

# Z LINKAGE OF FEMALE PROMISCUITY GENES IN THE MOTH *UTETHEISA ORNATRIX*: SUPPORT FOR THE SEXY-SPERM HYPOTHESIS?

Vikram K. Iyengar<sup>1,2</sup> and Hudson K. Reeve<sup>3,4</sup>

<sup>1</sup>Department of Biology, Villanova University, 800 Lancaster Avenue, Villanova, Pennsylvania 19085

<sup>2</sup>E-mail: vikram.iyengar@villanova.edu

<sup>3</sup>Department of Neurobiology and Behavior, Cornell University, Ithaca, New York 14853

<sup>4</sup>E-mail: hkr1@cornell.edu

Received July 9, 2009

Accepted November 12, 2009

Female preference genes for large males in the highly promiscuous moth *Utetheisa ornatrix* (Lepidoptera: Arctiidae) have previously been shown to be mostly Z-linked, in accordance with the hypothesis that ZZ–ZW sex chromosome systems should facilitate Fisherian sexual selection. We determined the heritability of both female and male promiscuity in the highly promiscuous moth *U. ornatrix* (Lepidoptera: Arctiidae) through parent–offspring and grandparent–offspring regression analyses. Our data show that male promiscuity is not sex-limited and either autosomal or sex-linked whereas female promiscuity is primarily determined by sex-limited, Z-linked genes. These data are consistent with the “sexy-sperm hypothesis,” which posits that multiple-mating and sperm competitiveness coevolve through a Fisherian-like process in which female promiscuity is a kind of mate choice in which sperm-competitiveness is the trait favored in males. Such a Fisherian process should also be more potent when female preferences are Z-linked and sex-limited than when autosomal or not limited.

**KEY WORDS:** Fisherian sexual selection, heritability, Lepidoptera, mating preferences, promiscuity, sex chromosomes.

Sexual selection theory makes different predictions about the number of mates each sex should take to maximize lifetime reproductive success (Andersson 1994). For males, the generally small investment of both time and resources results in the best strategy being able to fertilize as many females as possible. Until recently, the opposite was widely believed to be true for females, who usually maximize their fitness by selectively taking fewer mates of high quality (Bateman 1948; Trivers 1972; Arnold and Duvall 1994). There are often significant costs associated with promiscuity (Daly 1978; Thornhill and Alcock 1983; Arnqvist 1989; Chapman et al. 1995; Hurst et al. 1995; Chapman et al. 2003), and it is not uncommon for one mating to provide sufficient sperm for a female’s lifetime output of eggs (Ridley 1988; Bezzerides 2004). Many recent studies, however, have challenged the classical view of females as strictly choosy and monogamous

(Eberhard 1996; Hughes 1998; Birkhead and Møller 1998), as female promiscuity has been observed in many species across a wide variety of taxa (Arnqvist and Nilsson 2000).

How can female promiscuity evolve? Female promiscuity is particularly prevalent in insects in which females receive nuptial gifts containing nutrients and other chemicals that increase egg production and/or offspring survival (Wiklund and Kaitala 1995; Choe and Crespi 1997; Vahed 1998). Numerous explanations based on genetic rather than phenotypic benefits to females also have been offered to explain female promiscuity (Kokko et al. 2003). For example, females that mate multiply may obtain indirect genetic benefits by increasing their odds of finding a mate of superior genetic quality (Yasui 1998; Jennions and Petrie 2000). Alternatively, Halliday and Arnold (1987) suggested that selection for extreme male promiscuity may drive female promiscuity

nonadaptively through pleiotropic gene action—in this case, one would expect to see a genetic correlation of promiscuity among brothers and sisters.

Keller and Reeve (1995) proposed another hypothesis for the evolution of female promiscuity that has remained relatively untested. They argued that female multiple mating and male sperm competitiveness can coevolve in runaway, or Fisherian, process (the sexually selected sperm, or sexy-sperm, hypothesis). Low levels of multiple mating by females can result in selection of more-competitive sperm, such that the male offspring of promiscuous females possess both sperm competitiveness genes and the female promiscuity genes. Thus, selection for sperm competitiveness will fuel the subsequent spread of the genetically correlated female promiscuity genes in a positive-feedback process akin to conventional Fisherian sexual selection in which sperm competitiveness is the male Fisherian trait and postcopulatory sperm selection (choosiness for sperm) is promoted via female promiscuity. In essence, promiscuous females gain by producing sons with more-competitive sperm.

