The Evolution of Animal Nuptial Gifts

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Rich gifts wax poor when givers prove unkind
William Shakespeare, Hamlet, Prince of Denmark (3.1.101)

I. INTRODUCTION

A. WHAT ARE NUPITAL GIFTS?

Nuptial arrangements in many human cultures include gift-giving traditions (Cronk and Dunham, 2007; Mehdi, 2003), and this behavior plays an important role in the mating systems of other creatures as well (Boggs, 1995; Fabre, 1918; Gwynne, 2008; Lack, 1940; Thornhill, 1976; Vahed, 1998, 2007; Zeh and Smith, 1985). In species widely distributed across the animal kingdom, males transfer many different non-gametic materials to females during courtship and mating. Such materials can include lipids, carbohydrates, proteins, peptides, amino acids, uric acid, minerals, water, anti-predator defensive compounds, anti-aphrodisiac pheromones, and neuroendocrine modulators of recipient physiology. These nuptial gifts are an important aspect of reproductive behavior and animal mating systems (Andersson, 1994; Thornhill and Alcock, 1983). However, when compared to more conspicuous sexually selected traits such as male weaponry or ornamentation, such gifts have received relatively little attention from behavioral, ecological, and evolutionary research. Nuptial gifts heighten male reproductive investment, thus limiting male mating rates and altering courtship sex roles and sexual size dimorphism (Boggs, 1995; Gwynne and Simmons, 1990; Leimar et al., 1994). Selection acts on both gift-givers and receivers to shape nuptial gift structure and biochemical composition, as well as gift-giving behaviors. Not only do nuptial gifts form the basis for dynamic coevolutionary interactions between the sexes, but they also link

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together male and female resource budgets (Boggs, 1990). Because they are thus strategically poised at the intersection of nutritional ecology, sexual selection, and life-history evolution (Boggs, 2009), understanding the evolutionary origins and maintenance of nuptial gifts is of fundamental importance.

Animal nuptial gifts come in multitudinous forms (Fig. 1), including food offerings, various male body parts, hemolymph, salivary gland secretions, seminal fluid, spermatophores (sperm-containing packages manufactured by male reproductive glands), and love darts. Many birds engage in courtship feeding, during which males provide prey to their own pair-bond partner or to extra-pair females (Lack, 1940; Mougeot et al., 2006). Scorpionfly males offer females dead insects or secretions from their

Fig. 1. A sampler illustrating the extraordinary diversity of animal nuptial gifts: (A) During mating, a female dance fly (Diptera: Empididae) feeds upon a dead insect provided by her mate (Photo by Rob Knell). (B) Sperm rings are released from a spermatophore manufactured by male accessory glands in Photinus fireflies (Coleoptera: Lampyridae). (C) During mating, hermaphroditic land snails (Gastropoda: Achatinidae) shoot their partner with a love dart that delivers mucus gland secretions (Photo by James Koh). (D) A male scorpionfly (Mecoptera: Panorpodidae) secretes a white salivary mass that will be consumed by a female during mating (Photo by Arp Kruithof).
enlarged, sexually dimorphic salivary glands (Liu and Hua, 2010; Thornhill, 1981). In some ground crickets, females imbibe hemolymph from a specialized spur located on their mate’s hindleg (Gwynne, 1997; Piascik et al., 2010). In numerous animals (including salamanders, molluscs, crustaceans, annelids, leeches, and most insects), males transfer biochemically diverse spermatophores to females during mating (Mann, 1984). Nuptial gifts are not limited to animals with separate sexes, as during copulation many hermaphrodites inject chemicals that induce a physiological response in their partner (Koene and Schulenburg, 2005; Koene and Ter Maat, 2001; Michiels and Koene, 2006; Schilthuizen, 2005). Neither is gift-giving an exclusively male behavior: in heteropteran Zeus bugs, males feed upon glandular secretions provided by the female (Arnvist et al., 2003).

Clearly, if we intend to move beyond merely describing these traits to begin formulating and answering questions about how animal nuptial gifts have evolved, we will need to start with a carefully articulated, coherent definition that encompasses this remarkable diversity. In this review, we begin by proposing such a definition, and then offer a conceptual framework for systematically classifying nuptial gifts. We go on to discuss some ecological conditions and life-history traits that might favor the evolution of nutritive nuptial gifts, that is, those that contribute to female resource budgets. From the male perspective, gift-giving behavior will usually (but not always) provide a net benefit. We analyze these potential benefits by describing how nuptial gifts can increase male reproductive fitness over multiple selection episodes that take place before, during, and after copulation. As a case study, we describe previous work on the katydid Requena verticalis that has elucidated how gift-giving males benefit from this behavior. Rigorously testing the many scenarios that have been proposed about nuptial gift evolution requires a comparative phylogenetic approach, and we discuss results from three insect groups where such an approach has been applied: crickets and katydids, fireflies, and Drosophila fruitflies. We also summarize work on rates of evolutionary change in an important constituent of Drosophila nuptial gifts known as seminal fluid proteins. Finally, we suggest several directions for future research that promise to deepen our understanding of nuptial gift evolution.

### B. Toward a Broader View of Nuptial Gifts

Before considering how nuptial gifts might have evolved, it is essential to clarify some relevant terminology. Previous studies have most often relied on *ad hoc* definitions of nuptial gifts, an approach reminiscent of the infamous “I know it when I see it” definition of hard-core pornography that Justice Potter Stewart used in his written opinion on the US Supreme
Court case Jacobellis v. Ohio (1964). The *Oxford English Dictionary* (1989) provides a legal definition of gift as “the transference of property or a thing by one person to another, voluntarily.” Further, in colloquial English, the term “gift” generally implies some benefit for the recipient. However, because coevolutionary interactions between the sexes can continually alter costs and benefits for both givers and receivers, we contend that a broader view is essential for understanding the evolution of animal nuptial gifts. Within the scientific community, some researchers have limited the scope of nuptial gifts to encompass only “nutritive” gifts, that is, those that contain male-derived substances used by females to sustain metabolic activities (e.g., Andersson, 1994; Boggs, 1995; Gwynne, 2008; Thornhill, 1976). Others have excluded from consideration any gifts that are not contained within a consolidated package (e.g., Thornhill and Alcock, 1983). Again, we suggest that such restrictions may hinder progress toward the ultimate goal of understanding nuptial gift evolution.

As an alternative to this disjointed approach, we advocate the following definition (modified from South et al., 2011b; Lewis et al., 2011): *Nuptial gifts are materials beyond the obligatory gametes that are transferred from one sex to another during courtship or mating*. Importantly, this definition makes no assumptions concerning either: (1) how the gift currently affects fitness; thus, at certain times during its evolutionary trajectory, a gift might be beneficial, neutral, or detrimental to either sex, or (2) the presence or absence of gift-wrapping: thus, we include soluble proteins and other materials that are transmitted in seminal fluid or mucus as gifts, albeit unpackaged. In articulating this broad definition, we hope to unify what have previously been disconnected lines of investigation. For example, the protein content of insect spermatophores is often used as a measure of gift quality (Bissoondath and Wiklund, 1996; Cratsley et al., 2003; Wedell, 1994). This reasonable inference is based on female vitellogenesis being protein-limited (Wheeler, 1996), coupled with evidence that male-derived amino acids are incorporated into female eggs and soma (e.g., Boggs and Gilbert, 1979; Rooney and Lewis, 1999). However, male seminal fluid in *Drosophila melanogaster* contains soluble proteins secreted by reproductive accessory glands and the male ejaculatory duct (Chapman, 2008). Many of these reproductive proteins have been identified and demonstrated to alter female reproduction by stimulating ovulation and oviposition, increasing sperm storage, and lengthening females’ latency to remate (Avila et al., 2011; Wolfner, 2009). However, because these proteins are transmitted in seminal fluid and are not encapsulated within a discrete package, traditionally they have not been considered as nuptial gifts (but see Markow, 2002; Simmons and Parker, 1989; Vahed, 1998). Yet it is becoming clear that male
spermatophores contain many of the same protein classes (Andres et al., 2006, 2008; Braswell et al., 2006; Sonenshine et al., 2011; South et al., 2011a) and these components may produce similar effects on females. It could perhaps be argued that including seminal fluid makes our nuptial gift definition overly broad. However, because various constituents of seminal fluid have been shown to exert diverse effects on both male and female fitness (Gillott, 2003; Leopold, 1976; Poiani, 2006), such inclusion seems appropriate. Thus, we argue that drawing an arbitrary distinction between seminal products encased within a discrete package versus unpackaged seminal products transferred in a liquid ejaculate may have inadvertently obscured basic similarities in gift composition and function, as well as similarities in the evolutionary origin and maintenance of male reproductive accessory glands, the main gift-producing structures.

A key point is that this broad perspective on nuptial gifts allows for possible changes over evolutionary time in how gifts will affect the recipient’s net fitness. While some degree of cooperation is required for sexual reproduction to occur, males and females have distinct reproductive interests (Arnonqvist and Rowe, 2005; Parker, 1979; Trivers, 1972). As a result, coevolutionary interactions between the sexes will cause nuptial gifts to evolve dynamically in a manner that alters the cost/benefit ratio of nuptial gifts for each sex. Thus, a nuptial gift that originates because it provides mutual fitness benefits to both sexes may evolve into a gift that reduces the recipient’s net fitness, and vice versa.

In summary, even though some may find fault with our definition, there is an undeniable need for a more systematic approach to defining what exactly constitutes a nuptial gift. Furthermore, a broader definition such as the one we propose here will allow us to better track the changes in nuptial gift costs and benefits that are certain to occur over evolutionary time.

