Kinship and cannibalism in the Indian meal moth, *Plodia interpunctella*: No evidence of kin discrimination

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ABSTRACT

Generally, cannibals should avoid consuming related individuals so as to reduce indirect fitness costs. Here, I examine the effect of kinship on larval cannibalism in the Indian meal moth, *Plodia interpunctella*. First, a series of 'no-choice' experiments was performed in which third instar larvae were confined with either a second instar sibling or an unrelated second instar individual. Next, 'choice' experiments were performed in which third instar larvae were given the choice of a sibling or an unrelated individual, with all three individuals confined to one petri dish. The results from both experimental designs were consistent in that they showed no evidence that cannibals avoid siblings. Sibling cannibalism occured even when there was a choice of an unrelated individual. It is unclear whether this phenomenon is adaptive.

Keywords: cannibalism, discrimination, fitness costs, insect, kin selection, siblings.

INTRODUCTION

It is now well established that cannibalism is found under natural conditions in a diverse range of contexts and taxa, including the platyhelminthes (Armstrong, 1964), mollusca (Lipinski and Linkowski, 1988) and especially the arthropoda (Fox, 1975; Elgar and Crespi, 1992). It can be viewed simply as a part of a species' foraging behaviour, but several unique features lead to interesting ecological and evolutionary consequences. For example, it has been shown to be under genetic control and to be polymorphic in some species (Stevens, 1989). Cannibalism is often density-dependent and may act as a mechanism of population regulation affecting the population's age distribution (Park *et al.*, 1961) or the population dynamics themselves (Gurney *et al.*, 1983; Sait *et al.*, 1994). Another key feature of cannibalism is its age dependency, with different life-history stages acting alternatively as predators and prey (Dong and Polis, 1992). This, in turn, leads to a number of costs associated uniquely with cannibalism, including the risk of injury from attacking prey, which may also act as predators, and the chance of disease transmission from the predation of infected conspecifics (Elgar and Crespi, 1992; Boots, 1998; Pfennig *et al.*, 1998). It must be emphasized, however, that cannibalism provides important nutritional and competitive advantages to the individual; therefore, examining the costs to cannibalism is necessary if

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we are to understand why cannibalism, although taxonomically widespread, is relatively rare (Pfennig *et al.*, 1998).

In addition to the risk of injury and the transmission of disease, another unique cost of this form of foraging is the fitness cost associated with the cannibalism of related individuals (Polis, 1981; Pfennig *et al.*, 1993). Based on kin-selection theory (Hamilton, 1964a,b), cannibalism should be directed away from close relatives to reduce indirect fitness costs. Since inclusive fitness will, of course, be a balance of direct and indirect fitness, cannibalism of kin can be advantageous under some circumstances. However, if there are no direct fitness costs in doing so, cannibals should avoid their kin if they can recognize them. There is evidence that kin recognition is widespread (see Hepper, 1986), although it may be confused with group member recognition (see Grafen, 1990). Studying cannibalism is an ideal way of examining the more general phenomenon of how inclusive fitness affects behaviour, since both the indirect costs (death of a relative) and the direct benefits (nutrition leading to enhanced survival and reproduction) are clear and measurable (Walls and Blaustein, 1995).

A number of studies have shown that cannibals from a wide range of taxa, including insects (Wade, 1980; Klahn and Gamboa, 1983; Nummelin, 1989; Ratnieks and Visscher, 1989; Dickinson, 1992), are able to mediate the indirect costs of cannibalism by avoiding their kin (reviewed in Pfennig, 1997). However, some studies found that avoidance did not occur (Mumme *et al.*, 1983; Hoogland, 1985) and there is some evidence of preferential sib cannibalism (Walls and Blaustein, 1995). Here I use a series of choice and no-choice experiments to examine whether kinship mediates larval cannibalism in the Indian meal moth, *Plodia interpunctella*. Stage-dependent cannibalism occurs in this species with later instars cannibalizing earlier instars (Boots, 1998). Developmental stage differences between siblings are likely to occur because of differences in oviposition dates and environment leading to the potential for sibling cannibalism in natural populations. I therefore test the hypothesis that later-stage cannibals avoid eating younger kin.