It has recently been argued theoretically that ZZ/ZW genetic systems are especially conducive to Fisherian sexual selection when female preference genes lie on the Z chromosome (Reeve and Pfennig 2003; Kirkpatrick and Hall 2004). This occurs because females transmit their Z chromosomes to all of their sons, strengthening the genetic association between female preference genes and genes for the male traits that are targeted by those preferences; this increased correlation empowers Fisherian sexual selection. By logical extension, it follows that the sexy-sperm hypothesis also should be especially applicable to taxa with ZZ/ZW genetic systems, and that female promiscuity genes (which are analogous to female preference genes in conventional Fisherian models) should be especially likely to arise on Z chromosomes.

The moth *Utetheisa ornatrix* (Lepidoptera: Arctiidae), which, like all Lepidoptera, exhibits a ZZ/ZW sex chromosome system, is well suited for a test of the above prediction. Females are highly promiscuous over their 3–4 week life span and may take as many as 22 mates, each of whom delivers a substantial spermatophore containing both nongenetic and genetic material (Dussourd et al. 1988; LaMunyon and Eisner 1993). Females that mate multiply are known to accrue phenotypic benefits in the form of nutrient and pyrrolizidine alkaloid transmitted seminally by the male to the female in quantities proportional to his size (Dussourd et al. 1991; LaMunyon and Eisner 1994). The nutrient enhances female egg production (LaMunyon 1997) and the alkaloid provides chemical protection for herself (González et al. 1999) and her eggs (Dussourd et al. 1991). Female *U. ornatrix* do not compromise genetic benefits by mating multiply, as they are able to mate with multiple males yet use sperm selectively from the largest male (LaMunyon and Eisner 1993). Because body size is heritable (Iyengar and Eisner 1999a), females also can achieve

genetic benefits by using sperm from larger males, thereby having larger sons that are favored in courtship and larger daughters that are more fecund (Iyengar and Eisner 1999b).

Thus, female *U. ornatrix* appear to gain nutrients, chemical protection, and higher-quality offspring through promiscuity, but the possibility that they also gain sons with more-competitive sperm, in accordance with the sexy-sperm hypothesis, has not been addressed in this species. In other words, female promiscuity might benefit females through direct benefits, good genes, and Fisherian benefits simultaneously, because the corresponding sexual selection processes are not mutually exclusive and may well operate in concert in the evolution of costly female choice (Iwasa et al. 1991; Kokko et al. 2002). Indeed, direct benefits might have led to the initial evolution of multiple mating by females, setting the stage for the operation of the Fisherian sexually selected sperm mechanism that further enhances such female promiscuity. Only the sexy-sperm hypothesis entails a process that should be promoted by Z linkage of female preferences (Reeve and Pfennig 2003; Kirkpatrick and Hall 2004).

Therefore, we tested the prediction of the hypothesis that genes for female promiscuity should be especially likely to localize to the Z chromosome, as is known to be the case for the genes underlying female preferences for larger males (Iyengar et al. 2002). (Note: the Z chromosome in arctiid moths is comparable in size to autosomes and is genetically active [Traut and Marec 1997]. Because there are 30 pairs of autosomes, the Z chromosome thus appears to account for only a small fraction of the genome.) Specifically, we determined whether male and female promiscuity are inherited through the mother, father, or both parents. If female promiscuity genes localize to the Z chromosome, as predicted by the sexy-sperm hypothesis, then there should be low heritability of promiscuity between mothers and daughters, but relatively high heritability between paternal grandmothers and granddaughters because Z chromosomes are transmitted in the latter case but not the former. In addition, we tested the Halliday–Arnold nonadaptive pleiotropy hypothesis by comparing the heritability patterns for male and female heritability and examining the correlation in promiscuity between male and female siblings.

## Material and Methods

### MOTH REARING AND MATING

All *U. ornatrix* used were from laboratory colonies that were established from wild stock collected in Highlands County, FL. To ensure genetic diversity representative of that from the field, the first of the three generations of experimental moths were offspring of wild females. Larvae were reared on a pinto bean-based diet supplemented with seeds of *Crotalaria spectabilis*, a natural food plant of *U. ornatrix* (Conner et al. 1981). For any set of progeny, two groups of 8–10 larvae each were raised

under identical conditions to adulthood. Adults were weighed upon emergence and given access to a 5% honey–water solution on a sponge that was moistened daily.

