Ivy et al. 2005), the attractiveness of a given male will

vary predictably across matings leading to a low level of agreement between females in their mating preferences.

In the cockroach, *Nauphoeta cinerea*, male attractiveness depends on female assessment of a male-produced sexual pheromone (Moore 1997; Moore AJ and Moore PJ 1999). Females use a threshold mating tactic and respond more quickly to the courtship of attractive males (Moore AJ and Moore PJ 1988, 1999). Whereas males mate with as many females as they can attract, females only ever mate once per clutch and often only once in their lifetime, although some females remate between successive clutches (Roth 1964; Moore et al. 2001). Male mating history, however, has important implications for female fitness. Males become temporarily sperm depleted if they mate at a high rate, and female fecundity suffers as a direct consequence (Montrose et al. 2004). Accordingly, females actively discriminate against males that have recently consorted with a large number of females (Harris and Moore 2005). Males also influence female fitness by manipulating the length of gestation. Female *N. cinerea* are ovoviviparous, retaining the fertilized eggs in a brood pouch until parturition. The pheromone blend of some males has been found to accelerate gestation (Moore et al. 2003). Males benefit from this manipulation because it reduces the probability that females will remate between successive clutches, thereby ensuring that they sire any subsequent offspring (Moore et al. 2003). Females avoid mating with manipulative males because a shortened gestation time reduces female longevity (Moore et al. 2003).

Despite the vast number of reasons to expect the attractiveness of individual males to vary, the extent to which females actually agree (or disagree) during mate choice remains largely unexplored in most animal taxa (Jennions and Petrie 1997; Widemo and Sæther 1999). Even less is known about how this variation in mating preferences influences female fitness (Jennions and Petrie 1997). Here, we use a repeated-measures mating design, where each of 5 different females assessed the attractiveness of a given male, to examine the degree of between-female agreement in the mating preferences of *N. cinerea*. In addition, we relate these differences in mating preferences to variation in female reproduction. This not only allowed us to examine the effects of male attractiveness on female reproduction across different males but also to examine how female reproduction varies with the attractiveness and mating history of a given male. We conclude by discussing our findings in the context of mate choice theory and the operation of sexual selection in this species.

METHODS

Cockroach husbandry

The cockroaches used in this study were derived from a population that has been maintained in the laboratory for over 50 years. The population is maintained on dry rat chow and water at 28 °C under a 12:12 h light:dark photoperiod in multiple mass colonies consisting of many thousands of individuals, with gene flow among colonies enforced every few generations. Assessment of allozyme variation has shown that this population contains substantial levels of genetic variation (Corley et al. 2001). Last instar nymphs were selected at random from the mass colonies, sexed, and placed in single sex colonies. When adults emerged, they were isolated in individual plastic containers with ad libitum food and water until their use in the experiment. Males were returned to their original container after each mating.

Mate choice trials

We staged all mate choice trials under red light in a 28 °C constant room temperature during the dark phase of the 12:12 h light:dark photoperiod. A total of 45 males were mated sequen-

tially to 5 virgin females each, with a 3-day interval between successive matings ($n = 225$ mating trials). All males were virgin at the time of their first mating and were 10 days posteclosion. Likewise, all females were virgin and 10 days posteclosion at the time of mating. At this age, males have fully developed sexual pheromones (Moore et al. 1995), and it is the optimal time for females to mate (Moore PJ and Moore AJ 2001).

