

Sexual Conflict over Nuptial Gifts in Insects

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Abstract

Edible and seminal gifts that male arthropods transfer to their mates range from important material donations to items that provide little direct benefit. Recent reviews and research have emphasized the negative effect of gifts on female fitness, suggesting that male donations reduce the female's remating rate below her optimum or even that nuptial feeding is a net detriment to her fitness. However, comparative, experimental, and natural history evidence reveal that most edible gifts of prey or glandular products provide direct benefits to females. Gifts clearly supply nutrients when females compete for them or increase mating rates when food from other sources is limited. I point out the difficulties in determining that female remating rates are suboptimal and suggest several alternative hypotheses for the apparently low female mating rates in some gift-giving species. With regard to seminal contributions (absorbed from the ejaculate), I discuss how to separate hormonal (potentially manipulative) and material-benefit effects of male secretions on females.

Nuptial gifts:

materials eaten, or beneficial substances absorbed by the opposite sex during mating

Oral gifts:

gifts eaten that had been collected by the mating partner or were products from salivary, external, or reproductive glands

Seminal gifts:

potential material benefits absorbed in the female genital tract that can include nutrients or specialized defensive chemicals

Sexual conflict: the fitness interests of the sexes differ in the outcome of their reproductive interactions such as over mating rate

INTRODUCTION

Male arthropods can transfer important material gifts to their mates. For example, the edible spermatophylax that a male katydid *Isophya kraussi* (Orthoptera: Tettigoniidae) attaches to his spermatophore supplies all his mate's energy requirements for 1 to 2 days. As a female can mate every 2 to 3 days, she may obtain all her food by mating (113). This appears to be the case for female empidines, a group of predatory dance flies (Diptera: Empididae) in which females do not hunt at all and rely instead on gifts of prey from their mates (20, 24).

Nuptial gifts¹ are male material donations that are transferred during mating. For arthropods, gifts include prey, carrion, and plant products, items eaten by the female after being collected by the male. Oral gifts also include secretions from male glands, such as the katydid spermatophylax, the male's own soma, his hemolymph (32), and specialized body parts (e.g., 23). Gifts also include certain ejaculated substances absorbed in the female's genital tract (10, 48, 103, 107). Genitally absorbed male donations (seminal gifts) (96) might include non-nutritional products beneficial to females, such as immunostimulatory or antibiotic components (84), water (4), minerals, ions such as zinc (10), and specialized defensive substances. For example, in the beetle *Neopyrochroa flabellata* (Coleoptera: Pyrochroidae), males eat cantharidin (Spanish fly) and transfer it through the ejaculate, thus allowing the female to imbue her eggs with a chemical defense against predation (10, 27, 28).

The mating biology of *Isophya* katydids and empidine flies might indicate that nuptial gift giving is mutually beneficial because females feed while males inseminate (48, 100). Indeed, until the selective thinking revolu-

tion in evolutionary theory, largely inspired by Williams in 1966 (123), researchers often viewed mating in general as a sexually cooperative endeavor. Williams' (123) critical analysis, which included a discussion of mating adaptations, predicted "an evolutionary battle of the sexes" in which "genic selection will foster a skilled salesmanship among the males and an equally well-developed sales resistance and discrimination among females." Ever since Williams, sexual selection theory has acknowledged the potential for sexual conflict.

Sexual conflict has long been noted as a potential force in the origin (11) and selective maintenance (102) of nuptial gifts (13, 88, 110), and there are a number potential sources of this conflict (7, 10, 13, 82, 88, 110). Thus even male *Isophya* katydids and empidine flies could reduce the maximum fitness of females if males are selected to use gifts to maximize fertilizations—gifts as mating effort; see the sidebar, The Function of Nuptial Gifts in Males (2, 75)—particularly given that in many systems the longer it takes to eat the gift, the more sperm is transferred (10, 48, 88, 107). Male gift givers can be selected in a salesmanship context when they add non-nutritious substances that make offerings more attractive or that maximize gift-handling time by females (110). In some species males may reduce the quality of oral gifts while maintaining phagostimulatory (good-tasting) ingredients (88, 110). In a few species, such as certain male empidine flies who offer silk or seed fluff to females (67, 85, 110), the gift, presumably functioning to increase male mating success, carries negligible material benefit. Finally, males are known to reduce gift quantity if prey leftovers can be used to attract additional mates, as in scorpionflies (Mecoptera: Bittacidae) (102), empidid flies, and a spider species (110) in which male termination of copulation is followed by a struggle with the female over who retains the prey. Less sexual conflict is expected if males maximize the material benefits of gifts to increase the fitness of their own offspring, i.e., eggs that they fertilize and

¹The term gift (the act of giving) does not necessarily refer to an item of high value. For example, male insects might give low-value and symbolic items that females eat. Thus I prefer the use of the nonfunctional term nuptial gift over nuptial or courtship meal, which implies that gifts provide benefits.

to which they contribute these benefits (i.e., parental effort; see the sidebar, The Function of Nuptial Gifts in Males) (48, 107).

