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PREZYGOTIC MALE REPRODUCTIVE EFFORT IN INSECTS: WHY DO MALES PROVIDE MORE THAN SPERM?

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SYNOPSIS

Males' incentives for providing benefits to females and/or their offspring are ambiguous during the period prior to zygote formation. The benefits may function to increase the number of available eggs fertilized by a male and/or enhance the production and survival of his offspring. In some cases, male prezygotic investment may be an adaptation to secure fertilizations despite the fact that it incidentally benefits the female or her offspring. More often, the benefits to offspring production and survival are not simply incidental and probably account, in part, for the magnitude of the male investment. Regardless of the adaptive significance of male provided benefits, they typically reduce the females' costs of producing surviving offspring while raising the males' costs. The extent to which provisioning of benefits increases males' costs and decreases females' costs will affect the degree to which females limit male reproduction (or *vice versa*). If male-provided benefits (prezygotic or otherwise) are more costly than female costs of offspring production, reproductively-ready males will act as resources limiting female reproduction. From an evolutionary perspective it is important to consider the effect of male-provided benefits. The primary function of the investment (e.g., to maximize sperm transfer) is irrelevant in terms of the degree to which one sex limits the other's reproduction.

"Women and men move back and forth in between effect and cause. Just beyond the range of normal sight, this glittering joker was dancing in the dragon's jaws"

(B. Cockburn)

During the past two decades there has been considerable interest in Darwin's (1871)

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theory of sexual selection. In various theoretical discussions, authors have attempted to identify the key variables affecting the operation and intensity of sexual selection (Trivers 1972, Emlen and Oring 1977, Wade and Arnold 1980, Gwynne 1984a, Thornhill in press. At the same time, other studies have investigated the mechanisms through which sexual selection is mediated, specifically, intrasexual competition and mate choice (for a review of these processes in insects see Thornhill and Alcock 1983). These two approaches ask very different questions—what causes sexual selection? *and* what is the function of adaptations that arise through selection processes? In this paper we will adopt Williams' (1966) use of "function" to mean that the characteristic being considered was fashioned by natural selection for the goal attributed to it. When such a relationship is not intended we will use the term "effect" to imply that certain consequences of the characteristic may not necessarily be the goal fashioned by natural selection (see Williams 1966).

Relative parental contribution by the sexes has long been considered a key variable influencing the operation of sexual selection. Bateman (1948) proposed that the unequal energetic expenses of gamete production led to the typical pattern of courtship in animals. He found that in *Drosophila melanogaster*, female reproduction was limited by the number of eggs laid while male reproduction was limited by the number of females inseminated. Thus, females could be viewed as a limiting resource for which males were expected to compete. Females are selected to be more discriminating in their choice of mates because they have more to lose (their initial gametic investment) from mating with a genetically incompatible or otherwise unsuitable mate.

Trivers (1972) provided a more general hypothesis to explain interspecific differences in the operation of sexual selection, proposing that the amount of parental investment by the sexes was the key variable influencing the operation of sexual selection. He defined parental investment as "any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offspring." Trivers concluded that parental investment, measured as a cost to other parenting efforts, ultimately explained sexual differences in such life history variables as age of first breeding, differential mortality, and adult sex ratio, as well as the differences in sex roles during mating.

Insect females typically provide almost all parental investment in their production of eggs. However, in some species parental investment is shared. An example of parental investment by a male insect comes from the work of R. L. Smith (1979a, 1979b, 1980) in his studies of the giant waterbug *Abedus herberti*, and other Belostomatidae. These males provide oviposition sites (on their backs) for the eggs of their mates and provide care for those eggs. Paternal care involves aeration of eggs and brood pumping, a behavior that expedites the escape of young from the egg. This paternal care involves a cost to the male's ability to invest in other offspring because back space is limited. The extra drag associated with swimming while encumbered, as well as brooding behaviors, may increase risks of predation and decrease success at capturing prey (Smith 1979b, 1980). This increased time and risk associated with paternal care excludes encumbered males from mating and apparently affects the operational sex ratio (Emlen and Oring 1977), as well as the courtship roles.