Matings were staged in rectangular plastic boxes ($17 \times 12 \times 6.5$ cm) containing no food or water. Males and females were introduced into the boxes, and their mating behavior continuously observed until they had copulated successfully. Two females refused to mate and were replaced with other females after 60 min. Courtship is initiated when the male raises his wings perpendicular to his body to expose the sternal glands that produce and emit the sex pheromones (Clark et al. 1997). Females respond to male courtship by climbing onto the back of the male (Clark et al. 1997). This behavior is under female control and is necessary to achieve the stereotypic end-to-end mating position (Clark et al. 1997). These behaviors are distinct enough to allow an observer to record the timing to the nearest second. As has been done in previous studies on *N. cinerea* (Moore AJ and Moore PJ 1988, 1999; Moore 1990; Clark et al. 1997), we used the time interval between these 2 behaviors as our measure of female preference. A female finds a given male more attractive if she requires less courtship to mount him. After copulation, each female was placed in an individual plastic box ($11 \times 11 \times 3$ cm) with food and water provided ad libitum. We monitored the boxes daily for hatching offspring. When clutches appeared, we counted the offspring resulting from each mating to obtain a measure of reproductive success. Gestation time was calculated as the interval (in days) between mating and parturition.

We examined the consistency of male attractiveness across different females (i.e., the degree of between-female agreement over male attractiveness—not the consistency of the mating preferences of individual females) as well as the consequences for female reproduction, using repeated-measures analysis of variance. Using the variance components derived from these models, we calculated the repeatability (R) of male attractiveness, gestation time, and offspring production, according to Becker (1984):

$$R = \frac{\sigma_w^2}{\left(\sigma_w^2 + \sigma_w^2\right)},$$

where σ_W^2 is the between-male variance component and σ_E^2 is the within-male variance component. The standard error (SE) of R was calculated as described by Becker (1984):

$$SE = \sqrt{\frac{2(1-R)^2\left[1 + R(k-1)^2\right]}{k(k-1)(n-1)}},$$

where k is the number of repeat measures per male (i.e., $k = 5$) and n is the total number of males examined. In our mating trials, $n = 45$ males. However, because not all matings produced offspring, this number is considerably reduced ($n = 21$) for gestation time and offspring production.

All analyses were conducted in SPSS (version 14.0) on log-transformed data to ensure a normal distribution. However, for ease of interpretation, untransformed data are presented in figures. All data are presented as mean $\pm$ 1 SE.

RESULTS

The consistency of male attractiveness across females

There was significant between-male variation in attractiveness (Table 1), indicating that females, on average, found certain

Table 1

Repeated-measures ANOVA model (Type III sums of squares) examining the variance in attractiveness between different males and within the same male across five consecutive matings to different females

Source of variation	df	Mean Squares	F	P
Between males	44	0.230	1.518	0.031
Within males	180	0.152		
Mating number	4	0.253	1.692	0.154
Residual	176	0.149		
Total	224	0.207		

Figure 1
Mean (±SE) attractiveness (a) across different males and (b) with mating number. In both cases, time from wing raise to female climb is our measure of male attractiveness with a longer time between male display and female response, meaning that the male is less attractive to a female.

males more attractive than others (Figure 1a). In contrast, the within-male variation in attractiveness was not significant (Table 1), demonstrating that different females were largely in agreement when assessing the attractiveness of a given male across matings and that male attractiveness did not depend on male mating history (Figure 1b; Table 1). Accordingly, male attractiveness to different females was low but significantly repeatable (0.094 ± 0.061). Taken collectively, these results suggest that although different females largely agree with each other in their mating preferences, the extent of this agreement is not particularly strong.

Gestation time

There was no significant between-male variation in gestation time (Table 2). There was, however, significant within-male variation in gestation time (Table 2). This within-male variation occurred because gestation time increased with number of females that the male had previously mated with (Figure 2). Not surprisingly, gestation time was not repeatable across the 5 females mating to each male ($R = -0.095 \pm 0.048$).

Previous work on N. cinerea has shown that females actively discriminate against males that accelerate their gestation (Moore et al. 2003). In agreement with this study, we found a significant negative correlation between mean attractiveness and mean gestation time across different males in their first mating ($r = -0.332$, $N = 45$, $P = 0.03$).