C. Classifying Nuptial Gift Diversity

In any contest, insects would surely emerge as the undisputed champions of gift diversity. For comprehensive insight into this fascinating diversity, readers are referred to excellent reviews by Boggs (1995) and Vahed (1998). Here, we highlight just a few notable patterns observed among insects before proposing a classification scheme that will encompass animal nuptial gifts.

First, gifts are conspicuously diverse, not only between different insect groups, but also within particular clades. For example, spermatophores are ubiquitous within the insect order Lepidoptera, yet they are absent in the Diptera and occur only sporadically within the Coleoptera (Davey,
Within the beetle family Lampyridae (fireflies), some males pass elaborate spermatophores while firefly males of other species transfer free (unpackaged) ejaculates (Lewis and Cratsley, 2008; South et al., 2011b). Beyond spermatophores, orthopteran nuptial gifts have flowered into an especially impressive display of diversity (described in Section IV.A).

A second notable pattern is that some groups show surprising plasticity in their gift-giving behavior. For example, male Panorpa scorpionflies (Mecoptera: Panorpidae) pursue alternative mating tactics using different gift types (Sauer et al., 1998; Thornhill, 1981). In P. cognata, gift-giving behavior depends on a male’s nutritional state: well-fed males secrete salivary masses that females consume during copulation, while low-nutrition males instead offer females a dead arthropod (Engqvist, 2007b). Similarly, in several empidid dance flies (Diptera: Empididae), males optionally offer females either a dead prey insect or inedible tokens such as silk balloons or seed tufts (Preston-Mafham, 1999; Vahed, 2007).

Here we propose a taxonomy for animal gifts that we hope will facilitate mapping the landscape of nuptial gift evolution (for other classification schemes see Gwynne, 2008; Simmons and Parker, 1989; Vahed, 1998). Table I presents four nuptial gift categories, with examples of relevant structures and behaviors from various taxa. One key distinction is based on the method of gift production. Thus, we distinguish between endogenous gifts that are manufactured by males themselves and exogenous gifts that consist of externally procured food items such as seeds or prey that males gather and then transfer to females. Another important distinction is based on how gifts are absorbed by the recipient. Gwynne (2008) distinguished oral gifts that are taken in through the female digestive system (e.g., food items, spermatophylaces, hindwing secretions), from gifts we term genital gifts that are absorbed through the female reproductive tract: this includes both unpackaged secretions from male reproductive glands (conveyed in liquid seminal fluid) as well as those encased in discrete packages (spermatophores). We propose here another category consisting of transdermal gifts that are injected through the skin into the partner’s body (e.g., snail love darts, intradermally implanted squid spermatophores, hypodermic insemination in leeches and bedbugs). Although nuptial gifts are often commingled together into a single category (e.g., Arnqvist and Nilsson, 2000), we believe the distinctions drawn here will prove useful as a basis for future studies of the evolution of nuptial gift structure and composition. The primary reason for proposing this classification scheme is because, as discussed below, very different predictions can be made about how various gift types might affect fitness of both sexes (see also Simmons and Parker, 1989 and Section III).
<table>
<thead>
<tr>
<th>Gift production</th>
<th>Gift absorption</th>
<th>Nuptial gift examples</th>
<th>Taxonomic group and references</th>
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<tbody>
<tr>
<td>Endogenous</td>
<td>Oral</td>
<td>Hemolymph from tibial spurs</td>
<td>Ground crickets (Piascik et al., 2010)</td>
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<td></td>
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<td>Spermatophylax</td>
<td>Katydids and crickets (Gwynne, 1997)</td>
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<td>Salivary secretions</td>
<td><em>Panorpa</em> scorpionflies (Engqvist, 2007a)</td>
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<td>Anal secretions</td>
<td><em>Drosophila nebulosa</em> (Steele, 1986)</td>
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<td>Metanotal secretions</td>
<td>Tree crickets (Brown, 1997; Bussiére et al., 2005)</td>
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<td>Male body (sexual cannibalism)</td>
<td>Red-backed spider, mantids (Elgar and Schneider, 2004)</td>
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<tr>
<td>Endogenous</td>
<td>Genital</td>
<td>Spermatophores</td>
<td>Salamanders, lepidopterans, molluscs, copepods, crabs, spiders (Mann, 1984)</td>
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<td>Seminal fluid proteins</td>
<td><em>Drosophila</em> spp. (Chapman, 2008; Markow, 2002; Wolfner, 2007)</td>
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<td>Endogenous</td>
<td>Transdermal</td>
<td>Love darts</td>
<td>Land snails (Koene and Schulenburg, 2005)</td>
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<td>Setal gland injection</td>
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<td>Intradermal spermatophore implantation</td>
<td>Squid (Hoving and Laptikhovsky, 2007), leeches (Mann, 1984)</td>
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<td></td>
<td>Hemocoelic injection of seminal fluid</td>
<td>Bedbugs (Stutt and Siva-Jothy, 2001)</td>
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<tr>
<td>Exogenous</td>
<td>Oral</td>
<td>Courtship feeding</td>
<td>Birds: kestrels, shrikes (Lack, 1940; Mougeot et al., 2006)</td>
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<td>Seeds</td>
<td>Lygaeid bugs (Carayon, 1964)</td>
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1. **Exogenous Oral Gifts**

These consist of food items that males capture or collect, so these are most likely to contain nutritive materials (defined as substances that contribute to female metabolic reserves). Thus, most exogenous oral gifts are predicted to deliver net fitness benefits to females, measured as increased lifetime fecundity. From the male perspective, these gifts are generally predicted to increase male fitness across several selection episodes (reviewed in Gwynne, 2008; Vahed, 1998, 2007). First, because they can be assessed (visually or by gustation) prior to mating, exogenous oral gifts should affect a male’s ability to attract and successfully mate with females. Second, because females remain stationary while feeding, food gifts may make it easier for males to initiate copulation. Third, because females feed on these gifts while copulating, such gifts are expected to increase both copulation duration and the quantity of sperm transferred.

2. **Endogenous Oral Gifts**

This category includes diverse materials that are secreted by male salivary, reproductive, and other glands, as well as parts or the whole of the male’s body; these materials are then consumed by females before, during, or after copulation (reviewed by Boggs, 1995; Elgar and Schneider, 2004; Vahed, 1998). Thus, in Oecanthus nigricans tree crickets (Orthoptera), females feed upon proteinaceous secretions produced by dorsally located male glands, while females of some true flies (Diptera) and scorpionflies (Mecoptera) consume male salivary secretions, and female Allonemobius ground crickets drink hemolymph from male hindleg spurs (Bidochka and Snedden, 1985). Females in many katydids and crickets (Orthoptera) consume a spermatophylax, a gelatinous portion of the spermatophore produced by male reproductive glands. Many mantids and orb-weaving spiders engage in sexual cannibalism, where females kill and consume males either before or after insemination (Elgar and Schneider, 2004); in both cases, the male body represents an endogenous oral gift under our definition, even when it is given involuntarily (i.e., gifts can have a negative effect on male fitness).

Since they derive from such diverse sources, endogenous oral gifts are likely to have quite varied effects on females. Some endogenous oral gifts, such as hemolymph or male body parts, may closely resemble exogenous gifts of prey or other food items in contributing to females’ nutrient budgets (Boggs, 1995; Gwynne, 2008). Rather than replicating whatever nutritional mixtures are available in the diet, however, glandular gifts have the potential to provide more targeted dietary supplements. These specialized glandular gifts might supply nutrients which are otherwise absent or limited in
female diets, such as macronutrients (proteins, lipids, carbohydrates), micro-
utrients (sodium, zinc), or defensive compounds (cantharidin, pyrrolizidine
alkaloids, cyanogenic glycosides). In cockroaches (Dictyoptera: Blattidae),
males provide endogenous oral gifts that constitute an important nitrogen
source for females and their eggs (reviewed by Boggs, 1995; Vahed, 1998).
In many cockroaches, males accumulate uric acid in their accessory glands
before packaging it into their spermatophore; after mating, females expel
and eat the spermatophore. In other roaches, females feed directly on uric
acid as it is secreted from male glands.

On the other hand, sexual conflict theory predicts the evolution of male
glandular gifts that benefit males even though they may adversely affect
female net fitness (Arnqvist and Nilsson, 2000; Arnqvist and Rowe, 2005;
Rice, 1998). Through reciprocal sexual coevolution, an escalating arms race
might then ensue in which females evolve the ability to metabolize
or otherwise counteract manipulative male substances (Arnqvist and
Nilsson, 2000; Eberhard, 1996). However, it has been pointed out
(Gwynne, 2008) that such oral gifts might be less likely to contain manip-
ulative substances because those would be subject to degradation while
passing through the digestive tract. Thus, the category of endogenous oral
gifts is diverse and includes nuptial gifts that may have positive, negative, or
no effects on female fitness.

From the male perspective, when endogenous oral gifts (such as secreted
salivary masses) can be inspected by females, they could resemble exogen-
ous gifts that increase male mating success, copulation duration, and possi-
bly sperm quantity transferred during copulation. For example in spiders,
sexual cannibalism that takes place after insemination can benefit the
sacrificed male by prolonging copulation duration, thus increasing sperm
transfer and male paternity share, in addition to increasing female fecundity
and offspring survival (Andrade, 1996; Elgar and Schneider, 2004;
Herberstein et al., 2011; Welke and Schneider, 2012). For orally ingested
 glandular gifts, such as the orthopteran spermatophylax, males may be
selected to incorporate phagostimulants that increase their gifts’ gustatory
appeal for females (Sakaluk, 2000; Vahed, 2007). Selection may also alter
male gift composition to slow female consumption rates if this allows more
time for males to transfer sperm. For example, in many crickets and katy-
dids (Orthoptera: Ensifera), the male spermatophylax has a sticky, gelati-
 nous consistency that prevents rapid ingestion by females (Vahed, 2007).

