FROM FLIES TO MICE—AND BACK AGAIN

DONALD A. DEWSBURY*

As the laws of nature must be the same for all beings, the conclusions furnished by this group of insects must be applicable to the whole organic world...

Henry Walter Bates, 1910, p. 348

SYNOPSIS

Our goal in science is to generate principles of generality. Information on insects has been important in the development of our program of research on rodent reproductive behavior; I hope that the reverse effect might also be realized. Mammalian copulatory patterns can be classified with respect to locking, thrusting, multiple intromissions, and multiple ejaculations; application of a similar classification scheme might be useful with insects. In both insects and rodents variation in male genitalia and accessory glands appear correlated with reproductive behavior. Patterns of sperm competition are focal to the evolution of mating systems. Because there are important species differences in sperm competition, detailed study of both the basic pattern and the dynamics of sperm competition in a variety of species is warranted. There is evidence for female mate choice in both insects and rodents. Further, in both insects and rodents the capacity of males to produce ejaculates is limited; this implies a role for male choice in mate selection. Principles of the greatest generality will be developed if investigators can synthesize information from a wide range of taxa.

Our goal in developing a science of behavior is to elucidate principles of broad generality. Such principles ought to be applicable, with appropriate caution, across a wide range of taxa. However, there is an increasing trend in the biological sciences for students of different groups of animals to isolate themselves from other such groups. I believe that such isolation is detrimental to the search for general principles and that there is much to be gained by efforts to break down such barriers. Hopefully, the result will be hybrid vigor—not hybrid sterility.

I am a student of the evolution of mammalian reproductive behavior. However, one of my trade secrets is that many of my research ideas have come from the insect literature. In many respects the insect literature is ahead of that on mammals. This may be because of the short generation time of most insects, the low cost of maintenance, and the enormous diversity of biological material. Nevertheless, there may be some areas in which entomologists might benefit from considering the mammalian literature. I shall explore some parallels between the reproductive behavior of rodents and insects, some examples of cross fertilization, and some possibilities for future cross fertilization.

---

*Donald A. Dewsbury is Professor of Psychology at the University of Florida. He received his Ph.D. from the University of Michigan in 1965 and is a Past-President of the Animal Behavior Society His research is focused on the evolution of mammalian reproductive behavior. Address: Department of Psychology, University of Florida, Gainesville, Florida, 32611.

Patterns of Copulatory Behavior

We begin with the matters of description and classification. I have reviewed the mammalian literature and proposed that mammalian patterns can be classified according to four criteria: locking, thrusting, multiple intromissions and multiple ejaculations (Dewsbury 1972). I know of no similar effort for insects but I believe that such a system might usefully be employed.

A lock is a mechanical tie between the male and female genitalia and is found in such mammalian species as dogs, short-tailed shrews, golden mice, and grasshopper mice (Dewsbury 1972). Analogous genital locking is found in insects as well. Most notable are the locks of the familiar Florida love bug that last an average of 56 h (Thornhill 1976).

Whereas many mammalian species, such as virtually all primates, display intravaginal thrusting, many others cease thrusting when insertion is achieved. Descriptions of such post-insertion thrusting appear less common for insects but thrusting does occur in various species such as giant water bugs (Smith 1980), damselflies (Waage 1979), and crickets (Loher and Rence 1978).

In many species of rodents and primates there is a pattern of multiple intromissions prior to ejaculation. Typically, the male repeatedly mounts the female, gains insertion, and dismounts without ejaculating. Such multiple intromissions are prerequisite to ejaculation. I know of no comparable pattern in insects.

Finally, whereas the copulatory activity of a male-female pair in some mammalian species is terminated with the occurrence of the first ejaculation, in other species pairs continue to copulate for several ejaculations. Repeated copulations are common in some insect species, such as giant water bugs (Smith 1980). The most dramatic example of a single ejaculation species is the honey bee, in which males make a "suicidal" donation of the genitalia as a "plug" and die soon thereafter (Michener 1974).