METHODS

The Indian meal moth, *Plodia interpunctella*, is a cosmopolitan pest of stored products. In nature, the omnivorous moth is found feeding on a wide range of stored products, including dried grain and fruit. It commonly shows a level of cannibalism that is believed to influence its population dynamics, maintaining cycles along with larval competition (Gurney *et al.*, 1983; Sait *et al.*, 1994). Cannibalism has also been shown to be a route for the transmission of a fatal viral pathogen in the Indian meal moth (Boots, 1998). The moths used were taken from a large outbred stock that had been maintained under laboratory conditions for many generations. There is, therefore, likely to be significant variation in the population and, as a consequence, sibs and non-sibs should differ substantially. Since they are stored product pests, the laboratory environment in which the insects are kept is similar to that in which they have evolved.

A laboratory culture of *P. interpunctella* was maintained on a mixture of wheat germ, dried milk, yeast, honey and glycerol at a constant room temperature of $28 \pm 1°C$ under a 16 h : 8 h light–dark regime. Adults from the stock containers were removed and discarded. Then, individual pairs of newly emerged adults were allowed to mate in small plastic containers. Eggs were removed daily and raised separately on small amounts of the feeding medium. All experimental larvae were removed from this food and were therefore 'recently

fed' at the beginning of the experiments described below. The adults were allowed to mate and oviposit for 4–5 days and therefore cohorts of sibs with an age of up to 5 days were produced. Most viable eggs, however, were produced within 3–4 days of mating and, as a consequence, the siblings differed in age by 2–3 days only (although at different larval stages). The siblings used in the experiments were full sibs from the same pair of individuals. The non-siblings were taken from different pairs of the same group of adults that had emerged together. The siblings and non-siblings were therefore produced from adults of the same age.

I have previously shown that cannibalism by third instar larvae on second instar larvae is substantial (Boots, 1998). There is no cannibalism by earlier instars on healthy later instar larvae (Boots, 1998). Second instar larvae also prey on first instar larvae, but the first instars are too difficult to manipulate experimentally. Third instar larvae were therefore chosen to act as cannibals and second instars as their prey. First, a series of no-choice experiments was performed to determine the absolute rates of cannibalism of sibs and non-sibs. An individual early third instar larva was placed in a small (9 cm) petri dish with a second instar larva. Each time, 20 pairs were set up, 10 with sibs and 10 with unrelated individuals, and the experiment repeated 10 times. In total, 200 pairs were used, in 100 of which the larvae were sibs. They were left for 1 day, and the occurrence of cannibalism was recorded.

Next, choice experiments were performed in which a single third instar larva was placed in the same-sized petri dish as before, with two second instar larvae, one of which was the third instar's sib. The sib and non-sib were distinguished by marking either the front or rear half of one of the larvae. This marking process was randomized between sibs and non-sibs to avoid bias due to the marking. Observations were made every 2 h and the first individual attacked was recorded. In cases where both individuals were attacked within a 2 h sampling period, the replicate was discarded (five replicates were discarded for this reason, while further replicates were discarded due to death or escape of one of the larvae). Twenty combinations were set up each time and the experiment was repeated 10 times. Food was not added to either the choice or the no-choice experiments.

RESULTS

Chi-square tests indicated that the data from the repeated experiments were homogeneous and could therefore be pooled (Zar, 1984). In the no-choice experiment, the rates of cannibalism were similar to those found in previous experiments under similar conditions (Boots, 1998). The rate of cannibalism of the full sibs was not significantly different to that of unrelated individuals (Fisher's exact test, $P = 0.16$) (Table 1). Care should be taken when concluding that there was no difference between the rates of cannibalism; rather, there was no evidence of a difference. In the choice experiment, there was also no significant difference in the rate of cannibalism of related and unrelated individuals (binomial test with the normal approximation, $P = 0.396$). The trends in the two experiments were different, with more non-sibs cannibalized in the no-choice experiments, while sibs were marginally preferred in the choice experiments. One possible cause of this is that the choice experiments were inevitably more crowded and this may in itself have influenced the outcome. This contrast in the trends does, however, further suggest that there is no real preference for either siblings or non-relatives.

