

MALE NUPTIAL GIFTS: PHENOTYPIC CONSEQUENCES AND EVOLUTIONARY IMPLICATIONS

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I. DESCRIPTION OF MALE NUPTIAL GIFTS

A. DEFINITION

Male insects of many species give a nuptial gift to females. Nuptial gifts, as used here, are potentially nutritious substances given to the female by the male in conjunction with mating and used by the female in her resource budget. Such gifts can be as extreme as allowing the female to eat part of the male,¹⁻⁴ as behaviorally complex as presenting a female with a prey item on which she feeds during copulation,⁵⁻⁷ or as mundane as passing nutritive accessory gland fluid into the female's reproductive tract along with sperm.⁸ Thus, nuptial gifts are an investment by the male in a female and/or her prezygotic offspring with potential selective consequences. Activities such as guarding offspring⁹ or feeding offspring¹⁰ are a postzygotic investment and are not included in my definition of nuptial gifts. Tallamy¹¹ reviews postzygotic investment in insects.

Male nuptial gifts are widespread across insect orders, including those with a range of feeding habits and in a diversity of environments. Groups and the type of donation are tabulated in several recent reviews.^{6,12-15} Such tables therefore will not be duplicated here.

Nuptial gifts have ramifications throughout the biology of both males and females. Individual-level physiology and behavior, as well as population demography and genetics, may be affected in ecological and evolutionary time. Much of the work to date has focused on only a few aspects of nuptial gifts, in part because nuptial gift giving is an excellent vehicle to test sexual selection theory. However, nuptial gifts function in a much broader biological context. While I review the more well-known aspects of nuptial gift giving, I also point out areas that are currently begging for exploration.

B. PREY ITEMS AND REGURGITANTS

Males of some mecopteran, dipteran, hymenopteran, and heteropteran species present a prey item to the female for her feeding during copulation.⁵⁻⁶ The male sometimes may feed on the prey item himself before finding a mate. In the most well-described cases in Mecoptera, bittacid males capture an insect prey, dangle in the vegetation, and call females by means of a pheromone; once a female approaches, the prey is presented to the female for feeding during copulation.^{5,16-17} If the prey is small or has been largely eaten, females may prematurely terminate copulation.^{5,17} Otherwise, the male and female may fight over the prey item once males terminate copulation,^{5,17} with the male retaining the prey most of the time. Prey may then be reused by the male in another courtship. In at least one species, *Harpobittacus similis*, males with larger prey did not call as much as males with small prey, but still attracted females.¹⁷

Dance flies (Diptera: Empididae) exhibit a variant on this theme. Males catch prey, but the two sexes meet either at male¹⁸ or female⁷ leks. Prey items in *Empis borealis* can include conspecifics.⁷ Other empidids have altered nuptial gift giving in a stereotyped way.¹⁸⁻¹⁹ While male *E. borealis* simply present prey to females to feed on during mating, in more advanced species prey are wrapped in silk (*Hilara* species) or covered with a frothy balloon (*Empis* species). In yet other species, the silk or balloon surround inedible dried prey fragments; finally, in some species the male presents the female only with an empty wrapping. Females do not feed on this package, but only manipulate it during mating. By my definition, neither of these last two types of gifts qualify as nuptial gifts.

Panorpa (Mecoptera: Panorpidae) males may adopt a mixed strategy with respect to nuptial gift giving.²⁰ Prey may be caught and advertised to females; alternatively males may place a salivary gland secretion on a leaf to attract a female or may attempt forced copulations with no gift at all. Prey presentation is the most successful strategy, followed by salivary gland secretions and then by forced copulation. A single male may employ all of these strategies during his lifetime.

Feeding females regurgitants or anal secretions may be widespread within *Drosophila* (Diptera: Drosophilidae).²¹ In *Drosophila subobscura* and other members of the *obscura* species group, males regurgitate crop contents, forming a drop that females may eat during courtship. Females are more likely to eat the drop if they are on a low-nutrient diet than if they are well fed. In *D. nebulosa* (and probably other members of the *willistoni* species group), gut contents are expelled from the anus and eaten by the female during courtship.

C. ACCESSORY GLAND PRODUCTS

1. Nonspermatophore Secretions

The primary function of many male accessory gland fluids passed to the female at mating has nothing to do with nutrient donation. Such fluids include oogenesis inducers,²²⁻²³ mating refractory period inducers,²²⁻²³ sperm longevity or activation factors,²⁴ or sperm transfer facilitators.²⁵ However, at least some of these compounds do show up in oocytes.²⁵⁻²⁶ Further, in studies of sperm activation in Lepidoptera, Osani and coworkers have shown that spermatophores have proteolytic activity and release free amino acids.^{24,27} These amino acids could be taken up by the female, perhaps passively through diffusion or in competition with their use by sperm. Such effects may be minor in the overall context of the female's resource budget, but could be important to specific organs.

Still, some accessory gland compounds (other than spermatophores described below) could be nutrient donations from males to females. Mating plugs are formed from accessory gland material in Lepidoptera,²⁸ and could conceivably be absorbed by females. Many Lepidoptera also have both a bursa copulatrix (where the spermatophore is deposited) and a smaller appendix bursa.²⁹ The appendix bursa is filled with fluid at mating.³⁰ The function of this fluid is unknown; one possibility is that it is a source of female nutrition. Finally, *Drosophila* do not have spermatophores, but females of those species which show a mass in the reproductive tract after mating (an insemination reaction) also incorporate male nutrients into developing eggs.³¹

2. Spermatophores

Spermatophores are specialized structures produced by the male accessory gland. Orders possessing spermatophores include Orthoptera, Lepidoptera, Trichoptera, Neuroptera, Diptera, Odonata, Coleoptera, Hemiptera, and Psocoptera.³²

Spermatophores used by females as nutrient sources can be deposited internally or externally to the female. If deposited internally, spermatophores are absorbed; if deposited externally, they are eaten. Among the more well-studied groups, Lepidoptera and Coleoptera have internal spermatophores, ranging in size from 1.5 to 15% of the male's body weight.³³⁻³⁵ Orthoptera and some Megaloptera have external spermatophores, ranging from 0.2 to 30% of the male's body weight.³⁶⁻³⁸

Orthopteran spermatophores vary in complexity. Within the Ensifera (crickets and katydids), the Gryllidae (with the exception of the Gryllinae) generally have simple, externally attached spermatophores. The female often eats these after mating, sometimes interfering with sperm transfer.³⁹⁻⁴⁰ The frequency with which the spermatophore is eaten probably varies among species and habitats. Bidochka and Snedden⁴ found that female *Allenomobius fasciatus* ate the spermatophore after 58% of lab matings — but the male ate it after 27% of matings.

Within the nongrylline Gryllidae, females of some species may mate with the same male more than once.³⁹⁻⁴¹ In *Nemobius sylvestris*, multiple mating takes on an added dimension: at

the first mating, the male deposits an empty spermatophore which the female consumes; at a rapidly ensuing second mating, the male deposits a sperm-containing spermatophore which the female eventually also eats.⁴²

Males of the Gryllinae, Tettigonidae, katydids, and Stemopelmatidae (Jerusalem crickets) make complex spermatophores with sperm-containing ampulla and attached bi-lobed spermatophylaxes.^{39,43} Females in these species detach and eat the spermatophylax while sperm is moving from the ampulla to the spermatheca for storage; once the spermatophylax is consumed, the ampulla is often also eaten.³⁹

Spermatophores in general vary in composition, but virtually all contain protein and carbohydrates, and some contain lipids.²² For example, Marshall⁴⁴ found that *Colias philodice eriphyle* (Lepidoptera: Pieridae) spermatophores contain proteins, hydrocarbons, triglycerides, diglycerides, sterols, and phospholipids.

Spermatophores may contain significant amounts of ions or minerals. *Heliothis virescens* (Lepidoptera: Noctuidae) males put about one third of their zinc supply into the spermatophore.⁴⁵ Sodium is transferred to the female in other Lepidopteran species;⁴⁶⁻⁴⁷ young males feed at damp mud to obtain sodium,⁴⁸ which is then transferred to females. Transferred sodium can be important to the female's sodium budget⁴⁷ and affect egg survival.⁴⁶ The proportion of older lepidopteran females feeding at damp mud is inversely related to the species-specific average number of matings obtained by females for five species from four families; females that mate only once tend to feed at mud during old age much more frequently than females from multiple mating species.^{49,50} This suggests that insufficient sodium is transferred at mating to last throughout a female's life in some singly-mating species.