A Broader View of Sexual Conflict

The recognition that the fitness interests of the mating male and female are often at odds (81) has in recent years developed into a much broader view of the pervasiveness of sexual conflict in nature (reviewed in 7, 16). This view suggests that animal mating interactions are primarily governed by female strategies to decrease or avoid mating costs rather than, for example, acquire adaptive benefits such as good genes from high-quality males (26, 54). In fact, any such genetic benefits from remating may be expected to fall short of compensating for these costs (56; but see discussion of polyandry below). A key focus in this broader view is on sexual differences in the optimal number of copulations with different mating partners. Because male-fertilization gains from each additional mate typically overcome male mating costs (8), the optimal number of different mates for males is likely to be higher than for females. This is expected to lead to a conflict over the remating rate in which males coerce nonvirgin females into remating with them while attempting to restrict female rematings with rival males. Females then evolve strategies to foil such coercion (53). This broader view of sexual conflict is important in clarifying an alternative hypothesis to the traditional ones originally raised by Darwin—intrasexual competition and mating preferences (21)—for some of the patterns of sexual dimorphism that he sought to explain. Examples of sexual dimorphism that likely evolved in a sexual-conflict context include male grasping devices in gerrid hemipterans and female devices that thwart grasping attempts by males (5, 6).

Recent work has applied this broader view of sexual conflict to arthropods that use nuptial gifts, suggesting both that substances in gifts (3, 110), including ingredients in oral gifts (30, 89), commonly decrease female mat-

THE FUNCTION OF NUPTIAL GIFTS IN MALES

This review covers material (direct) benefits to females, and there is good evidence that females gain by discriminating in favor of males bearing large gifts (e.g., 102). Gifts are male traits, however, and the adaptive significance of males donating nutrients or other beneficial gifts involves two main contexts that are not mutually exclusive (41, 96, 107). Gifts function as mating effort if material donations to females increase paternity by allowing males to transfer more sperm or substances that induce refractoriness in females. Conversely, gifts can function as parental effort, analogous to cases in which the male cares directly for their offspring (41, 101) if his contributions directly increase the fitness or number (82) of offspring sired by him.

ing rates below optimum and that direct benefits from gifts may not compensate females for mating costs (3, 7, 110). One review (3) states that gifts result from “sexual conflict, manipulation and extortion rather than sexual confluence” and even that the term gift itself may be misleading for male ejaculate donations, including oral gifts (e.g., the spermatophylax), owing to the manipulative substances they are likely to contain (3, 7). However, the evidence marshaled by these papers (mainly evidence of the kind of sexual conflict highlighted in the Introduction, above), including individual case studies, shows little evidence that nuptial feeding decreases female fitness as these suggestions (3, 7, 110) predict. In fact comparative evidence (3) supports the hypothesis that nuptial feeding in general provides material benefits to females. I emphasize this generalization because gifts are expected to vary between species in their net benefit to females, with some gifts even lacking material benefits, such as the willow fluff used by males of certain *Empis* dance flies (85).

The Objectives of This Review

I review comparative and case study evidence necessary to demonstrate, or strongly infer,

Mating costs:

energetic costs and risks, such as predation, disease, and injury

Fecundity: the number of eggs or live offspring produced

that a nuptial gift provides a net fitness (material) benefit for females. In case studies, evidence can come from the natural history and biology of gifts, from the physiological and fitness effects of gifts on females (particularly if her life span is increased), and from studies on the number of mates per female. Particularly important support comes from demonstrations that food-restricted females increase mating rate or compete for gift-bearing males (**Table 1**). I conclude that there is strong support from comparative and focal species studies that many oral and certain seminal contributions from males provide direct benefits to females. For seminal contributions I highlight how to separate the effects of allohormonal (69) (and potentially manipulative) substances that may increase fecundity from nutritious substances that contribute to increased fecundity. This discussion also serves as a reminder that allohormonal substances reducing female receptivity or inducing oviposition may have evolved in contexts other than sexual conflict. Finally, I discuss several alternative hypotheses for the apparently low mating rates of gift-acquiring females, rates that have been attributed to male manipulation (3, 7, 30).

In addition to mating rate, there are other potential sources of sexual conflict in nuptial-gift-giving species that I do not discuss here. Examples include conflict over timing and female allocation of nutrients (10, 82) and conflicts in which females gain by eating the male. Males clearly lose if they are commonly eaten before copulation, as in praying mantids (64, 72), or before full insemination has occurred, as in some spiders (2, 35). Soma donation by males is reviewed in References 57 and 77. Other reviews of nuptial gifts include the broad diversity of orthopteran offerings (48) and two thorough reviews on the function and consequences of nuptial gifts in insects (10, 107).