Offspring production

Male mating history had a significant effect on the risk of females failing to produce a clutch ($\chi^2 = 19.89$, degrees of freedom = 4, $P < 0.001$). The proportion of unsuccessful clutches were 1 out of 45 in the first mating (2.22%), 3 out of 45 in the second mating (6.67%), 4 out of 45 in the third (8.89%), 12 out of 45 in the fourth and fifth mating (26.67%). The probability of clutch failure in one or more matings, however, was unrelated to mean attractiveness of the male (logistic regression: Wald $\chi^2 = 0.040$, $N = 45$, $P = 0.84$).

In matings that were successful, there was no significant between-male variation in the number of offspring produced (Table 3). There was, however, significant within-male variation in the number of offspring produced (Table 3), with the number of offspring produced decreasing with the number of females that the male had previously mated with (Figure 3). Consequently, the number of offspring produced by a given male was not repeatable across the different females he was mated to ($R = 0.058 \pm 0.082$). The mean number of offspring produced by females mated to a given male was unrelated to his mean attractiveness ($r = 0.233$, $N = 45$, $P = 0.132$).
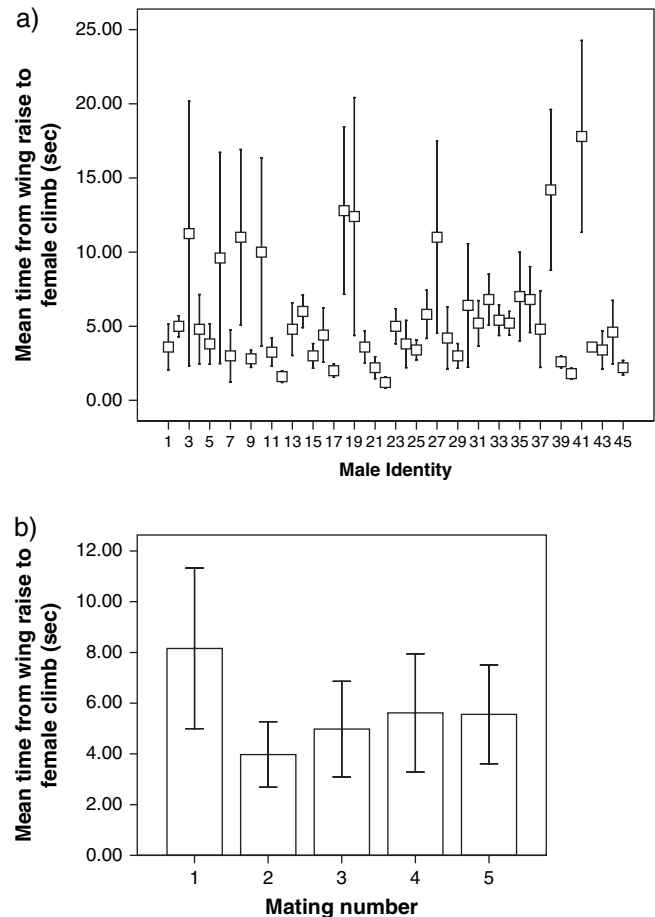
DISCUSSION

Here, we show that when males of the cockroach N. cinerea were assessed by 5 different females across successive mating attempts, there was significantly greater variation between males than within males in their attractiveness to females. This finding provides a number of insights on how female mate choice operates in N. cinerea. First, it shows that females find some males in the population consistently more attractive than others. Second, it demonstrates that females largely agree on what makes a male attractive. However, although the repeatability of male attractiveness across females ($R = 0.094 \pm 0.061$) was statistically significant, it was low suggesting that the extent of this agreement is not particularly large. Finally, it illustrates that females do not base their mate choice decisions on male mating history, at least over the time frame of our experiment. This is particularly interesting given that females mating with more experienced males suffer a direct cost, either through a higher probability of complete clutch failure or by producing fewer offspring if a clutch is successful.