Various roaches cover the spermatophore with urates from the male's uricose glands after the spermatophore is put in the female's genital pouch.^{22,51} After sperm transfer, the female expels and eats the spermatophore and urates, although several days may elapse between expulsion and eating.⁵¹ *Xestoblatta hamata* females feed on urate secretions directly from the male after mating.⁵² Mating takes about the same time as that needed for emptying the female's gut, increasing her willingness to feed on male urates. Ingested urates are important in the female's nitrogen budget, and uric acid *per se* is incorporated into eggs in *Blattella germanica* (Dictyoptera: Blattellidae);⁵¹ in *X. hamata*, mature oocytes are nearly 28% uric acid.⁵² Bacterial endosymbionts transferred to oocytes by the female may be responsible for urate catabolism in eggs as occurs in adult fat body.⁵³

Males may also donate defensive compounds. Cantharidin is not synthesized by female spanish flies *Lytta vesicatoria* (Coleoptera: Meloidae),⁵⁴ but is obtained from the male at mating.⁵⁴⁻⁵⁵ Male monarch butterflies *Danaus plexippus* (Lepidoptera: Nymphalidae) may donate cardenolides.⁵⁶ Male ithomiine butterflies (Lepidoptera: Nymphalidae) transfer up to half their pyrrolizidine alkaloid stores into the spermatophore; females can obtain significant amounts of alkaloids in this manner.⁵⁷ *Utethesia ornatrix* (Lepidoptera: Arctiidae) behave similarly.⁵⁸ *U. ornatrix* males transfer about 15% of their alkaloid to females, which in turn put 90% of the combined female reserves and male donation into eggs. Females are able to increase the amount of alkaloid in eggs by nearly a third through mating donations.

The composition of spermatophores can change as a function of the previous number of matings by a male.⁵⁹ In *Pseudaletia punctella* (Lepidoptera: Noctuidae), spermatophore mass and total lipids decreased as the number of previous male matings increased, but hydrocarbon content remained unchanged. Compositional changes are likely affected by resources available to males. Quantity of a resource type donated at a mating should not fluctuate much from mating to mating for resources available to the male either in large quantities or renewable through adult feeding. However, quantity of resource types only available from larval feeding, or generally scarce resource types, may decline with increasing mating numbers.

D. BODY PARTS AND HEMOLYMPH

The most extreme form of male nuptial gifts is cannibalism of the male by the female. This occurs in three insect orders,¹² including the mantids and ceratopogonine flies. In three ceratopogonine tribes, females pierce the mating male's head or thorax and completely consume him during mating.¹ It is not known if males are always eaten. Numbers of matings obtained by females and effect of the male meal on female foraging and reproduction are not known for these species. However, since cannibalism ends further male reproduction, selection pressures operating on this behavior should be quite large. Buskirk et al.⁶⁰ argue that a low expected lifetime number of matings for males (independent of cannibalism) and a significant increase in the male's reproductive success with cannibalism are the two factors selecting for sexual cannibalism.

A similar, but less drastic, form of nutrient donation occurs in some Orthoptera. Within the Haglidae, female *Cyphoderris buckelli* chew on a male's fleshy hind wings, ingesting both tissue and hemolymph.^{2,61} Females begin feeding before copulation. The male's "gin trap", or pinching organ which holds the female by the venter, restricts females from leaving before copulation. Feeding is terminated by the male. Females may eat as much as one third of a male's wings at a mating and also consume a sizeable spermatophylax. Other orthopterans feed on hemolymph from wounds inflicted on males. Included in this group are *A. fasciatus* (Gryllidae) females, who open a male's tibial spur with a mandible and feed on the exudate.^{4,42} Finally, some orthopteran females feed from secretions from male metanotal glands. Included here are female *Oecanthus* (Gryllidae) and some Eneopterinae and Gryllinae.^{3,42}

E. SPERM

Sperm serve as a male nutrient donation to the female in insect species with haemocoelic insemination, including the bedbug families Nabidae, Cimicidae, Plokiophilidae, and Polyctenidae (Hemiptera: Cimicoidea).⁶² In primitive groups, the sperm and accessory fluids are injected into the female's haemocoel and some sperm are digested. In other groups, the sperm are injected into a specialized tissue, the mesospermalege, and absorbed either by free phagocytes or by specialized cells in the mesospermalege. Hinton⁶² argued that haemocoelic insemination was advantageous because females got a meal thereby, although no data exist on the effects of sperm phagocytosis on female fitness.

Some groups, such as Lepidoptera, produce both apyrene (anucleate) and eupyrene (nucleated) sperm. Apyrene sperm have been proposed to function as nutrient resources for the female or the eupyrene sperm. However, there is no evidence for this, and apyrene sperm do not contain much energy.⁶³

II. OVERVIEW OF ADAPTIVE FUNCTIONS OF MALE NUPTIAL GIFTS

As background to examination of the effects of male nuptial gifts on insect physiology, ecology, fitness, and evolution, we need to understand the potential adaptive functions of the nutrient donations. Male nuptial gifts are part of male reproductive effort. This effort can have two potentially adaptive functions: investment in the female's resource budget and/or in obtaining or guarding a mate.^{12,64} Both forms of effort can increase male reproductive success. Contributions of resources used by females can increase female fecundity directly through an increase in nutrients available to make eggs, or potentially indirectly through an increase in nutrients available to support female survival. Use of resources as bribes to obtain a mate or to prevent or delay female remating can also increase a male's reproductive success through increasing the number of eggs that he fertilizes. These two forms of effort, contribution to a female's resource budget and control of mating opportunities, are not mutually exclusive. Contributions that influence mating opportunities may also be used by the female to make eggs.

III. PHYSIOLOGICAL COSTS AND BENEFITS OF MALE NUPTIAL GIFTS: EFFECTS ON RESOURCE AND TIME BUDGETS

Nuptial gifts are associated with physiological costs and/or benefits, affecting the resource and time budgets. Changes in resource and time budgets in turn may affect foraging, survival, and reproductive strategies, and thence fitness. I deal with specific impacts on fecundity and survival below under demographic fitness component consequences of nuptial gifts; here, I focus on underlying physiological effects.

A. FEMALE PERSPECTIVE

The benefit gained by females from a nuptial gift will depend on the usable donation size relative to the female's total resource pool. Types of nutrients that are limiting to females should have more effect than those available in abundance.⁶⁵⁻⁶⁶

Male-derived nutrients can be allocated as are nutrients derived from other sources: to egg production, to maintenance, to defense, and to foraging activity. The specific allocation pattern of male-derived nutrients should depend on the type of nutrients donated by males, the female's other available reserves, and state of ovarian development.⁶⁶ If males donate compounds that can be used directly in egg production with minimal processing and mating occurs during or just prior to a peak of vitellogenic activity in the ovaries, then such compounds should be more likely to be used in egg production. For example, in *X. hamata*, females feed on male-produced urates after mating, and the timing of mating during a reproductive cycle corresponds to the period when uptake of uric acid by the developing eggs is at a peak. As noted earlier, large amounts of male-derived uric acid may be incorporated into eggs in this species.⁵²

Male-derived nutrients can reduce the need for females to forage on their own for food; this occurs in *Hylobittacus apicalis*, *E. borealis*, *Heliconius charitonius* and *Heliconius cydno*.^{5,7,18,66} I have suggested that reduction in foraging by females with increasing male-derived nutrients is most likely to occur when non-nutritional factors limit egg production such that females cannot increase fecundity by maintaining foraging levels.⁶⁶ Such factors may include mortality risk to the female while foraging, time restrictions for oviposition, or body size limitations on the number of oocytes that can be matured at once.

Male nuptial gifts fed on by the female, such as prey items, external spermatophores, and male body parts, will be incorporated into the female resource budget at the same rates as any other similar quality food item to be used, stored or excreted. As noted above, however, rates and targets of allocation of these items could be affected by the male if males have control over the composition of the gift. Internal spermatophores and male accessory gland compounds that are absorbed by the female may be treated differently. The donation is initially present within the female in a form of storage. Donation usage rates should depend on the balance of draw down of other forms of storage such as fat body, use of free nutrients from newly absorbed food, and use of the "stored" male accessory gland products. The dynamics and priority of use of various types of nutrients from these sources in reproduction, survival, and foraging remain to be examined. Timing and amount of reproduction, feeding sources for the adult and juvenile female, effects of storage on risk of predation, etc., may also influence allocation patterns. Such studies, in combination with information on patterns of paternity, will give us an understanding of the effect of the nuptial gift on the female's resource budget and on the reproductive success of each sex. This in turn will provide a mechanistic basis for answers to questions about the evolution of specific forms of nuptial gifts as outlined below.

We have initial information on absorption rates of internal spermatophores and on the usage rates in oogenesis of materials from both internal and external donations. Most of these data come from radiolabel experiments. Males are labeled with radioactive amino acids and

mated with females; then eggs and/or females are tested for radioactivity at intervals after mating. In both an orthopteran, *D. verrucivorus*, and two lepidopterans, *D. plexippus* and *H. hecale*, the amount and timing of incorporation of labeled compounds into eggs is independent of the previous female mating history.^{8,67} In all Orthoptera and Lepidoptera examined to date, label is incorporated into the next eggs laid by a female although the peak of incorporation may be delayed by several days.^{8,64,66-70} Timing of the peak of incorporation varies from immediately after mating in *Colias eurytheme*,⁶⁹ to 10 days after mating in *D. verrucivorus*.⁶⁷ Elevated levels of label may be found in eggs for only 5 to 6 days as in *C. eurytheme*,⁶⁹ for 7 to 10 days as in *Dryas julia*⁶⁴ or *D. plexippus*,⁸ or for up to 15 to 20 days as in *Heliconius erato*,⁸ *H. charitonius*,^{64,66} or *D. verrucivorus*.⁶⁷ This timing agrees with data on rates of decrease in size of internal spermatophores: spermatophores of *D. plexippus* reach a baseline size within 7 to 10 days,⁷¹ spermatophores of *Pontia protodice*, with a biology similar to *C. eurytheme*, reach a baseline size within 5 days,⁷² and spermatophores of *H. charitonius* are absorbed within about 14 days.⁶⁴ In *Acanthoscelides obtectus* (Coleoptera), radiolabel declines within 48 hours in the spermatophore, peaks in eggs laid at 36 hours, and declines by 48 hours.⁷³ In essentially all studies, all eggs laid by females after mating with a labeled male contain at least a small amount of radioactivity. This would be expected if nutrients are incorporated into eggs at all stages of development, such that eggs that are in late development stages and incorporating large amounts of nutrients are heavily labeled, whereas eggs in early stages of development, incorporating small amounts of nutrients, are lightly labeled.