3. Endogenous Genital Gifts

This category includes materials that are produced by secretory tissue in
the male reproductive tract, transferred in seminal fluid or spermatophores,
and absorbed through the female genital tract. Although spermatophores
may have originated to prevent sperm loss or desiccation (Davey, 1960; Khalifa, 1949), in many animals these structures have become vastly elaborated (Mann, 1984; Thornhill, 1976). Many ideas have been proposed about the evolutionary origin of elaborated male ejaculates such as spermatophores. Wickler (1985) proposed that spermatophores originated as a way for males to prevent females from digesting sperm, as an adaptation secondary to intrasexual selection for greater sperm quantity. It has also been suggested that female choice, based on the quality or quantity of nonsperm ejaculate components, might have favored the elaboration of male ejaculates (Cordero, 1996). Arnqvist and Nilsson (2000) proposed that elaborated male ejaculates represent “manipulative and sinister superstimuli” that evolved through sexual conflict over female remating rates. However, given the wide taxonomic distribution and diversity of endogenous genital gifts, it is unrealistic to expect a single explanation for their evolution. Rather, even a brief overview of gift constituents indicates that endogenous genital gifts have probably had multiple evolutionary origins and diverse trajectories.

Like orally ingested glandular gifts, the products of male reproductive glands can also supply nutrients that are absent or limited within female diets. The geometric framework in nutritional ecology may provide a useful perspective for thinking about the evolution of nutritive nuptial gifts. This framework is based on locating an organism’s nutritional requirements and dietary choices within a multidimensional resource space (Raubenheimer, 2011; Raubenheimer et al., 2009). Importantly, rather than replicating nutritional mixtures that are available in the female diet, nuptial gifts could provide a vector that targets the female-specific requirements for vitellogenesis (Boggs, 1990). Thus, selection may shape male glandular products to augment females’ resources by providing them with entirely different nutritional mixtures compared to those gained through feeding. Empirical studies of numerous Orthoptera, Lepidoptera, and Coleoptera have demonstrated that diverse substances derived from endogenous genital gifts are incorporated into female somatic tissue and eggs; these substances include amino acids, zinc, phosphorus, and sodium transferred in male spermatophores (reviewed by Boggs, 1995; Vahed, 1998). For example, many lepidopteran males engage in puddling behavior on damp soil, dung, or carrion where they obtain sodium, which is a scarce nutrient for most folivores (Molleman, 2010). Males accumulate this element in their reproductive glands and transfer sodium-rich spermatophores during mating; in the moth Gluphisia septentrionis, a single spermatophore contains >50% of the male’s total body sodium content (Smedley and Eisner, 1996). Females pass sodium along to their eggs, and in the skipper, Thymelicus lineola, such gifts enhance larval survivorship (Pivnick and McNeil, 1987, but see
Molleman et al., 2004). In addition, reproductive glands can serve as a reservoir for defensive compounds that males derive from dietary sources, and these compounds are later transferred to females within spermatophores or seminal fluid (reviewed by Vahed, 1998). Thus, endogenous genital gifts can contain defensive compounds that protect the female or her eggs against predators or microbial attack; such gifts include cantharidin in *Neopyrochroa flabellata* beetles (Eisner et al., 1996), pyrrolizidine alkaloids in *Utetheisa ornatrix* moths (Eisner and Meinwald, 1995), cyanogenic glycosides in several *Heliconius* butterflies (Cardoso and Gilbert, 2007), and vicilin-derived peptides in *Callosobruchus maculatus* cowpea beetles (Alexandre et al., 2011).

On the other hand, some components of endogenous genital gifts may reduce female fitness. In some male insects, reproductive accessory glands manufacture compounds that have diverse effects on female reproductive physiology and behavior (Eberhard, 1996; Gillott, 2003). In *D. melanogaster*, for example, seminal fluid proteins have been shown to heighten female oogenesis and oviposition, increase sperm storage and utilization, and to reduce female remating rates and life span (reviewed by Chapman, 2008; Chapman and Davies, 2004; Ravi Ram and Wolfner, 2007a,b; Wolfner, 2007). For most taxa, little is known concerning the nature of these secretions, although recent work has elucidated seminal fluid composition in *Aedes* mosquitoes (Sirot et al., 2008), *Gryllus* and *Allochroaobius* crickets (Andres et al., 2006; Braswell et al., 2006), *Heliconius* butterflies (Walters and Harrison, 2010), *Tribolium* flour beetles (South et al., 2011a), and honeybees (Baer et al., 2009; Collins et al., 2006). In many species, male gifts contain anti-aphrodisiacs that reduce a female’s likelihood of remating (*Tenebrio* beetles, Happ, 1969; *Pieris napi* butterflies, Andersson et al., 2004; *Heliconius* butterflies, Estrada et al., 2011). Selection on males to reduce sperm competition risk favors inclusion of such substances, yet anti-aphrodisiacs can lower female net fitness if they depress remating rates below some female optimum.

Thus, endogenous genital gifts are complex mixtures that have likely been shaped by multiple selective forces. While it has been argued that male ejaculate composition will be selected primarily to manipulate female reproductive physiology and should carry a net fitness cost borne by gift recipients (Arnqvist and Nilsson, 2000; Arnqvist and Rowe, 2005), it is clear that understanding the complex effects that male ejaculates have on females will require a broad and balanced perspective.

### 4. Endogenous Transdermal Gifts

These nuptial gifts include male seminal and glandular products that are transferred and absorbed outside the female’s digestive or reproductive systems. This happens during extragenital insemination in bedbugs (Stutt
and Siva-Jothy, 2001) and intradermal spermatophore implantation in deep-sea squid (Hoving and Laptikhovsky, 2007). In the bedbug, *Cimex lectularius*, male ejaculates include (in addition to sperm) antioxidants, micronutrients, and antibacterial compounds (Reinhardt et al., 2009). Hypodermic injection of seminal products is particularly widespread among simultaneous hermaphrodites such as leeches, sea slugs, and poly-clad flatworms (Michiels and Koene, 2006). Another type of transdermal gift consists of allohormones, substances that induce a direct physiological response in the recipient (Koene and Ter Maat, 2001). These can be injected through the skin of a mating partner during copulation while sperm are being passed to the reproductive organs. This mode of delivery allows male products to bypass both digestive and reproductive tracts, where various gift components might get broken down. During copulation, hermaphroditic earthworms *Lumbricus terrestris* use their ventral copulatory setae to inject their partner with setal gland products that induce sperm uptake and storage (Koene et al., 2005). A similar benefit for male function occurs in *Helix aspersa* land snails, which penetrate their partners with a calcareous dart coated with allohormones produced by a mucus gland; these substances inhibit sperm digestion and enhance sperm storage by the recipient (Koene and Schulenburg, 2005; Schilthuizen, 2005). As in other endogenous gifts, selection on transdermal gift production may favor the inclusion of compounds that benefit males yet are detrimental to female fitness.

II. Effects on Recipient Fitness

Empirical studies in numerous taxa have documented how male gifts affect several different female fitness components (including egg and clutch size, rate and timing of offspring production, longevity), as well as female net fitness (lifetime fecundity measured as the total number of eggs or offspring produced). Many studies have found that nuptial gifts can provide females with direct material benefits measured as an increase in the recipient’s net fitness. Such evidence has been compiled and summarized by previous literature reviews for arthropod nuptial gifts (Boggs, 1995; Gwynne, 2008; Rooney and Lewis, 1999; Vahed, 1998, 2007) and for sexual cannibalism (Elgar and Schneider, 2004), as well as by some meta-analyses (Arnqvist and Nilsson, 2000; South and Lewis, 2011).

Rather than recapitulating these synopses here, we simply advocate that the term nuptial gift be used in its broadest sense, that is, independently of whether such materials currently exert a positive, a negative, or no effect on recipient net fitness (Fig. 2). Others have used narrower terminology, using
nuptial gifts to mean only nutritive gifts or those that increase female fitness (i.e., those falling within the upper-right cell of Fig. 2). On the other hand, because male and female reproductive interests are not perfectly aligned, sexual conflict may drive the evolution of nuptial gifts that provide fitness benefits to males while reducing female net fitness. Arnqvist and Nilsson (2000) and Arnqvist and Rowe (2005) suggested that the term “Medea gift” (named after a mythological Greek sorceress who used a beautifully embroidered, poisonous robe to murder a rival) should be used for any gifts that reduce female net fitness (i.e., those falling within the upper-left cell of Fig. 2). However, because coevolutionary interactions are expected to create dynamic changes over time in gifts’ cost/benefit ratios for their recipients, we believe such restrictive terminology is counterproductive to the goal of understanding nuptial gift evolution. One example of this shifting balance of costs and benefits is seen in the bedbug *C. lectularius*. Although traumatic insemination through the abdominal wall causes wounding that reduces female life span (Stutt and Siva-Jothy, 2001), male ejaculates contain compounds that increase female net fitness via increased lifetime fecundity and oviposition rate, and delayed reproductive senescence (Reinhardt et al., 2009). One evolutionary scenario proposed by these authors is that male ejaculates were originally detrimental and that subsequent female counteradaptations evolved to neutralize, and eventually reverse, these harmful effects. Alternatively, they suggest, male ejaculates may have positively affected female net fitness when they originated. While distinguishing between these evolutionary trajectories must

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**Fig. 2.** Our nuptial gift definition encompasses a range of possibilities for how nuptial gifts might influence male and female net fitness (benefit minus cost). Gifts that provide a net fitness benefit to males can have negative, positive, or no effects on female fitness (top row). When gifts provide a net fitness benefit for females, they can be maintained whether or not males derive a fitness benefit; thus, sexual cannibalism would fall into the rightmost column (e.g., cases when the male is consumed before insemination would fall into the bottom right cell). The position of any gift is likely to shift over evolutionary time, as sexual interactions modify costs and benefits for each sex. (Gray areas indicate that evolutionary maintenance is unlikely as these gifts carry net fitness costs for one or both sexes.)
await future phylogenetic studies coupled with ancestral trait reconstruc-
tion, it is clear that a more holistic framework will be required to under-
tand the evolution of nuptial gifts.