In this paper, we consider costly investments by male insects *before* they fertilize the eggs of females. We investigate the adaptive significance of such prezygotic investments, and examine the impact of these benefits on the operation of sexual selection. We consider the contention that prezygotic male investment is best considered mating effort (Low 1978) and not parental investment. We conclude that from an evolutionary perspective, the effects of the investment, and not the primary function, are the critical factors.

CATEGORIES OF MALE PREZYGOTIC INVESTMENT

Males often minimize their investment in offspring. This is because males produce many energetically inexpensive sperm compared with few expensive eggs produced by females (Bateman 1948). Male reproduction is typically limited by the number of females inseminated, a potentially great number. By providing parental effort rather than seeking other copulations, males potentially experience greater losses of other reproductive opportunities than would females who make additional investments in offspring. Additionally, males may not be certain of the paternity of their mate's offspring and therefore risk investing in the offspring of other males (Thornhill and Alcock 1983). Despite the substantial costs, males of many insect species often provide benefits to females before the females's eggs are fertilized. Such prezygotic investments include:

1. nuptial prey items consumed by the female (Downes 1970, Thornhill 1976a, 1980, 1983 and references).
2. spermatophores and/or accessory gland secretions
 - a. ingested orally by the female (Boldyrev 1927, Alexander and Otte 1967a, Mullins and Keil 1980, Sakaluk and Cade 1980, Gwynne 1981, 1983, 1984b, Bowen *et al.* 1984, Sakaluk 1984, 1985)
 - b. absorbed in the female's reproductive tract (Friedel and Gillott 1977, Boggs and Gilbert 1979, Sivinski 1980a, Boggs 1981, Greenfield 1982, Marshall 1982, Rutowski 1982, Schal and Bell 1982, Markow and Ankney 1984, Pivnick and McNeil ms)
3. secretions from glands other than the accessory glands (Fulton 1915, Mays 1971, Walker 1978, Bell 1980a,b, Bidochka and Snedden 1985)
4. portions of the male's body (Alexander and Otte 1967b, Dodson *et al.* 1983, Hubbell 1985)
5. protection of the female from predators (Sivinski 1980b, 1983)
6. reduction of harassment of the female by other conspecific males (Waage 1979, 1983, Borgia 1981, Wilcox 1984)
7. assistance in the collection of suitable oviposition substrate such as dung or carrion (Klemperer 1983, Tyndale-Biscoe 1984, Wilson and Fudge 1984)
8. provisioning of a burrow in which the female can rear her offspring (Walker 1980, 1983).

Trivers specifically excluded effort spent finding or subduing a mate from his concept of parental investment, except in those cases where such effort affects the survival chances of the offspring. For example, defense of a territory that benefits offspring survival, providing nuptial gifts, and other behaviors providing "incidental" benefits to offspring were included as parental investment. Low (1978) proposed that reproductive effort be divided into two components, mating effort and parental effort. The division and attendant definitions have resulted in a roundabout redefinition of parental investment that stresses the primary function of the investment rather than any effects it might have on offspring survival or production costs.¹

Alexander and Borgia (1979) and Gwynne (1984a) continued to stress the primary function of the components of reproductive effort (Low 1978). The former argued that because males have little control over the fate of their gametes or their mates' uses of prezygotic paternal contributions, such investments would be best considered mating effort. Gwynne (1984a) similarly identified prezygotic reproductive effort by males as mating effort² and suggested a further subdivision to distinguish effort influencing the operation of sexual selection. His "non-promiscuous mating effort" refers to effort providing benefits to offspring or mates at a cost of lost reproductive opportunities, while "promiscuous mating effort" provides no such benefits (Gwynne 1984a). Non-promiscuous mating effort, as defined, is similar to parental investment in its effect on sexual

selection. However, in species where males offer no more than sperm to females, substantial male investment in courtship, guarding, or fighting (promiscuous mating effort) also can influence the operation of sexual selection and lead to male mate choice or even sex role reversal in courtship behavior (Hatzios and Caldwell 1983, Johnson and Hubbell 1984 and references). Furthermore, as mentioned earlier, the classification of such effort as a type of mating effort is based on the primary function of the effort or the "intention" of the male.

