Mating status and kin recognition influence the strength of cannibalism

Whitney Parsons, Wenborui Zhong, Volker H. W. Rudolf*

Department of Ecology and Evolutionary Biology, Rice University, Houston, TX, U.S.A.

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.
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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

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

laid eggs every 24 h for 3 consecutive days. The 3-day limit assured that eggs did not hatch before the end of an experiment (eggs typically hatched within 6 days). After this period we added one female and 8–10 (depending on a female's fecundity) of her own eggs and an equal number of unrelated eggs, collected from randomly selected females from another stock colony, into a 7-dram plastic vial with 4 g of white flour medium. Eggs were mixed into the flour before a female was introduced into the vial. After 72 h we removed the female and counted the remaining eggs. This procedure was repeated for 32 females.

In experiment 1b, we stained the eggs using red food colouring, because preliminary trials indicated that beetles strongly preferred eggs stained in this manner. Indeed, we found that beetles were up to five times more likely to cannibalize stained eggs than unstained eggs (unequal variance t test: $t_{20.6} = 11.09$, $P < 0.0001$). We then divided females haphazardly into two groups; in one group, related eggs were stained by dipping them in droplets of food-colouring using a fine brush and unrelated eggs were left unstained, and in the other group, unrelated eggs were stained and related eggs were left unstained. Females were then allowed to forage for 48 h. This experiment was designed to infer kin discrimination indirectly by testing whether females would consume fewer or more of the dyed eggs when the eggs were related or unrelated.

Experiment 2: Reproductive Status and Cannibalistic Behaviour

For this experiment, half of the females were randomly assigned to one of two mating treatments: half of the females were allowed to mate and the other half (virgin females) were kept in all-female groups until the experiment started. Mated and virgin females were then placed individually into 6-dram vials filled with 2 g of flour medium and 10 unrelated eggs (from another colony). Although mated females generally laid few eggs during the experiment (see Results), they could potentially consume their own newly laid eggs instead of the unrelated eggs, resulting in an underestimation of the cannibalism rates of mated females. To account for this potential bias, we used red food colouring, as in experiment 1b, to stain unrelated eggs and we limited the experiment to 24 h, at which point we counted the remaining eggs. We used less flour than in experiment 1 to account for the reduced number of eggs and to increase the potential for cannibalism. We tested 15 mated and 15 virgin females, but two virgin females died during the experiment and were thus excluded from the analyses. All females (virgin and mated) were tested at the same age (i.e. days after metamorphosis).

Experiment 3: Male Mating Status and Cannibalistic Behaviour

Finally, we tested whether male cannibalistic behaviour varies with mating status. To compare cannibalism rates of males and females, we ran simultaneous trials with mated females as a control to ensure that the timing of the experiment did not influence cannibalistic behaviour in the colonies. Female cannibalism rates did not differ significantly between experiment 2 and experiment 3 (t test: $t_{22} = 1.17$ $P = 0.350$), suggesting that there was no change in female cannibalistic behaviour. The methods of experiment 3 were identical to those of experiment 2 except that we tested nine mated females (control), 11 mated males and nine virgin males. Two of nine virgin males died during the experiment and were excluded from the analyses.

Data for all experiments were analysed with two-tailed Student's or Welch's (for unequal variances) t tests using R software (R Foundation for Statistical Computing, Vienna, Austria). When variances were unequal, we calculated degrees of freedom using Welch's approximation of the degrees of freedom.

RESULTS

Experiment 1: Kin Discrimination and Cannibalism

When females were exposed to their own eggs and unrelated eggs from other females (experiment 1a), they consumed more than twice as many unrelated eggs (mean $\pm$ SE difference = 2.15 ± 0.35 times the number of eggs; two-tailed paired t test: $t_{31} = -2.91$, $P = 0.007$), regardless of colour treatment (two-tailed t test: $t_{29.5} = 0.15$, $P = 0.881$). Females consumed on average a total (related + unrelated eggs) of 38% of the eggs (Fig. 1). In experiment 1b, which used red food colouring to make eggs more 'attractive' as a food source, females consumed relatively fewer related red-stained eggs than they did unrelated red-stained eggs (unequal variance t test: $t_{25} = 2.87$, $P = 0.004$).

Experiments 2 and 3: Reproductive Status and Cannibalistic Behaviour

In experiment 2, where eggs were dyed with red food colouring, virgin females consumed almost twice as many eggs as did mated females (unequal variance t test: $t_{20.9} = 2.55$, $P = 0.019$; Fig. 2). We recovered only one to two newly laid (unstained) eggs from two of the 32 vials with females at the end of feeding trials.

