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Mating status and kin recognition influence the strength of cannibalism

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Adults that cannibalize juvenile conspecifics gain substantial energy and nutrients that are potentially limited in their normal diet, but they may also face the risk of filial cannibalism: the consumption of an individual's own offspring. However, the potential costs and benefits of cannibalism change with the reproductive status of an individual during its lifetime. Once adults become reproductively active, they suddenly face the potential loss of inclusive fitness associated with filial cannibalism, but they also have higher energy demands that could easily be met with cannibalism. Thus, selection should favour any behaviour that reduces the risk of filial cannibalism while maximizing the nutritional and other benefits of cannibalism. Here we take an experimental approach to examine the relative importance of kin discrimination, reproductive status and sex differences in influencing cannibalistic behaviour (including filial cannibalism) of adults using confused flour beetles, *Tribolium confusum*, as a model system. Using a series of complementary experiments, we show that the cannibalistic behaviour of *T. confusum* is driven by a combination of two factors that both reduce the risk of filial cannibalism. First, reproductive females preferred to cannibalize unrelated eggs over related eggs, indicating clear kin discrimination. In addition, females also showed a dramatic reduction in the general propensity for cannibalism after becoming reproductively active. Interestingly, the onset of reproduction also reduced cannibalism rates in males, indicating that this change in cannibalistic behaviour is consistent across sexes. Mating status had a greater influence on cannibalism rates than did sex. Together, kin discrimination and mating-status-dependent shifts in cannibalism rates reduced the risk of filial cannibalism by up to six-fold. In general, our findings suggest that evolution can alter the cannibalistic behaviour of individuals in multiple ways to reduce the risk of filial cannibalism while still maximizing the benefits of cannibalism.

Although cannibalism, the killing and consumption of conspecifics, has initially been considered to be an abnormal behaviour in a few species (Eibl-Eibelsfelt 1961), cannibalism has been documented in more than 1300 species across a diverse group of taxa, ranging from protists and arthropods to vertebrates (Fox 1975; Polis 1981; Elgar & Crespi 1992; Richardson et al. 2010). It is now clear that cannibalism is not only ubiquitous in natural communities (Fox 1975; Polis 1981; Woodward et al. 2005) but is also a major factor driving the dynamics of populations (Claessen et al. 2004; Wise 2006; Wissinger et al. 2010), species interactions (Rudolf 2008a, b, c), and even entire natural communities and ecosystems (Persson et al. 2000, 2003; Rudolf 2007a, b). Thus, understanding the factors that determine cannibalistic behaviour of organisms has broad ecological and evolutionary implications.

The evolution of cannibalism is generally expected to be driven by the balance of its benefits and costs (Pfennig 1997; Rudolf et al. 2010). Conspecifics represent a high-quality food source in the right stoichiometric ratio (you eat what you are) (Via 1999; Schausberger & Croft 2000; Mayntz & Toft 2006; Simpson et al. 2006; Alabi et al. 2008). Furthermore, cannibalism can also remove potential competitors (Polis 1981; Elgar & Crespi 1992), either for the individual itself or for its offspring (e.g. selective filial cannibalism increases offspring survival; Klug & Bonsall 2007), thereby indirectly benefiting cannibals. However, cannibalism can also be costly. One potential cost is the consumption of an individual's own offspring (i.e. filial cannibalism), which dramatically reduces the direct and indirect fitness of cannibals (Pfennig 1997). Based on the rules of kin selection (Hamilton 1964), cannibalistic behaviour should depend on the ratio of its fitness (direct and indirect) costs and benefits. Thus, any factor that changes the ratio of fitness costs and benefits should also result in a shift in cannibalistic behaviour (Pfennig 1997; Manica 2004; Rudolf et al. 2010).

A change in the reproductive status of individuals (i.e. reproductive versus nonreproductive) is particularly likely to have dramatic consequences on cannibalistic behaviour, but predicting how it affects cannibalistic behaviour has proven to be challenging. While some species show increased cannibalism rates in