With such a system we can classify copulatory patterns and search for evolutionary trends. Similar systems could be developed for a variety of taxa.

A notable characteristic of insect copulatory patterns is the ability to alter copulation duration. For example, in the southern green stink bug copulation ranges from 5 minutes to 14 days (McLain 1980). Mammalian species appear much less variable in this regard. Perhaps copulation duration is more "hard wired" in mammals than in some insects!

Anatomy

Taxonomists of both insects and mammals have used the structure of male genitalia as important characters in classification. As noted by Lloyd (1979) such characters may be used to predict behavioral variability.

Fortunately, Emmet Hooper and his associates (e.g., Hooper & Musser 1964) did a thorough job of describing penile anatomy in the rodents of the superfamily Muroidea. A decade ago we noted that variations in penile anatomy were correlated with behavioral variability. In species in which males either lock or thrust (and which have a "simple" glans penis) the glans is thicker, relative to length, than in other species (Dewsbury 1974,

1975). Further, the spines that line the glans surface are enlarged in locking species. In the decade since this proposal we have studied additional species and successfully predicted other copulatory patterns from penile anatomy. We also noted that males that lock possess a reduced complement of accessory glands in the reproductive tract.

The males of most rodent species deposit a copulatory plug with each ejaculate (Hartung and Dewsbury 1978, Baumgardner et al. 1982). Interestingly, locking species, with their reduced reproductive tracts, deposit no such plugs. Males of nonlocking species also have penile spines. We have proposed that they, together with the multiple intromission pattern described earlier, function in removing plugs and sperm—sometimes those of other males (Dewsbury 1981a).

In conducting these analyses we marched in parallel with developments on insects. In insects, coupling is mediated by a bewildering array of mandibles, genital claspers, antennae, and modified legs (Wing et al. 1983). In some butterflies a product of the male accessory glands appears to cement the pair together (Leopold 1976). In *Lytta nuttalli* specialized dorsal and ventral penile spines catch onto folds in the vaginal wall to maintain coupling (Gerber et al. 1972).

Males of many insect species deposit a copulatory plug. Often these are the remnants of spermatophores, as in *Pteroptyx* fireflies (Wing et al. 1983). The reproductive tracts of some insect species are simplified in ways parallel to those of rodents. However, whereas in rodents it is species with long copulations (i.e., locks) that have simplified tracts, in insects it appears to be those with brief copulations. This may be because, in insects, long copulations are associated with the passage of complex accessory gland secretions (Gerber et al. 1971, Wing 1984).

Male insects too are adapted to remove plugs and sperm from the female tract. Most dramatic are the specialized adaptions for sperm removal of the damselfly penis described by Waage (1979, 1983). Lloyd (1979) wrote of a "veritable Swiss Army knife of gadgetry" in insect anatomy designed to function in such a context.

Clearly, in both insects and rodents, reproductive behavior and anatomy have evolved interactively. The adaptations of rodents and insects often appear parallel.

SPERM COMPETITION

Among the very few papers most influential to the development of our research program was G. A. Parker's (1970) "Sperm Competition and its Evolutionary Consequences in the Insects." With that paper, Parker both provided a basis for interpreting many curious patterns of insect reproductive behavior and stimulated students of other taxa to study analagous phenomena. Parker defined sperm competition as "the competition within a single female between the sperm from two or more males for the fertilization of ova" (p. 527). The species-typical pattern of sperm competition is of great importance to the evolution of mating strategies. Females may manipulate sperm and males must compete within rules set by females (Lloyd 1979).