These different treatments of prezygotic male reproductive effort can result in the identification of an effort that benefits offspring as either a parental investment (Trivers 1972, Thornhill 1976b, Boggs and Gilbert 1979, Morris 1979, Mullins and Keil 1980, Zeh and Smith 1985) or a mating effort (Alexander and Borgia 1979, Gwynne 1984a, Thornhill *in press*). The basis for this difference is whether male-provided benefits are viewed according to the effect on offspring production or according to the primary function of the investment.

ADAPTIVE SIGNIFICANCE: WHY DO MALES PROVIDE MORE THAN SPERM?

The selective advantages to males providing benefits to mates and offspring include two main categories. First, such investments may increase the number of eggs fertilized by the male's sperm by: a) increased sperm transfer to the female; b) increased utilization of that male's sperm by the female; and/or c) increased number of females inseminated. Second, male-provided benefits may increase the production and survival of offspring. Male-derived selective advantages in the second category would be devalued if some or all of the benefited offspring were fathered by other males³.

The evolution of beneficial prezygotic investments by males is more likely in species in which males can provide useful services (e.g., protection from predators) or collect and/or defend resources that potentially limit reproduction. In species where reproduction is limited by protein or nutrients that are contained within the sperm or sperm transfer device, females are expected to digest any materials as long as this does not result in costly infertility of eggs. Thus, particularly in species engaging in multiple mating, females may make use of sperm as a nutritional resource.

Many of the examples of male prezygotic investment provide both increased fertilizations and increased survival or production of offspring. For example, mate guarding by male damselflies and dragonflies increases the male's likelihood of fertilizing eggs, diminishes predation on the mate (and hence her offspring) and increases oviposition by the female by reducing harassment by other males (Waage 1979, 1983). Detailed examples from crickets (Orthoptera: Gryllidae) and katydids (Orthoptera: Tettigoniidae) will help illustrate the functions and effects of male prezygotic contributions.

First consider the adaptive significance of the spermatophylax produced by male decorated crickets. *Gryllodes supplicans* (Sakaluk 1984, 1985). In crickets, copulation ends when a male transfers the sperm-containing vessel (spermatophore) to the female. The spermatophore of most cricket species consists of a small sperm-containing ampulla that remains outside the female's body after mating. This ampulla is drained as the sperm enter the female genital tract. Later the female often eats the evacuated spermatophore (Alexander and Otte 1967a, Loher and Rence 1978, Sakaluk and Cade 1980, 1983), but premature removal is prevented by the male who remains with and antennates his mate (Loher and Rence 1978). Interestingly, *G. supplicans* males produce a bipartite spermatophore consisting of the ampulla plus a spermatophylax, a larger gelatinous portion devoid of sperm (Alexander and Otte 1967a, Sakaluk 1984, Sakaluk and O'Day 1984). Immediately after mating, the female removes the easily detached spermatophylax from the ampulla with her mouthparts and begins to feed on it. The time required for a female to consume this nuptial 'meal' completely, increases with