THE EVOLUTIONARY ORIGINS OF NUPTIAL GIFTS

This review is mainly concerned with the evolutionary maintenance of nuptial gifts from the perspective of females (for the male perspective, see the sidebar, The Function of Nuptial Gifts in Males). It is important to distinguish maintenance from evolutionary origins because the function of male

Table 1 Evidence that a male oral gift or seminal substance is a material benefit to the female (nutrient or otherwise) rather than an allohormone that stimulates egg production

Mating and reproduction evidence:
1. The male donation is a complex compound used by the female for defense against natural enemies (e.g., in her eggs) (18, 27, 28, 60, 61).
2. Nutrients are expected to be differentially translocated to eggs or somatic storage (e.g., fat body) rather than to an effector organ as in the case of certain allohormones. Any mimicry to or triggering of a female hormone is evidence of allohormone function (25).
Ecological, behavioral and fitness evidence:
3. There are positive effects on life span, as found in meta-analysis of gift-giving insects (3).
4. The substance is costly. Allohormones are expected to be of low cost (e.g., the male can deliver equivalent amounts in multiple copulations) (25). Evidence of cost could come both from reduced investment over successive matings and from a decrease in male remating rates (25).
5. There is evidence for polyandry as foraging when female mating frequency shows a negative relationship with foraging rate (9).
6. Females low on gift nutrients solicit matings with males.
7. Increased female mating frequency and costs that limit male remating lead to role reversals in mating in which females compete for access to male donations (e.g., 47).

Table modified from Reference 25.

contributions may have changed. For example, sexual conflict over the remating rate is one hypothesis for the origin of large male ejaculate meals (82, 95). Researchers have proposed several scenarios. Males may have initially manipulated females by ejaculating chemicals that limited female remating, thus decreasing sperm competition. Females then evolved resistance to this male coercion by metabolizing these ejaculate components (3, 7, 31). Components could thus evolve into direct material benefits (seminal gifts) by males as ejaculates increase in size through a “co-evolutionary arms race between the sexes” (3). Boldyrev (11) suggested another conflict scenario almost a century ago. For certain orthopterans he argued that in response to females eating the spermatophore before full insemination, males evolved oral glandular gifts to distract their mates. Gifts included the spermatophylax attached to the spermatophore; meals from male external glands; and a partitioning of the sperm into many small spermatophores transferred in repeated matings, each spermatophore acting as a proteinaceous hors d'oeuvre that together provided a nutritious feed for the female while allowing the male to complete insemination (11, 70, 90).

THE EVOLUTIONARY MAINTENANCE OF NUPTIAL GIFTS

Comparative Studies

Gifts may be currently maintained by their benefits to females that more than compensate for any mating costs. If this is the case in general (across species), polyandry (mating by females with multiple males) should increase female fitness. This expectation was supported in a meta-analysis (3) showing that polyandry in insects with nuptial gifts not only greatly increased egg and offspring production by 35%–85%, but also had a weak positive effect on female life span. This test was probably conservative in that large spermatophores

of some species assumed to be nuptial gifts (3) may function not in providing nutrition but in other contexts such as housing large (sperm-competitive) ejaculates (116) (see below).

For non-gift-giving species, polyandry was associated with a decrease in life span (3). Although in this group an increase in fecundity from polyandry outweighed the negative effects on life span, there were diminishing returns to females of mating with too many males. The effect of polyandry on egg-hatching rate, in part probably due to replenishment of sperm stores (93), was positive but did not differ between species with and without nuptial gifts. From their results, Arnqvist & Nilsson (3) concluded that female fitness in general increases greatly (and monotonically) in gift-giving insects. The overall greater positive effects of polyandry on egg production in gift-giving insects compared to nongift species are particularly important as these fitness gains likely represent the effects of direct material benefits over and above other positive effects of multiple mates on egg production, for example, additional fecundity-enhancing allohormones (93) or females favoring a high-quality mate by increasing oviposition rate (12, 104). The widespread nature of gift benefits in insects suggests that when gifts originated, any net decrease in female fitness due to sexual conflict was quickly overcome.

Despite the overall polyandry benefits of nuptial gifts, however, recent papers have challenged the contention that direct benefits of nuptial feeding outweigh mating costs for females (110) or have stated that the direct benefits hypothesis for gifts cannot account for female choice of gifts, suggesting instead that gifts function in exploiting females (88). Similarly, Arnqvist & Nilsson (3) themselves argued that nuptial gift systems are probably governed by coevolutionary struggles over remating rates, suggesting that female mating rates, particularly in Lepidoptera, are suboptimal owing to male manipulation (discussed below). Their arguments (see also 7) focus primarily on oral and seminal gifts of male

Sperm

competition: when sperm from different males compete for fertilizations

Repeated mating:

females copulate repeatedly with the same male

Polyandry:

mating system in which females copulate with more than one male

Allohormone:

substance that bypasses sensory organs to induce a physiological response in an individual after transfer from another individual

secretions. Arnqvist and colleagues (3, 7) suggest that these male substances originated, and are adaptively maintained, as manipulative devices to control the potential for remating by females, stating that large gifts may “represent manipulative and sinister superstimuli . . . rather than amicable and nutritional meals.”