Possible evolutionary trajectories leading to manipulative male gifts have
been presented in detail by others (e.g., Arnqvist and Rowe, 2005; Eberhard,
1996; Rice, 1998; Sakaluk, 2000). Here we focus on circumstances that might
lead to the evolution of nutritive nuptial gifts, that is, those providing
material benefits that directly increase fitness for the gift recipient.

Among the ways that nuptial gifts might increase a male’s fitness relative
to other males in the same population is by enhancing female fecundity
relative to other females in the population. The enhanced fecundity hypoth-
esis for paternal investment was proposed by Tallamy (1994), who sug-
gested that male investment will evolve whenever males can provide
materials whose availability constrains female reproductive output. While
he mainly focused on postzygotic male investment (e.g., paternal brood
care), Tallamy pointed out that this hypothesis should also apply to the
evolution of nuptial gifts (i.e., prezygotic male investment). In addition,
recent theoretical work has shown that depending on the degree of fecund-
ity enhancement, male nuptial gifts can alter intersexual coevolutionary
dynamics and lead to a stable evolutionary equilibrium with mutual fitness
benefits for both sexes (Alonzo and Pizzari, 2010).

In general, female reproduction will be resource-constrained because of
the higher gametic investment by this sex (Trivers, 1972); in oviparous
organisms, all the nutritional resources required for embryogenesis must
be contained within each egg. Female egg production is most often limited
by protein availability (Wheeler, 1996). In insects, as in most oviparous
animals, oocyte development is fueled mainly by vitellogenin, a female-
specific glycolipoprotein; insect eggs also contain lipids and some carbohy-
derates in the form of glycogen (Klowden, 2007). Females need to obtain
these macronutrients from larval feeding, from adult feeding, or from male
nuptial gifts (Boggs, 1990). Thus, the enhanced fecundity hypothesis pre-
dicts that selection for nuptial gifts will be influenced by the availability and
quality of specific nutritional resources needed for female reproduction.
Resource availability will in turn depend on organismal life-history traits, as
well as on temporal and habitat variation within a particular species. Below
we consider some combinations of ecological conditions and life-history
traits that are expected to favor the evolution of nutritive gifts that enhance
female fecundity through male contributions to female resource budgets
(Boggs, 1990, 1995). We do not discuss mating systems; while several
studies have explored the relationship between nuptial gifts and polyandry
(e.g., Karlsson, 1995; Karlsson et al., 1997), it is difficult to determine causal
relationships between these two highly correlated features.
First we discuss some life-history features that are expected to lead to female-specific resource limitation. These include location of a species along the continuum between income and capital breeding, temporal dynamics of female oogenesis, and requirements for female dispersal and flight. Income breeders are those that fuel reproduction using current energetic income, while capital breeders support their reproduction with energy stores accumulated at an earlier life stage (Houston et al., 2007; Stearns, 1992). In purely capital breeders, male nuptial gifts could provide resources to supplement reserves that otherwise would be depleted over a female’s reproductive life span. One such example is Photinus ignitus firefly beetles (reviewed by Lewis and Cratsley, 2008; Lewis et al., 2004), which are capital breeders that entirely lack adult feeding. Both sexes mate repeatedly over their 2-week adult life span. Males manufacture a complex spermatophore from several reproductive glands, and spermatophore-derived proteins are allocated to females’ developing oocytes. Females that receive multiple spermatophores gain increased lifetime fecundity. In addition, a seasonal reversal in courtship roles occurs: late in the mating season when both sexes face depleted resource stores, females compete for access to gift-providing males and males selectively mate with more fecund females (Cratsley and Lewis, 2005).

Nuptial gift evolution may also depend on interspecific life-history differences in the temporal dynamics of female oogenesis (Boggs, 1990, 1995, 2009). In some insect taxa, adult females emerge with their entire complement of eggs already matured (e.g., mayflies), while in others (e.g., P. ignitus fireflies) females will continue to mature eggs throughout their reproductive lives (Jervis and Ferns, 2004; Jervis et al., 2005 compiled relevant data for many parasitoid wasps). When egg maturation is distributed over time, selection should favor male nuptial gifts that could enhance female reproductive output by replenishing resources.

A final life-history trait that may alter selection for nuptial gifts relates to female mobility. If females must fly in order to locate food, mates or suitable oviposition sites, to disperse, or to escape predators, then wing-loading constraints may restrict how many mature eggs a female can carry at any point in time. In addition, females face a trade-off between allocating resources to flight or to oogenesis (Boggs, 2009; Wheeler, 1996). Lewis and Cratsley (2008) presented a conceptual model proposing that because flightless (wingless) females can devote all their resources to egg production, selection for nuptial gifts will be relaxed due to limited scope for any further increases in females fecundity. A recent evolutionary trait analysis in fireflies supported this predicted intersexual correlation between female flight ability and male nuptial gifts (South et al., 2011b; see Section V.B below). Females of ancestral fireflies most likely were fully winged and
received male nuptial gifts in the form of spermatophores. In several lineages, after females lost their flight ability (possibly driven by fecundity selection), males subsequently lost the ability to produce these nuptial gifts.

Selection for nuptial gifts should also be influenced by within-species variation in the availability and quality of specific resources required for female reproduction. When such resources are limited, females may increase their mating activity to gain access to nutritive nuptial gifts (Boggs, 1990; Gwynne, 1990). For example, in the pollen katydid *Kawanaphila nartee* (Orthoptera: Tettigonidae), scarcity of pollen (a protein-rich food source for both sexes) generates intersexual competition among females for access to endogenous oral gifts in the form of the male spermatophylax (Simmons and Bailey, 1990). In the pollen-feeding butterfly *Heliconius cydno*, pollen load varies among females and is negatively correlated with number of matings, and thus nuptial gifts, that females acquire (Boggs, 1990). In addition, many experimental studies have found that nuptial gifts provide larger fecundity increases when females are food-limited (Gwynne and Simmons, 1990; reviewed by Boggs, 1990; Gwynne, 1991, 2008). Finally, Leimar et al. (1994) provided comparative data from butterflies suggesting that variation in available resources (rather than average) will increase selection for nuptial gifts. Similarly, another comparative study across butterfly species found increased polyandry with greater variation in female body size, again indirectly suggesting that species with more variable larval food resources might experience increased selection for nuptial gifts (Karlsson, 1995).

Thus, several ecological conditions and life-history traits linked to female resource allocation are predicted to favor the evolution of fecundity-enhancing male gifts. Indeed, an entire suite of correlated life-history traits seems likely to select for fecundity-enhancing nuptial gifts. Based on the connections outlined here between nuptial gifts, life-history traits, and nutritional ecology, testing hypotheses about trait combinations that favor the evolution of nutritive nuptial gifts seems like an important and relatively unexplored research area. As Boggs (1995) pointed out nearly 20 years ago, we still need rigorous comparative phylogenetic studies focused on testing for evolutionary associations between nuptial gift presence (and type) and interspecific variation in resource conditions and life-history traits.

III. Potential Gift Benefits for Males

Considerable evidence indicates that the collection and manufacture of nuptial gifts is costly for males (reviewed by Boggs, 1995). In addition, males have been shown to strategically allocate their gifts depending on female reproductive status or age (e.g., Simmons et al., 1993; Sirot et al.,
2011; Wedell, 1992). While colloquial usage views gifts as something given voluntarily, in the case of sexual cannibalism there may also be involuntary gift-giving that carries a net fitness cost for males (Elgar and Schneider, 2004, lower-right cell of Fig. 2). Yet as mentioned above, in some species cannibalized males gain posthumous benefits through increased paternity share and decreased likelihood of the female remating (Andrade, 1996; Herberstein et al., 2011: upper-right cell of Fig. 2). In most cases, however, the male structures that produce nuptial gifts and the various behaviors associated with gift-giving will only be maintained if they confer a net fitness benefit on males; that is, the gift-giving males must be able to sire more offspring compared to other males in the same population. These fitness advantages could accrue across different reproductive episodes, including through higher mating success, increased paternity share relative to other males mating with the same female, and/or enhanced female fecundity compared to other females in the population.

