



## Evolution of worthless gifts is favoured by male condition and prey access in spiders



Maria J. Albo\*, Valentina Melo-González, Matilde Carballo, Fabiana Baldenegro, Mariana C. Trillo, Fernando G. Costa

Laboratorio de Etología, Ecología y Evolución, Instituto de Investigaciones Biológicas Clemente Estable, Montevideo, Uruguay

### ARTICLE INFO

#### Article history:

Received 2 December 2013

Initial acceptance 13 January 2014

Final acceptance 12 February 2014

Available online xxx

MS. number: A13-01003

#### Keywords:

female mate choice  
male body condition  
nuptial gift content  
*Paratrechalea ornata*

Males from gift-giving species attempt to obtain food to offer to females. Therefore, food access may affect both their body condition and their reproductive success. In some species, males reduce the costs associated with giving gifts by reusing gifts, or by offering inedible items. Males from the spider *Paratrechalea ornata* (Trechaleidae) offer fresh prey or 'genuine gifts' to females, but also offer prey leftovers or 'worthless gifts'. We examined gift weight and content, and their relation to male condition in the field. We also investigated how gift content, male condition and female reproductive status (virgin/mated) affect male mating success. In the field, most gifts were worthless; genuine gifts were heavier than worthless ones; and gift weights (both genuine and worthless gifts combined) were positively correlated with male condition. In the laboratory, males in good condition had higher mating success than males in poor condition. Males offering gifts (genuine or worthless) to virgin females enjoyed similar mating success and duration; neither differed significantly when compared to males without gift. In contrast, mated females behaved differently. Males without gifts were consistently rejected by mated females, while those that offered worthless gifts achieved matings. The interplay between male condition, prey access, female mating history and female preferences for gifts can favour the evolution of worthless gifts under certain conditions. Females do not penalize males with non-nutritive items by not mating or by reducing mating duration, but penalties may be potentially exerted via postcopulatory process.

© 2014 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Sexual conflict and a coevolutionary arms race may occur when sexes' interests diverge (Arnqvist & Rowe, 2002, 2005). In such cases, adaptations in one sex may be disadvantageous for individuals of the other sex, favouring counteradaptations to minimize costs. The degree of conflict can be influenced by ecological conditions, such as the spatial and temporal distribution of resources (Emlen & Oring, 1977; Gwynne, 1990; Simmons & Bailey, 1990). Indeed, the amount of food during the reproductive season strongly influences female reproductive success in spiders, as it determines the number and quality of eggs and offspring (Wise, 1975, 2006). In contrast, obtaining food during this period is not as relevant for males (Foelix, 2011) unless they have a particular interest in acquiring nutrients to offer to females as nuptial gifts.

In gift-giving species, females should favour those males that offer nutritional resources. In some bird species, males supply food

and guard the progeny until they are independent, while potentially reducing the risk of female extrapair copulations (Mougeot, Arroyo, & Bretagnolle, 2006; Stokes & Williams, 1971). Male nuptial feeding is also a common behaviour in many invertebrates (Austad & Thornhill, 1986; Burela & Martín, 2007; Gwynne, 2008; Lewis & South, 2012; Vahed, 1998, 2007). In general, males benefit from offering food gifts to females as these usually increase mating success, copulation duration and number of offspring. However, males can also suffer from costs of gift production (Albo, Toft, & Bilde, 2011; Engels & Sauer, 2006; Gwynne, 1990; Immonen, Hoikkala, Kazem, & Ritchie, 2009; Vahed, 2007). Just as in many other secondary sexual traits, nuptial gifts can be condition dependent. For example, in some scorpionflies, food availability regulates male salivary secretion, and well-fed males produce more secretion and are able to obtain more matings than poorly fed ones (Engels & Sauer, 2006).

Thus, contrary to females' interests, males may evolve to minimize costs of gift production when food is scarce, reducing gift quality while maximizing their reproductive chances. In some insect and spider species, males offer prey gifts, and they have been

\* Correspondence: M. J. Albo, Laboratorio de Etología, Ecología y Evolución, Instituto de Investigaciones Biológicas Clemente Estable, Avenida Italia 3318, Montevideo, Uruguay.

E-mail address: [mjalbograna@gmail.com](mailto:mjalbograna@gmail.com) (M. J. Albo).

observed to reuse gifts after one mating (Thornhill, 1976) or to offer inedible items, so-called worthless gifts (Albo, Winther, Tuni, Toft, & Bilde, 2011; LeBas & Hockham, 2005; Preston-Mafham, 1999). Such deceptive behaviours may allow males to increase the number of matings compared to males without gifts, and minimize costs of prey searching and capturing compared to males with genuine gifts. In the spider *Pisaura mirabilis* (Pisauridae), the male captures a prey (typically an arthropod), wraps it in silk, and offers it to the female during courtship (Bristowe, 1958). Field studies indicate that approximately 38% of the gifts are inedible items, such as prey leftovers, and offering worthless gifts to females has been suggested to constitute an alternative male mating tactic in this species (Albo, Winther, et al., 2011). Males with worthless gifts not only increase their chances of being accepted by females but also prolong mating time compared to males without a gift. However, females prefer genuine nutritive gifts and penalize males offering worthless gifts by reducing mating duration and probably the number of sperm stored (Albo, Bilde, & Uhl, 2013; Albo, Winther, et al., 2011).