The differences among species in temporal pattern of radiolabel incorporation into eggs should depend on: (1) species-specific timing of incorporation of specific nutrient types into eggs; (2) the particular compounds that are labeled; (3) pool sizes of those compounds; (4) the rate at which male compounds are absorbed through the gut or reproductive walls; (5) whether more than one day's batch of eggs is matured at once; (6) the number of eggs laid per day; and (7) the total usable size of the male investment relative to mass of individual eggs or clutches of eggs. These factors have been explored to some extent in *B. germanica*,⁵³ where timing of uptake of uric acid into developing eggs is known, as is timing of ingestion of male-derived urates. However, for the most part we know little about factors affecting different patterns observed among species. It would also be interesting to expand the studies on physiology of female use of male-derived nutrients to Trichoptera, as Khalifa⁷⁴ reports differences among species in the size and timing of absorption of the spermatophore.

The interaction of nuptial gifts with female time budgets is also not well understood. Mating may not interact with the foraging or reproductive time budgets in some species. For example, monarch butterflies (*D. plexippus*) can mate overnight,⁷⁵ a time when the female would not be actively engaged in foraging or searching for oviposition sites anyway. However, for many species in which females mate more than once, this lack of impact on the time budget is likely to be the exception rather than the rule. Conflicts over the time spent mating could affect the evolution and maintenance of nuptial gift-giving behavior, particularly if mating is prolonged to allow male nutrient donations. In such cases, the time cost and nutritional rewards of foraging by a female will be balanced against the costs and rewards of male nuptial gifts.

Females may pass up opportunities to use male nuptial gifts altogether. Although *Melanoplus sanguinipes* (Orthoptera: Acrididae) females incorporate protein derived from male accessory gland products into eggs,²⁶ the amount of material transferred into the female's spermatheca is small, about 5 μg , while the amount of protein in eggs laid between matings is large, on the order of 100 mg.²⁵ However, the spermatophore, which could represent a larger male investment, was observed to be rubbed off the female's ovipositor and discarded in this species.²⁵ Why females should bypass cheaply available nutrients is unknown. The answer could depend on the composition of the spermatophore, or the conditions under which observations were made.

B. MALE PERSPECTIVE

Nuptial gifts affect the male's resource and time budgets. Resources spent on large ejaculates or capturing prey are not available for other uses; time spent mating, replenishing accessory glands, or capturing nuptial prey is not available for other uses.

Impacts of nuptial gifts on the energy and resource budget may in turn affect ability to attract mates. *Cyphoderris strepitans* males produce an external spermatophore, eaten by the female, and allow females to eat part of their hind wings and hemolymph during mating.⁷⁶ Virgin males of this species call for significantly longer than recently mated males, suggesting that energy reserves needed for calling have been reduced by mating and/or that intensity of calling depends on distension of the male's accessory glands. Similarly, *Requena verticalis* males on low-protein diets maintain spermatophore mass, but reduce calling, probably as a result of energy limitation.⁷⁷

Nuptial gifts may result in matings lost because of a refractory period while accessory glands are replenished or fresh prey are obtained. The form of this cost differs among insect orders. As Gwynne⁷⁸ points out, Lepidoptera will mate before they have replenished the accessory glands; matings simply take longer, presumably to include time for glands to be refilled and an ejaculate formed. Even so, smaller spermatophores are formed if remating occurs rapidly,^{30,64,78-79} which could affect male reproductive success. Further, in at least one lepidopteran, recently mated males' courtship persistence time was an order of magnitude lower than males that had not mated recently,⁸⁰ which will also affect male success. Orthoptera, Megaloptera, and Coleoptera, however, have a male refractory period during which time males will not attempt mating and accessory glands are replenished. The length of this refractory period depends on the relative size of the spermatophore: in two species without spermatophylaxes, *Gryllus bimaculatus*³⁷ and *Gryllus veletis*,⁸¹ male refractory periods are 1 hour and 30 minutes, respectively; in a species with a relatively small spermatophylax, *Grylloides sigillatus*,⁸¹⁻⁸² male refractory period is 3 hours; and in a species with a relatively large spermatophylax, *R. verticalis*,⁷⁸ the male refractory period is about 3 days. Megaloptera exhibit a similar pattern. *Protohermes immaculatus* males have smaller spermatophores relative to male body weight than do *P. grandis* males; *P. immaculatus* males can remate daily, whereas *P. grandis* males have a refractory period of about 2 days.³⁸ Differences among species in the length of the refractory period may also result from differences in the normal diet. Within Meloidae (Coleoptera), seed feeding species can mate every 4 hours, whereas species feeding on relatively protein-poor flower petals have a refractory period of 1 to 2 days.⁵⁵

Nuptial gifts may also affect survival through impacts on the energy budget. This is discussed in detail below.

Nuptial gift size should affect the relative costs to the male's resource and time budgets. Size of the nutrient donation is expected to vary within species with the male resource budget, female ability to receive and process nutrients, and sperm precedence patterns. First, ejaculate or spermatophore size is positively correlated with male size (and hence, presumably nutrient reserves) within a species in many groups, including *Lytta magister* and *Tegrodera alogra* (Coleoptera: Meloidae),⁵⁵ *H. charitonius* and *D. julia* (Lepidoptera: Nymphalidae),⁶⁴ *C. eurytheme* (Lepidoptera: Pieridae),³⁰ *Papilio machaon* (Lepidoptera: Papilionidae),⁸³ *Plodia interpunctella* (Lepidoptera: Pyralidae),⁶⁸ *Ostrinia nubilalis* (Lepidoptera: Pyralidae),⁸⁴ *G. sigillatus* (Orthoptera: Gryllidae),⁸⁵⁻⁸⁶ *R. verticalis* (Orthoptera: Tettigonidae),⁸⁷ *Conocephalus nigropleurum* (Orthoptera: Tettigonidae),⁸⁸ and *D. verrucivorus* (Orthoptera: Tettigonidae).^{67,89} In *G. sigillatus* and *D. verrucivorus*, the correlation occurs because the male's investment in the spermatophylax or whole spermatophore, respectively, is a constant proportion of his body weight;^{85,89} male investment as a proportion of body weight actually declines with male size in *R. verticalis*.⁸⁷ The data suggest that absolute spermatophore size is more constrained in *R. verticalis* than in the other two species. These differences could be related to differences among species in diet, in spermatophore size relative to male body size, and/or in spermatophore function.

In contrast, no relationship was found between male size and ejaculate mass or volume in *P. protodice* (Lepidoptera: Pieridae)⁷² or *Pararge aegeria* (Lepidoptera: Satyridae).⁹⁰ Rutowski⁷² suggests that this may be due to differences in the primary function of the spermatophore among Lepidoptera, with *P. protodice* donations functioning more to prevent female remating than as a nutrient investment. This idea is explored in more detail below.

Among species, Reiss⁹¹ argues that the investment *per unit time* in reproduction by either sex should scale allometrically with body weight, with a coefficient between 0.5 and 0.9; the precise predictions for each group will depend on the allometries of energy intake and nonreproductive expenditure with body weight. Extensive data to test this hypothesis do not exist for male nutrient donations.

Male ejaculate or spermatophore size increases with male age in virgin male *D. plexippus*,⁹² but not in *O. nubilalis*.⁸⁴ This suggests that males of some species may need time after eclosion to reach complete sexual maturity (as measured by filling of the accessory glands) and/or that adult feeding contributes to the formation of spermatophores.

Spermatophore size decreases with number of previous matings by a male in some Orthoptera,⁸⁹ Lepidoptera^{30,72,84,93} and Trichoptera.⁷⁴ Change in size of spermatophores with previous mating history is likely to be determined by the opportunity for males to replenish reserves from feeding, the average and range in number of matings by males, and the intensity of selective pressure for maintaining a minimum size to guarantee sperm transfer.

Quality of the male's diet and presence of parasites affect the male's resource budget and hence may affect the size of the nutrient donation. Zuk⁹⁴ showed that the number of spermatophores produced in 24 hours decreased with number of gregarine parasitic cysts in the feces of *G. veletis* and *G. pennsylvanicus* (Orthoptera: Gryllidae), but no relationship existed for shorter term spermatophore production measures. Further, *R. verticalis* males infected with a protozoan gut parasite had lower mating frequencies than uninfected males when fed a poor diet. However, the effect of parasitic infection disappeared when males were maintained on a rich diet, indicating that parasites have the effect of lowering experienced diet quality as far as impact on mating success is concerned.⁹⁵

Female ability to receive or process the nutrient donation could constrain the size of the nuptial gift, placing upper limits on size variation. In species with an internal spermatophore, female size and previous number of matings (if the spermatophore is not completely absorbed) may constrain the size of the male's nutrient investment due to space available in the bursa copulatrix or appendix bursa. Some evidence for this comes from *D. julia*, where female winglength interacted with other parameters to affect spermatophore size.⁶⁴ Finally, female mating status has an effect on spermatophylax and ampulla size in *D. verrucivorus*; virgin females obtain larger spermatophores.⁸⁹

IV. EFFECTS OF NUPTIAL GIFTS ON DEMOGRAPHIC FITNESS COMPONENTS

Fecundity and survival are components of individual fitness and, as noted earlier, observed patterns of birth and death may be direct consequences of male nutrient donations because of the impact of these donations on the time and resource budgets of each sex. In this section, I explore the translation of effects on time and resource budgets into effects on fecundity and survival. Explicitly evolutionary relationships between nuptial gifts and fitness components are dealt with later.

