CANNIBALISM, OPTIMAL EGG SIZE AND VULNERABLE DEVELOPMENTAL STAGES IN INSECT PREDATORS

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ABSTRACT

Cannibalism in insect predators is widely reported and commented on. However, the reasons for the high levels of cannibalism observed, the vulnerability of certain developmental stages, and its adaptive significance are poorly understood. Here we show that unlike in parasitoids there could be advantages for a predator in laying many small eggs, rather than fewer large eggs. The temporal incidence of cannibalism within a patch is possibly a consequence of changes in the ratio of predator to prey numbers and/or changes in the vulnerability of the developmental stages of the predator. Cannibalism is advantageous for cannibals because conspecifics are a rich source of food for larval development or egg production, and it reduces intraspecific competition. Adults reduce the cannibalism of their offspring by not ovipositing in patches of prey where conspecific larvae are present.

Keywords: adaptive significance, Coccinellidae, fitness, selection, survival

Introduction

Cannibalism is widely recorded in many insect predators and is now regarded as part of their normal foraging behaviour. The general reviews of cannibalism by Dong and Polis (1992), Elgar and Crespi (1992), and Fox (1975) regard it as a means of re-deploying resources. In the predatory ladybirds cannibalism, although recorded (Nadel and Biron 1964; Kehat 1968), is less frequently commented on in studies of coccidophagous than in those of aphidophagous species of ladybirds. In this study, models were applied to data available on cannibalism in aphidophagous ladybirds with the objective of arriving at a better understanding of its adaptive significance and incidence.

Number and size of eggs laid in a patch

Parker and Begon (1986) studied the trade-offs between clutch size and egg size in insects. They assumed there is an inverse relationship between clutch size and egg size: for a given reproductive output, a female either produces a few large or many small eggs. Reproductive output is constrained by energy, so this assumption seems to be quite general. Assuming then that a female has to travel from a feeding site to an oviposition site, Parker and Begon (1986) predict that increasing intensities of both sib and non-sib competition select for fewer and larger eggs. The latter assumption undoubtedly holds for insect parasites, where females first feed and then look for potential hosts in which they can deposit their eggs. Insect predators, however, may feed and lay eggs in the same patch of prey but more importantly their larvae have to hunt for prey. In this case what determines the optimum egg size?

Following Parker and Begon (1986), we first assume that fitness f of a larva depends only on the absolute amount of resources, m, in an egg, that $f(m)$ increases monotonically up to some asymptote, and that a certain minimal provisioning is necessary to ensure that the larva can develop (Fig. 1). Maternal fitness, w, is then defined by $w(m) = f(m)/m$. To find the optimal egg size, m^*, set $\partial w(m)/\partial m = 0$, which gives

$$f'(m^*) = f(m^*)/m^*. \tag{1}$$

This is the familiar marginal-value theorem (Charnov 1976; Parker and Begon 1986), illustrated in Fig. 1.

In insect predators, f, as a function of only m, is likely to be very steep, as in Fig. 1b. The size of a hatchling larva is closely correlated with the size of the egg from which it emerged and unlike in insect parasites, there is a more definite lower size below which a larva is too small to pursue and/or subdue its prey and above which a larva is generally successful and survives (Dixon 1958). In this case the marginal-value theorem predicts that egg size should be close to the minimum (Fig. 1). This results in more eggs being laid and therefore more larvae in a patch, especially when predators are abundant.
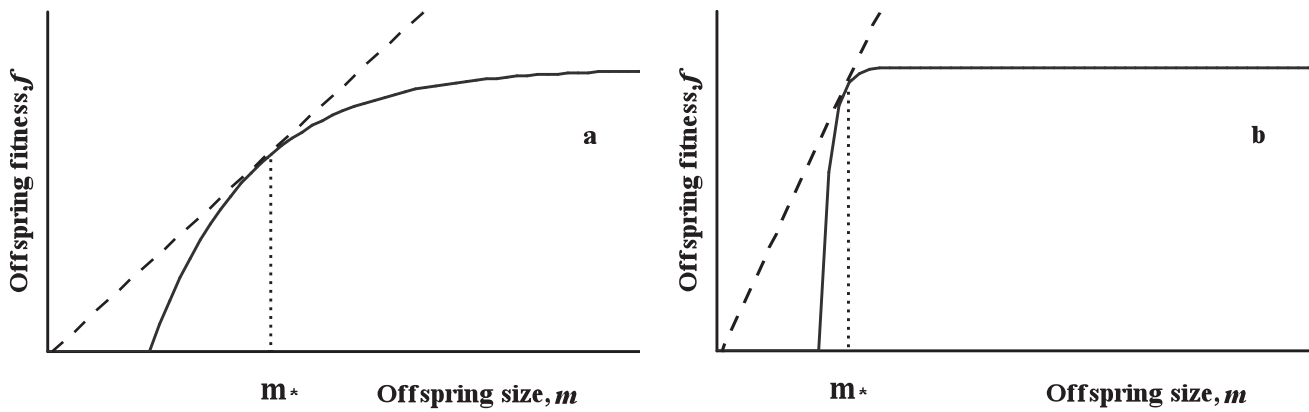
Fig. 1 Offspring fitness, f, as a function of their initial size m – solid line; its tangent – broken line; $m*$ is the optimal offspring size.