spermatophore weight (Sakaluk 1985). Within several minutes of eating the spermatophylax, the female removes and eats the sperm ampulla and the remaining contents. Thus a male that provides a small spermatophylax will have his ampulla removed sooner than a male providing a larger one. Because the ampulla must be attached for a minimum of about 50 min to be emptied completely of sperm (Sakaluk 1984), males providing under-sized spermatophylaxes will not transfer a full complement of sperm. However, the average time at which females removed sperm ampullae was 52 min, which matches the time required for complete sperm transfer (Sakaluk 1984). Therefore males, on the average, provide females with a nuptial meal no larger than that required to prevent the premature removal of the ampulla. The ease with which the spermatophylax breaks off is important to fulfilling the function of preventing premature removal of the ampulla. Furthermore, male *G. supplicans* are definitely less intense in their post-copulatory interaction with the female than other crickets, which are known to rely on direct contact and antennation for prevention of premature ampulla-removal by females (Loher and Rence 1978). This suggests that the spermatophylax "replaces" contact guarding and that the function of the bipartite spermatophore is to maximize sperm transfer (Alexander and Otte 1967a).

The largest possible sperm transfer is expected to be particularly important in species where sperm from a number of males are mixed in the spermatheca and fertilization success is essentially by lottery (Parker 1970, Sakaluk in press). It appears that the function of the spermatophylax, or more specifically the bipartite nature of the spermatophore, is to ensure the maximum transfer of a male's sperm. There are other possible beneficial effects of this nuptial offering, such as increasing production and survival of offspring or inducing a female refractory period (i.e., a period when the female refrains from mating). However, the bipartite spermatophore of *G. supplicans* was not likely designed by natural selection to provide these other possible benefits. There may be additions to the spermatophore that serve those other functions, such as substances included in the spermatophore that promote a female refractory period or that provide nutrition for the young. It appears likely that the evolution of the spermatophylax itself did not require males to reap these extra benefits. Thus, some of these benefits may be incidental to the evolution of the spermatophylax.

The size of a spermatophylax represents a continuous variable. Costs of producing a spermatophore are not trivial; in *G. supplicans*, the spermatophore can assume up to about 6% of the male's body weight and males require 3.3 ± 0.1 h for spermatophore replenishment before they can remate (Sakaluk 1985). This may be a considerable cost if mating opportunities are lost during this period of replenishment. In other crickets, males transfer small unipartite spermatophores consisting of a sperm ampulla alone and remate within as little as 15 min (Alexander and Otte 1967a). The costs can be viewed as time or energy, but ultimately as lost reproductive opportunity. These costs are weighed against the benefits—increased likelihood of fertilizing available eggs and increased number of surviving offspring. In *G. supplicans*, secondary benefits to increased spermatophylax size, such as potentially increased production of surviving offspring, may be small. Nevertheless, the determination of the optimal spermatophylax size by natural selection involved the balancing of all benefits against all costs.

Research by D. T. Gwynne and colleagues (Gwynne 1984b, Gwynne *et al.* 1984, Bowen *et al.* 1984) on the katydid *Requena verticalis* serves to illustrate the impact of secondary benefits on optimal investment in a continuous character. The bipartite spermatophores produced by males of this species are huge, representing about 20% of male body weight (derived from Table 2 in Bowen *et al.* 1984). Again, females consume the spermatophylax fully before removing and eating the sperm ampulla. However, the spermatophylax in this species is almost twice as large as necessary to protect the ejaculate (Gwynne *et al.* 1984). Protein from the spermatophylax is incorporated into

the batch of eggs produced after the mating (Bowen *et al.* 1984). This suggests that one function of the large spermatophylax is the production of surviving offspring because it is likely that the male providing the spermatophylax fathers those young. Gwynne (1984b) allowed female *R. verticalis* raised on a low protein diet to eat 0, 1, 3 or 7 spermatophylaxes, then recorded numbers and weights of eggs produced. Volumes of sperm and other contents of the ejaculate were held constant between treatments. He found significant increases in both egg weight and egg number produced as a function of increased numbers of spermatophylaxes eaten. While other benefits to males providing large spermatophylaxes might exist, the production of surviving offspring may be important to males. Gwynne (1982) found that when given the choice between two singing male katydids (*Conocephalus nigropleurum*), females always mated with the larger individual. This may represent an adaptive choice since spermatophore size correlated positively with male body weight. The potential role that female choice or the inducement of a refractory period could have played in the evolution of large spermatophylaxes remains to be investigated. Indeed, multiple benefits to male reproduction, some promoting fertilization of eggs and others favoring production of surviving offspring, appear to be responsible for the large spermatophylax produced by *R. verticalis*.