A. AGE-SPECIFIC FECUNDITY PATTERNS

Mating can affect age-specific fecundity patterns either through hormonal mechanisms stimulating oogenesis and/or oviposition²²⁻²³ or through alteration of the female's resource budget via nuptial gifts. These two causes can be difficult to separate, especially in species

with internal spermatophores. Here, I am not concerned with oogenesis or oviposition stimulating factors, but rather with effects on fecundity via effects on the female's resource budget.

Male nutrient donations may affect fecundity independently of whether nuptial gifts arose and/or are maintained specifically in the selective context of increasing female reproductive success (and hence, male success). Rather, whether fecundity is affected by nuptial gifts should depend on the size and composition of the donation relative to the female's overall nutrient stores and the timing of the donation relative to oogenesis.⁶⁶ Fecundity enhancement is expected if: (1) at least some oogenesis occurs after mating; and (2) the type of nutrient donated is a limiting factor in egg production. A nutrient may be limiting either due to lack of foraging opportunities either in the adult or juvenile stage or due to an evolutionary history during which females have become dependent on male donations to replace foraging. In these cases, we expect that egg numbers will increase over the short term after mating, consistent with timing of incorporation of male nutrients into eggs outlined above. Alternatively, lifetime fecundity may also be enhanced if male donations allow females to reduce foraging and by so doing, decrease death rates from predation or increase time available to lay eggs. This means that species which live either in harsh or dangerous environments or which use ephemeral but nutritious resources, are likely to show an effect of male donations on fecundity.^{13,62}

Some support exists for these ideas, as outlined by Boggs.⁶⁶ Within Orthoptera, spermatophylax consumption has an effect on the next few days' fecundity in several species, including *R. verticalis*⁶⁵ and *Chorthippus brunneus*.⁹⁶ This impact is affected by the quality of the diet fed to experimental females. More directly, spermatophylax consumption and a seasonally available high quality diet had equivalent effects on female fecundity in an unnamed zaprochiline katydid.⁹⁷ Not all tettigonids show an effect of male-donated nutrients on fecundity, however. Even on a restricted diet, no effect was detected for *D. verrucivorus*.⁹⁸ The spermatophylax in this species is just large enough to ensure that all sperm are transferred to the female after mating,^{67,99} and has a relatively low protein content,⁶⁷ suggesting little opportunity for male-donated nutrients to be important in the female's resource budget, and, hence, to affect fecundity — unless mating were to occur frequently. Within Lepidoptera, larger spermatophores increased post-mating fecundity in *C. eurytheme*.¹⁰⁰ Females in this experiment were fed a relatively poor diet consisting of a 10% sucrose solution; we do not know how often females are food stressed in the field. Within Diptera, semi-starved *D. subobscura* females showed an increase in fecundity the first 2 days after mating if they were fed by males as compared to not fed.²¹ A comparison of crop sizes in wild and lab-fed or lab-starved flies showed no difference in crop size between wild and starved flies, but wild flies had significantly smaller crops than fed flies.²¹ This suggests that females are frequently nutrient stressed in the field. Hence, male-donated nutrients likely play an important role in egg production in this species. In *Drosophila mojavensis*, receipt of a large male donation increases early fecundity only if females are held without access to yeast.¹⁰¹ Further, females of *Panorpa* spp. feeding on dead arthropods during mating showed increased fecundity compared to those not feeding.²⁰ Thornhill²⁰ found evidence for interspecific competition for food in this group, and for significant mortality when individuals forage from spider webs, suggesting that food was scarce and costly to obtain. Finally, within Coleoptera, unfed *Caryedon serratus* females show higher fecundity if allowed multiple matings instead of only one mating, although the authors are not convinced that their results were due to a nutritional rather than hormonal stimulus effect.³⁴

B. SURVIVAL PATTERNS

In cases of sexual cannibalism, male nutrient donation ipso facto reduces male survival rate. The effect of donations on male survival is seldom this severe for other types of male donations. Nonetheless, we lack a detailed understanding of the impact of nutrient donations and mating numbers on male survival. Interesting questions include: Do males whose nutrient

donation is a sizeable portion of their body mass suffer a relatively greater survival cost than males with a relatively smaller donation? Does the survival rate differ depending on whether specialized male structures are eaten or accessory gland products are donated? If accessory gland products are involved, does the effect on survival depend on the match between the composition of the male-donated nutrients and the composition of the adult male diet and hence the ability to replenish the nutrient pool? Understanding the answers to these questions will allow us to understand physiological costs of mating to the males and how such costs translate into fitness-related survival patterns.

Refractory periods found in Orthoptera and Megaloptera, or the decrease in nutrient donations with frequent matings seen in Lepidoptera, may act to buffer survival rates against effects from reproductive expenditures by limiting reproduction. Within Lepidoptera, *D. plexippus* males given the opportunity to mate every day had the same life span as males with no opportunity to mate;¹⁰² a similar result was obtained for *P. aegeria*⁹⁰, the orthopterans *G. sigillatus* and *G. veletis*,⁸¹ and the megalopterans *Prothermes grandis* and *P. immaculatus*.³⁸ This lack of effect could stem from a limitation on reproductive expenditure, from compensatory feeding by males with more matings¹⁰³ as occurs in *H. charitonius*,¹⁰⁴ or from a lack of impact of mating expenditures on types of nutrients important in survival.

In an interesting twist, a *lack* of opportunity to pass nutrients to females can impact male survival under some conditions in at least one roach. *X. hamata* males fed on foods with a high nitrogen content (as are chosen in the lab and field) can die from uric acid toxicity if not allowed to mate and give some urates to females.⁵² How important this is under field conditions as a source of mortality is unknown, but if the variance in distribution of mating numbers among males is at all high, significant numbers of males could be exposed to this mortality source under appropriate nutritional environments.

Effects of male donations on female survival are somewhat more variable than those seen to date on male survival. No survival effect of increasing the quantity of male nutrient donations has been found for *D. plexippus*^{75,79} or *O. nubilalis*⁸⁴ within Lepidoptera, or *D. verrucivorus*⁹⁸ within Orthoptera. However, increasing male nutrient donations increased female survival in *C. eurytheme*¹⁰⁰ and *Psuedaletia unipuncta*¹⁰⁵ within Lepidoptera, and *G. sigillatus* and *G. veletis*⁸¹ within Orthoptera. As for males, the observed results may be affected by possibilities (in the field or lab) for compensatory feeding if females receive small donations, or by the type of nutrients donated by males at mating and their importance to survival processes.⁶⁶ In the latter case, it is also possible that a shortage of male-donated nutrients normally used for survival could cause a reallocation of female-derived resources away from reproduction, maintaining female survival rates at the expense of reproduction. Such reallocation driven by decreases in male-derived nutrients has not been explored, but *Speyeria mormonia* females (Lepidoptera: Nymphalidae) reallocate resources from reproduction to survival in the face of adult female food shortages.¹⁰⁶

Effects on survival may occur not just through impacts on the resource budget, but also through increases or decreases in exposure to predators because of changes in foraging activity by either males or females. Through feeding on nuptial gifts rather than foraging on their own, the incidence of spider predation is apparently reduced in the hanging fly *H. apicalis*, as females are found significantly less frequently than males in webs, whereas there is no difference by sex in a similar species without nuptial prey gifts.¹⁶ Conversely, in mormon crickets and conocephaline katydids, the sex competing for mates (and hence, with a relatively smaller investment) is more active and suffers more wasp predation.¹⁰⁷

Finally, nuptial gifts can affect offspring survival rates. Increasing the female's supply of defensive compounds, such as pyrrolizidine alkaloids in ithomiine butterflies⁵⁷ or moths,⁵⁸ could increase the survival rates of offspring. Offspring survival can also be increased if male donations increase the female's supply of trace nutrients, including sodium, as seen in *Thymelicus lineola*.⁴⁶ The same effect may explain data for *R. verticalis*:⁶⁵ females eating more or larger spermatophylaxes laid larger eggs; larger eggs have higher over-winter survival

rates, and, if male, differ in developmental rate compared to smaller eggs. Improved female diet alone did not increase egg size in this species.

V. EFFECTS OF NUPTIAL GIFTS ON POPULATION STRUCTURE

Individual fecundity and survival influence fitness relative to the fecundity and survival of other members of a population. The composition of the population is affected by its age structure, individual dispersal habits, and effective population size. Male nuptial gifts can have effects on these three parameters, and hence on the population context within which selection may occur.