Cannibalism among members of the same clutch, however, reduces the prospects of a larva surviving. If $s(n)$ is the component of fitness of a larva that declines with increasing clutch size, n, then, according to Parker and Begon (1986), the optimal egg size is defined by

$$f'(m^*) = \frac{f(m^*)}{m^*} \left[\frac{s(n) + ns'(n)}{s(n)} \right]. \qquad (2)$$

As $s(n)$ is assumed to decrease monotonically, that is, the gradient, $s'(n)$, is negative, the term in the square brackets of (2) is smaller than one. Hence, for the same m^* and f, the right-hand side of (2) is smaller than that of (1), and therefore the optimal egg size, m^*, is larger in this case. In other words, increasing the intensity of sib or non-sib cannibalism selects for the production of fewer, larger eggs (Parker and Begon 1986).

This leads to the prediction that predators that experience high levels of cannibalism should lay fewer and larger eggs than those that experience little cannibalism during their development. The literature on ladybirds indicates that cannibalism in coccidophagous species is relatively uncommon whereas it is frequently reported and very common in aphidophagous species (Dixon 2000). However, the size of the eggs laid by similar sized aphidophagous and coccidophagous species is similar (Dixon and Hemptinne 2001). This indicates that cannibalism is unlikely to have been an important factor in the evolution of egg size in ladybirds. This is further supported by the outcome of contests between developmental stages, which is determined more by their relative ages and/or developmental stage than their birth size (Yasuda and Shinya 1997; Yasuda et al. 2001). For example, when a larva encounters an egg its size does not affect whether it is eaten or not. Thus cannibalism is likely to select for laying eggs early rather than for larger eggs as the larvae hatching from these eggs will be the oldest in the patch. Being the first discoverer of a prey patch thus becomes the most important component determining a mother's fitness. This will now be illustrated using a specific example.

Aphid-ladybird population dynamics

Aphids occur in patches that vary in space and time. Early in the season they very rapidly increase in abundance. After that, they may equally rapidly decline in abundance when they switch to producing winged individuals and/or disperse to establish patches elsewhere. This may occur even if natural enemies are not abundant. The time for which a patch lasts is very similar to the time it takes an aphidophagous ladybird to complete its development from egg to pupa (Kindlmann and Dixon 1993). In addition, if a patch of aphids is exploited by a large number of a particular species of ladybird and other aphidophaga, then the dynamics of the prey is likely to change; the peak abundance could be lower and the decline in abundance could occur earlier. That is, aphids become very scarce or disappear before the ladybird larvae can complete their development. Another feature of the aphid-ladybird population dynamics is that some aphids can respond to the presence of ladybird larval tracks and switch to producing winged forms, which leave before the ladybird larvae reach a large size and pose a serious predation risk to the aphid (Dixon and Agarwala 1999; Weisser et al. 1999). This could have disastrous consequences for the ladybird larvae present in a patch, as the aphid becomes scarce well before the ladybird can complete its development.