In determining what specific benefits a male might derive from his gift-giving behavior, much previous work has been caught up in a largely unproductive semantic debate. For several decades many attempts were made to distinguish between two particular hypotheses for the origin and maintenance of male gifts (Alexander and Borgia, 1979; Gwynne, 1984; Sakaluk, 1986; Simmons and Parker, 1989; Vahed, 1998). The mating effort hypothesis suggested that gifts function to ensure mating and sperm transfer, while the paternal investment hypothesis suggested that gifts function to increase the number or quality of the gift-giver’s own offspring. However, attempts to sort nuptial gifts neatly into these two categories were unsuccessful, and a fatal terminological quagmire gradually developed (see also Gwynne, 2008; Simmons, 1995; Simmons and Parker, 1989; Vahed, 1998; Wickler, 1985). Among the reasons for this failure was that these two hypotheses represent two nonindependent gift functions (i.e., the latter depends on the former), and also that the paternity data necessary for empirical tests of the paternal investment hypothesis were lacking.

Moving forward, we suggest that a more constructive approach will be to think about nuptial gifts as selection targets during several sequential episodes that occur before, during, and after mating (Fig. 3). A similar approach was suggested by Gwynne (1997; his Table 6-1). For example, nuptial gifts may enhance a male’s mating success by increasing his ability to attract females (episode 1) and to successfully copulate with them (episode 2). During copulation, nuptial gifts may improve a male’s insemination success (episode 3, measured as whether or not any sperm transfer occurs), or increase the number of sperm transferred (episode 4). After mating, nuptial gifts may increase the viability and storage of male sperm within the female reproductive tract (episode 5). In competitive mating situations
(polyandry or polygamy), providing a nuptial gift may increase male paternity share (proportion of offspring sired by the gift-giving male) relative to other males mating with the same female (episode 6); this may occur through cryptic female choice favoring certain male or gift traits, or by increased sperm defense or offense. As discussed in Section II, nuptial gifts may also increase a male’s fitness by enhancing overall female fecundity (episode 7), as well as egg and offspring survival (episode 8), relative to that of other females in the population. Numerous experimental or observational studies of nuptial gift function have demonstrated that larger or more nuptial gifts lead to higher male fitness during one or more of these sequential selection episodes; we provide just a few examples below.

Many oral nuptial gifts (both exogenous and endogenous) provide a benefit to males by attracting females and also by increasing the likelihood that females will copulate once they have been attracted. Among such gifts are...
The edible and inedible gifts offered by male empidid dance flies (Lebas and Hockham, 2005; Preston-Mafham, 1999), prey and salivary secretions provided by Panorpa scorpionflies (Engqvist, 2007a), and food regurgitated by Drosophila subobscura males (Steele, 1986). Some oral gifts, such as male hindwings and hemolymph in Cyphoderris hump-winged crickets (Eggert and Sakaluk, 1994), also facilitate successful insemination, as males can more readily accomplish sperm transfer when females hold still while feeding.

Oral nuptial gifts (both exogenous and endogenous) also function during mating to increase the quantity of sperm transferred to the female reproductive tract; these include the spermatophylax in several crickets and bushcrickets (Sakaluk, 1984; reviewed by Gwynne, 1997; Vahed, 1998, 2007), prey gifts in Bittacus hangingflies (Thornhill, 1976), and salivary secretions in Panorpa scorpionflies (Engqvist, 2007a).

Other nuptial gifts benefit males during postcopulatory episodes of selection, including enhancing female storage of sperm that will later fertilize eggs. Acp36DE is a seminal fluid protein (endogenous genital) transferred by D. melanogaster males that causes an increase in sperm numbers stored within the female reproductive tract (Qazi and Wolfner, 2003). Similarly, hermaphroditic H. aspersa garden snails penetrate their partner with a mucus-coated dart (endogenous transdermal gift) that increases sperm storage (Rogers and Chase, 2001).

Many endogenous gifts (both oral and genital) also include materials that inhibit the female’s mating receptivity (thus reducing the risk of sperm competition) and/or increase her latency to remate (thus increasing sperm defense). Such receptivity-inhibiting materials include Drosophila sex peptide, unknown ejaculate components in R. verticalis katydids (Gwynne, 1986), nonfertilizing apyrene sperm in Lepidoptera (Wedell, 2005), and salivary secretions of Panorpa scorpionflies (Engqvist, 2007a). In addition, many spermatophores (endogenous genital) contain anti-aphrodisiacs that deter other males from approaching a mated female (e.g., Estrada et al., 2011; Happ, 1969).

Although we lack information on male paternity share for most gift-giving taxa, nuptial gifts can also influence what proportion of offspring produced by a multiply-mated female gets sired by the gift-giving male. For example, larger salivary secretions (endogenous oral gifts) offered by male Panorpa scorpionflies increase male paternity share by increasing copulation duration (Engqvist et al., 2007; Sauer et al., 1998). Also, larger spermatophores (endogenous genital gifts) increase the paternity share of male Photinus greeni fireflies (South and Lewis, 2012a). Many nuptial gifts (including exogenous oral, endogenous oral, and endogenous genital gifts) have been demonstrated to play a role in increasing female fecundity, either through nutritive contributions or allohormones that stimulate female
ovulation or oviposition (see Arnqvist and Nilsson, 2000; Boggs, 1995; Eberhard, 1996; Gwynne, 2008; South and Lewis, 2011). A central concern is that these gifts will provide a fitness benefit to males only if they increase the total number of offspring sired by the gift-giving male, yet the requisite information on offspring paternity is often not gathered.

As described in Section I.C.3, endogenous genital gifts can contain chemical defenses that protect a female and/or her eggs against predators, thus increasing offspring survival (e.g., cantharidin in spermatophore of male Neopyrochroa beetles [Eisner et al., 1996], pyrrolizidine alkaloids in U. ornatrix moths [reviewed by Eisner and Meinwald, 1995]).

Thus, male costs incurred in manufacturing or procuring nuptial gifts are apparently outweighed by fitness benefits that can accrue during multiple selection episodes before, during, and after mating. Endogenous nuptial gifts are especially likely to contain complex mixtures that will operate across multiple selection episodes to increase male fitness. Also, nuptial gift composition and the associated male fitness benefits will shift dynamically over time due to coevolutionary interactions between the sexes.

IV. A Case Study of Male Benefits: Requena verticalis

A. Orthopteran Nuptial Gifts

Orthopteran insects (grasshoppers, crickets, and katydids) display a dazzling array of endogenously produced nuptial gifts (Fig. 4); these include male body parts and glandular secretions that females absorb orally, genitally, or in some cases, both. Female Pteronemobius and Allonemobius (Gryllidae: Nemobiinae) ground crickets receive an endogenous oral gift by chewing on a modified hindleg spur and drinking the male’s hemolymph (Fedorka and Mousseau, 2003; Mays, 1971). Similarly, female Cyphoderris hump-winged crickets (Tettigonioida: Haglidae) drink hemolymph after feeding on the male’s fleshy hindwings (Dodson et al., 1983; Morris, 1979). In Oecanthus tree crickets (Gryllidae: Oecanthinae), females consume secretions produced by dorsal glands on the male’s thorax (Brown, 1997); such metanotal gland feeding also occurs in many other orthopterans (see Vahed, 1998). Many species with endogenous oral nuptial gifts also transfer a genital gift during mating in the form of a spermatophore (Gwynne, 2001; Vahed, 1998). In most species within the suborder Ensifera (katydids, crickets, and wetas), males produce spermatophores that can comprise between 2% and 40% of their total body weight. These two-part structures are produced by two distinct accessory glands: the smooth glands produce the small, sperm-containing ampulla, while the rough glands produce the
larger, gelatinous spermatophylax (Gwynne, 1997, 2001). During copulation, the ampulla tube is inserted into the female’s genital opening, while the remainder of the gift is deposited externally. When the male departs after coupling, the female ingests the spermatophylax while sperm and associated seminal fluid drain from the ampulla into the female’s reproductive system. Once the female finishes consuming the spermatophylax, she removes and consumes whatever remains of the ampulla (Gwynne, 1984; Gwynne et al., 1984; Sakaluk, 1984).

The Australian katydid *R. verticalis* (family Tettigoniidae) has been extensively studied as a model system for understanding the costs and benefits of nuptial gifts for both sexes. Thus, this species provides an excellent case study for illustrating the episodes of selection framework presented in Section III. Like other tettigonids, *R. verticalis* males produce a two-part spermatophore that is approximately 15–20% of total male body weight (Davies and Dadour, 1989). The spermatophylax
alone (without the sperm-containing ampulla) comprises 78% of total spermatophore weight (Bowen et al., 1984). The spermatophylax is composed of 13.5% protein (Bowen et al., 1984). In this species, both sexes mate multiple times and both courtship and mating are costly to males. The chirping acoustic signals that males use to attract females require an energetic investment that averages 3.2 kJ/h (Bailey et al., 1993) and spermatophore production requires 1.1 kJ (Simmons et al., 1992); together these two components make up approximately 70% of a male’s daily energy budget (Simmons et al., 1992). Nuptial gift costs also limit male mating frequency. After mating, males require 2.5–5 days (depending on diet quality) to manufacture another spermatophore before they are able to mate again (Davies and Dadour, 1989; Gwynne, 1990). Furthermore, when male diet is restricted, males invest less energy into courtship signals but nuptial gift production remains constant (Simmons et al., 1992).

What fitness benefits might balance out these well-established costs of nuptial gifts for R. verticalis males? Below we expand on Gwynne’s (1997) analysis of current gift function to examine the fitness benefits that males derive from spermatophylax production across multiple selection episodes that occur before, during, and after mating.