To study sperm competition, one needs to determine the paternity of the offspring resulting from an episode of copulatory activity. In insects this

has generally been done either with marker genes or by sterilizing one of two males so that the eggs that do not hatch are assumed to be sired by him. One must control for the order of mating by the two males, the timing of the matings, and the differential fertilizing capacity of the sperm from the males of the two genotypes. The most common result of insect studies is that the last male to copulate enjoys a differential advantage. However, there are many species with a first-male advantage, such as *Culicoides melleus* (Linley 1975), the parasitic wasp *Nansonia vitripennis* (Holmes 1974), and the southern green stink bug (McLain 1980). Gwynne (1984) interprets this variability in relation to the pattern of non-promiscuous mating efforts and/or parental effort characteristic of the males of each species. Similarly, Smith (1980) noted that a last male advantage is to be expected in species, such as giant water bugs, in which there is appreciable paternal investment. If males are to make a large paternal investment, it is critical that it be for their own offspring.

Although Parker predicted minimal sperm competition in mammals, there is good evidence of multiple-male copulations by female rodents in the field and we were stimulated to investigate the phenomenon (Dewsbury 1984). We have used marker geses affecting both coat color and transferrin, as assessed with electrophoresis. In one series of studies, females mated with each of two males for an equal number of ejaculations with the timing and order of mating controlled. In several studies we have found no order effects in either deer mice or laboratory rats. It did not matter whether a male was the first or last to ejaculate. Clearly, plugs do not prevent subsequent inseminations. By contrast, Levine (1967) found a first-male advantage in house mice. There is some indication of a last-male advantage in golden hamsters, although caution must be used in interpreting these results (Oglesby et al., 1981). We found a last-male advantage in prairie voles (Dewsbury and Baumgardner 1981). Prairie voles appear to display substanial male paternal investment and appear sometimes monogamous in the field (Getz and Carter 1980). Whether this correlation between sperm competition pattern and male investment will prove general must be determined by future data.

The pattern of sperm competition is one of the most important characteristics of the reproductive system of any species. Yet it is known for too few species. In their recent book, Thornhill and Alcock (1983) repeatedly used phrases like "Suppose we assume a 'last-male-to-mate advantage'," (p. 249), "If sperm precedence occurs" (p. 261), and "We shall assume that it occurs" (p. 334) in interpreting insect mating patterns. It is critical that more basic studies of sperm competition be conducted in insects.

More research on the dynamics of sperm competition would also be of interest. In rodents, we have found that the relative number of ejaculates deposited by two males is critical in determining litter composition. Imposition of a two-hour delay between males was found to have little effect. However, it appears that a male deer mouse can essentially cancel another male's ejaculate by mating with the same female within one minute—presumably by disrupting sperm transport. Detailed studies of such dynamics can provide a more solid basis for understanding the pressures affecting the evolution of mating systems.

FEMALE CHOICE

Charles Darwin (1871) distinguished between natural selection and sexual selection, selection for traits that increase an individual's success in getting mates. Darwin proposed two components: intrasexual selection, generally male-male competition, and female choice. His logic was summarized by Thornhill (1980a) and has generally been accepted by most biologists. In contemporary terms, it is the difference in parental investment (Trivers 1972) that is responsible for the pattern of "ardent" males and "coy" females. As reviewed by Thornhill, male-male competition has often been studied, although I might add that the full consequences have not always been fully documented (Dewsbury 1982a). Female choice has been more difficult to demonstrate. Thornhill's concerns related to 1) the nature of the evidence of female choice, 2) the view that those traits that may be preferred appear unrelated to fitness, and 3) that choice may not be heritable.

There is much evidence suggestive of female choice in insects. For example, Thornhill (1980b) showed that female hangingflies appear to prefer males with prey of an optimal size. The benefit to the female is well documented. Borgia (1981) demonstrated choice by female dung flies, for large males and related it to 1) reduced harm in struggles, 2) more rapid copulation and oviposition, and 3) ability to escape danger during copulation. Partridge (1980) showed that female fruitflies permitted to choose among males produced offspring that were more fit in tests of intraspecific competition than did females not permitted to choose. Mate choice in the two-spot ladybird appears heritable (Majerus et al. 1982).