These proposals (3, 7, 110) followed those of Eberhard (25) who concluded that many glandular substances that increased oviposition rate are unlikely to serve a nutritional role. Rather than sexual conflict, however, Eberhard suggested that the context for the evolution of these secretions was one of chemically signaling male (genetic) quality that evolved by female discrimination among males. This signaling hypothesis introduced intersexual selection to an existing argument that such male chemicals were mutually beneficial in most species because it was to the female’s advantage to become refractory for some time (105, p. 403). Eberhard connected two bodies of literature: investigations of the physiological effects of seminal products on female behavior (reviewed in 17, 38, 39) and studies of sexual selection and nuptial contributions (107). Many ejaculate components almost certainly serve functions other than as material benefits to the female, including aiding sperm capacitation, sperm competition, and fertilization (reviewed in 84). Sperm-competition functions include allohormonal signals to the female to become nonreceptive or to begin oviposition (69, 84). The last effect means that one cannot conclude a nutritional function when delivery of the ejaculate is followed by increased fecundity (107, 110). Furthermore, large ejaculate size is expected not only for gifts, but also for sperm competition (110). Proteinaceous spermatophores in many insects function primarily to house sperm, and this was likely their ancestral function (1, 22, 68). Moreover, proteinaceous substances in the male ejaculate commonly function as non-nutritional allohormonal signals to females (39, 69). Eberhard (25) thus concluded that for studies of large male ejaculates, there was little evidence supporting the nutri-

tious gift hypothesis over alternatives such as an allohormone function. He did regard a few studies concluding a nutritional function for ejaculates—including some katydids in which ejaculates are eaten by females—as “relatively convincing although still incomplete.”

Focal Species Studies: Seminal Gifts

Genitally absorbed substances are the most difficult to examine for their effects on female fitness in part because seminal fluids include a blend of components (84), for example, a mix of nutritional and allohormonal substances (124) or a combination of beneficial substances [nutritional and defensive chemicals (61)]. Highly specialized gifts or those rich in simple but important chemicals, such as sodium (83), can provide benefits as long as one can rule out nutritive or protective (e.g., antioxidant properties of carotenoids; see p. 143 in Reference 7) benefits to sperm (reviewed in 84). The large amount of alkaloid defensive chemicals that males of some beetles and moths ejaculate into females (18, 27, 28, 60, 61; see also 107) serves in a direct-benefit context rather than an exploitative or signaling context because the chemicals provide direct survival value to the female or her offspring.

Many focal species studies showing the positive effects of male contributions on fecundity and supporting a nutritional effect have not ruled out obvious alternative hypotheses. Studies of genitally absorbed substances (including studies of Lepidoptera in which each ejaculate is 10%–20% of male body mass) have lacked controls for the effects of manipulative or signaling allohormones that could potentially increase the rate of egg maturation or oviposition following mating (25, 107). Even experiments in which the effects of mating on fecundity are more pronounced in food-deprived females (78) are problematic. For example, starved females may have a reduced life span (and residual reproductive value) and thus ramp up egg production as a consequence. Eberhard (25) also

correctly pointed out that the proteinaceous nature of certain all hormones and the fact that their target organs can be the ovaries mean that tracing male substances to the ovaries (e.g., using radio labels) is weak support for the nutrition hypotheses. Conversely, finding that the male substance directly influences a female effector organ other than the ovaries does support a non-nutritional function (25). Other support listed by Eberhard (25) for a non-nutritional function includes the following: when the substance has a messenger function or is a precursor of such a chemical signal and when male products are of low cost or are not limiting to males. Two final points noted by Eberhard do not appear to offer exclusive support for all hormone hypotheses. The first is that the products' effects on fecundity are species specific: Certain nutrients allocated by males are specialized (45) and potentially species specific. Second, effects are too rapid to have allowed time for nutritional incorporation. This overlooks the possibility that a female may invest immediately in egg production from her own reserves while nutrients from males are processed.

What kind of evidence would support a material-benefit function for seminal products (Table 1, items 1 and 2)? One important source concerns the effects of copulation on polyandry and subsequent behavior, which is discussed below. As with oral gifts, the biology of seminal gift giving can also provide evidence that some components provide material benefits to females. For example, in male *Photinus* fireflies, labeled spermatophore proteins are translocated to ovaries and have a positive effect on female fecundity (73), but they alone do not support a nutrition function. However, details of the nature of spermatophore transfer, together with fecundity and other data, indicate a gift function. The spermatophore is a complex gelatinous device with the sperm located only at its anterior end. Nonsperm parts move to a specialized sac in the female in which they are digested over several days (73). Such sacs, also found in other beetle species (and some mites and tri-

clad flatworms), provide support for a likely nutritional function of spermatophores (25). Finally, the life history of *Photinus* fireflies is one in which male donations might be expected owing to the expected importance of such nutrients to females (62, 73). As these insects do not feed as adults, they are capital breeders, relying on larval-acquired resources for reproduction. Other aspects of life history might also be useful in predicting whether a species might be expected to evolve gifts, such as insects in which the eggs of newly eclosed females are not fully matured and thus may need additional proteins (62).