There appears to be good reason why female N. cinerea prefer the same males. Previous studies on this species have shown that the components of the male sex pheromone that increase attractiveness (3-hydroxy-2-butanone) also influence the time it takes for offspring to develop from eggs to

Table 2

Repeated-measures ANOVA (Type III sums of squares) examining the variance in female gestation time between different males and within the same males across five consecutive matings to different females

Source of variation	df	Mean Squares	F	P
Between males	20	16.146	0.566	0.925
Within males	84	28.524		
Mating number	2.187	200.151	4.471	0.015
Residual	43.744	44.765		
Total	104	26.143		

Males with one or more failed clutches have been excluded from the analysis. The sphericity assumption of a repeated measures ANOVA was violated and we therefore present Greenhouse-Geisser adjusted degrees of freedom for the within male analysis (Quinn and Keough 2002).

Table 3

Repeated-measures ANOVA model (Type III sums of squares) examining the variance in the number of offspring produced across different males and within the same male across five consecutive matings to different females.

Source of variation	df	Mean Squares	F	P
Between males	20	75.407	1.305	0.199
Within males	84	57.762		
Mating number	3.415	385.643	7.450	0.001
Residual	68.296	51.762		
Total	104	61.155		

Males with one or more failed clutches have been excluded from the analysis. Type III sums of squares were used. The sphericity assumption of a repeated measures ANOVA was violated and we therefore present Greenhouse-Geisser adjusted degrees of freedom for the within male analysis (Quinn and Keough 2002).

parturition (Moore et al. 2003). Females actively avoid manipulative males that accelerate gestation because this has a negative effect on female longevity (Moore et al. 2003) and generate a female-biased offspring sex ratio (Moore et al. 2001). In contrast, males benefit from a shortened time to parturition because females with a short gestation period remain unreceptive to courting males and are therefore less likely to remate between successive clutches (Moore et al. 2003). Our finding that gestation time is negatively correlated with male attractiveness further corroborates these findings and suggests that mate choice to reduce male manipulation is an important component of the mating system of *N. cinerea* (Moore et al. 2001, 2003).

Repeatability estimates for female mating preferences vary considerably across species, ranging from as low as $R = 0.00$ in the flour beetle *Tribolium castaneum* (Boake 1989) to as high as $R = 0.65$ in the stickleback *Gasterosteus aculeatus* (Bakker 1993). Although differences in sample sizes between studies is undoubtedly a large source of this variation (Forstmeier and Birkhead 2004), repeatability estimates for female mate choice are known to vary temporally (e.g., Johnsen and Zuk
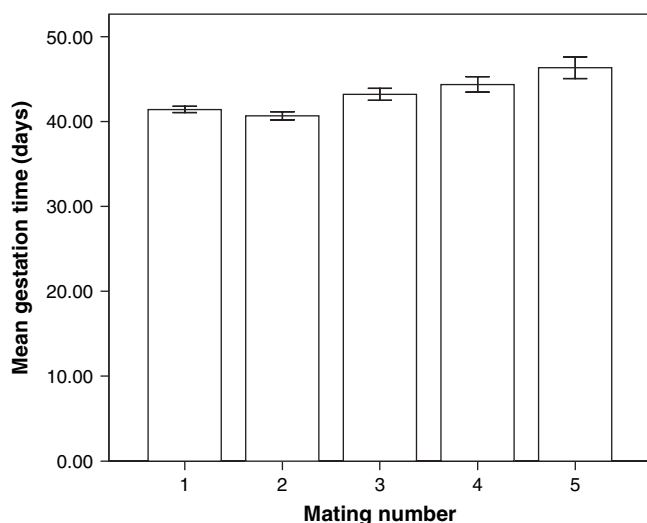
1995; Ligon and Zwartjes 1995) and even according to the specific apparatus used to assess female mating preferences (e.g., Kodric-Brown and Nicoletto 1997). In our study, we cannot rule out that the low repeatability estimate for male attractiveness is partly a consequence of the way we quantified female mating preferences. Our measure of female preference is based on the amount of courtship required by a male to obtain mating. Thus, our measure encompasses all traits that contribute to male attractiveness in *N. cinerea* (e.g., sex pheromones, cuticular hydrocarbons, and courtship behavior). Consequently, more variance between females may be found for such a measure relative to those where only a single male trait is examined (often controlling for all other male traits) (e.g., Wagner et al. 1995) or appears to be most important in the mating system (e.g., Bakker 1993; Godin and Dugatkin 1995). This would be particularly likely if females assess multiple cues during mate choice so that no single trait determines male attractiveness. Indeed, a recent study on zebra finches showed that although female mating preferences across females were significantly repeatable, the degree of female agreement was low ($R = 0.11$) and no single male trait
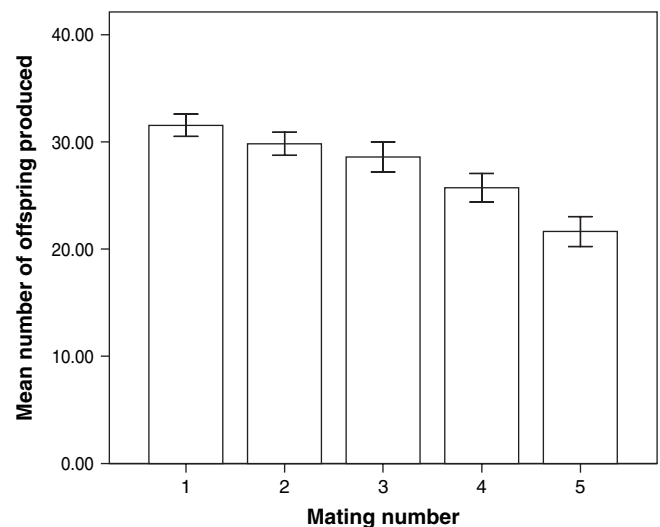