The methodological problems outlined by Thornhill (1980a) are important. If preference is tested in a naturalistic situation one cannot be certain that association is due to true female choice rather than male coercion or some other factor. If choice is tested in artifical situations greater control is possible, but the very artificiality is open to criticism. Our approach is one of convergent methodologies. We are trying to study mate choice in a variety of situations in the hope that consistent findings will be generated. In a semi-natural enclosure, for example, female deer mice approach dominant males more frequently than subordinate males (Dewsbury 1981b). However, this could be because dominant males tend to be quite active and accessible, whereas subordinates often appear to be hiding. We are currently studying female choice in a small cage with the dominant and subordinate males anesthetized. Should the results of both situations be consistent, we believe we will have a strong case for female choice.

We have also studied female choice in a test chamber in which two males are tethered at opposite ends. Female prairie voles, but not female montane voles, prefer to mate with a male with which they have copulated previously rather than a novel male. The experience of copulation appears to "stamp in" a preference in the monogamous species, prairie voles, but not the non-monogamous species, montane voles. An analagous effect of mating experience on female choice has been found in *Drosophila* (Pruzan 1976, O'Hara et al. 1976).

MALE CAPACITY AND MALE CHOICE

Much biological thought appears to indicate that in promiscuous species the cost of sperm is trivial and male choice should be nonexistent (e.g., Bateman 1948; Dawkins 1976). We have argued that the correct unit for consideration is the ejaculate, and that males are limited in their capacity to produce ejaculates (Dewsbury 1982b). This limitation suggests the existence of some degree of male choice even in promiscuous species.

Rutowski (1982a) drew similar conclusions from his studies of moths and butterflies: "Because males are limited in their ability to make these secretions they also should be selective in whom they court and inseminate" (p. 78). There are numerous demonstrations in insects of the limited ability of males to produce ejaclates; examples include oriental fruit moths (George and Howard 1968), mosquitoes (Jones 1973), fruitflies (Markow et al. 1978), and spruce budworms (Outram 1971). There is also evidence of male selectivity in mate choice. For example, in the white checkered butterfly, males selectively court young and large females and this appears adaptive (Rutowski 1982b). Male Mormon crickets, which produce large spermatophores, reject many potential mates, preferring more fecund females (Gwynne 1981).

We reasoned that male voles ought to mate preferentially with unmated rather than mated females. By so doing, they could avoid the certain consequences of sperm competition. We studied the preference of male voles for tethered mated versus unmated females. Male prairie voles spent more time with and copulated more with unmated rather than mated females. Because such differences could be due in part to active female resistance by mated females we repeated the study with the two females anesthetized and obtained similar results. Although male prairie voles preferred to mate with unmated females, there was no such preference in montane voles. In another study we permitted one male vole to copulate with one, two, or four receptive females. As might be expected, prairie vole males tended to concentrate their copulations on a smaller number of females, whereas montane voles mated less selectively (Fuentes and Dewsbury 1984).

Recency of mating is also a factor in male choice in insects. Male *Drosophila melanogaster* preferentially court virgin rather than inseminated females, even when the females are decapitated and do not extrude their genitalia (Cook and Cook 1975), Virgin females emit pheromones that stimulate males to court; males produce a pheromone that inhibits courtship (Tompkins and Hall 1981a, 1981b). Male flour beetles prefer virgin to fertilized females (Graur and Wood 1982).

The large investments by male insects in spermatophores are of nutritional benefits to the females (e.g., Boggs 1981, Boggs & Gilbert 1979). In rodents sperm not involved in fertilization may function in facilitating embryo development (Chaykin and Watson 1983, Watson et al. 1983).

Male newts that have mated repeatedly and have a reduced capacity to produce spermatophores also decrease the intensity of their courtship displays and thus might be termed "honest salesmen" (Halliday and Houston 1978). Rutowski (1979) argued for a similar phenomenon in the checkered white butterfly. Although mosquitoes appear "honest" (Jones 1973) (and may not even resume courting when supplies have recuperated), species such

as coddling moths (Howell et al. 1978) and spruce budworms (Outram 1971) appear less honest.

