



If you eat, I eat: resolution of sexual conflict over consumption from a shared resource



Natalie Pilakouta^{*}, Jon Richardson, Per T. Smiseth

Institute of Evolutionary Biology, School of Biological Sciences, University of Edinburgh, Edinburgh, U.K.

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Sexual conflict arises whenever males and females have divergent reproductive interests. The mechanisms mediating the resolution of sexual conflict have been studied extensively in the context of parental care, where each parent adjusts its decision about how much care to provide based on its partner's workload. However, there is currently no information on the mechanisms mediating the resolution of sexual conflict over personal consumption from a shared resource. We address this gap in the burying beetle *Nicrophorus vespilloides*, which breeds on small vertebrate carcasses. The carcass serves as a source of food for both the developing larvae and the caring parents, and parents feed from the carcass for self-maintenance. To study the mechanisms mediating conflict resolution, we experimentally varied the two parents' body size to create variation in carcass consumption. We then assessed whether each parent adjusted its consumption based on its own size, its partner's size and its partner's consumption. As expected, large parents gained more mass than small parents. Furthermore, males paired to large females gained more mass than males paired to small females, and females responded to their partner's mass change, gaining more mass when their partner did. Our study provides insights into the resolution of a new form of sexual conflict, showing that it is mediated through both matching and sealed-bid responses. Our findings also suggest that the resolution models developed in the context of sexual conflict over biparental care may apply more generally than previously thought.

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Sexual conflict arises whenever males and females have divergent reproductive interests and can occur in various contexts before mating (e.g. male harassment and female resistance; Arnqvist & Rowe, 2005), during mating (e.g. duration of copulation; Schneider, Gilberg, Fromhage, & Uhl, 2006) or after mating (e.g. contribution to parental care; Houston, Székely, & McNamara, 2005). Even though previous research has examined many types of sexual conflict (Arnqvist & Rowe, 2005; Houston et al., 2005; Parker, 2006), one type of conflict that so far has been neglected is that over the consumption of a food resource that is shared by the two parents and their offspring.

Sexual conflict over the consumption of a shared food resource might be common in species with biparental care. For example, in many birds, the two parents share a breeding territory, within which each parent searches for food, both for its own consumption and to provision its nestlings. Also, in many insects with biparental care, the two parents share resources in the form of

dung, carrion or wood that serve as food for the parents as well as the developing larvae (Tallamy & Wood, 1986). Each parent benefits personally by consuming from the shared resource, as it allows that parent to invest in self-maintenance and thereby enhance its future reproductive potential (Billman, Creighton, & Belk, 2014; Creighton, Heflin, & Belk, 2009). However, given that resources are finite, increased consumption by one parent leaves less of the resource for the offspring and the partner. A study on the burying beetle *Nicrophorus vespilloides* suggested that sexual conflict over shared resources during the breeding attempt may negatively affect female longevity (Boncoraglio & Kilner, 2012). Thus, there is evidence for a conflict battleground between the two sexes over personal consumption from the shared resource, with each parent preferring to consume more resources than would be optimal from its partner's perspective. Nevertheless, the mechanisms underlying the resolution of this form of conflict are still unexplored.

We suggest four mechanisms that might be involved in the resolution of sexual conflict over consumption from a shared resource. The first potential mechanism is coercion based on physical interference between the two parents. If coercion is mediating the resolution of this conflict, consumption of the

^{*} Correspondence: N. Pilakouta, Ashworth Laboratories Room 102, King's Buildings, School of Biological Sciences, University of Edinburgh, Edinburgh EH9 3JT, U.K.

E-mail address: n.pilakouta@gmail.com (N. Pilakouta).

resource should depend on asymmetries in fighting ability between the two parents, as the stronger parent might be in a position to control the feeding behaviour of its partner. The other three possible mechanisms (negotiation, matching and sealed-bid decisions) derive from theoretical models for the resolution of sexual conflict over contribution towards parental care. Negotiation and matching occur when each parent adjusts its own contribution in direct response to its partner's contribution (Johnstone & Hinde, 2006; McNamara, Gasson, & Houston, 1999). When there is negotiation, the focal parent responds to a reduction in the amount of care provided by its partner by increasing its contribution (McNamara et al., 1999), while when there is matching, the focal parent matches any increase or reduction in its partner's contribution (Johnstone & Hinde, 2006). Sealed-bid decisions occur when each parent makes an initial fixed decision about how much to contribute that is independent of its partner's contribution (Houston & Davies, 1985). We suggest that these mechanisms might also apply to the resolution of sexual conflict over consumption from a shared resource because there are clear analogies between these two forms of conflict. Sexual conflict over contributions to parental care occurs because the benefits of care are shared between the two parents while the costs of care are personal (Lessells, 2012), whereas sexual conflict over consumption from a shared resource occurs because the costs of consumption are shared between the parents while the benefits of consumption are personal.