Focal Species Studies: Oral Gifts

Natural history reveals interspecific variation in the nutritional quality of edible (oral) gifts. This includes variation in collected gifts—from nutritious prey donations to gifts of low quality such as inedible plant parts (71, 85). Other investigations have revealed variation in protein content in glandular gifts such as the spermatophylax (115) and have even suggested that such gifts can contain phagostimulant ingredients (88; see 110). Although a thorough test of the costs and benefits to females of eating gifts should include the costs of polyandry (e.g., 31, 110), evidence from focal species studies showing clear material benefits from gifts strongly infers that female fitness is enhanced.

Demonstrating that gifts are nutritious [for either mating or parental effort (107); see the sidebar, The Function of Nuptial Gifts in Males] is easier for oral than seminal male donations. First, collected oral gifts such as prey are obviously a source of nutrition if, as is apparent in many species (107), they are of a decent size, not distasteful (102), in good condition, and not greatly modified by male secretions (e.g., 85, 98). Second, one can test a nutritional hypothesis for oral gifts because edible parts are often separated from components transferred to the genital tract (sperm and associated potential all hormones). Thus potential gifts can be experimentally

manipulated to examine their direct effect on female fitness. Although relatively few studies have done this (107), researchers have altered experimentally edible products to demonstrate the positive effects on female reproduction in some cases of glandular (12, 44, 79, 91) and hemolymph (31) gifts but not in others, such as glandular gifts (108, 111, 117, 122). However, it is important to note that in some studies showing no effect, experimental gift delivery to virgin females came—perhaps unnaturally—after substantial egg maturation (9, 117; compare 49 with 40).

A third reason why oral gifts are likely to be material donations is that they are unlikely to contain specialized allohormonal chemicals that affect specific target tissues in the female (**Table 1**); virtually all such substances known are absorbed from the ejaculate, or diffuse into or are injected directly into the hemolymph (69). Complex chemicals taken orally, particularly those that compromise female fitness, would probably be subjected to enzymatic breakdown in the gut. However one study (89; see also 3 and 30) did conclude that an oral gift is laced with manipulative allohormones. While being inseminated, the female cricket *Gryllodes sigillatus* (Gryllidae) eats a spermatophylax, a gift that is argued to have little material benefit (59, 88; but see 58, 66) and may have manipulative ingredients. In experimental studies, researchers fed *Gryllodes* spermatophylaxes to females of non-gift-giving gryllid species because the recipient species are expected to lack an evolved female resistance to male manipulation via gifts. Taken together, these studies outline two potential types of manipulation. First, phagostimulatory ingredients (analyses of the gift suggest a blend of amino acids that signal high food quality but are short on essential amino acids) may increase spermatophylax consumption time and thus allow a longer insemination time (attachment of the sperm ampulla) (88). Second, and central to the discussion here, Sakaluk and colleagues (89) concluded that receptivity-inhibiting chemicals lengthened the refractory period. However, there

are alternative explanations for the effects on refractoriness: Substances in the *G. sigillatus* oral gift may be costly to digest (e.g., toxic) for the sole experimental recipient species (*Acheta domesticus*), causing reduced motivation to remate. Alternatively, phagostimulants in the gift (88) might signal to females that they have recently fed, thus inducing a delay in remating in *A. domesticus* related to digestion. This alternative explanation invokes the male manipulation of females but by a reduction in amino acid quality rather than through allohormones. A demonstration that oral gifts contain manipulative allohormones requires the analysis of gift components, followed by experimental manipulation of candidate chemicals in mated females.

EFFECTS OF POLYANDRY

As mentioned above, comparative studies show that polyandry increases fecundity, with a higher rate of egg production in species with nuptial gifts. There is also an overall positive effect of polyandry on hatching success (3), but is this effect due to material benefits or genetic benefits from multiple sires? Tregenza & Wedell (106) pioneered a useful method to address this in an experimental design that manipulates the number of mates and number of matings. A second approach that is more important in directly assessing the material benefits of multiple mating examines certain life history and behavioral consequences of nuptial feeding, including the transfer of seminal gifts (see 10).

Manipulating Polyandry and Mating Frequency

In the Tregenza & Wedell design (106), the fitness of females mating with different males is compared to those who repeatedly mate the same number of times with the same male. Male mating history in both treatments is held constant. This is important in studies of nuptial-feeding insects because mating can deplete the male's ability to provide gifts

(particularly glandular gifts), thus potentially affecting the fitness of the mates of nonvirgin males (reviewed in 93; see also 34). Three studies have examined species with gifts. Mating female ground crickets *Allonemobius socius* (Gryllidae) imbibe hemolymph secretions after chewing male tibial spurs. Although in single matings, there were positive effects of meal size on egg production, polyandrous females produced fewer eggs and did not live as long as females that repeatedly mated to the same male (31). These results are exceptional in light of the comparative studies (meta-analyses) on nuptial-feeding orthopteroids and Lepidoptera, showing that polyandry increases both egg production and life span (3) (see above). Therefore, blood feeding in ground crickets did not appear to offset the egg-production costs of multiple mating. Instead the benefits of polyandry came from enhanced hatching success and survivorship of offspring, which was attributed to the positive genetic effects on offspring from multiple sires (31; see also 33). Engqvist (29) reached a similar conclusion in a study of polyandry in *Panorpa cognata* (Mecoptera: Panorpidae), a scorpionfly in which females eat male salivary gland secretions. Again there was greater hatching success for polyandrous than repeatedly mated females.