Although we found that the sperm counts of male deer mice in successive ejaculates within a session became progressively lower, we could not get males to deliver numbers of ejaculates in a range where the decreased sperm counts would have functional consequences for pregnancy initiation or sperm competition. We termed male deer mice "honest ejaculators" (Dewsbury & Sawrey 1984).

CONCLUSION

Our quest is for principles of generality. In this quest we should employ whatever information appears useful, whatever the source. Our research program on rodents has profited from some knowledge of research on insects. There are some striking similarities and some important differences in the patterns of copulatory behavior, anatomy, sperm competion, female choice, and male capacity and choice in insects and rodents. My hope is that students of insect behavior might learn something of interest from our studies of rodents. If Henry Walter Bates was correct that the laws of nature must be the same for all beings then the applicability of conclusions from rodents, like those from insects, may be quite broad.

ACKNOWLEDGMENTS

LITERATURE CITED

BATEMAN, A. J. 1948. Intra-sexual selection in *Drosophila*. Heredity 2: 349-68.

BATES, H. W. 1910. The naturalist on the River Amazons. John Murray, London.

BAUMGARDNER, D. J., T. G. HARTUNG, D. K. SAWREY, D. G. WEBSTER, AND D. A. DEWSBURY. 1982. Muroid copulatory plugs and female reproductive tracts: A comparative investigation. J. Mammal. 63: 110-17.

BOGGS, C. L. 1981. Selection pressures affecting male nutrient investment at mating in Heliconiine butterflies. Evolution 35: 931-40.

BOGGS, C. L., AND L. E. GILBERT. 1979. Male contribution to egg production in butterflies: Evidence for transfer of nutrients at mating. Science 206: 83-84.

BORGIA, G. 1981. Mate selection in the fly *Scatophaga stercoraria*: Female choice in a male-controlled system. Anim. Behav. 29: 71-80.

CHAYKIN, S., AND J. G. WATSON. 1983. Reproduction in mice: Spermatozoa as factors in the development and implantation of embryos. Gamete Res. 7: 63-74.

COOK, R., AND A. COOK. 1975. The attractiveness to males of female *Drosophila melanogaster*: Effects of mating, age and diet. Anim. Behav. 23: 521-26.

DARWIN, C. 1871. The descent of man and selection in relation to sex. John Murray, London.

DAWKINS, R. 1976. The selfish gene. Oxford University Press, Oxford.

DEWSBURY, D. A. 1972. Patterns of copulatory behavior in male mammals.

Quart. Rev. Biol. 47: 1-33.

————. 1974. Copulatory behavior of white-throated wood rats (*Neotoma albigula*) and golden mice (*Ochrotomys nuttalli*). Anim. Behav. 22: 601-10.

————. 1975. Diversity and adaptation in rodent copulatory behavior. Science 190: 947-54.

————. 1981a. On the function of the multiple-intromission, multiple-ejaculation copulatory patterns of rodents. Bull. Psychonomic Soc. 18: 221-23.

————. 1981b. Social dominance, copulatory behavior, and differential reproduction in deer mice (*Peromyscus maniculatus*). J. Comp. Physiol. Psychol. 95: 880-95.

————. 1982a. Dominance rank, copulatory behavior, and differential reproduction. Quart. Rev. Biol. 57: 135-59.

————. 1982b. Ejaculate cost and male choice. Am. Nat. 119: 601-10.

————. 1984. Sperm competition in muroid rodents. Pages 547-571 in R. L. Smith ed. Sperm competition and the evolution of animal mating systems. Academic Press, New York.

————, AND D. L. BAUMGARDNER. 1981. Studies of sperm competition in two species of muroid rodents. Behav. Ecol. Sociobiol. 9: 121-33.

