



Gift carrying in the spider *Pisaura mirabilis*: nuptial gift contents in nature and effects on male running speed and fighting success

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Males of the spider *Pisaura mirabilis* offer prey items as nuptial gifts to females. While gift giving in this species has received attention in captivity, the ecological context of these gifts remains largely unknown. First, we examine the occurrence of gift carrying by males in nature. Field data reveal that gift-carrying males are frequent in nature (40% of captured males), and that all gifts contain fresh arthropod prey. Gift mass was positively correlated with the longest diameter of the gift. Thus, males do not appear to ‘cheat’ by inflating their gifts with inedible items, air or loosely wrapped silk. Second, we examine two ecological costs to gift-carrying males: the effects of gifts on male running speed and male fighting success. Gift carrying reduced male running speed, but did not affect male fighting success in male–male contests. The former result is the first demonstration of a transportation cost associated with gift carrying in an arthropod.

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In many arthropods, males provide nuptial gifts to females, which can consist of captured food, glandular or salivary secretions, spermatophores, or the male’s body parts (reviewed in: Simmons & Parker 1989; Vahed 1998, 2007; Gwynne 2008). The evolution of nuptial gifts can lie in a combination of fitness benefits to the male, such as increased mating success and/or increased paternal investment (increase the quality and quantity of his offspring), and to the female, in the form of nutrition used to increase female fitness and/or offspring quality and probability of survival (Simmons & Parker 1989; Vahed 1998, 2007).

While nuptial gifts can offer benefits to male and female fitness, they involve costs to both sexes as well. The particular form of the cost will often depend on the form of the donation itself. In some species, the costs of donations are quite obvious to the male, such as gryllid crickets in which the female chews and consumes a male body part, typically reducing the male’s future reproductive success (Fedorka & Mousseau 2002; Sakaluk et al. 2004; Piascik et al. 2010). A more extreme nuptial offering can be found in the males of the

Australian redback spider, *Latrodectus hasselti*, which somersault into the females’ mouthparts during copulation, risking death for the sake of prolonging copulation (Andrade 1996). In other species, donations are energetically costly, such as large spermatophores produced by male tettigoniids (Simmons 1990; Simmons & Gwynne 1991; Wedell 1994; Vahed 2007).

In some arthropods, males carry gift items as they search for or court females. This form of nuptial gift occurs in dance flies (Diptera: Empididae), hangingflies and scorpionflies (Mecoptera), and some spiders (Bristowe 1968; Austad & Thornhill 1986; Vahed 1998; Costa-Schmidt et al. 2008). These gifts are often procured before the male contacts the female (Nitzsche 1988), requiring the male to retain and carry the item in his travels. In these species, then, the gift item may pose ecological costs for males, including movement costs and possible lost opportunities for feeding. In the context of courtship, gift items carried by male dance flies may reduce manoeuvrability or flight efficiency for the males (Sadowski et al. 1999; LeBas et al. 2004). With regard to travel involved in searching for females, the effects of gift transport on male behaviours, such as movement and intermale competition, have eluded experimental examination in gift-giving arthropods.

We examine the ecological costs of gift carrying to males in the spider *Pisaura mirabilis*. In this spider, males wrap prey items in silk, hold them with their chelicerae, and offer the items to females. The

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female may accept the item into her chelicerae; as she feeds, the male transfers sperm (Austad & Thornhill 1986; Stålhandske 2001a, b). Previous research demonstrates the importance of possessing a gift to male mating success in this species. In some populations, females appear to require the prey item for insemination to occur (Austad & Thornhill 1986; Prokop & Maxwell 2009). Copulation duration increases with gift size and, in turn, copulation duration positively correlates with fertilization success (Stålhandske 2001a). It is suspected that males carry gift items in the field as they search for females (Nitzsche 2011), as in other gift-giving spiders (Costa-Schmidt et al. 2008; Albo et al. 2009).

Despite these benefits to male mating success, the gifts' costs to males remain poorly understood. For example, authors differ on whether silk production and gift wrapping are energetically costly (Lang 1996; Albo et al. 2011a), and costs associated with gift carrying have not been examined. The present study examines ecological costs associated with gift carrying. First, we investigate the incidence of male gift carrying in nature, to document this behaviour and to describe the characteristics and contents of field-collected gifts. We are particularly interested in whether males 'inflate' the gifts by adding inedible items as a possible way of reducing the effort involved in acquiring prey to package as gifts, as suggested by some authors (Nitzsche 2011; Albo et al. 2011b). Second, we examine the effects of gift carrying on two male behaviours: running speed and male–male fights. *Pisaura mirabilis* is a ground-dwelling spider, and males are commonly found crawling on the ground or on vegetation in nature (P. Prokop, personal observation). We ask whether male running speed is affected by holding a gift item. With regard to male–male fights, such fights are common in captive colonies (Nitzsche 2011), and are expected to occur in nature (Nitzsche 1988). We therefore ask whether possession of a gift confers an advantage or a disadvantage to the male in combat.