Figure 2
Mean ($\pm$SE) gestation time (in days) of females in their first clutch when mating to the same males but with different levels of mating experience. Failed clutches have been excluded from the analysis.

Figure 3
Mean ($\pm$SE) number of offspring produced by females in their first clutch when mating to the same males but with different levels of mating experience. Failed clutches have been excluded from the analysis.

was a strong overall predictor of male attractiveness (Forstmeier and Birkhead 2004). More studies examining the repeatability of mate choice are needed, however, to test the generality of this pattern.

When mating with a male that had previously mated more than 3 times, females in our study suffered an increased risk of failing to produce a clutch, and when successful in producing a clutch, produced fewer offspring. This is likely to be the result of the depletion of viable sperm (Montrose et al. 2004). While male fertility is typically restored to normal levels after 5 days without mating (Montrose et al. 2004), our study suggests that 3 days is insufficient for males to make a full recovery. Consequently, mating with a male during this recovery period comes at a substantial reproductive cost to females, particularly because females typically only mate once prior to the birth of their first clutch (Roth 1964). Despite this cost, however, we showed that females do not discriminate between males depending on their prior mating history when males have 3 days between successive matings. This contrasts previous work on *N. cinerea* showing that females discriminated against males that had mated multiple times (Harris and Moore 2005). This effect was not caused by mating per se as physical contact with females (but without mating) was sufficient to reduce male attractiveness, suggesting that females use chemical cues transferred from other females, such as cuticular hydrocarbons (Everaerts et al. 1997), to assess male mating history. A likely reason for the difference between these studies is the time frame over which males were permitted to interact with females. In the study by Harris and Moore (2005), attractiveness was tested immediately after the male had simultaneously interacted with 5 females over a 2-day period, whereas in our current study, there was a 3-day interval between successive matings. This suggests that the chemical cue used by females in Harris and Moore (2005) is likely to be short lived and may be dependent on the absolute number of females that the male has interacted with immediately prior to being assessed. This is largely consistent with the action of cuticular hydrocarbons that are often dose dependent in their effect and volatile (Wyatt 2002).