Table 1. Results of the 'no-choice' experiments showing the percentage cannibalism found with siblings and non-relatives, and results of the 'choice' experiments showing the number of times that the sibling and non-sibling were attacked first ($n = 139$)

	Siblings	Non-siblings
No-choice	37.4% ($n = 91$)	50.5% ($n = 93$)
Choice	75	64

DISCUSSION

I did not detect any consistent difference in the rates of cannibalism of siblings and non-siblings in either the choice or the no-choice experiments. The absolute rates of cannibalism are dependent on the details of the experimental design, which in turn determine the nutritional states of both the cannibal and the victim. Here, however, I was only interested in the relative rates of cannibalism of non-sibs and sibs. It is clear that *Plodia interpunctella* larvae may eat their smaller kin and that there is no evidence that the cannibals distinguish between kin and non-kin even when they have a choice. It may be that the nutritional state of the larvae can also influence whether a choice is made between sibs and non-sibs. For example, well-fed larvae may be more discriminating than starved ones (Pfennig *et al.*, 1993). Although the larvae in the present study were well fed before the experiment, I still could not detect a difference in their cannibalistic preference.

There are numerous examples in the literature of antagonism between relatives, but these usually involve species which live in family groups and which do not normally encounter unrelated conspecifics (Walls and Blaustein, 1995). Clearly, antagonism – of which cannibalism is an extreme form – to close kin is more likely when there are only related conspecifics available to a malnourished individual (Pfennig, 1997). In the present study, an extreme form of antagonism – cannibalism – occurred even when there was a choice of relatives and non-relatives. In a study on salamanders, Walls and Blaustein (1995) also demonstrated that sibling cannibalism occurs even when there is a choice of an unrelated individual. They also suggested that there was some evidence of preferential sibling cannibalism. The results of the present study support the observation that siblings may be harmed even when there is the possibility of the cannibalism of a less related individual. Here, however, there is no evidence that *Plodia interpunctella* larvae show preferential sibling cannibalism.

The present findings diverge from the results of a number of behavioural studies of cannibalism in a broad range of species where individuals have been shown to avoid cannibalizing their sibs (see Pfennig, 1997). Many of these studies have been on amphibians (e.g. Pfennig, 1992; Pfennig *et al.*, 1993) and other species distantly related to the Indian meal moth (e.g. Loekle *et al.*, 1982), but avoidance has been demonstrated in insects (e.g. Klahn and Gamboa, 1983; Nummelin, 1989; Ratnieks and Visscher, 1989; Dickinson, 1992). One explanation for the lack of avoidance of sibs is that later instar larvae may not often co-exist under natural conditions with siblings that are at the previous instar. This may be a consequence of adult dispersal, which leads to eggs being laid at different locations on different days. If there is a low risk of sibling cannibalism under natural

conditions, there may not have been strong selection for avoidance of siblings. Another possibility is that, when younger larvae do co-exist with their older siblings, the younger larvae are stunted due to poor competitive ability or poor conditions. The fitness costs of consuming these individuals will be lower than the costs of consuming vigorous siblings. There is also the possibility that sibling recognition itself may involve fitness costs. It should also be borne in mind that the cannibalism of close kin can evolve if the disadvantages of decreasing the indirect fitness of the cannibal are outweighed by the consequences of starvation or reproductive failure due to not cannibalizing the related victim (Pfennig, 1997). There is also the possibility that a victim may, under certain circumstances, sacrifice itself to related victims to increase its indirect fitness (Pfennig, 1997).

In species that do discriminate between relatives, the interaction with disease transmission deserves investigation. On the one hand, it has been suggested that infection is more likely to occur through cannibalism of siblings (Pfennig *et al.*, 1998), perhaps through the increased likelihood of pathogen transmission between phenotypically similar individuals. However, if – as in the granulosis virus of *P. interpunctella* (Boots, 1998) – infection means that reproduction cannot occur, there are no indirect fitness costs associated with cannibalizing infected related individuals. This intuition cannot be tested in *P. interpunctella*, however, because, as has been demonstrated here, there is no discrimination between relatives and non-relatives. In cannibalistic species that do discriminate between sibs and non-sibs, however, we might expect higher cannibalism of siblings infected by a parasite that stops host reproduction compared to infections that allow reproduction. However, even when infected sibs can still reproduce, they will have a lower chance of survival; therefore, the indirect fitness cost of their cannibalism will always be less than that of healthy sibs.

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