A. AGE STRUCTURE

Adult age structure is affected by development time of juveniles, as well as age-specific death rates of adults. Male nuptial gifts may interact with juvenile development time through impacts on the resource budget of each sex. If nutrients gathered during the juvenile stage are used by males in procuring or making nuptial gifts, then longer development times resulting in larger male resource stores and consequently larger donations should be favored, all else being equal.¹⁰⁸ Conversely, females receiving substantial nutrient input from males could have shorter development times if resources normally obtainable only in the juvenile stage are provided by males and juvenile mortality rates are high. These ideas could be tested using selection experiments in a species with a suitably short life cycle. Alternatively, development times could be compared for closely related species from the same habitat with similar food sources and sperm precedence patterns, but which differ in male nutrient donations.

Further, sperm precedence patterns favoring protandry, or adult emergence of males before females, may also affect the size of male nutrient donations.⁸⁹ If sperm from multiple matings mix, then a male's net fitness increment from mating with a female decreases with increasing number of previous matings by the female. Males could offset this decline by increasing the number of sperm transferred, which in Orthoptera can entail a larger nutrient donation to ensure sperm transfer. However, the net gain from a given increase in number of sperm transferred diminishes with increasing numbers of previous matings by the female. As predicted in a protandrous system with sperm mixing and in which the male nutrient donation is just large enough to ensure complete sperm transfer, *D. verrucivorus* males make their largest contribution to virgin females, independent of male mating status.⁸⁹

B. DISPERSAL

Male nuptial gifts may interact with dispersal in two ways: nutrient donations may provide necessary resources for successful dispersal by females, or females may view males as a resource and refrain from leaving areas with males.¹⁰⁹

The first idea, that nuptial gifts allow females to disperse or to migrate, has been explored in monarch butterflies (*D. plexippus*).¹¹⁰⁻¹¹² Overwintering monarchs in Mexico and coastal California have different mating regimes before the spring migration.¹¹⁰ In Mexico, nearly a third of migrating females are virgins, and males and females leave the colony at about the same time. For virgin females, mating presumably occurs on the trip north, since females oviposit on milkweeds during the migration. Prior to migration, mating males are more worn and smaller than the average for the population, whereas mating females are less worn and larger, and males attempting matings appear to discriminate against mated females.¹¹¹ In coastal California, 95% of females mated between 1 and 7 times before moving north, and many males may not leave the colony at all. Thus, there are different patterns in these two populations for the timing of entry of male-derived nutrients into the female resource budget with respect to the timing of migration. These differences could be affected by sperm precedence patterns, physical environmental parameters, activity levels of over-wintering individuals, and distance to the nearest milkweed.¹¹⁰

Wells et al.¹¹² have shown that female lipid content increases once mating begins in the California monarch aggregations, while male lipid content continues to decline. They attributed this difference to a shift of nutrients to the female from males at mating. Using measured energy expenditures by monarchs, the amount of energy estimated to be obtained at each mating by the female, and the timing of first access to milkweed plants for oviposition in the spring, they did Monte Carlo simulations examining expected long-term fate of monarch populations. Their results indicate that multiple mating upon leaving the winter roosting site is necessary for long-term persistence of the population.

Experimental measurements of effects of male nutrients on either dispersal ability or on reproductive ability once a new habitat has been reached have not yet been published. However, several authors have turned the prediction around, arguing that species which are long-lived migrants should be expected to have large nutrient donations from the male to the female.¹⁰⁵ *P. unipuncta* is one such case, as female fecundity and life span are increased by multiple mating in this migrant.¹⁰⁵

An alternative effect of significant male nutrient donations is for females to refrain from dispersing and to remain in areas with males, using males as a nutrient resource. Monarch butterflies in Australia, which do not form overwintering aggregations but breed year-round, may provide an example of this effect.¹⁰⁹ Female density is lower inside dense milkweed patches than on the edges, and male density shows the reverse pattern, suggesting that male harassment may drive females away from the center of the patches. However, if males are removed from an area, females tend to disperse, whereas if population density is simply reduced, the effect is not seen. Use of males as a resource, and hence females remaining in an area with males, need not be the only explanation for this result, but it is certainly a possible cause. It could be instructive to test this hypothesis by contrasting the female dispersal patterns in *Hylobittacus apicalis*, whose females depend on male-provided prey items,^{5,16} with related species with no prey gifts and whose females hunt.

C. EFFECTIVE POPULATION SIZE

The effective population size (N_e) is a measure of the number of individuals actually contributing offspring to the next generation, as opposed to the total number of individuals in a population. Among other things, effective population size governs the power of genetic drift as a significant evolutionary factor. As the effective population size becomes smaller, drift may play a more powerful role affecting evolutionary change.

A given population will exhibit a characteristic mean number of matings per individual, but some individuals will mate more often than others. Male nuptial gifts may affect N_e by affecting the male refractory period after a mating, as noted for Orthoptera and Megaloptera.^{37-38,78,81-82} The male refractory period in turn affects the size of the pool of males available to mate by removing males from the pool for a length of time equal to the refractory period. Thus, the identity of the males in the pool of potential mates is constantly changing, with some turnover rate dependent on the size of the donation. The larger the pool of males available for mating relative to the absolute number of males, the greater the chances that the pool contains males that have recently mated, and thus the greater the chances that a male that has already mated will secure the next mate, or that a male that has not yet mated will not secure the next mate. Note that this effect only occurs if the operational sex ratio is male biased. Otherwise, all males in the pool at any point in time should be able to obtain matings, since there are more females willing to mate than males available, resulting in all males in the population obtaining at least one mating.

The practice of males donating nutrients at mating may also affect N_e through resource-based effects on the operational sex ratio (OSR). When the OSR is biased towards one sex, the possibility exists that not all members of the over-represented sex will obtain matings and contribute to the effective population size. Hence, the component of N_e determined by mating success (a first step in representation in the next generation) may be significantly lower than

the actual observed population size for the over-represented sex, but close to the actual observed population size for the under-represented sex. The OSR can be affected by resource availability in populations with large nutrient donations at mating. If females are in a resource-poor environment, they attempt to replace nutrients unavailable from the environment with nutrients from males at mating; conversely, males may experience longer refractory periods since a given donation is more expensive relative to available resources. The OSR may become female biased under such conditions. In a rich resource environment, females are less willing to spend time mating, since nutrients are not scarce and males experience shorter refractory times. The OSR may become male biased under such conditions, even in the same population.

Male refractory times are not the only item that may constrain the pool of available males in a resource-poor environment. In species with nuptial prey, the abundance of prey items in the environment may affect hunting times, which could in turn affect the number of males with prey available as mates, affecting male N_e . In environments with low prey availability, males which are better hunters or more able to steal prey items may get more matings, increasing the number of males with zero lifetime reproductive success and decreasing N_e .

Species for which diet affects the male refractory period or the size of the male nuptial gift, or for which prey availability is important, then, may experience fluctuations in N_e as a function of variation in the nutrient environment, even without fluctuations in observed numbers of individuals. These fluctuations may have important consequences for the population genetic structure, and the role of genetic drift.

Data on effects of donation size on N_e do not currently exist; for that matter, population data on insect lifetime reproductive success in reasonably natural environments are scarce.¹¹³ Species which alter the size of donations as a function of the food environment would be good candidates for study.

VI. PATTERNS OF THE EVOLUTION OF NUPTIAL GIFTS

A. ORIGINS: PHYLOGENETIC HISTORY

Nuptial gifts may be a very old trait within Insecta. Khalifa⁷⁴ and Davey^{29,43} argue that presence of spermatophores is a primitive trait within this class and has been lost multiple times during radiation of various groups. Thysanura possess spermatophores, as do the orthopteroids and neuropterans. Davey²⁹ points out that other groups without spermatophores often retain reduced accessory glands. The antiquity of spermatophores within Insecta means that the *potential* for male nutrient donations via the spermatophore or similar accessory gland secretions is probably at least as old as the class. Although spermatophores are believed to have arisen in the context of facilitating sperm transfer in a terrestrial environment,⁴³ the possibility of using the structure as a means to provide females with extra nutrients was present. Thus, spermatophores may have been exaptations for male nutrient donations.

Within orders, or genera, phylogenetic history can be an important determinant of both the presence and size of male nutrient donations. Pitnick et al.¹¹⁴ found that monophyletic species groups in *Drosophila* have similar sized ejaculates and similar levels of incorporation into ovaries and female soma of radiolabeled male nutrient donations. This is in spite of the fact that species compared within a species group differed in nutritional ecology and habitat. Likewise, comparison of *D. mojavensis* and *D. pachea*, both cactophilic species endemic to the Sonoran desert but members of different species groups, showed that these two species differ dramatically in ejaculate size and incorporation by the female, but were similar to other members of their species group.

Phylogenetic history undoubtedly plays an important role in determining the degree of male nutrient donation within Orthoptera as well. As noted above, families differ in the presence or absence of a spermatophylax, which increases the size of the male donation. Boldyrev¹¹⁵ argues that the ancestral spermatophore was probably similar to a simple ampulla

without the spermatophylax; in that case, the spermatophylax could have evolved as an elaboration in circumstances where increased male nutrient donation was favored.⁶⁵ There is some uniformity of spermatophore structure within families,¹¹⁶ so the elaboration of the spermatophore occurred relatively early. Many of the relationships between male nutrient donations and other aspects of the biology of a given orthopteran species may be constrained by the phylogenetic history associated with spermatophore production.