Our study also shows the potential for male mating history to have a positive effect on female reproduction. We found that gestation time increased consistently with the number of previous matings by the male. Females may benefit from this because female longevity is reduced with short gestation periods (Moore et al. 2003). This may counter the negative effect of male mating history on female fertility and make it beneficial for females to mate with males even though there is still a risk that they have not regained full fertility. However, to obtain a more complete picture of the consequences for female fitness, further tests are needed that examine the effects of male mating history on the total number of offspring produced by a female in her lifetime.

Our findings have a number of important implications for the operation of sexual selection in *N. cinerea*. First, it has been suggested that the degree to which different females in the population agree in their mating preferences may provide important insights into the evolution of mate choice (Forstmeier and Birkhead 2004). In particular, it has been argued that if females choose males based on good genes, then there should be relatively strong agreement between females in their mate choice decisions, whereas if the evolution of female choice is largely driven by genetic incompatibility, a low degree of agreement between females is expected (Forstmeier and Birkhead 2004). However, the utility of this approach may be limited when, as appears to be the case in *N. cinerea*, it is more important for females to assess the direct costs associated with mating than to find the best genes for their offspring. The ubiquity of costly male manipulations and

sexual conflict suggests that this may frequently be the case (Arnqvist and Rowe 2005). Females would then be expected to have preferences influenced by the costliness of mating with males of a certain phenotype. This could lead to either uniform or varying preferences depending on whether the costliness of male manipulations varies between females. Consequently, caution should be taken when using repeatability estimates to infer the mechanisms underlying the evolution of female mate choice, particularly if done so in isolation from the direct fitness consequences of mate choice. A complete understanding of how mate choice evolves requires both an appreciation of how females agree in their mating preferences and the complex interplay between the direct and indirect costs and benefits of exerting these preferences (Kokko et al. 2002).

Second, our results highlight the potentially complex effects that male mating history can have on female fitness. There will often be both negative (e.g., through sperm depletion) and positive effects (e.g., through reduced male manipulations) of mating with sexually experienced males. Although the attractiveness of male *N. cinerea* was affected negatively by consorting with females in an earlier study (Harris and Moore 2005), our results suggest that it is restored quickly and that female assessment of recent male mating history has only a limited effect on variance in male mating success in this species. There is no reason to believe, however, that this will be the case in all mating systems. Future work should take this potentially important, yet largely unexplored, component of female mating behavior into account when studying the evolution of female mate choice (Harris and Moore 2005; Ivy et al. 2005).

Finally, even though our repeatability estimate for male attractiveness suggests that the intensity of sexual selection operating on male traits is not likely to be strong, it nevertheless indicates that it is persistent. Theoretically, persistent sexual selection is expected to erode the genetic variance that exists in male attractiveness (Kirkpatrick and Ryan 1991). However, high levels of additive genetic variance has been maintained in male attractiveness (Moore 1990), as well as the male sex pheromones, which are a major determinant of attractiveness in this species (Moore 1997). One mechanism that may explain the maintenance of genetic variation in these male traits is balancing sexual selection (Moore AJ and Moore PJ 1999). In *N. cinerea*, the same 3 male sex pheromones (3-hydroxy-2-butanone, 2-methylthiazolidine, and 4-ethyl-2-methoxyphenol) are involved in both female mate choice and male–male competition (Moore 1988; Moore AJ and Moore PJ 1999). The most attractive pheromone profile differs from that which confers high status to males (Moore AJ and Moore PJ 1999). Dominant males still enjoy a relatively high mating success because they can bypass mate choice by physically excluding other rival males from mating (Moore et al. 2001). More work is needed, however, to show that sexual selection in this species is purely balancing and thus capable of maintaining genetic variance.

FUNDING

REFERENCES

Andersson M. 1994. Sexual selection. Princeton (NJ): Princeton University Press.