All matings involved confining pairs of unrelated individuals in humidified cylindrical containers (0.35 L) in the evening, when most mating occurs in nature (Conner et al. 1981). Pairs were monitored at 6-h intervals overnight to check on mating success, as copulation lasts 10–12 h in *U. ornatrix* (LaMunyon and Eisner 1994). Each pair consisted of a focal individual (whose promiscuity we were measuring) and a randomly selected 2-, 3-, or 4-d-old opposite-sex virgin from the colony. To ensure that the focal individual's decision to mate was not caused by lack of interest by the potential partner, we monitored events in the first hour to determine that the potential female partner was receptive (indicated by her abdominal pulsing; Conner et al. 1980) or the potential male partner was actively courting (indicated by eversion of his pheromonal glands; Conner et al. 1981). We presented each focal individual with a different potential partner each night throughout his or her lifetime, recording whether or not mating occurred.

#### DAILY MATING PROBABILITY

The daily mating probability (DMP) for the focal individual was calculated by dividing the total number of matings by the number of days alive. We determined the degree to which the genetically variable components of promiscuity for each sex are inherited through both parents (i.e., autosomally) or primarily through one parent exclusively (i.e., sex-linked). To assess inheritance through the father, who may not express female promiscuity if it were sex-limited, we had to examine inheritance patterns by calculating DMPs for three generations. Families were excluded from experiment if there were fewer than four full sisters and full brothers (third generation) for whom promiscuity was measured, or any of these focal individuals lived fewer than 10 d. Within each family included in our analyses ( $n = 41$  families), DMP was assessed for four or five full sisters, four or five full brothers, their mother, their father, and their paternal grandmother.

#### STATISTICAL ANALYSES

Parent–offspring regression analyses were used to measure the heritability of promiscuity and longevity in a manner similar to that of previous work on the inheritance of physical and behavioral traits in *U. ornatrix* (Iyengar and Eisner 1999a; Iyengar et al. 2002). To estimate heritability of promiscuity in the narrow sense—that is, the proportion of phenotypic variance attributable to additive genetic effects—the DMP of offspring (the average of—four to five full sisters or the average of—four to five full brothers) was regressed on the DMP of their mother, father, and their paternal grandmother (an indication of inheritance via the father for Z-linked female traits in lepidopterans; Iyengar et al. 2002). Heritability was calculated based on the slope of the re-

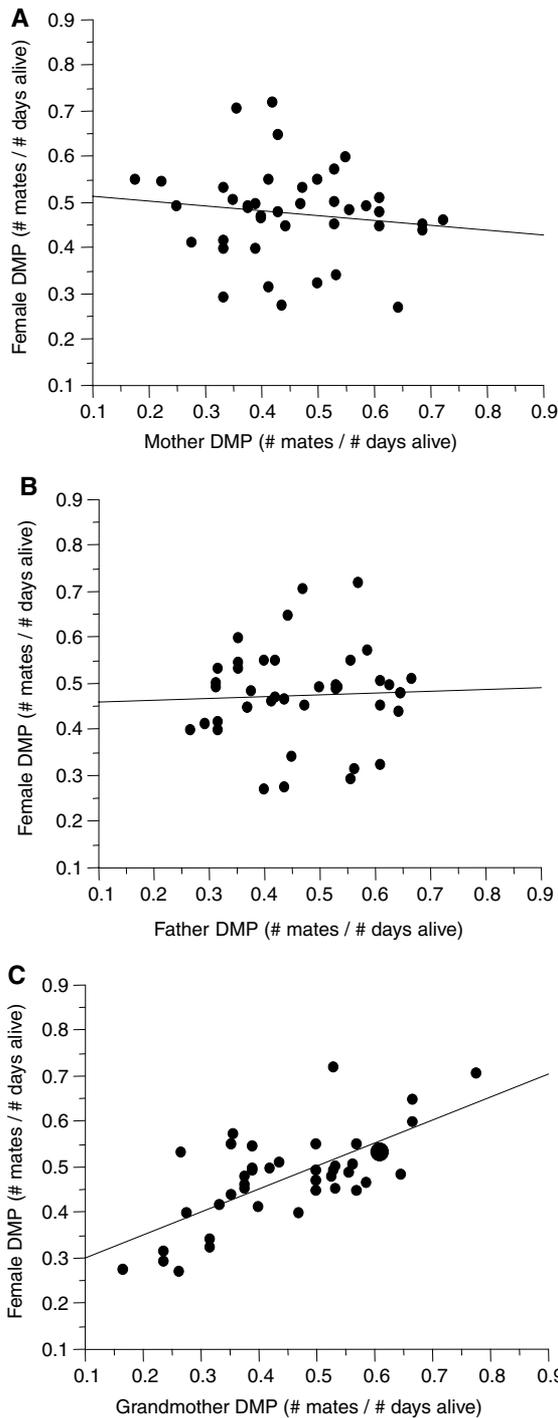
gression: twice the slope of sons or daughters on a single parent, or four times the slope of offspring on a grandparent (Lynch and Walsh 1998). However, if there was evidence of sex linkage (e.g., a significant correlation of female and paternal grandmother DMP only), the slope of the regression was multiplied by 2 rather than 4 because females share one-half of their sex chromosomes, and only one-fourth of their autosomes, with their paternal grandparents (Lynch and Walsh 1998).