Interestingly, the change in cannibalistic behaviour with reproductive status was even stronger in males: virgin males cannibalized 5.2 times more eggs than did mated males (unequal variance t test: $t_{11.2} = 3.95$, $P = 0.002$; Fig. 2). Furthermore, we found no difference in cannibalism rates between mated males and mated females (two-tailed t test: $t_{16} = 0.78$, $P = 0.445$), but cannibalism rates of virgin males were 3.3 times higher than those of mated females (two-tailed t test: $t_{13} = -3.21$, $P = 0.007$; Fig. 2). Cannibalism rates of mated females in experiments 2 and 3 also did not differ, nor did cannibalism rates of virgin females in experiment 2 and virgin males in experiment 3 (two-tailed t test: $t_{20} = -0.30$, $P = 0.77$). Thus, mating status, but not sex, influenced adult cannibalism rates.

DISCUSSION

Filial cannibalism, the consumption of an individual's own offspring, typically reduces the fitness of cannibalistic individuals. As a consequence, theory suggests that evolution should select for
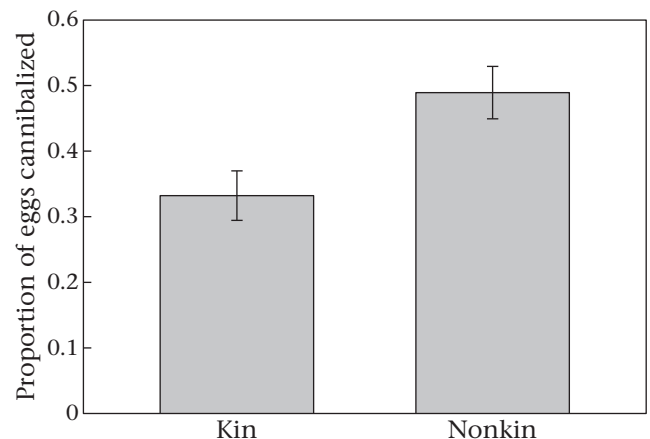

Figure 1. Kin discrimination in cannibalistic *Tribolium confusum* females. Mean $\pm$ SE proportion of kin (own eggs) and nonkin (eggs from unrelated conspecific females) cannibalized by females. Both kin and nonkin were present in equal abundance (8–10 eggs each).
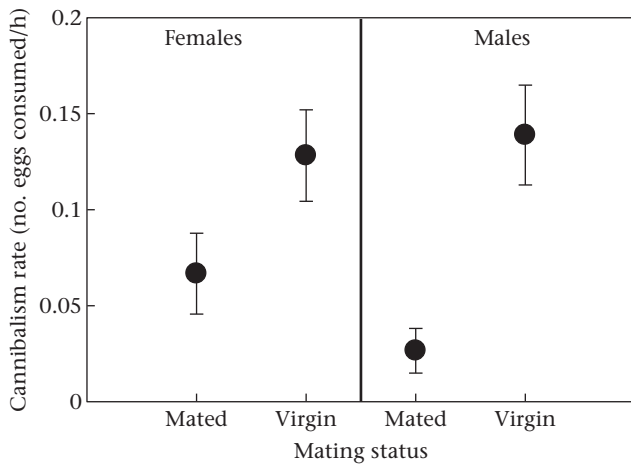
Figure 2. Mean ± SE number of eggs consumed/h by adult female and male *T. confusum* depending on their mating status.

any behaviour that reduces the risk of filial cannibalism while still maximizing its benefits (Pfennig 1997; Rudolf et al. 2010). Here we show that the cannibalistic behaviour of *T. confusum* is driven by two factors that reduce the risk of filial cannibalism. First, reproductive females strongly preferred to cannibalize unrelated 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 occurs in both sexes. In general, this suggests that evolution can alter the cannibalistic behaviour of individuals in multiple ways to reduce the risk of filial cannibalism while still maximizing the benefits from cannibalism over an individual's lifetime.

Cannibalistic individuals incur a high cost for filial cannibalism. Thus, it is not surprising that kin discrimination is common in a range of cannibalistic invertebrate and vertebrate species such as tiger salamanders, spadefoot toads, various rodent species, social amphipods and isopods, various mite species and many fish (Pfennig 1997; Schausberger 2003). Kin discrimination can occur through a range of mechanisms that do not necessarily imply kin recognition (Penn & Frommen 2010). For instance, in many species, spatial or temporal associations are used as an indirect proxy to discriminate among kin and nonkin (reviewed in: Elwood 1994; Pfennig 1997). However, in our experiments, females were given a choice to cannibalize their own eggs or unrelated eggs in a novel environment, thereby eliminating any potential for using spatial or temporal proxies as cues. Yet, females clearly preferred to cannibalize unrelated eggs over related eggs. Note that the consumption of newly laid eggs in experiment 1 did not affect our results, because the design specifically made relative comparisons among two groups of stained eggs. So, while consumption of any newly laid, unmarked eggs might influence the total number of eggs consumed, it had no effect on the relative consumption rates of stained eggs. Furthermore, when we made eggs more 'attractive' by staining them with red food colouring, females consumed significantly fewer red-dyed eggs when they were related than when they were unrelated. Together, these results indicate that female flour beetles are able to recognize their offspring. As in many other studies, it is unclear which of the many possible mechanisms influence kin recognition in this species (Pfennig 1997; Penn & Frommen 2010), and future studies are needed to answer this question. To the best of our knowledge this is the first demonstration of kin discrimination in a *Tribolium* species.

