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Emerging issues in the evolution of animal nuptial gifts

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Uniquely positioned at the intersection of sexual selection, nutritional ecology and life-history theory, nuptial gifts are widespread and diverse. Despite extensive empirical study, we still have only a rudimentary understanding of gift evolution because we lack a unified conceptual framework for considering these traits. In this opinion piece, we tackle several issues that we believe have substantively hindered progress in this area. Here, we: (i) present a comprehensive definition and classification scheme for nuptial gifts (including those transferred by simultaneous hermaphrodites), (ii) outline evolutionary predictions for different gift types, and (iii) highlight some research directions to help facilitate progress in this field.

1. Introduction

Humans, birds, snails, squid, crickets, ladybird beetles, bedbugs, butterflies and fireflies are known to exchange gifts during courtship or copulation. These nuptial gifts include food, body parts, salivary gland secretions, love darts and sperm-containing packages known as spermatophores (reviewed by [1–3]). Although more cryptic than peacock tails, these morphological, physiological and biochemical traits play vital roles in both precopulatory and postcopulatory sexual selection. They link sexual selection with nutritional ecology, and it has long been recognized that gift economics can alter courtship roles, mating rates and sexual size dimorphism [4–6].

However, these important sexually selected traits have attracted limited theoretical attention (e.g. [7–9]), and we still have only a rudimentary understanding of how such gift diversity evolved. We believe progress in this area has been hindered by lack of a unified conceptual framework. In this opinion piece, we propose an updated definition and classification scheme to encompass the astounding diversity of nuptial gifts. We offer distinct predictions concerning gift economics and selective forces for these different gift types. Finally, we call for focused research in three key areas to meet the compelling need for a better understanding of nuptial gift evolution.

2. A comprehensive definition

While an extensive literature describes nuptial gifts in various taxa, little attention has been given to formally defining this term. Here, we offer an inclusive definition (updated from [3]) that encompasses gift diversity and explicitly includes gift-giving by simultaneous hermaphrodites: 'Nuptial gifts are materials (beyond the obligatory gametes) provided by a donor to a recipient during courtship or copulation in order to improve donor fitness'. In animals with separate sexes, gift donors are typically male and recipients female (but see [10]), while in many simultaneous hermaphrodites copulating pairs engage in bidirectional gift transfer (e.g. [11]).

An important feature of our definition is that it avoids making assumptions concerning how the gift affects recipient fitness: thus, it includes not only nuptial gifts that currently provide net fitness benefits to recipients, but also gifts that carry a net fitness cost as well as gifts that are neutral with respect to recipient fitness. This contrasts with some previous usage: for example, Arnqvist & Nilsson [12] suggested that the term 'Medea gift' be used for manipulative gifts that are detrimental to recipient fitness. We consider this approach problematic because it fails to account for changes in gift function that are expected over evolutionary time, driven by sexual selection and antagonistic coevolutionary interactions between the sexes [13]: gifts that initially benefit recipients may frequently evolve into detrimental gifts, and *vice versa*.

Many historically prominent reviews have implicitly or explicitly restricted their focus to include only 'nutritive' gifts; that is, materials that could be used to sustain metabolic activities (e.g. [1,14,15]). Similarly, some authors (e.g. [2,16]) have used the term 'nuptial feeding' interchangeably with 'nuptial gift' (acknowledging that intake need not necessarily be oral). Yet, many materials transferred during copulation are not nutritive. For example, gifts of some male insects contain sequestered defensive alkaloids that reduce predation on females' eggs and larvae (e.g. [17]). Additionally, some land snails inject their partners with mucus-covered darts during copulation, triggering physiological effects that can reduce recipient fitness [11]. We argue that restricting nuptial gifts solely to those that currently serve a nutritive function is undesirable because dynamic sexual interactions will alter gift composition as well as gift function over evolutionary time. For example, male gifts that are initially nutritive may drive selection for females to mate multiply, instigating sexual conflict and favouring the evolution of manipulative gifts to reduce the likelihood of female remating.

3. Nuptial gift classification and predictions

Although nuptial gifts are diverse, we propose that most of this diversity can be captured in just two dimensions [3]. The first is based on gift source: *endogenous* gifts are those manufactured or sequestered by donors, whereas *exogenous* gifts are food items that donors capture or collect. The second dimension describes how the gifts are taken in by recipients: *oral* gifts are absorbed through the digestive system, *genital* gifts are absorbed through the reproductive tract and *transdermal* gifts are injected through the recipient's body wall.