The adaptive significance of benefits provided by males during the prezygotic period may include increases in both fertilization of eggs and production of surviving offspring. The male's cost of providing such benefits is the loss of reproductive opportunity. The arguments by Alexander and Borgia (1979) identifying such investments as mating effort ignore the contributions to offspring production.

PREZYGOTIC BENEFITS AND THEIR INFLUENCE ON SEXUAL SELECTION

Under some conditions the benefits to offspring production and survival provided by males are probably incidental to their attempts to fertilize eggs. For example, mate-guarding from copulation until oviposition by some odonates presumably evolved to protect the male's genetic interests by reducing the competition among his sperm and that of other males. Assuming that benefits of increased fertilization by the male guarding exceed the costs of guarding, the benefits obtained by the female (a period free of harassment by other males during which she can choose a suitable oviposition site; Waage 1983) are probably incidental or secondary from the male's perspective, although this remains to be demonstrated. Because carefully chosen oviposition sites may lead to increased survivorship of young and because male guarding may enable the female to take significantly greater care in selecting her site, the effect of this effort by males could include increased survival of his offspring and reduced female costs for producing surviving young. In some odonates the method of guarding precludes investment by males in other mating attempts, and so limits a male's ability to invest in other offspring. A similar case can be made for mate-guarding that incidentally reduces female predation risk prior to oviposition, as in the stick insect *Diaperomera veliei* (Sivinski 1980b, 1983). Assuming the simultaneous existence of other reproductive opportunities for males, investments of this sort alter the degree to which females limit reproduction, and thus decrease the competition for mates by males.

The distinction in classification of reproductive effort between the prezygotic and postzygotic periods suggested by Alexander and Borgia (1979) is misleading when reproductive effort is viewed in terms of its effect on the degree to which one sex *versus* the other limits reproduction (*sensu* Trivers 1972). Male contributions affecting the production of surviving young during the postzygotic period usually can be seen easily as parental effort (Low 1978). We suggest that the main reason postzygotic investments are easier to understand as parental investment is that in most cases the primary

function is unequivocally for the production and survival of offspring. The primary function of a prezygotic investment does not alter the investment's effect as limiting reproduction. Various types of prezygotic and postzygotic investments involving benefits provided by males reveal that irrespective of their primary functions, the impact on sexual selection's intensity is the same (see Gwynne 1984a). A similar conclusion was reached independently by Zeh and Smith (1985). Increases in male reproductive effort that enhance offspring survival may reduce female costs of producing independent offspring and increase the degree to which female reproduction is limited by the male's ability to provide that effort. This in turn should lead to reduced intensity of sexual selection on males.

Male contributions to offspring do, indeed, influence the operation of sexual selection and affect the courtship roles adopted by male and female insects. In the giant waterbug, *A. herberti*, females are aggressive in courtship, although male display is an essential element of the courtship (Smith 1979b). Sex roles in this species are not completely reversed, probably because the costs of egg production and paternal care are equivalent (Smith 1979b). When parental investments by males and females are equal, theory predicts that the sexes should be equally eager to mate (Trivers 1972). Gwynne's (1981) study of Mormon crickets, *Anabrus simplex*, showed that prezygotic male investments can have an equal or greater impact on sex roles in courtship. During mating, a male *A. simplex* transfers a very large spermatophore that accounts for up to 27% of a male's body weight to the female. Females consume the proteinaceous spermatophylax and then the ampulla after it has been emptied of sperm. Gwynne demonstrated that females compete for access to males whereas males exhibit mate preference, actively rejecting smaller, less fecund, females as potential mates.