The data were not transformed because they met the assumptions of normality (normal probability plot) and linearity (Lowess test). Furthermore, there was no need to adjust regression coefficients or standard errors for unequal variances because the variances were not significantly different for all comparisons (two-tailed variance ratio test,  $P > 0.25$  for all comparisons). Heritabilities (regression slopes) were compared using analyses of covariance (ANCOVAs; Lynch and Walsh 1998). Such regression analyses are necessary to determine whether a trait is sex-linked or subject to maternal effects, and are essential in discriminating among the competing hypotheses regarding the evolution of promiscuity.

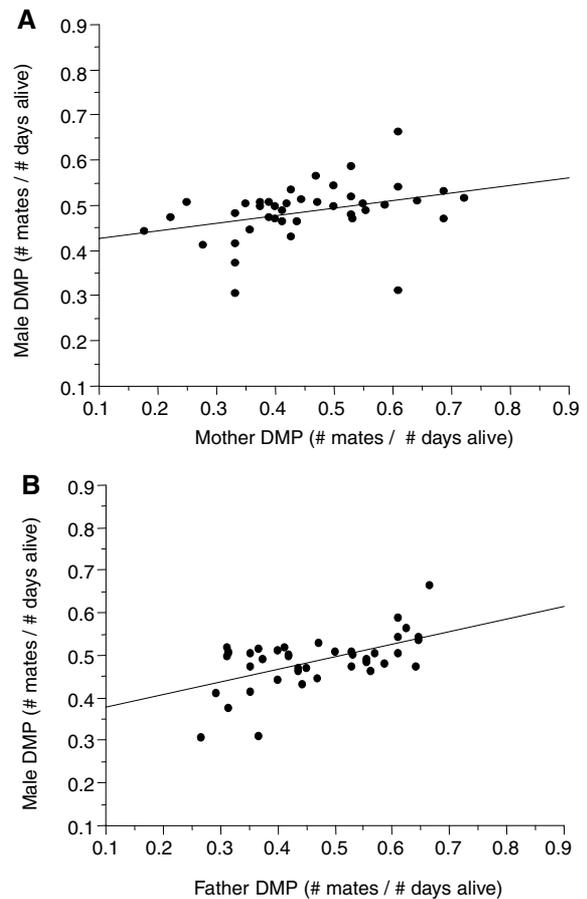
## Results

The DMPs of females did not significantly correlate with those of their mothers, indicating that female promiscuity not inherited from the mother (Fig. 1A). The DMPs of females also did not correlate with those of their fathers (Fig. 1B) or their brothers ( $R^2 = 0.003$ ;  $F_{1,39} = 0.119$ ;  $P = 0.7324$ ). Additionally, there were no differences between female inheritance of promiscuity from their father versus their mother (ANCOVA:  $F_{1,78} = 0.597$ ,  $P = 0.4422$ ). Although the lack of heritability from father to daughter indicates that promiscuity is not inherited through the father, the DMPs of females and their paternal grandmothers were significantly positively correlated (Fig. 1C). Furthermore, the heritability of female–paternal grandmother DMP was significantly different from those of both female–mother (ANCOVA:  $F_{1,78} = 17.003$ ,  $P < 0.0001$ ) and female–father (ANCOVA:  $F_{1,78} = 8.946$ ,  $P = 0.0037$ ). These results together indicate that female promiscuity is sex-linked and sex-limited, that is, females inherit promiscuity from their paternal grandmothers via the Z sex-chromosomes of their fathers.