In another gryllid cricket, *G. sigillatus*, a spermatophylax gift appears to confer little nutritional benefit to females (see discussion above). Ivy & Sakaluk (59) showed that the survivorship of offspring of females from polyandrous matings was much greater than from repeatedly mated females. Hatching success was not affected. Taken together, the results with three systems suggest that polyandry in these gift-giving insects is more important in its genetic effects on offspring survival than on increased fecundity. Indeed such effects have been found in studies of species lacking nuptial gifts as well (93). Could females in species with highly nutritious glandular gifts, such as certain scorpionflies and katydids, use multiple mating to increase fecundity (3; see the next section)

but multiple mates to improve offspring performance?

For such species, the effects of multiple mates on offspring survival are attributed to an increased probability of mating with males of high genetic quality. However, an alternative hypothesis is that these effects are a result of higher quality gifts supplied by these males. In the tree cricket *Oecanthus nigricornis* (Gryllidae), larger males, apparently of higher genetic quality (13–15), provide glandular gifts that are higher in protein (copulating female *Oecanthus* eat secretions from male dorsal glands) (14). Moreover, there is experimental evidence that in the katydid *Requena verticalis*, increasing the number of spermatophylax gifts (harvested from different males) increases offspring performance (44). In the end, however, the hypothesis that the genetic effects of polyandry in gift-giving insects directly affect offspring survival is more consistent with polyandry-manipulation studies of all species showing that increased embryo viability (a small but significant meta-analysis result) is a general benefit for females (93). This review does caution, however, that differential allocation by females in individual offspring from males of high genetic quality, rather than direct genetic influences per se, may explain the increase in offspring viability. Finally, differential allocation by females raises an alternative hypothesis for any positive effects on fecundity from experimentally increasing polyandry in nuptial-feeding insects. The increased probability of mating with a male of high genetic quality can result in females favoring such males by increasing oviposition rate following mating (cryptic female choice) as reported for gland-feeding *O. nigricornis* tree crickets (12) and prey-eating *Harpobittacus* scorpionflies (104).

Ecological and Behavioral Evidence for Direct Benefits of Multiple Mating

One can determine the direct-benefit (nuptial-feeding) effects of polyandry by

examining the demographic, ecological, and behavioral consequences of material transfer to females. An examination of long-term or lifetime fitness is important as it focuses on the central predictions of hypotheses about male-substance function, i.e., whether any cost of remating by females (including manipulative gift ingredients) is compensated by the direct benefits received (110). One aspect is the survival of the female herself (see 82): how seminal or oral male donations affect life span. Given the expected direct costs to females of remating [e.g., male ejaculates, polyandry, and reduced life span in certain seed beetles (36; but see 19)], any positive effects of polyandry or multiple mating on female life span are almost certainly owing to material benefits, assuming that lifetime reproduction is not compromised by longer life. Evidence comes from the positive effects on life span (and fecundity) revealed in comparative (3) and some focal species studies of oral glandular gifts, of several orthopterans (10, 12, 74; but see 31, 58), and seminal gifts, of some Lepidoptera (10).

Boggs (9, 10) pointed out that an important (but overlooked) effect over the life of the female is the effect of food intake on long-term or lifetime mating frequency. If nonspecialized nutrients are obtained from mating, and acquiring these nutrients spurs polyandry, then additional copulations are expected to reduce the need for females to feed. Boggs (9) studied heliconiine butterflies in which adult females obtain nitrogen both by absorbing proteinaceous ejaculates and by ingesting pollen mixed with nectar. Boggs predicted that adult feeding is inversely correlated with female mating frequency and supported this by finding for the polyandrous *Heliconius cydno* that approximately 40% of the variation in mating frequency is explained by pollen-ingestion rates. Variation in pollen feeding in the first place may be a result of differences in the ability of females to compete for pollen or from temporal variation in pollen availability. Further evidence comes from puddling in butterflies. In five species in four families, the

frequency of female visits to puddles, in which mud is eaten to obtain certain nutrients, correlates with mating; the proportion of (older) puddling females was inversely proportional to the species-specific average number of matings (10). Correlations between nutrient acquisition and mating frequency are not predicted by hypotheses that male genital donations are non-nutritious manipulative devices or signals of male quality. This important prediction needs to be tested in other species for which ejaculates have been hypothesized to serve as a general source of nutrition.