B. Fitness Benefits to R. verticalis Males

1. Male Insemination Success and Number of Sperm Transferred

When R. verticalis females are deprived of a spermatophylax they will remove and eat the ampulla, effectively halting sperm transfer (Gwynne et al., 1984). Gwynne et al. (1984) demonstrated that while sperm drainage from the ampulla is completed within 3 h, females take ~5 h to eat the spermatophylax before moving on to consume the ampulla. In some other orthopteran species, in contrast, male spermatophylax size attains only the minimum necessary to ensure complete sperm drainage (e.g., the cricket Gryllodes supplicans; Sakaluk, 1984). Thus, the R. verticalis spermatophylax serves to protect male ejaculates by insuring insemination and maximizing the number of sperm transferred (Fig. 3, selection episodes 3 and 4).

2. Paternity Share

Male nuptial gifts in R. verticalis also affect male paternity share postmating (Fig. 3, episode 6). Laboratory studies indicate that R. verticalis generally show complete first-male sperm precedence; that is, the first male that mates with a virgin female will sire all of her offspring even when the female remates (Gwynne, 1988a; Simmons and Achmann, 2000). When females were given a longer intermating interval and allowed to oviposit between
matings, second males gained ∼20% paternity share (Gwynne and Snedden, 1995). In addition, first males that had greater spermatophore mass retained higher paternity share. Radiolabeling studies show that amino acids derived from second males become incorporated into eggs that were fertilized by the first male; thus, second male gifts are allocated to offspring sired by another male. However, such cuckoldry may happen infrequently under natural conditions, as field estimates of female polyandry suggest that females in nature remate less frequently than in the lab (Simmons et al., 2007).

The high degree of first-male paternity seen in R. verticalis suggests that males should be selected to preferentially mate with virgin females, but males appear incapable of discriminating females’ mating status (Lynam et al., 1992; Simmons et al., 1993, 1994). This may represent sexual conflict, with selection acting on females to hide their mating status to obtain the benefits provided by additional spermatophores (Simmons et al., 1994). However, Simmons et al. (1994) did find that males are able to discriminate among potential mates based on female age. By preferentially mating with younger females, males may increase their chance of mating with virgins and may thus gain higher paternity share.

Sperm competition theory predicts that males should strategically allocate their ejaculates depending on female mating status (Simmons, 2001); when mating with a previously mated female, males should maximize sperm number in the ampulla (to increase their sperm offense ability), but minimize spermatophylax investment due to their the low probability of siring offspring. Instead, Simmons et al. (1993) found that when mating with young females, R. verticalis males transfer identical spermatophores regardless of female mating status; however, males transfer spermatophores with 50% more sperm and 25% less spermatophylax material when mating with older compared to younger females. Thus, R. verticalis males appear to strategically allocate their ejaculates when mating with older females to increase their sperm offense ability, and thus their potential paternity share.

Nuptial gifts produced by R. verticalis also affect male postcopulatory fitness by increasing sperm defense. Given the high cost of producing nuptial gifts, males should be selected to increase female latency to remate as a mechanism of reducing sperm competition. By experimentally manipulating ampulla attachment times, Gwynne (1986) demonstrated that the ampulla contains receptivity-reducing substances that act in a dose-dependent fashion, normally rendering females non-receptive for approximately 4 days. Substances in the ampulla also appear to negatively affect female longevity. Wedell et al. (2008) found that when females received the contents of three male ampullas (each without a spermatophylax), they had significantly shorter life spans, and this negative effect was not counteracted by spermatophylax consumption.
3. Female Fecundity and Egg/Offspring Survival

Finally, nuptial gifts can also increase male fitness through effects on female fecundity and the survival of offspring sired by the gift-giving male (Fig. 3, selection episodes 7 and 8). Radiolabeling experiments demonstrated that male protein derived from the *R. verticalis* spermatophore is incorporated into the female’s eggs (Bowen et al., 1984; Gwynne, 1988a). Furthermore, females that consume more spermatophylacies produce more and heavier eggs (Gwynne, 1984), and offspring from larger eggs had greater overwintering survival (Gwynne, 1988b). If receiving spermatophylax nutrients directly benefits female fitness, nutrient-limited females would be expected to seek out matings to obtain additional nuptial gifts. Indeed, female *R. verticalis* females kept on a low-quality diet remate more often than females kept on a high-quality diet (Gwynne, 1990).

By applying this framework in *R. verticalis*, we see that nuptial gifts increase male fitness across several episodes of selection, ultimately increasing the number of offspring sired by the gift-giving male. A complete spermatophore (ampulla + spermatophylax) is necessary for insemination to occur (i.e., ejaculate protection), as otherwise the ampulla will be removed and eaten before sperm transfer. Presence of a spermatophylax increases the duration of ampulla attachment, and spermatophylax size exceeds that required for complete sperm transfer. Unidentified substances present in the male ampulla act to reduce female receptivity to additional matings, helping to ensure a male’s paternity share relative to his rivals. Additionally, males discriminate against older females that have likely already mated as a mechanism to reduce incidence of cuckoldry. Spermatophylax consumption increases female fecundity and has the potential to enhance fitness by increasing the number of offspring sired by the gift-giving male. Paternity success of second mating males increases if they mate with a female after she has had an opportunity to oviposit. Finally, spermatophylax consumption increases egg size, which enhances survival of a male’s offspring. Thus, this work on *R. verticalis* clearly illustrates how costly nuptial gifts might provide males with demonstrable fitness benefits measured across several sequential episodes of selection.

V. PHYLOGENETIC INSIGHTS INTO THE EVOLUTION OF NUPTLIAL GIFTS

Despite the key role that nuptial gifts play in the reproductive ecology of so many animals, surprisingly few studies have rigorously examined the evolution of nuptial gifts using a comparative phylogenetic approach. To
thoroughly test the various evolutionary scenarios that have been proposed for nuptial gifts, it will be essential to map gifts and other relevant traits onto robust phylogenies developed for particular taxa. Using this approach will provide insight into the evolutionary sequence of gift trait transitions and will also allow tests of correlated evolution between nuptial gifts, life-history, and ecological traits. To date, however relatively few studies have applied these methods. Here we review work from three insect taxa where a comparative phylogenetic approach has provided insight into nuptial gift evolution: 1) endogenous oral gifts within katydids and crickets (Ensifera: Orthoptera), 2) correlated evolution of wingless females and male nuptial gifts in fireflies (Lampyridae: Coleoptera), and 3) patterns of male ejaculate incorporation, as well as rates of seminal fluid protein evolution, in the genus *Drosophila* (Drosophilidae: Diptera).

### A. Endogenous Oral Gifts in Katydids and Crickets

The first comparative phylogenetic study of nuptial gift evolution was presented by Gwynne (1995, 1997, 2001), who examined the origins and elaboration of edible glandular gifts within the orthopteran suborder Ensifera (katydids, crickets and their allies). Gwynne’s (1995) phylogenetic reconstruction was based upon morphological characters and suggested that the ancestral trait in this group was an exposed spermatophore (essentially a naked sperm-containing ampulla) that was deposited externally on the female genitalia (Fig. 5). Female consumption of this unprotected spermatophore was hypothesized to be ancestral for all ensiferans, followed in the superfamily Tettigonioidea by the origin of the spermatophylax as an edible addition to the spermatophore. In the evolutionary branch leading to the family Gryllidae (true crickets), there were numerous origins of diverse glandular gifts consumed by females before and after mating, along with male spermatophylaces.

A more detailed analysis (Gwynne, 1995, 1997) showed a total of 11 origins of males producing endogenous oral gifts within the Ensifera; these included 3 origins of a spermatophylax, 4 origins of metanotal glands, 1 tibial gland, and 3 others instances where females feed on other male body parts. This work also indicated several independent spermatophylax losses or size reductions; these occurred in some wetas (Stenopelmatidae; loss in *Deinacrida*, size reduction in *Hemideina*) and katydids (Tettigonidae; loss in *Tympanophora*, *Decticina*, size reduction in *Neoconocephalus*). Interestingly, such losses were often associated with origins of other endogenous gifts, such as secretions from metanotal or tibial glands. Within the Grylloidea, Gwynne’s analysis reveals that there were also seven likely losses of nuptial gifts and three origins of postcopulatory mate guarding.
This analysis supports an evolutionary scenario in which males first used a simple, externally attached ampulla to transfer their sperm (for review see Gwynne, 2001). Food limitation may have initially driven females to consume this proteinaceous package, leading to sexual conflict over ampulla attachment times. Selection on males to maximize sperm transfer could have lead to the origin of male reproductive glands that produced an additional spermatophore component, the edible spermatophylax. Thus, the spermatophylax likely originated as an ejaculate protection mechanism, prolonging ampulla attachment times and allowing sufficient time for sperm to fully drain from the ampulla into the female reproductive tract. Further elaboration of the spermatophylax might have occurred if male gifts increased the number of offspring sired by increasing female fecundity and/or offspring survival. As females increased their mating rates to obtain nutritional supplements from these oral gifts, male ejaculates (genital gifts) would have undergone selection to include compounds that suppress female receptivity to further matings, thus reducing sperm competition risk.

While this analysis provides considerable insight into the evolution of orthopteran nuptial gifts, additional work could increase taxon coverage and incorporate more detailed information on species’ life-history and ecological traits. Further studies could also help elucidate what conditions
led to the spermatophylax loss seen across several ensiferan lineages, and what factors underlie the explosion of nuptial gift diversity seen among modern day Orthoptera.