Phylogenetic history may also play a role in the development of presentation of prey items to females at mating or other behaviors associated with male nuptial gifts. Certainly the variations seen in *Empis* or *Hilara* species, ranging from presentation of a prey item in primitive species to wrapping the prey item in silk or a balloon to presentation of an empty wrapping in the most derived species, indicate that phylogeny can have significant effects.¹⁸⁻¹⁹ At a more basic level, a survey of mecopteran species which do and do not have male nuptial gifts, examining both phylogenetic relationships and habitat or ecological specialization, could be instructive as to the relative roles of phylogeny and ecology or habitat in influencing the evolution of presentation of nuptial prey.

B. CURRENT VARIATION AND FUTURE PROSPECTS: HERITABILITY

Male nuptial gifts range from secretions, whose evolution must be based on metabolic control of resource allocation, to presentation of prey items, whose evolution must be based on behavioral adaptations. The discussion so far assumes that variation in nuptial gifts has a genetic basis, and hence selection and evolutionary change is possible. However, the genetics underlying nuptial gift giving is not yet understood for any species. In fact, in only one case has heritability of any aspect of the nuptial gift been measured. Based on father-son regressions, Sakaluk demonstrated a ~47% heritability for spermatophylax mass/male body mass in *G. sigillatus*.⁸⁵⁻⁸⁶ None of ampulla mass/male body mass, ampullas mass alone, or spermatophylax mass alone showed significant heritabilities. Sakaluk points out that this result suggests that the size of the ampulla and spermatophylax are genetically uncoupled. This makes sense given that the composition of the two are not the same, and hence the two are likely produced through different metabolic pathways with the potential for differing control. Further, the fact that percent body mass allocated to spermatophylaxes showed heritable variation while absolute spermatophylax mass did not suggests that the controlling factor is an enzyme regulating allocation rate from some finite pool to male accessory glands and/or gene(s) affecting the relative size of the accessory glands.

Sakaluk suggests that variation for relative spermatophylax size may be maintained by fluctuating food environments. In a high food environment, a large spermatophylax may not increase the female's fecundity, but may decrease the number of matings a male obtains due to a longer male refractory period. The disadvantage of a longer refractory period still holds in low food environments, but female fecundity may be increased by a large spermatophylax. Similarly, lack of heritable variation for ampulla mass may have resulted from lack of variation in selection pressures affecting ampulla mass since the costs or benefits of number of sperm transferred do not vary with environmental food availability.

C. INTERACTION OF NUPTIAL GIFTS WITH MATE COMPETITION AND MATE CHOICE

Given the possible adaptive function of nuptial gifts in enhancing female fecundity and securing matings, we can ask whether or not aspects of the reproductive biology of insects are coadapted with male nuptial gift giving. That is, are types, compositions, sizes, or timing of nuptial gifts coadapted with female fecundity, security of paternity, mate competition, or choice, or mating system? Are there patterns of association among traits which have high fitness value and could be selected for in natural environments over evolutionary time? I first consider interactions with sex roles, then with mating systems, then with age-specific fecundity, and then I conclude by pointing out that these interactions themselves are not independent.

Coadaptation of nuptial gifts occurs not just with mating systems, but with the combination of mating systems and age-specific fecundity.

1. Sex Roles and Sexual Selection: Theory

Much of the work on insect nuptial gifts has been done to explore the effects of relative reproductive investment by each sex on sex roles and the operation of sexual selection. This work was stimulated by a series of authors, beginning with Darwin. Before examining the results of experiments relating male nuptial gifts to sexual selection, I will explore the conceptual context for those experiments.

Trivers¹¹⁷ built on arguments by Darwin,¹¹⁸ Fisher,¹¹⁹ Bateman,¹²⁰ and Williams,¹²¹ and argued that differences between the sexes in amount of investment in offspring should control the operation of sexual selection. Trivers defined this critical parameter, 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."¹¹⁷ Thus, individual fitness is the currency in which parental investment is measured; investments must increase the fitness through one offspring's survival at the cost of ability to realize fitness increases through other offspring. Trivers goes on to argue that the sex with the larger parental investment will limit the realized reproductive success of the sex with the smaller investment. Thus, the sex with the smaller investment should experience intrasexual competition for mates. Further, the sex with the larger investment has more to lose from a bad choice of mates than does the sex with the smaller investment. Thus, the sex with the larger investment should exhibit mate choice. Presumably to avoid circularity, Trivers defined parental investment explicitly to exclude investment in obtaining mates through "sexual competition for mates".¹¹⁷

Trivers' definition has led to a proliferation of papers on male nuptial gifts as parental investment vs. mating investment.^{99,102,122-127} This distinction is critical to testing Trivers' hypothesis, since only shifts in relative parental investment are predicted to lead to shifts in sex roles.

Taking a different approach to the problem of sex roles, Emlen and Oring¹²⁸ examined environmental and ecological effects on mating systems. They argued that which sex experiences intrasexual competition for mates depends on the Operational Sex Ratio (OSR), defined as the sex ratio of individuals currently ready to mate. That is, if receptive females are present in smaller numbers than reproductively active males, females represent a scarce resource for males, and males should compete among themselves for access to females and *vice versa*. As Gwynne^{78,129} pointed out, the OSR may be driven by parental investment patterns if the size of the parental investment affects the amount of time spent out of the mating pool by either sex.

Recently, these arguments have been substantially expanded by Clutton-Brock and Parker.¹³⁰ They include time in their analysis, build explicit connections between investment and the OSR, and acknowledge a variety of other factors that may influence the OSR or intrasexual mate competition. They begin by stating that the OSR determines which sex will compete for mates, using arguments similar to Emlen and Oring's.¹²⁸ However, rather than parental investment, Clutton-Brock and Parker focus on potential reproductive rates of each sex as the major factor determining the OSR, along with the local adult sex ratio and sexual differences in survival rates. Potential reproductive rates are in turn affected by investment in offspring, courtship, and mating, as well as physiological and environmental constraints. In effect, Clutton-Brock and Parker have interposed the OSR and potential reproductive rates as intermediary steps between parental investment and mate competition, and have acknowledged other factors that can affect the outcome as to which sex is competitive.

Clutton-Brock and Parker's¹³⁰ theory does not require the distinction between mating and parental investment required by Trivers. Each type of investment is important in so far as it affects the potential reproductive rate. Since a nuptial gift may serve both functions, as for

example nuptial prey in Mecoptera or spermatophores in some Lepidoptera, this theory is more amenable to experimental test.

There is a remaining problem yet unaddressed. Many authors explicitly or implicitly assume that where intrasexual mate competition occurs, mate choice must be occurring in the opposite sex or that conditions leading to mate competition produce mate choice by the opposite sex. Clutton-Brock and Parker¹³⁰ are obvious exceptions to this pattern, as they only address mate competition in their analysis. Trivers,¹¹⁷ however, considers factors affecting the operation of sexual selection in general, and does not examine potential differences in causes of intrasexual competition and intersexual mate choice.

There is no expectation for mate choice to automatically accompany mate competition or vice versa, however. Males may compete with each other for access to a female's feeding territory, or, in some *Heliconius*, males defend female pupae from each other.¹³¹ In these cases, the female is not exerting mate choice. Alternatively, in *Colias*, females choose mates,¹³²⁻¹³⁴ but males are not competing with each other for access to females.

Three factors are important prerequisites for the mate choice to be expected. First, more than one potential mate must be reliably available, to allow a choice to be made. This does not mean that the operational sex ratio must be skewed towards the nonchoosy sex, although that certainly helps. Second, fertility (for females) or paternity (for males) must be assured, unless choice is to be made among potential mates on the basis of which one will assure genetic representation of the chooser in offspring. Third, one sex must be able to control resources needed by the other,^{6,128,135} AND there must be differences among individuals in quality or quantity of the resources controlled, in order for a basis for choice to exist. Such resources may be genetic, nutritional, or portions of habitat. Thus, choice is likely to be seen in populations with skewed OSRs due to density or lekking behavior, in populations whose individuals mate multiply and/or show last male sperm precedence, and in species in which variation in male nutrient donations or female fecundity are discernible due to age, size, or behavioral differences among differing individuals.

2. Experimental Evidence: Nuptial Gifts, OSR, and Mate Competition

Mate competition can take at least two forms in insects with nuptial gifts. The first is the standard one of fighting between members of one sex for access to a receptive individual of the opposite sex. Fighting for access to mates has been documented within Orthoptera^{36,129,136} and some Lepidoptera.¹³¹ Within Lepidoptera, some *Heliconius* species' males find a female pupa and sit on it about 24 hours before female emergence. Two males will fit on a pupa, one on each side. Males may attempt to take over pupae by dislodging resident males in much the same way they attempt to take over matings in other species. One defending male then mates with the female either just before or at female eclosion.

The second form of mate competition is theft of nuptial prey items, as occurs in *H. bittacus*.¹⁶ Males can act as "transvestites", approaching a calling male as if for mating; in one study, calling males actually offered the prey item to the thief 67% of the time.¹⁶ Males which gain a prey item may also thereby be able to gain a mate at the expense of delayed mating possibilities by the male losing the prey item.