The DMPs of males were significantly positively correlated with those of both their mothers and their fathers (Fig. 2). These heritabilities were significantly greater than zero but not different from each other (ANCOVA:  $F_{1,78} = 1.554$ ,  $P = 0.2163$ ), indicating that male promiscuity is not sex-limited and inherited either autosomally or from the Z chromosomes or both. We also conducted additional comparisons to determine the pattern of gene transmission, and found marginal but nonsignificant differences between father–son and father–daughter heritabilities (ANCOVA:



**Figure 1.** Mean daily mating preference (DMP) of females (four to five full sisters) plotted as a function of the DMP of their mother (A), father (B), and paternal grandmother (C) for 41 families. The DMP values of females are not correlated with those of their mothers ( $R^2 = 0.019$ ;  $F_{1,39} = 0.7337$ ;  $P = 0.3969$ ;  $y = 0.522 - 0.106x$ ) or their fathers ( $R^2 = 0.002$ ;  $F_{1,39} = 0.0710$ ;  $P = 0.7913$ ;  $y = 0.458 + 0.036x$ ). However, the MPI values of females and their paternal grandmothers are positively correlated ( $R^2 = 0.478$ ;  $F_{1,39} = 35.72$ ;  $P < 0.0001$ ;  $y = 0.249 + 0.505x$ ), indicating that female promiscuity is sex-linked and paternally inherited ( $h^2 = 1.009 \pm 0.168$  [mean  $\pm$  S.E.]).



**Figure 2.** Mean daily mating preference (DMP) of males (4–5 full brothers) plotted as a function of the DMP of their mother (A) and father (B) for 41 families. The DMP values of males is positively correlated with those of their mothers ( $R^2 = 0.1199$ ;  $F_{1,39} = 5.3141$ ;  $P = 0.0266$ ;  $y = 0.408 + 0.169x$ ;  $h^2 = 0.338 \pm 0.146$  [mean  $\pm$  S.E.]) and their fathers ( $R^2 = 0.3084$ ;  $F_{1,39} = 17.3886$ ;  $P = 0.0002$ ;  $y = 0.347 + 0.297x$ ;  $h^2 = 0.585 \pm 0.142$  [mean  $\pm$  S.E.]).

$F_{1,78} = 2.883$ ,  $P = 0.0935$ ) and mother–son and mother–daughter heritabilities (ANCOVA:  $F_{1,78} = 3.669$ ,  $P = 0.0591$ ).

### Discussion

The high degree of female promiscuity in *U. ornatrix* provided the opportunity to distinguish among hypotheses regarding the evolution of multiple mating by females. One such hypothesis proposes the female promiscuity evolves through pleiotropic effects and selection for male promiscuity (Halliday and Arnold 1987). The sexy-sperm hypothesis suggests an alternative mechanism for the evolution of female promiscuity in which female multiple mating and male sperm competitiveness coevolve in a runaway, or Fisherian, process (Keller and Reeve 1995). Under this scenario, one would predict that the genes responsible for female promiscuity would be especially likely to accumulate on the Z chromosome, which is only inherited through fathers, as Z-linked female promiscuity genes should strengthen the genetic

correlation that empowers the Fisherian positive-feedback process (Reeve and Pfennig 2003; Kirkpatrick and Hall 2004).

In this study, we investigated the inheritance of both male and female promiscuity in *U. ornatrix*. We found that male promiscuity is inherited from both parents, as the father–son and mother–son heritabilities were both significantly positive and not significantly different from each other, as would be expected if the underlying genes were not sex-limited in origin and localized to either autosomes or Z chromosomes. Female promiscuity, on the other hand, is not inherited in the same manner. In fact, the promiscuity of females resembled their paternal grandmothers, but not their fathers, mothers, or brothers, as expected if the underlying genes are sex-limited and Z-linked. Indeed, the heritability of female promiscuity from the paternal grandmother is significantly higher than those from all other relatives measured. In sum, all of our data were most consistent with the conclusions that (1) female promiscuity is influenced by mostly by Z-linked sex-limited genes, and (2) male promiscuity is influenced only by non-sex-limited genes of either autosomal or sex-linked origin (see Appendix for a detailed discussion of how our heritability pattern is explained by (A1) and (A2)).