Andersson M, Simmons LW. 2006. Sexual selection and mate choice. Trends Ecol Evol. 21:296–302.

Anthony LL, Blumstein DT. 2000. Integrating behaviour into wildlife conservation: the multiple ways that behaviour can reduce N_e. Biol Conserv. 95:303–315.

Arnqvist G, Rowe L. 2005. Sexual conflict. Princeton (NJ): Princeton University Press.

Bakker TCM. 1993. Positive genetic correlation between female preference and preferred male ornaments in sticklebacks. Nature. 363:255–257.

Bateman PW, Gilson LN, Ferguson JWA. 2000. Male size and sequential mate preference in the cricket Gryllus bimaculatus. Anim Behav. 61:631–637.

Becker WA. 1984. Manual of quantitative genetics. Pullman (WA): Academic Enterprises.

Boake CRB. 1989. Repeatability: its role in evolutionary studies of mating behaviour. Evol Ecol. 3:173–182.

Brooks R, Kemp DJ. 2001. Can older males deliver the good genes? Trends Ecol Evol. 16:308–313.

Chapman T, Liddle LF, Kalb JM, Wolfner MF, Partridge L. 1995. Cost of mating in Drosophila melanogaster is mediated by male accessory gland products. Nature. 373:241–244.

Clark DC, DeBano SJ, Moore AJ. 1997. The influence of environmental quality on sexual selection in Nauphoeta cinerea (Dictyoptera: Blaberidae). Behav Ecol. 8:46–53.

Corley LS, Blankenship JR, Moore AJ. 2001. Genetic variation and asexual reproduction in the facultatively parthenogenetic cockroach, Nauphoeta cinerea: implications for the evolution of sex. J Evol Biol. 14:68–74.

Everaerts C, Fenaux-Benderitter F, Farine JP, Brossut R. 1997. Male dominant/subordinate relationship, cuticular profiles and sex pheromones in Nauphoeta cinerea (Dictyoptera, Blaberidae). Insect Soc. 44:277–287.

Fisher HS, Rosenthal GG. 2006. Female swordtail fish use chemical cues to select well-fed males. Anim Behav. 72:721–725.

Forstmeier W, Birkhead TR. 2004. Repeatability of mate choice in the zebra finch: consistency within and between females. Anim Behav. 68:1017–1028.

Fowler K, Partridge L. 1989. A cost of mating in fruit flies. Nature. 338:760–761.

Godin JJ, Dugatkin LA. 1995. Variability and repeatability of female mating preference in the guppy. Anim Behav. 49:1427–1433.

Gray DA. 1999. Intrinsic factors affecting female choice in house crickets: time costs, female age, nutritional condition, body size and size related reproductive investment. J Insect Behav. 12:691–700.

Harris WE, Moore PJ. 2005. Female mate preference and sexual conflict: females prefer males that have had fewer consorts. Am Nat. 165:S64–S71.

Hunt J, Brooks R, Jennions MD. 2005. Female mate choice as a condition-dependent life-history trait. Am Nat. 166:79–92.

Ivy TM, Weddle CB, Sakaluk SK. 2005. Females use self-referent cues to avoid mating with previous mates. Proc R Soc Lond B Biol Sci. 272:2475–2478.

Jennions MD, Petrie M. 1997. Variation in mate choice and mating preferences: a review of causes and consequences. Biol Rev. 72: 283–327.

Johnsen TS, Zuk M. 1995. Repeatability of mate choice in female red jungle fowl. Behav Ecol. 7:243–246.

Kirkpatrick M, Ryan MJ. 1991. The paradox of the lek and the evolution of female mating preferences. Nature. 350:33–38.

Knell RJ. 1999. Sexually transmitted disease and parasite mediated sexual selection. Evolution. 53:957–961.

Kodric-Brown A, Nicoletto PF. 1997. Repeatability of female choice in the guppy: response to live and videotaped males. Anim Behav. 54: 369–376.