In this study, we investigated the mechanisms underlying the resolution of sexual conflict over carrion consumption in the burying beetle *N. vespilloides*, an insect that breeds on carcasses of small vertebrates (Eggert, Reinking, & Müller, 1998). The carcass serves as a source of food for the two parents and their developing offspring, so the more each parent consumes from the resource, the less will be left for its partner and the offspring (Boncoraglio & Kilner, 2012; Scott, 1989). Previous work in the burying beetle *Nicrophorus orbicollis* has shown that there is substantial variation in the parents' mass change over the breeding attempt and that this mass change serves as a proxy for investment in future reproduction (Billman et al., 2014; Creighton et al., 2009). Because we were interested in whether each parent adjusts its carrion consumption in response to that of its partner, we experimentally varied the body size of the two parents on the assumption that larger individuals consume more carrion. This asymmetry in body size inadvertently introduced asymmetry in the physical strength of the two parents (Otronen, 1988), allowing the possibility that the larger parent might enforce their feeding optimum by eating more while interfering with its partner's access to the carcass. Evidence for physical interference between partners has been observed in the closely related *Nicrophorus defodiens*. In this species, females behave aggressively towards their male partner to prevent him from attracting additional females (Eggert & Sakaluk, 1995).

To study the mechanisms mediating conflict resolution and assess whether each parent adjusts its consumption based on its own size, its partner's size and its partner's consumption, we recorded (1) the amount of time spent feeding on the carcass by each parent during a 30 min observation and (2) the change in the mass of each parent over the reproductive attempt (Billman et al., 2014; Creighton et al., 2009). If sexual conflict over carrion consumption is resolved through negotiation, we predicted that the focal parent would reduce its consumption in response to an increase in consumption by its partner. If it is resolved through matching, we predicted that the focal parent would increase its consumption in response to an increase in consumption by its partner. If the conflict is resolved through sealed-bid decisions, each parent's decisions about how much to consume should be

independent of its partner's consumption. Lastly, if the conflict is resolved through coercion, we predicted that the larger parent would prevent its smaller partner from consuming from the carcass.

METHODS

General Methodology

We used virgin beetles from an outbred laboratory population maintained at the University of Edinburgh. The beetles used in this study comprised sixth-, seventh- and eighth-generation beetles from lines originally collected in Edinburgh, U.K. and Warmond, The Netherlands. They were housed individually in transparent plastic containers (12 × 8 cm and 2 cm deep) filled with moist soil and kept at 20 °C and constant light. Nonbreeding adults were fed raw organic beef twice a week.

Experimental Design

To induce variation in carcass consumption by the parents, we first generated small and large beetles using a full-sib design based on previously established methodology (Pilakouta, Richardson, & Smiseth, 2015; Steiger, 2013). For each of these 90 broods, we removed half of the brood from the carcass once the larvae reached the third instar, leaving the remaining larvae on the carcass until right before dispersal. We recorded the mass of each larva and kept the larvae in individual containers with moist soil. Larvae weighing less than 150 mg were categorized as small (mean ± SD: 111 ± 14 mg), while larvae weighing more than 150 mg were categorized as large (203 ± 24 mg). Larval mass at dispersal determines adult size, as larvae do not feed in the period between dispersal from the carcass and eclosion (Bartlett & Ashworth, 1988; Lock, Smiseth, & Moore, 2004).

All beetles were bred within 2 weeks after sexual maturity (10–24 days after eclosion) using a 2 × 2 factorial design: a large male paired with a large female ($N = 25$), a large male paired with a small female ($N = 25$), a small male paired with a large female ($N = 25$) and a small male paired with a small female ($N = 25$). Paired beetles were virgins and did not share common ancestors for at least two generations. The pairs were transferred to transparent plastic containers (17 × 12 cm and 6 cm deep) with moist soil and were provided with freshly thawed mouse carcasses (Livefoods Direct Ltd, Sheffield, U.K.) of a standardized size (22–25 g). For each of these matings, we recorded the mass of the carcass and the prebreeding mass of each parent. Immediately after eggs were laid, we moved the parents and the carcass to a new container. When the eggs started hatching, we generated experimental broods of 15 larvae by pooling larvae from eggs across all treatments (Mattey & Smiseth, 2015). This design ensured that there were no effects due to parent-offspring coadaptation (Lock et al., 2004) and that any differences in the parents' consumption of the carcass were not mediated through differences in brood size.

Twenty-four hours after providing the parents with a brood, we conducted behavioural observations using instantaneous sampling every 1 min for 30 min (Martin & Bateson, 1986; Smiseth & Moore, 2002; Smiseth, Darwell, & Moore, 2003). During this time, we recorded the number of scans that each parent spent feeding on the carcass. Parents were then allowed to care for the brood undisturbed until the larvae dispersed from the carcass about 4 days later. At dispersal, which corresponds to the end of the parental care period, we recorded the postbreeding mass of each parent. We calculated each parent's change in mass during the breeding period, by subtracting its prebreeding mass from its postbreeding mass.

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