The distinctness of the sets of genes underlying male and female promiscuity, and the lack of male–female sibling correlations in promiscuity, do not support the hypothesis that male promiscuity evolves as a nonadaptive byproduct of selection on female promiscuity (Halliday and Arnold 1987). Furthermore, it is highly unlikely that the genes for female promiscuity localized on the Z chromosome simply due to chance, as the Z chromosome is comparable in size to autosomes (Traut and Marec 1997) and makes up only 3% of the moth's genome (arctiid moths typically have 31 pairs of chromosomes; Sharma 1999). Another potential mechanism driving sex differences in inheritance patterns is genomic imprinting, in which alleles are conditionally expressed depending upon the parent from which they are inherited (Day and Bonduriansky 2004). There is no evidence for simple patterns of genomic imprinting in our study, however, because mother–daughter heritability was not different from father–daughter, nor was father–son heritability different from mother–son. Finally, we found no support for the presence of maternal effects, as we did not find any correlation between the promiscuity of mothers and daughters.

However, the genetic pattern is consistent with the prediction of the sexy-sperm hypothesis that female promiscuity and male sperm competitiveness can coevolve through a Fisherian process and is especially likely to apply to species with ZZ/ZW sex chromosomes, as in the Lepidoptera. Indeed, the widespread occurrence of high female promiscuity in the Lepidoptera (Drummond 1984) may be a reflection of such a genetic bias toward Fisherian promiscuity evolution throughout this taxon (V. K. Iyengar, H. K. Reeve, T. Eisner, unpubl. ms. ). A necessary and testable prediction of this hypothesis is that increased opportunity for multiple

mating should increase the sperm competitiveness of the sons resulting from such matings, as has been indicated for flour beetles (Bernasconi and Keller 2001).

#### ACKNOWLEDGMENTS

We wish to thank T. Eisner for his inspiration and his keen insight into the natural world. We also greatly appreciate the efforts of Dr. M. Deyrup, who made this project possible by collecting moths at the Biological Station in Florida. We are also grateful to undergraduate students S. Desai, L. Ly, and D. O'Shea for their assistance in maintaining the moth colonies at Villanova. VKI was financially supported during this period by a Summer Research Fellowship from Villanova University, and the research was funded by Research Initiation Grant 0720018 from the National Science Foundation.

#### LITERATURE CITED

- Andersson, M. 1994. Sexual selection. Princeton Univ. Press, Princeton, NJ.
- Arnold, S. J., and D. Duvall. 1994. Animal mating systems: a synthesis based on selection theory. *Am. Nat.* 143:317–348.
- Arnqvist, G. 1989. Multiple mating in a water strider: mutual benefits or intersexual conflict? *Anim. Behav.* 38:749–756.
- Arnqvist, G., and T. Nilsson. 2000. The evolution of polyandry: multiple mating and female fitness in insects. *Anim. Behav.* 60:145–164.
- Bateman, A. J. 1948. Intrasexual selection in *Drosophila*. *Heredity* 2:349–368.
- Bernasconi, G., and L. Keller. 2001. Female polyandry affects their sons' reproductive success in the red flour beetle *Tribolium castaneum*. *J. Evol. Biol.* 14:186–193.
- Bezzerides, A. 2004. Phenotypic and genetic benefits of promiscuity in an arctiid moth (*Utetheisa ornatrix*). Ph.D. dissertation. Cornell Univ., Ithaca, NY.
- Birkhead, T. R., and A. P. Møller. 1998. Sperm competition and sexual selection. Academic Press, San Diego, CA.
- Chapman, T., L. F. Liddle, J. M. Kalb, M. F. Wolfner, and L. Partridge. 1995. Cost of mating in *Drosophila melanogaster* females is mediated by male accessory gland products. *Nature* 373:241–244.
- Chapman, T., G. Arnqvist, J. Bangham, and L. Rowe. 2003. Sexual conflict. *Trends Ecol. Evol.* 18:41–47.
- Choe, J. C., and B. J. Crespi. 1997. The evolution of mating systems in insects and arachnids. Cambridge Univ. Press, Cambridge, U.K.
- Conner, W. E., T. Eisner, R. K. Vander Meer, A. Guerrero, D. Ghiringelli, and J. Meinwald. 1980. Sex attractant of an arctiid moth (*Utetheisa ornatrix*): a pulsed chemical signal. *Behav. Ecol. Sociobiol.* 7:55–63.
- Conner, W. E., T. Eisner, R. K. Vander Meer, A. Guerrero, and J. Meinwald. 1981. Precopulatory sexual interaction in an arctiid moth (*Utetheisa ornatrix*): role of a pheromone derived from dietary alkaloids. *Behav. Ecol. Sociobiol.* 9:227–235.
- Daly, M. 1978. The cost of mating. *Am. Nat.* 112:771–774.
- Day, T., and R. Bonduriansky. 2004. Intralocus sexual conflict can drive the evolution of genomic imprinting. *Genetics* 167:1537–1564.
- Drummond, B. A. 1984. Multiple mating and sperm competition in the Lepidoptera. Pp. 291–270 in R. L. Smith, ed. *Sperm competition and the evolution of animal mating systems*. Academic Press, New York, NY.
- Dussourd, D. E., K. Ubik, C. Harvis, J. Resch, J. Meinwald, and T. Eisner. 1988. Biparental defensive endowment of eggs with acquired plant alkaloid in the moth *Utetheisa ornatrix*. *Proc. Natl. Acad. Sci. USA* 85:5992–5996.
- Dussourd, D. E., C. A. Harvis, J. Meinwald, and T. Eisner. 1991. Pheromonal advertisement of a nuptial gift by a male moth (*Utetheisa ornatrix*). *Proc. Natl. Acad. Sci. USA* 88:9224–9227.