B. Firefly Spermatophores: Coevolution with Female Flight

Recent work on fireflies (Coleoptera: Lampyridae) also shows the power of a comparative phylogenetic approach and offers new insights into how nuptial gift evolution is linked to other life-history traits (South et al., 2011b). This analysis also allowed reconstruction of ancestral character states as well as the sequence of evolutionary transitions, and demonstrated trait coevolution between the sexes.

Based upon Tallamy’s (1994) enhanced fecundity hypothesis and Boggs’ (1990) female allocation model, Lewis and Cratsley (2008) developed a conceptual model to explore the evolution of nuptial gifts in lampyrids as a function of female allocation trade-offs between flight and reproduction. Because nuptial gifts can link together male and female resource budgets, they have the potential to alter the allocation strategies used by both sexes. Thus, selection for nuptial gifts might depend on female reproductive allocation, which in turn depends on allocation to other activities, including flight. If females do not require flight, fecundity selection can act to maximize female reproductive allocation. In this case, because female reproductive output is already at its maximum (\(E_{\text{max}}\) in Boggs, 1990), male nuptial gifts will have limited scope to further enhance female fecundity. On the other hand, when female reproductive allocation is constrained by the energetic and biomechanical demands of flight, nuptial gifts could provide larger proportional fecundity increases for females. Therefore, this model predicts that nuptial gifts would not be selected in species with flightless females. Fireflies present an opportunity to test this relationship, as they demonstrate variation in not only nuptial gift-giving, but also in female flight ability.

As fireflies are capital breeders and both sexes mate multiply, nuptial gifts can have major fitness consequences for both sexes (Lewis and Cratsley, 2008). Firefly nuptial gifts consist of spermatophores (endogenous genital gifts) that are manufactured by several accessory glands and transferred to females during mating (Lewis et al., 2004). Some female fireflies possess a specialized reproductive sac to receive and break down the spermatophore after sperm are released into the female spermatheca (van der Reijden et al., 1997). Radiolabeling experiments in Photinus fireflies have shown that spermatophore-derived proteins are incorporated into the female’s developing oocytes (Rooney and Lewis, 1999), and male gifts benefit females by increasing their lifetime fecundity.
Rooney and Lewis, 2002) and longevity (South and Lewis, 2012b). Gift production is costly for males, as spermatophore size declines across successive matings in *Photinus* (Cratsley et al., 2003). Among the 2000 extant species of firefly worldwide, spermatophores are present in some, yet absent in others (Hayashi and Suzuki, 2003; Lewis et al., 2004; South et al., 2008, 2011b; van der Reijden et al., 1997). Those species that lack spermatophores show reduced male accessory glands and females do not have a spermatophore-receiving sac (Demary and Lewis, 2007; South et al., 2011b). What accounts for such interspecific variation in nuptial gifts?

Fireflies also exhibit extensive interspecific variation in life-history traits. In some fireflies, females have greatly reduced wings and as a result are flightless, while in other species both sexes have normal wings and can fly (Jeng, 2008). Hayashi and Suzuki (2003) first proposed that female wing reduction might be negatively associated with male nuptial gifts in Japanese fireflies. Thus, the existing variation in both spermatophore production and female flight within the Lampyridae provided an opportunity to test Lewis and Cratsley’s (2008) model and to examine whether this life-history trait could help explain how nuptial gifts are distributed across fireflies.

South et al. (2011b) performed a phylogenetic analysis of the relationship between spermatophore production and female flightlessness within the Lampyridae (Fig. 6). These two traits were measured in 32 taxa and mapped onto a lampyrid molecular phylogeny constructed by Stanger-Hall et al. (2007). Ancestral state reconstruction revealed it was highly likely that firefly males originally produced spermatophores, but these nuptial gifts were subsequently lost in four separate lineages (Fig. 6, right). This reconstruction also revealed that ancestral fireflies had flight-capable females, and females then lost their flight ability at least five times (Fig. 6, left). Furthermore, this work revealed a remarkably congruent pattern between male nuptial gifts and female flight, with the correlated loss of both female flight and male gifts occurring in many lineages. This congruence (statistically confirmed by Pagel’s test of correlated evolution) demonstrated coevolution between two traits expressed in different sexes. Finally, transitional probability analysis demonstrated that first females lost their flight ability, subsequently followed by male spermatophore loss.

Thus, female flight ability provides a compelling explanation for observed patterns of nuptial gifts in fireflies, but what selected for female flight loss in the first place? Based upon considerable evidence demonstrating that flightless females can allocate more to reproduction, the most likely explanation for female-specific flight loss is selection for increased fecundity. Thus, these results strongly support the conclusion that male nuptial gifts are co-adapted with patterns of female reproductive allocation, at least
Fig. 6. Firefly beetles (Coleoptera: Lampyridae) show correlated evolution (Pagel's test, \( P < 0.001 \)) between male nuptial gifts (spermatophores) and female flight ability (based on presence of functional wings). For 32 worldwide firefly species, these two traits were mapped onto a lampyrid molecular phylogeny based on 18S, 16S, and \textit{cox1} DNA sequences (Stanger-Hall et al., 2007). For each trait, pie charts at each node indicate the proportional likelihood support for ancestral states (figure modified from South et al., 2011b).
in fireflies. These results could be broadly applicable to other capital breeders and could help explain patterns of nuptial gift evolution in other taxa. Further studies are needed to see whether variation in other ecological and life-history traits associated with resource allocation can provide additional insights into nuptial gift evolution.

C. Female Incorporation of Ejaculate-Derived Proteins in \textit{Drosophila} Fruitflies

In our taxonomy of nuptial gifts, the category of endogenous genital gifts explicitly includes seminal products that are transferred in a liquid ejaculate; this occurs in many Diptera, including \textit{Drosophila} fruitflies. \textit{Drosophila} species vary widely in several aspects of their mating systems, including female remating latency, male ejaculate composition, mating behavior, and the degree to which substances from male ejaculates are incorporated into female tissue (Markow, 2002; Markow and Ankney, 1984; Markow and O'Grady, 2005; Pitnick et al., 1997). Studies mapping reproductive traits onto a \textit{Drosophila} phylogeny provide insight into the evolutionary history of these unpackaged nuptial gifts.

For 34 species of \textit{Drosophila}, Pitnick et al. (1997) used radiolabeled amino acids to determine how much protein transferred in male ejaculates was incorporated into female ovarian or somatic tissue. \textit{Drosophila} species showed dramatic variation in the degree to which females incorporated male-derived proteins (Fig. 7). Females in most species, including those in the \textit{melanogaster} group, showed no incorporation into their ovarian tissue and about half showed no incorporation into somatic tissue. However, \textit{Drosophila} species within the \textit{subpalustris} group showed substantial incorporation into somatic tissue, and those within the \textit{mojavensis} cluster showed substantial incorporation of male-derived protein into both somatic tissue and oocytes.

By mapping these data onto a molecular phylogeny, Pitnick et al. (1997) showed that incorporation of male-derived protein into female somatic tissue has independently evolved multiple times (Fig. 7). In the \textit{mojavensis} cluster, high levels of ovarian incorporation were also seen to accompany high incorporation into somatic tissue. This phylogeny also reveals some degree of lability, as incorporation into both tissue types seems to have been subject to both gains and losses. Thus, this work provides evidence that multiple \textit{Drosophila} groups have evolved male ejaculates that contribute to female somatic maintenance or reproduction.

As pointed out by Pitnick et al. (1997), these patterns of female ejaculate incorporation might be related to differences among species in their nutritional ecology, as the host resources exploited by \textit{Drosophila} vary
Fig. 7. Phylogenetic distribution of nutritive male ejaculates in 34 species of *Drosophila* fruitflies (Diptera: Drosophilidae). Shading indicates the degree to which females have incorporated $^{14}$C-labeled proteins derived from male ejaculates into their somatic tissue (shown on left) and ovaries (shown on right) 6–8 h after mating. White bars indicate no female incorporation (0–50 corrected DPM), gray bars indicate a small degree of female incorporation (51–100 DPM), and black bars indicate substantial incorporation of male-derived protein by females (>100). Figure from Pitnick et al. (1997).
widely in quality (Markow and O’Grady, 2008). Species in the mojavensis group (D. mojavensis, D. navojoa, D. straubae, D. parisiena, D. mayaguana, and D. arizonae) all breed and feed on necrotic cactus (see Markow and O’Grady, 2005, 2008), which contains lower levels of both nitrogen and phosphorus compared to the fruit hosts used by the melanogaster group (Markow et al., 1999). In addition, by manipulating nutritional content of the cactus host, Brazner et al. (1984) showed that D. mojavensis are likely to undergo frequent nutritional stress. Markow et al. (1990) showed that D. mojavensis females kept on low-quality diets experienced enhanced fecundity from the receipt of male ejaculate, and suggested that nutritive ejaculates are more likely to evolve when adults are subject to nutrient limitation. Consistent with the enhanced fecundity hypothesis (Tallamy, 1994), females in some cactophilic, and presumably nutrient-limited, Drosophila species show a high degree of male ejaculate incorporation (Pitnick et al., 1997). In addition, Markow et al. (2001) found that in Drosophila nigrospiracula, a cactophilic species subject to larval phosphorus limitation, mated females incorporate phosphorus derived from male ejaculates into oocytes. Therefore, variation in resource availability among Drosophila species may be one factor in the evolution of nutritive male ejaculates that contribute to female somatic maintenance and reproduction.