Clutton-Brock and Parker's¹³⁰ theory predicts that changes in the potential reproductive rate of each sex, which may be driven by the relative value of the nuptial gift, affect the operational sex ratio and hence, determine which sex is the competitive sex. Evidence from Orthoptera is consistent with the theory. For example, at high food availability, mating frequency by a zaprochiline katydid female is reduced; at low food availability, female fecundity is maintained only through spermatophore consumption.⁹⁷ Thus, the fraction of females in the mating pool at any one time is lower at high food availability such that the operational sex ratio should be more likely to be male biased at high food availability and female biased at low food availability. As expected, males compete for mates when adult food is plentiful, but females compete for mates when adult food is scarce.¹³⁶ In another case,

Anabrus simplex occurs in either high or low density in Colorado, U.S.¹³⁷ Males in the high density site have lighter accessory glands than males in the low density site. Given the refractory period after a mating while glands are refilled, these data are consistent with the observation that few males were calling at the high density site. Average number of matings by females did not differ between sites. If high density led to longer male refractory periods at the high density site, the OSR may have been biased towards females at that site, and towards males at the lower density site. This would produce the observed sex role reversal between the two sites, with competitive females at the high density site only.

The fact that sex role reversals tend to be observed in Orthoptera with relatively large male investments and multiple matings by females is also consistent with the theory. Larger male investments lead to increased refractory times (see above), decreasing the number of sexually active males at any point in time. Further, the possibility of female dependence on male nutrient donations when other adult food resources are scarce means that the proportion of sexually active females in the population can increase under some circumstances. Thus, the OSR can swing from male to female biased depending on food availability, accompanied by changes in which sex competes for mates.

The interaction between energy needed for male nutrient donations and for mate calling can also produce a biased OSR, but only if noncalling males are not part of the mating pool. For example, *C. strepitans* males' wing pads are fed on by females during mating, impairing the ability of nonvirgin males to call for mates.⁷⁶ Likewise, *R. verticalis* males held on low diets maintain spermatophore size, but reduce calling for mates due to energetic limitations.⁷⁷ Since female competition has not been observed in the latter species, the theory predicts that male refractory periods should be relatively unchanged by low quality diets and that noncalling males really are part of the mating pool — that females are able to find them for mating purposes.

In species without direct mate competition, sex role reversals may take the form of shifts in the sex initiating courtship. This has been documented for the pierid butterflies *P. protodice*¹³⁸ *Colias philodice*, and *C. eurytheme*,¹³⁹ whose females approached males and elicited courtship chases once the bursal spermatophore contents were largely depleted. This system would be interesting to examine in the context of interactions among resource availability, potential reproductive rates, and the operational sex ratio.

3. Mate Choice Based on Nuptial Gifts

Mate choice can be accomplished in several ways. The first way is primary choice through rejection or acceptance of mating with a prospective mate. Secondary choice by females occurs if the female rapidly remates with another male (in systems without first male sperm precedence) or if females control the length of copulation and hence, the amount of sperm transferred, as occurs in some bittacids.⁵ In the orthopteran *Gryllus bimaculatus*, females use both approaches: females may remove some males' spermatophores before all sperm are transferred, but remain near large males, remating several times.¹⁴⁰

Above, I predicted that presence of choosiness should depend on reliable availability of mates, assurance of fertility or paternity, and ability of one sex to control resources needed by the other combined with distinguishable differences among individuals in ability to provide those resources. Available data for choice involving nuptial gift donations supports these predictions. First, food availability can influence choosiness in each sex through effects on mate availability. For example, in a zaprochiline tettigoniid, calling males were frequent under conditions of high food availability and females were choosy, rejecting males. However, females were eager to mate and receive nutrients under low food availability, the OSR was female biased, and males were choosy.¹³⁶

Second, in *D. julia* (Lepidoptera), females tend to mate on their second and subsequent matings with males who have had large numbers of matings, but have not mated recently; these males provide larger spermatophores than males that have mated more recently. This

pattern is not observed for the first matings by females.¹⁴¹ Females in this species can fertilize all eggs from a single mating if access to males is restricted.¹⁴² A similar increase in female discrimination is observed in *Colias* butterflies.¹⁴³ Thus, female choosiness can increase after a first mating if sufficient sperm are obtained from one mating to fertilize all of a female's eggs. In a twist on this idea, *D. verrucivorus* males contribute a larger spermatophore to virgin females than to nonvirgins, which constitutes a form of investment choice; males probably father more offspring of virgins than nonvirgins.⁸⁹

Both sexes can exercise mate choice simultaneously. For example, in *P. protodice*, male courtship duration depends on the type of female: larger, younger females are courted longer than others.¹⁴⁴ In the same species, females discriminate among males based on the duration and intensity of courtship.⁸⁰ Since choice can be exercised by both sexes simultaneously, then the identity of the choosy sex(es) cannot be dependent only on the operational sex ratio or on the relative amount of parental investment by each sex. An examination is needed of threshold conditions for choice, considering mate availability, fertility/paternity assurance, and discernible differences among individuals in resource control.

D. INTERACTION OF NUPTIAL GIFTS WITH MATING SYSTEMS AND SECURITY OF PATERNITY

Nuptial gifts can function as investments in obtaining a mate or in ensuring complete sperm transfer. A male either presents a prey or is expected to donate a spermatophore,⁸⁰ which gives the female sufficient net benefit that she is willing to mate with that male. Nuptial gifts may thus function as bribes, as an index of male genetic quality, or both. For species which have external spermatophores or which present arthropod prey for the female to feed on during mating, the size and quality of the male donation can determine whether the maximum number of sperm are transferred. For example, in *G. sigillatus*, the length of time the ampulla remains attached, allowing sperm to be transferred and stored in the female, depended on the size of the spermatophylax and how long it takes females to eat it; once they had eaten the spermatophylax, they removed the ampulla and ate it as well.^{86,122} Copulation duration in *H. apicalis* depended on size of the offered nuptial prey item, with a threshold size above which copulations lasted long enough for complete sperm transfer.⁵ In these cases, the function of the donation may differ, depending on the vantage point: for females, it is still an investment in their resource budget; for males, it is expenditure in obtaining a mate and not necessarily a direct investment in offspring.

A prediction following from this function is that a threshold investment in the female's resource budget exists, and males that cross that threshold obtain mates and/or complete sperm transfer. The threshold might shift, depending on the state of the female's resource pool, the relative time cost of mating, and the current risks associated with foraging herself. Quantitative shifts in thresholds have not been explored in detail yet, except in the extreme case where females are on very poor diets, which can lead to sex role reversals where females are willing to accept any male as they compete for males, rather than choosing among males.^{97,136-137}

Male nuptial gifts can also function to prevent females from remating. This can be accomplished in several ways. First, female refractory periods may be induced through compounds in the ejaculate.²²⁻²³ Second, mating plugs (which might also function as nuptial gifts if they are absorbed by the female) may be formed in the female's genital tract, which physically prevent other males from mating with the female.²⁸ Third, for some species with internal spermatophores, the spermatophore triggers a stretch receptor in the bursa, initiating nonreceptivity; this has been shown for *Pieris rapae*.¹⁴⁵ The decay of female nonreceptivity in another Lepidoptera, *D. plexippus*, is correlated with the initial size of the spermatophore;⁷¹ whether resumption of receptivity is cued by a threshold size of the absorbed spermatophore, by decay of some factor transferred by the male whose volume is correlated with spermatophore size, or by changes in the female's nutritional status as a result of decreasing input of spermatophore nutrients remains to be determined.

Males make a nutrient donation to the female prior to the transfer of sperm in all known cases, even if female utilization of that donation is delayed.³⁰ In Lepidoptera and other groups with internal spermatophores, the spermatophore is passed to the female prior to sperm movement; in Orthoptera, the sperm are often deposited in an external ampulla, and the ampulla, spermatophylax, and/or male body parts are available to the female prior to sperm movement into the female's body; in Mecoptera and Diptera with nuptial prey or salivary gifts, prey are presented to females prior to the onset of copulation. This uniformity among cases where the nutrient value of the donation to the female varies suggests that selective pressures associated with mate acquisition, complete insemination and mate guarding were crucial to the evolution of nuptial gifts. That is, males that were able to present gifts first obtained matings from females and also obtained complete inseminations. In some of these groups, then, female choice of mates with an initial gift may have played an important role in the evolution of the form and sequence of gift giving.

While mate acquisition, mate guarding, and security of paternity may have played a role in the evolution of male nutrient donations, male nutrient donations may also function as the selective context for changes in mating systems and sperm precedence patterns. In short, the two sets of traits, mating systems and donation quality/quantity, should be coadapted. In species whose females mate several times, the timing of remating can be closely linked to the timing of the decay of use of the previous male's nutrients in egg production. Female *C. eurytheme* remate after 4 to 6 days in a field population;³⁰ male nutrients are primarily found in eggs laid during the first 3 to 4 days after a mating.⁶⁹ However, both *R. verticalis* and *D. verrucivorus* females show a peak of incorporation of male nutrients into laid eggs much later than the end of the female refractory period.^{70,85,146} Actual timing of female remating in the field will depend on female access to mates as well as the length of the refractory period.¹⁴⁶ Inter-mating intervals may thus be longer than the refractory period which was observed under experimental conditions.

Differences not just in nutrient use as outlined above, but also in donation quality or quantity, are expected for related species that differ in expected number of female matings, sperm precedence patterns, and/or alternative mechanisms of mate guarding not involving the male nutrient donation. Extensive data to test this do not yet exist. We do know that spermatophore size is correlated with the duration of the inter-mating interval within some species but not others, and that the species-specific time required to regain the ability to make a normal sized spermatophore after a mating is correlated with mean number of matings in some groups.