In some species, reproductively active adults are more cannibalistic than their nonreproductive conspecifics. For instance, mated females of some mite species are more cannibalistic than virgin females (Schausberger 2003). The difference in cannibalistic behaviour could be driven by the concurrent changes in energy and nutrient needs with reproductive status. Reproductive adults require more energy and are often more nutrient limited (Harshman & Zera 2007), and cannibalism has been attributed to various protein and nutrient limitations (Polis 1981; Mayntz & Toft 2006; Simpson et al. 2006). For instance, caddisfly larvae appear to engage in cannibalism to supplement their normal nutrient-poor diet (Wissinger et al. 1996). *Tribolium* are particularly likely to be protein limited, given their main food source (flour). Indeed, previous experiments found that improving food quality reduces cannibalism rates in *Tribolium* (King & Dawson 1972; Via 1999), and that supplemental feeding with conspecific eggs significantly increases fecundity of *Tribolium* females (Via 1999). Given that all these factors should favour cannibalism, and that we found evidence of kin recognition in this species (this study), we might expect that the onset of reproduction might not change, or potentially even increase, cannibalism rates in *T. confusum*. Yet, we found the exact opposite: a clear and dramatic reduction in the propensity for cannibalism in both females and males once they became reproductively active.

Several lines of evidence suggest that the reduction in the propensity for cannibalism in our experiments was not an experimental artefact but instead indicates an adaptive change in cannibalistic behaviour consistent with kin selection theory. First, experiment 2 was specifically designed to reduce the risk of mated females cannibalizing their own newly laid eggs (see Methods), thereby eliminating, or at least strongly reducing, any potential bias in the estimation of cannibalism rates. Second, we found the exact same pattern in males: the cannibalism rate in mated males was one-third that observed in virgin males, but there was no difference in cannibalism rates between mated males and mated females. Indeed, we found that cannibalism rates were not influenced by sex-specific differences, but they were influenced by mating status. Together, these results strongly suggest that the reduction in the propensity for cannibalism was not simply driven by the consumption of eggs laid during the experiment. Instead, the observed reduction is consistent with an adaptive state-dependent change in behaviour to reduce the chance of filial cannibalism. Elwood (1994) reviewed a limited set of examples where adults (male and female) reduce or even cease cannibalism once they are likely to encounter their own offspring, arguing that such state- (or temporal) associated changes in cannibalistic behaviour are driven by kin selection. Interestingly, we found that males were just as likely to change their cannibalistic behaviour, even though females should have a better ability to fine-tune this change in behaviour given the internal fertilization in this species. This suggests that males may be just as likely as females to encounter their own offspring, but this remains to be tested. This is highly likely given that their natural habitat strongly confounds their movement, which should favour frequent encounters with their own offspring.

Although kin discrimination and mating status are both known to influence cannibalistic behaviour (reviewed in: Elwood 1994; Pfennig 1997), previous studies have typically not tested both together. However, given that each behaviour represents an alternative strategy to reduce filial cannibalism, identifying the presence and relative importance of both is crucial to identify any variation in either behaviour across species. For instance, it is conceivable that mating status has little effect on cannibalism rates if species can already reduce the risk of filial cannibalism via kin recognition. Here we found that *T. confusum* jointly uses kin discrimination and a change in the propensity for cannibalism with

mating status to reduce the risk of filial cannibalism. This clearly indicates that both strategies are not exclusive alternatives. Instead, selection may favour a very effective combination of both strategies to reduce filial cannibalism, while maximizing the potential benefits of cannibalizing unrelated conspecifics. Unfortunately, most studies on kin discrimination did not estimate whether mating status alters cannibalism rates or vice versa, making it difficult to determine how common such mixed strategies are in other species. Although *T. confusum* shows no parental care or other social or family structure, it is possible that changes in such social factors alter the relative importance and thus evolution of state-dependant changes in cannibalism rates versus kin discrimination for reducing filial cannibalism in other species. Thus, more studies are needed to determine whether there are certain species traits (e.g. carnivorous versus noncarnivorous) and environmental or social factors that drive the relative importance and evolution of both types of behaviours in a predictable pattern.

Acknowledgments

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