The presence of nutritive male ejaculates also shows strong phylogenetic correlations with other features of Drosophila mating systems (Markow, 2002). Across 21 Drosophila species, Markow (2002) found strong congruence between female mating frequency and exaggerated male ejaculates (these include nutritive male ejaculates). Additionally, Markow (2002) suggested that the evolution of nutritive male ejaculates may have been preceded by higher female remating rates. However, because so many reproductive traits covary with mating systems, additional work is needed to test the sequence of these evolutionary transitions. The extensive knowledge base for Drosophila concerning host use, life histories, and reproductive traits makes this a compelling system for examining specific factors that promote the evolution of endogenous genital gifts.

In summary, in this section we present previous work that has taken a comparative phylogenetic approach to describe and test hypotheses about nuptial gift evolution. To rigorously test the various evolutionary scenarios that have been proposed for nuptial gifts, it will be essential to map gifts and other relevant traits onto robust phylogenies developed for particular taxa. We emphasize how valuable it is to include life-history and ecological traits in such evolutionary analyses. This approach should provide insight into the evolutionary sequence of gift transitions and will also allow formal tests of correlated evolution between male gifts and other traits that can influence their evolutionary trajectory.
D. EVOLUTIONARY RATES OF DROSOPHILA SEMINAL PROTEINS

Drosophila male ejaculates are certainly the most well-characterized of all endogenous nuptial gifts. Their nonsperm components comprise a complex cocktail of molecules produced by male accessory glands and secretory tissues in the male ejaculatory duct. While many different types of molecules are transferred within Drosophila male ejaculates, research has focused on seminal fluid proteins (SFPs). Once transferred, these SFPs engage in dynamic molecular interactions within the female reproductive tract, and this sexual interplay is likely to influence SFP evolution. Because these molecules have been so well-studied, research on SFP evolutionary rates can contribute to a broader understanding of nuptial gift evolution.

Nearly 150 different SFPs have been identified from the ejaculate of D. melanogaster males, and these proteins initiate many physiological and behavioral changes within mated females (reviewed by Avila et al., 2011). Significant changes in female gene expression are seen 1–3 h following the receipt of ejaculate and are maximized at 6 h postmating. Conformational changes of the female reproductive tract allow for sperm storage, and the oviduct shows increased innervation and enhanced formation of myofibrils (Adams and Wolfner, 2007; Kapelnikov et al., 2008). Specific SFPs are necessary for female sperm storage and release, while others improve sperm survival (Ravi Ram and Wolfner, 2007a; Xue and Noll, 2000). Male SFPs increase female egg production and ovulation (Heifetz et al., 2000; Ravi Ram and Wolfner, 2007a,b), initiate the formation of a mating plug (a gelatinous mass containing sperm; Bretman et al., 2010; Lung and Wolfner, 2001), and cause females to actively reject courting males. Female activity levels also increase following mating, with increased foraging (Carvalho et al., 2006) and 70% less sleep (Isaac et al., 2010), possibly leading to shorter life spans for mated females (Isaac et al., 2010; Wigby and Chapman, 2005).

Notably, rapid evolution of genes encoding male SFPs has been documented in Drosophila as well as in other taxa (Clark et al., 2006; Swanson and Vacquier, 2002; Vacquier, 1998). Comparisons between D. melanogaster and D. simulans demonstrated high rates of nonsynonymous nucleotide substitution in SFP genes compared to non-SFP genes (Swanson et al., 2001). Sequence comparisons between D. melanogaster and D. pseudoobscura of 52 SFP-encoding genes from male reproductive accessory glands detected only 58% conserved as true orthologs (Mueller et al., 2005). Such rapid and dynamic evolution of SFPs is likely due to postcopulatory sexual selection (Clark et al., 2006; Panhuis et al., 2006; Swanson and Vacquier, 2002). Sperm competition (Birkhead and Moller, 1998), cryptic female choice (Eberhard, 1996), and sexual conflict (Parker, 1979) may all contribute to a coevolutionary arms race between and within sexes over control of reproductive outcomes.
Comparisons between *Drosophila* species can be used to test the prediction that SFP evolution will proceed more rapidly when postcopulatory sexual selection is more intense. Mating systems and reproductive ecology differ dramatically between species in the *repleta* group and those in the *melanogaster* group. *D. repleta* males transfer a nutritive ejaculate, and females remate more frequently (Markow, 2002; Markow and Ankney, 1984; Pitnick et al., 1997). In addition, many *repleta* species show an insemination reaction, consisting of an opaque mass that develops within the female vagina after mating. This is thought to prevent females from remating, thus protecting the male’s nutritional investment from cuckoldry by rival males (Markow and Ankney, 1984, 1988). Based on these differences in reproductive ecology, species in the *D. repleta* group appear subject to more intense postcopulatory sexual selection and thus are predicted to show faster rates of SFP evolution compared to *D. melanogaster*. Supporting this prediction, several studies have shown that SFP genes expressed by male accessory glands in the *repleta* group evolve more rapidly than those in the *D. melanogaster* group (Almeida and DeSalle, 2009; Wagstaff and Begun, 2005, 2007). In the *repleta* group, SFP genes also show high rates of gene duplication, which is suggested to facilitate adaptive protein evolution (Ohno, 1970; Walsh, 2003). Thus, *repleta* SFPs appear to be undergoing rapid evolution, potentially due to differences in their reproductive ecology.

Consistent with the prediction that sexual coevolution is responsible for rapid evolutionary changes in male gifts, some female reproductive proteins in the *repleta* group also show rapid adaptive evolution, and gene duplication has also been important in the evolution of these proteins (Kelleher et al., 2007). Of particular interest are several digestive proteases, which Kelleher et al. (2007) suggest might play a role in breaking down the mating-induced insemination reaction. Interestingly, male ejaculates in *D. mojavensis* contain protease inhibitors (Wagstaff and Begun, 2005), two of which have also experienced lineage-specific gene duplication events (Kelleher et al., 2009). The reproductive tract of female *D. arizonae* (a close sister species to *D. mojavensis*) shows exceptionally high proteolytic activity that is negatively regulated by mating (Kelleher and Pennington, 2009). Taken together, these results from different *repleta* species suggest active sexually antagonistic coevolution around the insemination reaction, with male protease inhibitors acting to prevent male ejaculate components getting broken down by female proteases.

Thus, rapid evolution of *Drosophila* nuptial gifts appears to be driven by a complex sexual interplay taking place at the molecular level. While some male-derived proteins are incorporated into female oocytes and somatic tissue, other SFPs may have evolved to counter defenses mounted by
females to prevent male manipulation. Further exploration of these
dynamic sexual interactions should provide many insights into the con-
stantly shifting balance between the costs and benefits of nuptial gifts.

VI. CONCLUSIONS AND FUTURE DIRECTIONS

Animal nuptial gifts take multitudinous forms, and their evolutionary
stories promise to be just as diverse. In this overview, we have tried to offer
a fresh perspective on the evolution of animal nuptial gifts. We argue for a
broader definition of nuptial gifts that can accommodate anticipated lability
of nuptial gift structure and function arising from coevolutionary interac-
tions both between and within the sexes. By systematically classifying
nuptial gifts according to how they are produced (endogenous vs. exogen-
ous) and how they are absorbed by the recipient (oral, genital, or transder-
mal), we hope to establish a robust framework for testing predictions about
how gifts influence both male and female fitness. Rather than attempting to
place potential benefits gained by gift-giving males into the falsely dichot-
omous categories of parental investment versus mating effort, we illustrate
how nuptial gifts might enhance male fitness across multiple selection
episodes that occur before, during, and after mating. Finally, we highlight
some studies that have greatly advanced our understanding by using com-
parative phylogenetic methods to examine how nuptial gifts and associated
life-history traits have changed over evolutionary time.

We hope this foundation will inspire future research efforts to enhance
our understanding of nuptial gift evolution. Despite many advances, there
remain several areas that clearly call out for more focused research efforts:

- We have detailed morphological descriptions of the glands which are
responsible for manufacturing many endogenous gifts (e.g., Leopold,
1976; Liu and Hua, 2010). In many taxa, nuptial gifts are the combined
productions of multiple glands, yet much work remains to fully char-
acterize these glandular products. Transcriptome studies of gene
expression within gift-manufacturing glands will provide insight into
differences and similarities in their gene products and associated func-
tions. For example, to what extent has convergent evolution occurred
between those male reproductive glands that produce oral versus
genital gifts, or between reproductive and salivary glands?

- In considering selection for nutritive nuptial gifts, the geometric frame-
work developed for nutritional ecology (Raubenheimer, 2011;
Raubenheimer et al., 2009) provides a powerful tool for testing
whether male gifts evolved to support female reproduction. Does
selection shape male glandular products to provide novel nutritional mixtures that will supplement females' dietary resources, that is, do such gifts act as vectors that specifically target the requirements of vitellogenesis? We need more detailed biochemical analyses of different types of nuptial gifts to test many of the predictions laid out here.

- Most importantly, there is a compelling need for additional phylogenetic analyses of nuptial gift traits that can provide insight into the evolutionary origin and maintenance of nuptial gifts across different taxonomic groups. Continuing to examine evolutionary patterns within the Orthoptera will be especially interesting, because their nuptial gift types are so variable. Phylogenetic analysis would also be worthwhile in the Lepidoptera, where reconstructing ancestral character states could shed light on possible trajectories of spermatophore evolution. Finally, because nuptial gifts lie at the intersection of nutritional ecology, sexual selection, and life-history evolution, testing informed predictions concerning evolutionary associations between nuptial gifts and relevant ecological and life-history traits is of fundamental importance.

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