METHODS

Study Organism

The nursery-web spider, *Pisaura mirabilis* (Pisauridae), is a predominantly diurnal predator (Nitzsche 2011), living in grasslands and deciduous woods. Its life cycle is annual in central Europe (Buchar et al. 1989). Spiderlings hatch in late June–August and reach maturity in April–May of the following year. Mature males can be found until June, whereas females may be seen into late summer (P. Prokop, personal observation). When a male detects a receptive female's draglines, he catches a prey item and wraps it with silk (e.g. Nitzsche 1988; Albo et al. 2011a). Males have also been observed to wrap prey and carry it as a nuptial gift soon after final moult, even in the absence of a female (Lang 1996; P. Prokop, personal observation), which allows a male to court a female upon detecting her (Albo et al. 2011a). The male then approaches the female, and the female seizes the gift. Once the female holds the gift in her chelicerae, the male swivels around and positions himself underneath the female's sternum, facing away from her anterior. While the female feeds on the gift item, the male inserts his pedipalp into the female's epigyne and transfers sperm.

Nuptial Gifts in the Field

To examine the contents of nuptial gifts in the field, we randomly captured 58 adult males through visual searching at two open woodland sites near Trnava, Slovakia (48°23'N, 17°35'E) during 8–14 May 2010. Early May is typically the peak mating season for *P. mirabilis* in Slovakia (P. Prokop, unpublished data), when males are most likely to be found carrying gifts in the field.

Searching and capture occurred during daylight hours (1300–1700 hours). Upon capture, each male was isolated in a ventilated cup (0.3 litre) with wet cotton to maintain humidity. Each male was anaesthetized soon after capture, and the gifts were carefully removed from the males' chelicerae to avoid consumption of the gifts. Gifts were weighed to 0.0001 g, and measured along the longest diameter to 0.01 mm. The contents of the gifts were then examined through dissection under a binocular microscope. On the following morning, each male was anaesthetized with CO₂, and prosoma width (to 0.01 mm) and body mass (to 0.0001 g) were measured. Throughout this study, we quantified male body condition as the residual of regression of body mass on prosoma width (Jakob et al. 1996). After all measurements, the spiders were returned to their sites of capture. These releases occurred after all spiders had been captured, so no male was captured more than once. All field work and experiments were performed in compliance with Slovakian laws.

Ecological Costs of Nuptial Gifts: Male Running Speed and Male–Male Fights

To examine ecological costs of nuptial gifts, we captured 125 subadult males from mixed woodlands near Trnava in April 2010. Each juvenile was isolated in a ventilated 0.3-litre glass jar provided with wet cotton, maintained at 20 °C, and exposed to natural photoperiod. The spiders were fed house cricket nymphs (*Gryllus assimilis*) three times per week (ca. five crickets per feeding), and were misted with water once per day. Each juvenile was checked daily for adult emergence; 119 subadults became adults. Adult males were fed daily with cricket nymphs on an ad libitum basis. Trials that examined running speed and male–male fights were conducted indoors, 20 °C, and exposed to indirect sunlight. From our field collections, we observed males actively crawling and carrying gifts during the day. Nuptial gifts used in the trials were freshly killed crickets (by CO₂) of standardized size (random sample of crickets: mean \pm SE = 0.014 \pm 0.0005 g, $N = 10$), being of comparable size to gift items used in other studies on *P. mirabilis* (e.g. range 2.3–29.1 mg, Stålhandske 2001a; mean = 15.5 mg, Stålhandske 2002; mean = 11.9 mg, Prokop & Maxwell 2009), as well as gift items reported from nature (Nitzsche 1988; Stålhandske 2001a, b; this study).

Effect of nuptial gifts on male running speed

For trials to test running speed, we randomly selected 10 adult males (mean mass \pm SE = 0.0984 \pm 0.007 g; mean prosoma width \pm SE = 3.58 \pm 0.12 mm; $N = 10$). Each male was 10–12 days postemergence. Each male was tested in two trials: one trial with a gift item (freshly killed cricket nymph: mean \pm SE = 0.0250 \pm 0.0002 g, $N = 10$), and the other trial without a gift item. Five of the males performed the trial with the gift first, followed by the trial without a gift. The other five males did the trials in reverse order.

Trials were conducted indoors between 1100 and 1300 hours. For each trial, the male was placed at one end of a wooden stick (1 m long, 2 cm diameter) that was fixed 15 cm above a horizontal surface. The stick was surrounded by white paper to reduce visual distractions to the spider. If the trial involved running with the gift, we first released the male in a glass terrarium (30 \times 20 \times 20 cm) lined with white paper that a virgin female had previously crawled on for 10 min. Female draglines induce male sexual behaviour (e.g. Nitzsche 1988; Stålhandske 2001a, b; Albo et al. 2011a) and stimulate males to wrap prey items with silk. We provided the cricket to the male in the terrarium. Once the male had wrapped the cricket in silk and held it in his chelicerae, we placed him on the stick. The

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