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individuals that are not yet reproductively active, the opposite is true in other species. For instance, in the amphipod *Gamarus pulex*, females that are not reproductively active are more cannibalistic than females that have recently reproduced (e.g. Lewis et al. 2010). In contrast, mated females are more cannibalistic than their virgin counterparts in some mite species (Schausberger 2003). Changes in reproductive status can alter the cost–benefit ratio of cannibalism in at least two major ways. On the one hand, individuals that are not yet reproductively active face no risk of consuming their own offspring, and thus experience lower costs (i.e. loss of inclusive fitness) of cannibalistic behaviour than their reproductive counterparts. Thus, the ratio of costs and benefits of cannibalism changes with reproductive status, which could select for a reduction in the propensity for cannibalism to reduce filial cannibalism. Indeed, this has been observed in several social species across a range of taxa, including isopods and amphipods, rodents (e.g. house mice, gerbils) and fish (e.g. African cichlids) (Elwood 1994). On the other hand, reproduction is also costly; individuals that reproduce have much higher energy needs than their nonreproductive counterparts (Harshman & Zera 2007). Given the high nutritional value of conspecifics, cannibalism could be an easy way to meet the increased energy and nutrient demands. While it has been suggested that this could explain the higher cannibalism rates in reproductively active individuals (Schausberger 2003), this prediction also requires that the risk of filial cannibalism is low. A low risk of filial cannibalism is particularly likely in species with kin discrimination. Kin discrimination is the behavioural manifestation of kin recognition, or the cognitive ability of an individual to differentiate between kin and nonkin (Tang-Martinez 2001). If individuals are able to recognize kin (i.e. discriminate between their own and other offspring), this would allow reproductive adults to preferentially cannibalize unrelated offspring, thus minimizing the loss of inclusive fitness resulting from filial cannibalism while still enjoying the benefits of cannibalism. Kin discrimination has been recorded in a range of cannibalistic vertebrates and invertebrates, such as tiger salamanders, spadefoot toads, various species of rodents, isopods, various mite species, milkweed beetles and poeciliid fish (Pfennig 1997; Schausberger 2003). Given kin discrimination, cannibalistic behaviour may not change with reproductive status since it already reduces the risk of filial cannibalism. Indeed, given the high costs of reproduction, one might expect that reproductive adults may show higher cannibalism rates than their nonproductive counterparts if individuals are able to discriminate against kin. The question is, however, which strategy (i.e. kin discrimination versus a shift in the propensity for cannibalism with reproductive status) is actually displayed in cannibalistic species.

Here we take an experimental approach to examine how kin discrimination, reproductive status and sex influence cannibalistic behaviour (including filial cannibalism) of adult confused flour beetles, *Tribolium confusum*. This species has served for decades as a model system to study the evolutionary and population dynamical consequences of cannibalism (Champman 1928; Park et al. 1965; Wade 1976). Adults and larvae heavily cannibalize eggs and pupae (Park et al. 1965; Alabi et al. 2008), and previous studies indicate substantial genetic variation and inheritance for the propensity of cannibalism in flour beetles (Wade 1980; Stevens 1989). However, little is known about how reproductive status influences cannibalism rates in *T. confusum* and whether this species shows kin recognition. *Tribolium confusum* is a widespread pest species that often experiences very high population densities. We predicted that these conditions should strongly favour behavioural strategies that minimize the risk of filial cannibalism, such as kin recognition and/or changes in cannibalistic behaviour with reproductive status. In particular, we conducted a series of complementary experiments to answer the following questions. (1) Do reproductive females show some type of kin recognition that reduces filial cannibalism? (2) Does the propensity for cannibalism vary with reproductive status (i.e. virgin versus mated) in females and males? (3) Are there sex-specific differences in the propensity for cannibalism and do they vary with mating status?

METHODS

Focal Species

Tribolium confusum is a widely distributed pest of stored grain and dry goods (King & Dawson 1972). It has a typical beetle life cycle that includes an egg, larval, pupal and adult stage. It completes its entire life cycle (egg–adult stage) in wheat flour or other stored goods in about 30–40 days, depending on specific environmental conditions (e.g. type of flour, temperature, humidity). Adults start to senesce after about 3 months but can live much longer depending on the specific environmental conditions. Within 3–5 days after emergence, adults become reproductively mature and remain reproductively active for most of their adult life span. Females lay single eggs into the flour that are frequently cannibalized by larvae and adults. Cannibalism is considered to be a major factor regulating *T. confusum* populations (Park et al. 1965).

Stock colonies were started from one standard strain obtained from the U.S. Department of Agriculture Stored Product Insect Research Unit (Manhattan, KS, U.S.A.). We divided these stock colonies to found a series of laboratory colonies, which were maintained for 1 year (~eight generations) in 250 ml plastic containers filled with unbleached, enriched white flour and 5% baker's yeast at ~28 °C and ~30% humidity. Every 6–8 weeks, we founded new colonies with 20 haphazardly selected adults, larvae and eggs from old colonies. We typically changed flour in stock colonies every 3–6 weeks.

General Experimental Procedures

For the individual experiments, we randomly selected pupae from each of the stock colonies. Pupae were separated by sex and kept in sex-specific groups of five individuals in petri dishes (1.5 cm diameter) with flour medium to prevent breeding and to minimize cannibalism of pupae. Seven days after adults emerged, we haphazardly selected one male and one female from the same original stock colony and transferred them to a new petri dish (1.5 cm diameter) with flour medium, where they were allowed to mate for 72 h. To easily identify each sex, we marked males with a white dot (using a White-Out pen) on the back prior to mating. No individual was tested more than once, and all individuals (mated and unmated males and females) were tested at the same age.

Experiment 1: Kin Discrimination and Cannibalism

To test whether females differentially cannibalize their own eggs or unrelated eggs, we conducted two experiments. In the first experiment (experiment 1a), we moved females after the mating period into a 7-dram vial (51 × 26 mm diameter, 26 ml) that contained a mixture of 4 g of white flour and 1.5% of either methylene blue or neutral red dye. Because the eggs have a very sticky surface, the coloured flour naturally stuck to and coated the eggs, allowing us to identify related and unrelated eggs by colour. In half of the trials, related eggs were dyed with neutral red and unrelated eggs were dyed with methylene blue, and in the other half of the trials, this colour scheme was reversed. We checked and collected newly