The evolution of worthless gift giving is potentially favoured when the male is in poor condition and/or has low access to food, because males may reduce the costs of gift production by eating the prey before offering it to females or by offering inedible items. We tested these hypotheses using the nuptial gift-giving spider *Paratrechalea ornata* (Trechaleidae). In this species, males also offer wrapped prey, and gift-giving males experience higher mating success and longer mating duration than males without a gift (Albo & Costa, 2010). Despite the benefits of gift giving, males sometimes attempt to mate without offering a gift, but they may wrap worthless items such as prey leftovers and occasionally plant parts when are rejected by females (Albo & Costa, 2010; see [Supplementary Video S1](#)). In addition, males in poor condition usually delay wrapping the prey in silk compared to males in good condition, suggesting that males in poor condition may feed on the prey before turning it into a gift and offering it to the female (Trillo, Melo-González, & Albo, 2014). Because of this plasticity in *P. ornata*'s behaviour, it is a particularly good model for studying sexual conflict over gift nutritional quality and for discussing the evolutionary processes involved.

We predicted that males in poor body condition would feed on their prey before wrapping it in silk, resulting in worthless gifts, while males in better condition would offer fresh genuine gifts. Since females are able to recognize gift content only after they have grasped the gift and mating has started, we expected females to accept matings with males offering gifts, regardless of the content (genuine or worthless), equally. But, if feeding on the gift is positively correlated with mating duration, we also expected the females to reduce mating duration for males offering worthless gifts as a counteraction to male deception. In addition, we expected that males in good condition would experience higher mating success and longer mating duration than males in poor condition independently of the gift.

## METHODS

*Paratrechalea ornata* is a crepuscular/nocturnal spider associated with rivers and streams in South America (Carico, 2005). During field surveys we collected males with gifts from three sites in Uruguay: Santa Lucía River (Paso del Molino, Arequita, Lavalleja, 34°16'40.10"S, 55°14'00.80"W), Yermal Chico stream (Treinta y Tres Province 32°55'30.50"S, 54°27'33.10"W) and Queguay River (Rincón de Perez, Paysandú Province, 32°10'37.98"S, 57°14'15.30"W). For the behavioural experiments we collected immature individuals from Santa Lucía River.

Spiders were sexed and kept in the laboratory in plastic jars (8.5 cm internal diameter and 7.5 cm high); experiments were performed in glass cages (30 × 14 cm base and 20 cm height), containing a layer of small pebbles and water, simulating their natural environment. Immature spiders were raised in a warm room (24.8 ± 1.9 °C) to accelerate development, and were checked daily for moults. We fed individuals three times a week with fruit flies (*Drosophila* spp.), and provided water in a wet cotton wool. Once individuals reached adulthood, we placed them in a room averaging 20.6 °C (±3.3 SD). Adult females received fruit flies twice per week; adult males were included in one of two different feeding groups (see below). Vouchers were deposited in the Arachnological collection of the Facultad de Ciencias, Montevideo, Uruguay.

Statistical analyses were performed using JMP 9.0 software (SAS Institute, Cary, NC, U.S.A.). Response variables were examined for normal distribution of residuals and homogeneity of variance with Shapiro–Wilk and Levene tests, respectively.

## Field Data

### Quantifying gift content and male condition

We examined how nuptial gift content varies in nature and whether there is a correlation between gift content and male body condition. To quantify male condition and gift content in the field, we collected males carrying gifts on eight dates during three reproductive seasons (2010, 2011 and 2012) and from the three localities mentioned above. To avoid manipulation of the gift by the males, we immediately removed the gift from each male's chelicerae and placed it in an eppendorf tube together with the corresponding male in a plastic bag. Within 24 h of field collection, we weighed and measured males. We calculated an index of male condition (residual index) as the residual of the regression of body mass on cephalothorax width (Jakob, Marshall, & Uetz, 1996). We also weighed the gifts, dissected them under a stereomicroscope using forceps, and registered the content. We classified the gifts according to Albo, Toft, et al. (2011) as 'genuine' (containing fresh prey) or 'worthless' (containing prey leftovers; i.e. empty exoskeletons and/or plant parts or other non-nutritive items; Fig. 1a, b). In the field, the number of prey in a gift package varied from one to three (Trillo et al., 2014), but for the aim of this study we did not quantify the prey. Thus, if a gift contained both genuine and worthless prey, we counted the gift as genuine. After silk wrapping, males search for a female, and during this time they do not feed on the prey, as they would need to dissolve their own silk package to do so. In addition, males seem not to carry gifts longer than 24 h (M. J. Albo, personal observations), eliminating the possibility of desiccation of gifts because of time. Thus, gift content accurately reflects what the male added before silk wrapping and what the female will receive.

We analysed gift weight with one-way ANOVA and we also calculated a linear regression between gift weight and body condition. We analysed the effects on gift content from the collecting date and the site using ANCOVA.

## Experiment 1

### Worthless gifts, male condition and reproductive consequences

We designed experiments in the laboratory to investigate how both gift content and male condition affect male mating success. The typical courtship behaviour of a *P. ornata* male, whether carrying a gift on his chelicerae or not, consists of nonlinear locomotion towards the female and foreleg vibrations. The male offers the gift to the female in a particular posture called 'hyperflexion' (Costa-Schmidt, Carico, & Araújo, 2008). Female mating acceptance

Download English Version:

<https://daneshyari.com/en/article/8490510>

Download Persian Version:

<https://daneshyari.com/article/8490510>

[Daneshyari.com](https://daneshyari.com)