There is also evidence from species with glandular oral gifts of inverse correlations between mating and feeding. Experimental reduction in food quality of the female katydid *R. verticalis* significantly increased female mating (spermatophylax-acquisition) rate (46; see also 95). Food deprivation not only increased the mating rates of females, but also decreased the rate at which the males can mate (i.e., produce gifts; males are unable to mate without supplying the spermatophylax). In fact, katydid species with larger gifts have longer male refractory periods (110). These effects on remating rates increase the relative number of sexually active females who compete aggressively for access to males (matings). Moreover, males become choosy (47, 50). These behaviors reflect the kinds of reversal in the mating roles observed in natural populations that were hypothesized to be food deprived (42, 94). Again these results support the hypothesis that polyandry in these species increases female fitness through material benefits, i.e., that spermatophylaxes are an important source of nutrition rather than coercive devices or signals of male quality. The results also reveal that there are material benefits to polyandry that offset any costs.

Evidence of mating role reversals in field studies of arthropods with male seminal or oral donations would thus appear to support the material benefits hypothesis (**Table 1**). This assumes no major female bias in the sex ratio due to pathogens, which can also induce

sexual competition among females (63). Researchers have shown sexual selection among females in the context of competition for edible gifts in katydids (e.g., 50) and dance flies (37, 99; reviewed in 48), but is there any evidence in species with genitally absorbed male secretions? Possible examples include some butterflies in which females solicit matings from males (86, 87, 119–121) and role reversal in certain stomatopod crustaceans. In *Pseudosquilla ciliata*, one study found that females initiate courtship and males are coy (preferring large females). The authors hypothesize that female multiple mating and role reversal are results of valuable nutrients in the ejaculate (52). Protein-rich male accessory gland secretions that are translocated into the ovaries were reported for *Squilla boloschista*, a species showing both polyandry and female solicitation of courtship.

Are Rates of Polyandry Suboptimal in Gift-Giving Species?

Male adaptations potentially push females away from their optimum mating rate both by coercing females into matings with them and by preventing or delaying females from copulating with rivals (80, 92). The hypothesis that male glandular gift substances impose refractoriness in females, as suggested by Arnqvist and colleagues (3, 7), is an example of the latter. Although acknowledging their meta-analytical result that female fitness in nuptial-feeding insects increases “markedly and monotonically” with increased mating rate (3), Arnqvist & Nilsson suggest that mating rates are “seemingly lower than optimal.” They point in particular to butterfly species in which genitally absorbed ejaculates increase female fitness (3 and references therein), yet lifetime mean mating rates in nature are often lower than two. For insects with oral gifts, there are apparently low polyandry rates that are commonly interpreted as being below the optimum for females. The two-week period before a *Kawanaphila* female remates (95) contrasts with just a few days in other katydids

(46). In scorpionflies the period ranges from several days (30) to several hours (102). Refractory periods in these species can be controlled by the duration of ejaculation (implicating allohormone effects) (43, 102) or by the size of the nuptial meal alone (30), yet in most recent studies all refractory periods are interpreted as male manipulation of female mating frequency (109).

However, a subjective assessment of the mating rate as low does not provide evidence that refractory period length is either male imposed or suboptimal for females. Female reproductive success is limited not by mating rate but by her lifetime fitness. Suboptimality thus is measured by decreased fitness. A relatively long refractory period may well be consistent with a mutual benefits hypothesis. In a bittacid scorpionfly, a male ejaculate factor passed only in a full ejaculate (supplied with a full nuptial meal) (105) both induces a refractory period in females and accelerates oviposition. The several-hour refractory period may benefit both partners, whereby the male increases paternity and the female gains from having time out to process and lay eggs and by passing these attributes to her offspring (102). Engqvist (30) raises this hypothesis to explain the several-day refractory period in a panorpid scorpionfly. However, he favors an alternative explanation, that male substances in the salivary-mass meal decrease the female mating rate below her optimum. However, in this scorpionfly it is the size of the nuptial meal that controls refractory period length. Given that oral gifts are unlikely to contain allohormones (see above), a more parsimonious hypothesis is that females remate when hungry and that refractory period length is close to the optimum.

Even the two-week refractory period of *Kawanaphila* katydids may represent an optimal mating rate of females in terms of the length of time needed for gift processing and oviposition. This hypothesis predicts that female interests would win out when deprived of the nutrition required to process eggs. Evidence in support of this comes from

Monandry: mating system in which a female copulates with only one male

experiments in which food-limited *Kawanaphila* females deprived of a spermatophylax meal (but completely inseminated) reduced the refractory period to just a few days (95). The ability of females to reduce the refractory period to this degree argues against a male manipulation hypothesis unless for hungry females there is a cost in disabling the effects of manipulative chemicals.