Distinct predictions concerning gift economics and selective forces apply to these different gift types. *Exogenous oral* gifts consist of seeds or prey that donors collect. These can increase the donor's mating success, copulation duration and sperm transfer, as recipients often assess gifts prior to mating and feed on them during copulation. These are the gifts most likely to be nutritive and to provide recipients with net fitness benefits (yet such gifts may sometimes be worthless, e.g. [18]).

Endogenous gifts may carry substantial manufacturing costs, whose affordability should depend on the donor's physiological condition. Some *endogenous oral* gifts consist of haemolymph or body parts that recipients consume during copulation; like exogenous gifts, these may directly augment the recipient's nutrient budget [19]. Other endogenous oral gifts are secreted by donor glands (salivary, reproductive or other), and may be consumed before, during and after copulation. These glandular gifts might provide nutrients otherwise scarce in recipient diets, including macro- and micro-nutrients, water and defensive chemicals. Conversely, donors may be selected to add non-nutritive phagostimulants that increase gifts' gustatory appeal [20], or substances that slow gift consumption rates [21,22].

Endogenous genital gifts are manufactured by donors' reproductive glands and then absorbed through the recipient's genital tract. According to our definition, this includes non-sperm ejaculate components that are transferred within seminal fluid as well as those transferred within discrete packages (e.g. spermatophores). Like endogenous oral gifts, these gifts might supply nutrients, water or defensive chemicals. On the other hand, glandular gifts deposited directly within the reproductive tract may be more likely to manipulate recipient physiology, driven by sexual conflict.

We recognize that our definition might be considered overly broad because it includes seminal fluid, a complex mixture produced by donor's reproductive glands that typically accompanies sperm transfer. However, we contend such inclusion is justified. Many seminal fluid components improve donor fitness not by protecting and nurturing sperm, but rather by exerting their effects on recipient reproductive behaviour and physiology [23,24]. For example, well-studied seminal fluid proteins in *Drosophila* increase storage and use of donor's sperm, heighten female oviposition and reduce female remating [25,26]; equivalent effects are triggered by donor spermatophores in other taxa. Furthermore, spermatophores and seminal fluid contain many similar proteins (e.g. [27]). By including seminal fluid components and unifying these closely related yet previously separate research arenas, we hope to facilitate progress in understanding nuptial gift function and evolution.

The final category consists of *endogenous transdermal* gifts, which include ejaculate and accessory gland products that are hypodermically injected into the recipient's body by the donor [28]. Such transdermal gifts include micronutrients, antibacterial compounds and numerous accessory gland products that alter recipients' physiology [29,30]. Such gifts have evolved in organisms with separate sexes (e.g. bedbugs, plant bugs and squid), as well as in simultaneous hermaphrodites (e.g. snails, slugs and earthworms). For the latter, theory suggests that sexual conflict may be particularly strong because copulation affords each individual the opportunity to gain fitness through its male as well as through its female function [31].

4. Conclusion and future directions

Clearly, much remains to be learned about nuptial gifts. We believe three avenues of investigation are particularly likely to provide new insights into the evolution of these important sexually selected traits.

- To rigorously test hypotheses for the evolution of nuptial gifts, we need additional comparative studies using well-supported phylogenies for different taxonomic groups (see [32–34]). Because nuptial gifts are so intimately linked to sexual selection, nutritional ecology and life histories [35], these analyses should include relevant mating system and life-history traits, such as degree of remating, mate-guarding behaviours and structures (e.g. genital claspers), and trophic ecology.
- Sexual conflict may be a powerful force driving nuptial gift evolution, yet surprisingly little is known about the counteradaptations that females/recipients have evolved to circumvent male manipulation. Also, functional studies focused on net fitness effects should allow us to compare the degree of sexual conflict within different endogenous gift categories: oral, genital and transdermal.
- Additional work is needed to characterize the biochemical composition of nuptial gifts, including proteomic analysis. Transcriptome studies of various gift-manufacturing glands will not only help characterize gift composition, but will provide crucial insights into functional similarities across taxa.

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