- Eberhard, W. G. 1996. Female control: sexual selection by cryptic female choice. Princeton Univ. Press, Princeton, NJ.
- González, A., C. Rossini, M. Eisner, and T. Eisner. 1999. Sexually transmitted chemical defense in a moth (*Utetheisa ornatrix*). Proc. Natl. Acad. Sci. USA 96:5570–5574.
- Halliday, T. R., and S. J. Arnold. 1987. Multiple mating by females: a perspective from quantitative genetics. Anim. Behav. 35:939–941.
- Hughes, C. 1998. Integrating molecular techniques with field methods in studies of social behavior: a revolution results. Mol. Ecol. 79:383–399.
- Hurst, G. D. D., R. G. Sharpe, A. H. Broomfield, L. E. Walker, T. M. O. Majerus, I. A. Zakharov, and M. E. N. Majerus. 1995. Sexually transmitted disease in a promiscuous insect, *Adalia bipunctata*. Ecol. Entomol. 20:230–236.
- Iwasa, Y., A. Pomiankowski, and S. Nee. 1991. The evolution of costly mate preferences II. The ‘handicap’ principle. Evolution 45:1431–1442.
- Iyengar, V. K., and T. Eisner. 1999a. Heritability of body mass, a sexually selected trait, in an arctiid moth (*Utetheisa ornatrix*). Proc. Natl. Acad. Sci. USA 96:9169–9171.
- . 1999b. Female choice increases offspring fitness in an arctiid moth (*Utetheisa ornatrix*). Proc. Natl. Acad. Sci. USA 96:15013–15016.
- Iyengar, V. K., H. K. Reeve, and T. Eisner. 2002. Paternal inheritance of a female moth’s mating preference. Nature 419:830–832.
- Jennions, M. D., and M. Petrie. 2000. Why do females mate multiple? A review of the genetic benefits. Biol. Rev. 75:21–64.
- Keller, L., and H. K. Reeve. 1995. Why do females mate with multiple males? The sexually-selected sperm hypothesis. Adv. Stud. Behav. 24:291–315.
- Kirkpatrick, M., and D. W. Hall. 2004. Sexual selection and sex linkage. Evolution 58:683–691.
- Kokko, H., R. Brooks, M. D. Jennions, and J. Morley. 2003. The evolution of mate choice and mating biases. Proc. R. Soc. Lond. B 342:335–352.
- Kokko, H., R. Brooks, J. M. McNamara, and A. I. Houston. 2002. The sexual selection continuum. Proc. R. Soc. Lond. B 269:1331–1340.
- LaMunyon, C. W. 1997. Increased fecundity, as a function of multiple mating, in an arctiid moth, *Utetheisa ornatrix*. Ecol. Entomol. 22:69–73.
- LaMunyon, C. W., and T. Eisner. 1993. Postcopulatory sexual selection in an arctiid moth (*Utetheisa ornatrix*). Proc. Natl. Acad. Sci. USA 90:4689–4692.
- . 1994. Spermatophore size as determinant of paternity in an arctiid moth (*Utetheisa ornatrix*). Proc. Natl. Acad. Sci. USA 91:7081–7084.
- Lynch, M., and B. Walsh. 1998. Genetics and analysis of quantitative traits. Sunderland Associates, Sunderland, MA.
- Reeve, H. K., and D. W. Pfennig. 2003. Genetic biases for showy males: are some genetic systems especially conducive to sexual selection? Proc. Natl. Acad. Sci. USA 100:1089–1094.
- Ridley, M. 1988. Mating frequency and fecundity in insects. Biol. Rev. Camb. Philos. Soc. 63:509–549.
- Sharma, V. L. 1999. Chromosome studies on two species of moths. Bionature 19:65–67.
- Thornhill, R., and J. Alcock. 1983. The evolution of insect mating systems. Harvard Univ. Press, Cambridge, MA.
- Traut, W., and F. Marec. 1997. Sex chromosome differentiation in some species of Lepidoptera (Insecta). Chromosome Res. 5:283–291.
- Trivers, R. L. 1972. Parental investment and sexual selection. Pp. 136–179 in B. Campbell, ed. Sexual selection and the descent of man. Aldine Publishing Co., London, U.K.
- Vahed, K. 1998. The function of nuptial feeding in insects: a review of empirical studies. Biol. Rev. Camb. Philos. Soc. 73:43–78.
- Wiklund, C., and A. Kaitala. 1995. Sexual selection for large male size in a polyandrous butterfly: the effect of body-size on male versus female reproductive success in *Pieris napi*. Behav. Ecol. 6:6–13.