————, AND D. K. SAWREY. 1984. Male capacity as related to sperm production, pregnancy initiation, and sperm competition in deer mice (*Peromyscus maniculatus*). Behav. Ecol. Sociobiol. 16: 37-47.

FUENTES, S. M., AND D. A. DEWSBURY. 1984. Copulatory behavior of voles (*Microtus montanus* and *M. ochrogaster*) in multiple-female test situations. J. Comp. Psychol. 98: 45-53.

GEORGE, J. A., AND M. G. HOWARD. 1968. Insemination without spermatophores in the oriental fruit moth, *Grapholitha molesta* (Lepidoptera: Tortricidae). Canadian Ent. 100: 190-92.

GERBER, G. H., N. S. CHURCH, AND J. G. REMPEL. 1971. The structure, formation, histochemistry, fate, and functions of the spermatophore of *Lytta nuttalli* Say (Coleoptera: Meloidae). Canadian J. Zool. 49: 1595-1610.

————, ————, AND ————. 1972. The anatomy, histology, and physiology of the reproductive systems of *Lytta nuttalli* Say (Coleoptera: Meloidae). II. The abdomen and external genitalia. Canadian J. Zool. 50: 649-60.

GETZ, L. L., AND C. S. CARTER. 1980. Social organization in *Microtus ochrogaster* populations. Biologist 62: 56-69.

GRAUR, D., AND D. WOOL. 1982. Dynamics and genetics of mating behavior in *Tribolium castaneum* (Coleoptera: Tenebrionidae). Behav. Genet. 12: 116-79.

GWYNNE, D. T. 1981. Sexual difference theory: Mormon crickets show role reversal in mate choice. Science 213: 779-80.

GWYNNE, D. T. 1984. Male mating effort, confidence of paternity and insect sperm competition. Pages 000-000 *in* R. L. Smith ed. Sperm competition and the evolution of animal mating systems. Academic Press, New York, in press.

HALLIDAY, T., AND A. HOUSTON. 1978. The newt as an honest salesman. Anim. Behav. 26: 1273-74.

HARTUNG, T. G., AND D. A. DEWSBURY. 1978. A comparative analysis of copulatory plugs in muroid rodents and their relationship to copulatory behavior. J. Mammal. 59: 717-23.

HOLMES, H. B. 1974. Patterns of sperm competition in *Nasonia vitripennis*. Canadian J. Genet. Cytol. 16: 789-95.

HOOPER, E. T., AND G. G. MUSSER. 1964. The glans penis in neotropical

cricetines (Family Muridae) with comments on classification of muroid rodents. Misc. Publ. Mus. Zool. Univ. Michigan 123: 1-57.

HOWELL, J. F., R. B. HUTT, AND W. B. HILL. 1978. Codling moth: Mating behavior in the laboratory. Ann. Ent. Soc. America 71: 891-95.

JONES, J. C. 1973. A study on the fecundity of male *Aedes aegypti*. J. Insect Physiol. 19: 435-39.

LEOPOLD, R. A. 1976. The role of male accessory glands in insect reproduction. Ann. Rev. Ent. 21: 199-221.

LEVINE, L. 1967. Sexual selection in mice IV. Experimental demonstration of selective fertilization. Am. Nat. 101: 289-94.

LINLEY, J. R. 1975. Sperm supply and its utilization in doubly inseminated flies, *Culicoides melleus*. J. Insect Physiol. 21: 1785-88.

LLOYD, J. E. 1979. Mating behavior and natural selection. Florida Ent. 62: 19-34.

LOHER, W., AND B. RENCE. 1978. The mating behavior of *Teleogryllus commodus* (Walker) and its central and peripheral control. Z. Tierpsychol. 46: 225-59.

MAJERUS, M. E. N., P. O'DONALD, AND J. WEIR. 1982. Female mating preference is genetic. Nature 300: 521-23.

MARKOW, T. A., M. QUAID, AND C. KERR. 1978. Male mating experience and competitive courtship success in *Drosophila melanogaster*. Nature 276: 821-22.