CONCLUSION

In some species, males provide "gifts" or services that aid in the production of surviving offspring. These aids to reproduction can be provided before or after zygote formation. During the prezygotic period the function of such investments may be exclusively to increase male success at fertilizing eggs. This is more likely to be the case for discrete adaptations such as a bipartite spermatophore. Continuous traits such as the size of a spermatophore represent a compromise between the benefits (increased number of eggs fertilized and increased number of sired offspring surviving) and the costs (lost reproductive opportunities).

The primary *function*, or "intention", of male reproductive effort has no bearing on the operation of sexual selection (i.e., the direction and intensity of the selection). Instead, what matters is the *effect* of that effort on the degree to which males *versus* females limit reproduction. We suggest that the classification of components of reproductive effort according to the "intentions" of the investor, or the primary function of the investment, should be avoided. The identification of function is operationally difficult, and the exclusion of "incidental" effects may result in erroneous conclusions. Furthermore, we suggest that the original concept of parental investment (*sensu* Trivers 1972) is most suitable for understanding the relationship between parental investment and sexual selection.

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APPENDIX

1. The concept of parental investment has become obfuscated. Low (1978) divided reproductive effort into two components, mating effort and parental effort. She defined mating effort as "any expenditure of nutrient or effort or taking of risks to secure matings." Parental effort was defined as "any expenditure of nutrient or effort or taking of risks in the production and raising of offspring or other kin." This divides reproductive effort according to the function of the effort (for mating or for production and raising of offspring) and removes the emphasis from the effect of the investment on production and survival of offspring. Furthermore, effort with multiple functions would be classified according to the primary function alone. In this scheme, incidental benefits to offspring production and survival are neglected. Despite the apparent inconsistency of this classification with that of Trivers (1972), Low considered parental investment to be that portion of parental effort received by an individual offspring.

2. Gwynne (1984a) also suggested that postzygotic investment by males could function as mating effort. Regarding the egg-brooding of male waterbugs, he stated "As long as there is space available for eggs on a male's back (there is some evidence that male backs are a limiting resource for females; Smith 1979a), the investment can be considered ME involved in advertising the male's parental abilities that may aid in the acquisition of matings with other egg-laden females." There are two problems with this interpretation. First, if the possession of eggs functions as a signal attracting other mates, "unattractive" males lacking eggs might be expected to accept eggs without requiring copulations. Males apparently do not allow oviposition on their backs unless they have just copulated with the ovipositing female (Smith 1979a, b). Furthermore, a partially egg-laden male must have been able to obtain at least one mating without having any eggs on his back. If egg-brooding functioned as a signal of a male's quality, it is not clear why a male would employ the signal if he were able to obtain matings without it, especially given its obvious costs. Second, that females exploit information made available to them by egg-brooding males, thereby allowing females to make optimal mate choices, could be an incidental effect of the behavior (see Otte's 1974 distinction between the evolved function and incidental effects of 'signals'). Gwynne (1984a) did concede that paternal care exhibited by *A. herberti* after the male is completely encumbered functions to increase the survival of the young.

3. Because females can store sperm and mate with more than one male, parentage is less certain for male than for female insects of many species. If benefit-providing males enjoy increased certainty of paternity over males that fail to provide benefits, then the degree of paternal certainty will affect the level of investment favored by natural selection. Whether or not males provide benefits is determined by natural selection according to the net benefits of available options (e.g., whether to provide benefits, and if so, to what extent). Males who provide benefits may experience enhanced offspring survival, and/or increased mate attraction and/or increased probability of fertilization of eggs, hence increased certainty of paternity (Zeh and Smith 1985). The cost of providing benefits may be the loss of other mating opportunities. Males that do not provide benefits may experience increased mating opportunities, but may have reduced offspring survival, and/or probability of mate attraction, and/or certainty of paternity.

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