- Yasui, Y. 1998. The genetic benefits of female multiple mating reconsidered. Trends Ecol. Evol. 13:246–250.

Associate Editor: G. Arnqvist

## Appendix

Let  $m$  represent the mother,  $f$  the father,  $d$  the daughter, and  $s$  the son. We shall derive the measured heritabilities of promiscuity expected if, as claimed, (A1) female promiscuity is influenced by both non-sex-limited autosomal or Z-linked genes with phenotypic effects denoted by  $A$  and by sex-limited Z-linked genes with phenotypic effects denoted by  $Z$  ( $A$  being uncorrelated to  $Z$ ), each having proportionate phenotypic weights  $(1 - z)$  and  $z$ , respectively, and (A2) male promiscuity is influenced only by the non-sex-limited autosomal or Z-linked genes ( $A$ ).

Father–daughter heritability is equal to

$$2 \frac{\text{cov}[A_f, (1 - z)A_d + zZ_d]}{\text{var}[A_f]} = 2 \frac{(1 - z)\text{cov}[A_f, A_d]}{\text{var}[A_f]} \quad (\text{A1})$$

(because  $A$  and  $Z$  are uncorrelated).

Father–son heritability is equal to

$$2 \frac{\text{cov}[A_f, A_s]}{\text{var}[A_f]} \quad (\text{A2})$$

Thus, a weaker father–daughter than father–son heritability is expected if  $z > 0$ , as we observed.

Mother–daughter heritability is equal to

$$\begin{aligned} & 2 \frac{\text{cov}[(1 - z)A_m + zZ_m, (1 - z)A_d + zZ_d]}{\text{var}[(1 - z)A_m + zZ_m]} \\ &= 2 \frac{z^2 \text{cov}[Z_m, Z_d] + (1 - z)^2 \text{cov}[A_m, A_d]}{\text{var}[(1 - z)A_m + zZ_m]} \\ &= 2 \frac{(1 - z)^2 \text{cov}[A_m, A_d]}{\text{var}[(1 - z)A_m + zZ_m]} \quad (\text{A3}) \end{aligned}$$

because  $A$  and  $Z$  are uncorrelated and  $\text{cov}[Z_m, Z_d] = 0$  (because mothers cannot transmit  $Z$  chromosomes to daughters).

Mother–son heritability is equal to

$$2 \frac{\text{cov}[(1 - z)A_m + zZ_m, A_s]}{\text{var}[(1 - z)A_m + zZ_m]} = 2 \frac{(1 - z)\text{cov}[A_m, A_s]}{\text{var}[(1 - z)A_m + zZ_m]} \quad (\text{A4})$$

It follows from a comparison of (A3) and (A4) that mother–son heritability will be stronger than mother–daughter heritability, as observed. In fact, if  $z$  is close to one, the mother–daughter heritability will be very close to zero. Under the latter condition, the mother–son heritability (A4) is also likely to be weaker than the father–son heritability, also as observed.

Thus, all of our heritability patterns are consistent with the idea that both  $A$  and  $Z$  genes exist, but that the  $Z$  genes have a much higher phenotypic contribution than do the  $A$  genes to promiscuity in females.