McLAIN, D. K. 1980. Female choice and the adaptive significance of prolonged copulation in *Nezara viridula* (Hemiptera: Pentatomidae). Psyche 87: 325-36.

MICHENER, C. D. 1974. The social behavior of bees. Harvard University Press, Cambridge, Massachusetts.

OGLESBY, J. M., D. L. LANIER, AND D. A. DEWSBURY. 1981. The role of prolonged copulatory behavior in facilitating reproductive success in male Syrian golden hamsters (*Mesocricetus auratus*) in a competitive mating situation. Behav. Ecol. Sociobiol. 8: 47-54.

O'HARA, E., A. PRUZAN, AND L. EHRMAN. 1976. Ethological isolation and mating experience in *Drosophila paulistorum*. Proc. Nat. Acad. Sci. USA. 73: 975-76.

OUTRAM, I. 1971. Aspects of mating in the spruce budworm, *Choristoneura fumiferana* (Leoidoptera: Tortricidae). Canadian Ent. 103: 1121-28.

PARKER, G. A. 1970. Sperm competition and its evolutionary consequences in the insects. Biol. Rev. 45: 525-67.

PARTRIDGE, L. 1980. Mate choice increases a component of offspring fitness in fruit flies. Nature 283: 290-91.

PRUZAN, A. 1976. Effects of age, rearing and mating experiences on frequency dependent selection in *Drosophila pseudoobscura*. Evolution 30: 130-45.

RUTOWSKI, R. L. 1979. The butterfly as an honest salesman. Anim. Behav. 27: 1269-70.

————. 1982a. Mate choice and lepidopteran mating behavior. Florida Ent. 65: 72-82.

————. 1982b. Epigamic selection by males as evidenced by courtship partner preferences in the checkered white butterfly (*Pieris protodice*). Anim. Behav. 30: 108-12.

SMITH, R. L. 1980. Evolution of exclusive postcopulatory paternal care in the insects. Florida Ent. 63: 65-78.

THORNHILL, R. 1976. Reproductive behavior of the lovebug, *Plecia nearctica* (Diptera: Bibionidae). Ann. Ent. Soc. America 69: 843-47.

————. 1980a. Competitive, charming males and choosy females: Was Darwin correct? Florida Ent. 63: 5-30.

————. 1980b. Mate choice in *Hylobittacus apicalis* (Insecta: Mecoptera) and its relation to some models of female choice. Evolution 34: 519-38.

————, AND J. ALCOCK. 1983. The evolution of insect mating systems. Harvard University Press, Cambridge, Massachusetts.

TOMPKINS, L., AND J. C. HALL. 1981. The different effects on courtship of volatile compounds from mated and virgin *Drosophila* females. J. Insect Physiol. 27: 17-21.

————, AND ————. *Drosophila* males produce a pheromone which inhibits courtship. Z. Naturforsch. 36C: 694-96.

TRIVERS, R. L. 1972. Parental investment and sexual selection. Pages 136-79 *in* B. G. Campbell ed. Sexual selection and the descent of man, 1871-1971. Aldine, Chicago.

WAAGE, J. K. 1979. Dual function of the damselfly penis: Sperm removal and transfer. Science 203: 916-18.

————. 1983. Sexual selection, ESS theory and insect behavior: Some examples from damselflies (Odonata). Florida Ent. 66: 19-31.

WATSON, J. G., J. CARROLL, AND S. CHAYKIN. 1983. Reproduction in mice: The fate of spermatozoa not involved in fertilization. Gamete Res. 7: 75-84.

WING, S. 1984. Reproductive anatomy and behavior of three firefly species. Unpublished manuscript.

————, J. E. LLOYD, AND T. HONGTRUKUL. 1983. Male competition in *Pteroptyx* fireflies: Wing-cover clamps, female anatomy, and mating plugs. Florida Ent. 86-91.