Kokko H, Brooks R, Jennions MD, Morely J. 2002. The evolution of mate choice and mating biases. Proc R Soc Lond B Biol Sci. 270:653–664.

Ligon JD, Zwartjes PW. 1995. Female red junglefowl choose to mate with multiple males. Anim Behav. 49:127–135.

Mays HL Jr, Hill GE. 2004. Choosing mates: good genes versus genes that are a good fit. Trends Ecol Evol. 19:554–559.

Montrose VT, Harris WE, Moore PJ. 2004. Sexual conflict and cooperation under naturally occurring male enforced monogamy. J Evol Biol. 17:443–452.

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

Moore AJ. 1990. Sexual selection and the genetics of pheromonally mediated behavior in Nauphoeta cinerea. Entomol Gen. 15: 133–147.

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

Moore AJ, Gowaty PA, Moore PJ. 2003. Females avoid manipulative males and live longer. J Evol Biol. 16:523–530.

Moore AJ, Gowaty PA, Wallin WG, Moore PJ. 2001. Sexual conflict and the evolution of female mate choice and male social dominance. Proc R Soc Lond B Biol Sci. 268:517–523.

Moore AJ, Moore PJ. 1988. Female strategy during mate choice: threshold assessment. Evolution. 42:387–391.

Moore AJ, Moore PJ. 1999. Balancing sexual selection through opposing mate choice and male competition. Proc R Soc Lond B Biol Sci. 266:711–716.

Moore AJ, Reagan NJ, Haynes KF. 1995. Conditional signalling strategies: effects of ontogeny, social experience and social status on the pheromonal signal of male cockroaches. Anim Behav. 50: 191–202.

Moore PJ, Moore AJ. 2001. Reproductive aging and mating: the ticking of the biological clock in female cockroaches. Proc Natl Acad Sci USA. 98:9171–9176.

Pitcher TE, Neff BD, Rodd FH, Rowe L. 2003. Multiple mating and sequential mate choice in guppies: female trade-up. Proc R Soc Lond B Biol Sci. 270:1623–1629.

Preston BT, Stevenson IR, Pemberton JM, Wilson K. 2001. Dominant males lose out by sperm depletion. Nature. 409:681–682.

Quader S. 2005. Mate choice and its implications for conservation and management. Curr Sci. 89:1220–1229.

Quinn G, Keough M. 2002. Experimental design and data analysis for biologists. Cambridge (UK): Cambridge University Press.

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

Ryan MJ, Perrill SA, Wilczynski W. 1992. Auditory tuning and call frequency predict population-based mating preferences in the cricket frog, Acris crepitans. Am Nat. 139:1370–1383.

Shuster SM, Wade MJ. 2003. Mating systems and strategies. Princeton (NJ): Princeton University Press.

Thrall PH, Antonovics J, Dobson AP. 2000. Sexually transmitted diseases in polygynous mating systems: prevalence and impact on reproductive success. Proc R Soc Lond B Biol Sci. 267: 1555–1563.

Torres-Vila LM, Jennions MD. 2005. Male mating history and female fecundity in the Lepidoptera: do male virgins make better partners? Behav Ecol Sociobiol. 57:318–326.

Tregenza T, Wedell N. 2000. Genetic compatibility, mate choice and patterns of parentage. Mol Ecol. 9:1013–1027.

Wagner WE Jr, Murray AM, Cade WH. 1995. Phenotypic variation in the mating preferences of female field crickets, Gryllus integer. Anim Behav. 49:1269–1281.

Wedell N, Ritchie MG. 2004. Male age, mating status and nuptial gift quality in a bushcricket. Anim Behav. 67:1059–1065.

Widemo F, Sæther S-A. 1999. Beauty is in the eye of the beholder: causes and consequences of variation in mating preferences. Trends Ecol Evol. 14:26–31.

Wyatt TD. 2002. Pheromones and animal behaviour: communication by taste and smell. Cambridge (UK): Cambridge University Press.