The typical two-week female refractory period of *Kawanaphila* is at the upper end of the range (from less than 1 day to approximately 18 days) reported for spermatophylax-eating tettigoniids (114). Comparative studies have interpreted a positive relationship across taxa between relative ejaculate mass (estimated using the size of the sperm ampulla part of the spermatophore) and the length of the female refractory period (109, 110) as evidence for male manipulation to decrease female mating frequency by means of inseminating a large ejaculate (spermatophylax gift size was either not a significant predictor of mating rate or was held constant in these analyses). However, such comparative evidence is also consistent with mutual benefits hypotheses; the signal transferred in the ampullar ejaculate cues the female to take time to process the nuptial meal (105, p. 403). This hypothesis predicts that larger nuptial gifts require longer processing times, thus explaining the inverse relationship between ampulla size (positively correlated with spermatophylax mass) and refractory period (109).

Curiously, the negative correlation between ejaculate size and polyandry in tettigoniids contrasts with a positive correlation for lepidopteran species (109, and references therein), which Vahed (109) suggests may result partly from the inherent differences between the two insect groups to resist manipulation by males. A more parsimonious explanation for lepidopterans, however, is that sperm competition, via more sperm and non-nutritional components in ejaculates (55), increases in intensity with increased polyandry.

Vahed (109) also suggests that, in contrast to tettigoniids, the lepidopteran analyses are

complicated because they probably include a number of “genuinely monandrous” species, i.e., a species in which monandry is a female adaptation rather than being male induced. Reductions in remating rate to the level of monandry can be adaptive for females even in species with seminal gifts. This can occur if the time taken to remate is costly because of climatic or seasonal restrictions (118) on time available for oviposition. Male *Pieris napi* butterflies transfer large and nutritious ejaculates to their mates (65), yet some populations are monandrous, whereas others are polyandrous. These differences are under genetic control (118). Monandry was suggested as an optimal female mating rate for populations experiencing a seasonal limitation on time for reproduction (118). Välimäki et al. (112) supported this hypothesis by showing that monandrous *P. napi* females had higher fecundity early in life than polyandrous individuals.

Even if the remating rate is suboptimal for females, there are evolutionary factors other than male coercion that could potentially determine this. For example, if the costs of producing nuptial gifts are high, the number of males available for mating may be limited. In fact a paucity of food in the environment could decrease the number of gift-giving males available, thus reducing the female remating rate below the optimum. This would occur either if gifts themselves were rare [e.g., in empidine dance flies whose proteinaceous food comes only from nuptial prey (20)] or because food limitation decreases the ability of males to manufacture proteinaceous glandular gifts (46). Moreover, these decreases in male availability and concomitant increases in female promiscuity due to the direct fitness gains that females obtain from polyandry (3) can cause suboptimal mating rates for some females owing to sexual competition for gift-giving males. In katydids there is direct evidence for reduced mating rates in some females at high population densities, e.g., those starved of protein (97), due to sexual competition among females. Greater sexual selection on females was evident in the greater variation

in lifetime polyandry rates (0–12 matings) at this site compared to low density sites (1–6 matings). As mentioned above, female katydids fought for access to males able to produce spermatophylax gifts, and males were selective of mates (42). Owing to the influence of diet on both female remating rate and the availability of males as mates, the outcome of limited food supply on the mean mating rate of females is difficult to predict. In fact, consistent with the lab studies mentioned above, field enclosures in which female *K. nartee* katydids were well fed—and thus showed typical mating roles—had a lower female mating rate (0.7 over 14 days) than food-stressed populations (1.4 over 14 days) (50). Mating rates of hungry females are probably suboptimal given the added value of male spermatophylax meals (95).

Potential influences on female mating rates due to sexual competition are not limited to populations showing complete reversal in mating roles. Food-deprived *R. verticalis* females in the lab reduce the refractory period

to approximately 2 days compared with 4 days with females on an ad lib diet (46). However, field evidence indicates that female remating intervals in nature are much longer, at approximately 2 weeks (51), possibly because virgins outcompete mated females (or are more motivated to mate than nonvirgin females under field conditions) (76).

These studies with nuptial-feeding katydids show a complex interaction between food availability and the effects of sexual competition and mating-induced refractory periods on female mating rates. This reinforces the conclusion that relatively low mating rates (long refractory periods) do not provide evidence that female mating rates are suboptimal. The suboptimality hypothesis could be tested by determining whether optimal polyandry rates for females (determined experimentally) are higher than natural rates. Furthermore, diet and gifts need to be manipulated in other species (see 95) to test whether food-restricted females can overcome male-imposed refractory periods.

SUMMARY POINTS

1. Comparative and experimental/observational evidence support the hypothesis that most edible (oral) gifts of prey or glandular products provide direct benefits to females.
2. Some seminal contributions from males (absorbed in the female genital tract) also provide direct benefits. These include both chemicals used in defense against natural enemies and nutrients.
3. Gifts clearly supply nutrients if females increase mating rates when food from other sources is limited. Sexual competition among females for gifts also supports a material benefits hypothesis.

DISCLOSURE STATEMENT

The author is not aware of any biases that might be perceived as affecting the objectivity of this review.

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3. Comparative analysis (meta-analysis) of the effects of polyandry on female fitness comparing gift-giving species with others.

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