Time since the last mating by the male is positively correlated with spermatophore size in several Lepidoptera.^{30,64,72,83-84,90,92} Further, male lepidopterans remate rapidly, increasing the time in copula if mating has occurred recently, whereas male orthopterans generally have a post-mating refractory period, with subsequent spermatophore sizes unaffected. This suggests differences between the two groups in mate acquisition strategies, with lepidopterans remating whenever possible even if a small spermatophore results, whereas orthopteran males appear to need the ability to make a minimum investment before mating will occur.⁷⁸

Differences in the mean number of lifetime matings among lepidopteran species are correlated with the rate of recovery of ability to produce a "normal" sized spermatophore.³⁵ Four species from a diversity of families with an average number of matings greater than 2.0 were able to make a spermatophore equal in mass to that of the first mating within 2 to 3 days after the first mating; individual males from three species with an average number of matings less than 2.0 had not recovered the ability to make normal sized spermatophores even 5 days post-mating. Further, male mating success is highly skewed in at least three species including one with mean number of matings less than 2.0; in *H. cydno*, *H. charitonius*, and *D. julia*, less than 15% of the males obtain half the matings.¹⁴⁷ This difference in recovery time, then, means that a significant number of females which only mate once may be receiving small spermatophores without the opportunity to obtain more nutrients from males at a later time.

E. INTERACTION OF NUPTIAL GIFTS WITH AGE-SPECIFIC FECUNDITY: FECUNDITY ENHANCEMENT

Female intake of male-donated food, in whatever form, is a contribution by the male to the female's resource budget.⁶⁶ Depending on subsequent allocation of that food by the female, it may also be an investment in offspring; depending on paternity patterns, it may be an investment in the donating male's offspring. Males can theoretically influence allocation patterns by the type of nutrients they donate; nutrients which are in short supply for egg production and which are usable with little modification should be allocated to offspring by the female. Although the fitness of the male may also be enhanced if "his" nutrients are allocated to female survival rather than invested in his offspring, this effect has never been experimentally tested.

From a female perspective, the nuptial gift may be regarded as another food source, with attendant risks and benefits which differ in detail from those of "ordinary" food sources. Females should be expected to allocate male-donated resources in a manner consistent with maximizing their own lifetime reproductive success. Thus, the possibility exists for conflict in evolutionary time between the sexes over female allocation of male-derived nutrients.¹⁵ Such conflicts may have molded the present-day size, composition and timing of male nutrient donations, and the consequent role donations have in enhancing female fecundity.

Most work has focused on the end product — number of eggs produced — as the trait affected by changes in available resources due to male nuptial gifts. However, other aspects of reproductive resource allocation patterns may be coadapted with nuptial gift giving. That is, the sources of resources and dynamics of their use in reproduction may be shifted in expectation of a given level of nutritional intake by the female from the male. This can have two manifestations: the first is allocation to reproductive reserves, and the second is ovarian dynamics.

Holometabolous insects in particular have the luxury of reallocating resources during metamorphosis to suit adult needs. Boggs¹⁰⁸ predicted that allocation of larval resources to body vs. reproductive reserves during metamorphosis should vary among species and sexes as a function of the expected adult intake of nutrients, including nuptial gifts, and output of nutrients in reproduction. Three species of heliconiine butterflies fit the predictions. These species differ in the quality of the spermatophore received by the female and in the number of matings. Thus, allocation of larval reserves to reproduction accommodates expected nuptial gifts.

Boggs⁶⁶ further suggests that the nutritional function of the male nuptial gift should be matched with the female's ovarian dynamics. Females whose eggs are matured after adult emergence have the opportunity to use male donations in egg production, rather than just for somatic maintenance. Species with large nutrient donations thus are expected to yolk eggs after adult eclosion.

F. NONINDEPENDENCE OF ADAPTIVE FUNCTION: INTERACTIONS BETWEEN FECUNDITY ENHANCEMENT AND MATING SYSTEMS EFFECTS OF NUPTIAL GIFTS

Nuptial gifts' interactions with mating systems can be affected by the interaction between nuptial gifts and female reproduction, and vice versa. For example, once male nutrient donations of whatever form exist, the size and quality of the donation should be affected by selective pressures related to female and male resource budgets for reproduction, in the context of security of paternity.^{15,148} The effectiveness of mechanisms delaying remating in species with sperm precedence will constrain the possible size/quality of the nutrient donation through pressure on males not to provide nutrients to make another male's offspring. For example, complete sperm precedence coupled with rapid female remating in particular should select for males to donate only small quantities of rapidly utilizable nutrients to females. The state of male and female resource budgets will depend on foraging efficiencies, food availability,

and demands of survival expenses on the resource pool. The fecundity-enhancement function of male nutrient donations thus should have been most strongly selected for in environments which are resource poor, because of low prey or high predator densities or low quality diets, and in species whose males have high confidence of paternity. Note that a species feeding on a highly dispersed but high quality prey could still be considered to reside in a resource-poor environment when compared with species feeding on less dispersed prey items. By this criteria, many parasites, including bedbugs, could be considered to reside in resource-poor environments. Quality of the resource environment should also put a constraint on the evolution of the fecundity-enhancement function of male nutrient donations, however. Nutritional environments which are very poor or risky should not be able to support the resource pools needed by males to make large donations. Tallamy¹¹ presents a variant of this hypothesis, including both prezygotic and postzygotic paternal reproductive expenditures. He provides extensive supporting evidence from a wide variety of arthropods.

Male nuptial gifts may thus have mixed functions, both as resource and mating investments — but only from the male's perspective. From the female's perspective, the sole role of the nutrient donation is as investment in her resource budget; what differs is the size of the investment, its possible uses, and the possibility of exercising choice among males with different quality gifts.

The observed relative importance of the two functions should depend on the following factors. Timing of oogenesis relative to mating and certainty of paternity should affect elaboration of the role of gifts as investment in the female's resource budget (from a male viewpoint). The ability of the female to terminate mating before sperm transfer is complete, the alternative behavioral or hormonal methods of mate guarding, the ability of the male to mate with unwilling females, and the availability of other female mates should all affect elaboration of the role of gifts as mating investment.

Within Orthoptera, we now know that spermatophores can function primarily as a mating investment guaranteeing complete sperm transfer, or have an additional primary function as an investment in the female's resource budget. Conclusions are based on size of the spermatophylax relative to that needed to ensure complete sperm transfer, protein content of the spermatophylax, and the sensitivity of its size to male diet.^{99,122-124} Similar studies have not yet been done in other groups.

VII. FUTURE PROSPECTS

Male nuptial gifts have primarily served as a case example to study theories of sexual selection. The focus has been testing hypotheses concerning the effect of the balance of investment between the two sexes on sex roles and the operational sex ratio. Work in this area should continue to expand, with a better understanding of causes of mate competition and mate choice and inclusion of study of the physiological and genetic underpinnings of observed behaviors.

Study of male nuptial gifts, however, has broader potential than just illuminating sexual selection theory. Like many other reproductive traits, male donations have effects at organizational levels ranging from individual physiology through behavior to population demography. As discussed above, effects of size or frequency of gift donation, for example, can impact the male's resource budget, affecting courting intensity, the operational sex ratio, sex roles, survival, and effective population size. Nuptial gifts also have the potential to affect the evolutionary pathway of traits within a population or of whole phylogenetic groups of organisms through direct effects on fitness or by interacting with other traits to affect fitness. Thus, we may expect to see suites of traits associated with a particular pattern of male nuptial gift giving in the context of a particular resource environment and constraints imposed by phylogenetic history. The degree of variability in the resource environment, the relative harshness of the environment, and the level of survival risk associated with obtaining resources

should be important environmental descriptors in this case. As a corollary, we should only see some combinations of traits as a transient state in evolutionary time, if at all. Traits at issue here include the size and composition of the nuptial gift, the timing of oogenesis, the mean and variance in number of matings by each sex, mate competition, mate choice, allocation of male-derived resources by females, time and allocation costs to males of mating, and age at maturity for each sex. Some of these traits will determine other traits considered above. For example, the mean and variance in number of matings, combined with total population size, determines the population effective population size.

In particular, male nuptial gifts provide a nearly unique opportunity to examine emerging ideas concerning resource allocation. Since male nutrient donations are an allocation to reproduction by the male, but a meal to the female, they are part of the life history strategy of one sex, but the foraging strategy, broad sense, of the other. Resource allocation links foraging and life history allocation; the study of male nutrient donations will allow us to link not only foraging and allocation, but the life strategies (*sensu* Gatto et al.¹⁴⁹) of both sexes. Other possibilities abound as well. Internal spermatophores are a form of "stored" nutrients for the female. Questions concerning the use of available vs. stored nutrients as a function of environmental food availability can be addressed in this system. Questions concerning the effects of variation in availability of different nutrient types at different times in the life cycle can be addressed as well. With the expansion of groups in which male nutrient donations have been studied, we can begin to examine the role of phylogenetic history in constraining allocations related to male nutrient donations, thus limiting suites of traits observed in nature. We should also be able to explore circumstances under which convergent evolution is more or less likely to occur.

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