A theoretical model developed by Kindlmann and Dixon (1993) suggests that as ladybirds are cannibalistic the optimum number of eggs laid by ladybirds in a patch of prey should be low. If this optimum number is exceeded, then cannibalism results in the total larval biomass per unit biomass of offspring laid in a patch of prey steeply declining. This poses the question: Is it reasonable to expect ladybirds to have this level of omniscience? Although this is unlikely, there are simple biological mechanisms, however, which enable ladybirds to lay a number of eggs close to the optimum number.

Empirical data indicate that ladybirds lay their eggs early in the development of an aphid patch and cease laying eggs when the risk to their eggs of being eaten

by conspecific larvae is high. They do this by responding to a simple cue that is associated with the risk; an oviposition deterring pheromone present in the tracks of conspecific larvae (Hemptinne et al. 1992; Růžička 1997; Doumbia et al. 1998; Magro et al. 2007; Ameixa and Kindlmann 2011; Šipoš et al. 2012). Although this would appear to imply ladybirds are contesting rather than scrambling for resources the few life tables available for ladybirds in the field indicate that the mortality of the immature stages is very high (Dixon 2000). In addition, cannibalism gives larvae and adults access to high quality nutrition, and a means of reducing intraspecific competition and increasing survival when prey are scarce. This is well supported by the empirical data (Koide 1962; Pienkowski 1965; Dimetry 1974; Kawai 1978; Takahashi 1987; Agarwala 1991; Agarwala and Dixon 1992). Therefore, it is likely that cannibalism, the *uncertainty* about the future quality of a patch of prey and the experience of adults of the average quality and abundance of patches of prey are likely to have shaped the egg laying strategy of aphidophagous ladybirds.

The tendency of adult ladybirds to avoid laying eggs in patches of prey where conspecific larvae are present (Hemptinne et al. 1992; Doumbia et al. 1998) is adaptive as it reduces the probability of their eggs being eaten. In addition this response also reduces the probability of adults being present in a patch along with their larvae. This is well supported by the few life tables that have been published (e.g. Yasuda and Shinya 1997). That is, ladybirds do not regularly coexist in space in age-structured populations, but mainly as a sequence of stages: adults, eggs, larvae and pupae, with little overlap between the stages.

## Occurrence in time and intensity of cannibalism within a patch

As indicated above the developmental stages of predators: adults, eggs, larvae and pupae tend to occur in a patch of prey in this sequence with little overlap between the stages. Empirical data tend to indicate that the incidence of cannibalism is greatest in the egg and prepupal/pupal stages (Yasuda and Shinya 1997; Kindlmann et al. 2000). That is, cannibalism is most marked early and late in the development of a patch of prey.

This patterning in the incidence of cannibalism in time is associated with changes in the relative abundance of predator and prey in time and in the asymmetry between cannibal and victim.

Early and late in the development of a patch of prey there are more predators per prey item than there are when prey are at their peak abundance mid way through the development of a patch. If one assumes that hungry predator larvae have a constant consumption rate and the proportion of conspecifics in their diet is proportional to their relative abundance (the "*meet and eat*" hypothesis) then the number eaten is:

$$f(x,y) = ay / (x + y) \qquad (3)$$

where x is the number of prey, y the number of predators, and a is a scaling constant (Kindlmann and Dixon 1993). This indicates that there should be a high incidence of cannibalism at the egg and last larval/pupal stages of development (Fig. 2). In addition, equation (3) predicts that if abundance of prey is kept constant the incidence of cannibalism will increase super proportionally with increase in predator abundance. At a higher density of prey there is a similar relationship but the rate of increase in the incidence of cannibalism with increase in predator abundance is less (Fig. 3). Alternatively if the number of predators is kept constant and that of the prey is varied then the model predicts that the incidence of cannibalism will decrease with increase in prey abundance (Fig. 3). That is, cannibalism should be density dependent and potentially capable of regulating the number of predators.
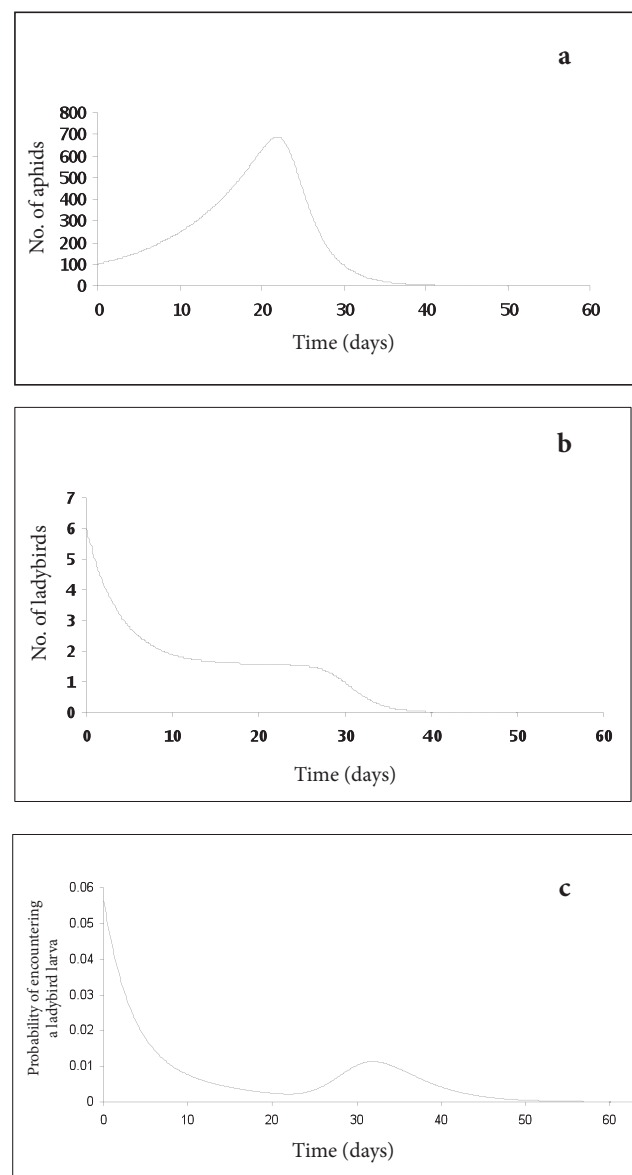
Fig. 2 Illustration of the trends in (a) aphid and (b) ladybird abundance in patches of prey and (c) the probability of ladybird developmental stages meeting a conspecific predicted by the Kindlmann and Dixon (1993) model.
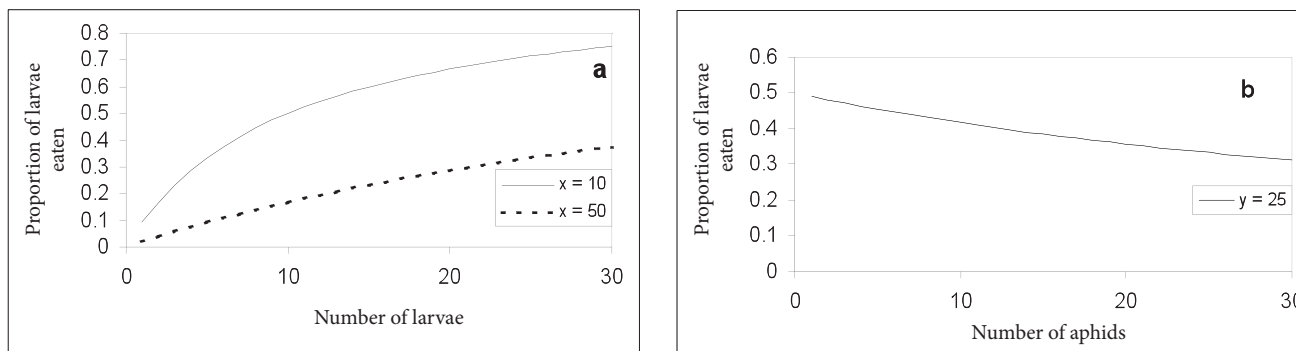
Fig. 3 Proportion of ladybirds eaten as a function of: (a) the number of ladybird larvae for a constant number of aphids, x; and (b) the number of aphids available for a constant number of ladybird larvae, y, predicted by equation (3).

The above predictions are well supported by empirical data. In addition to the stages most at risk, commented on above, egg cannibalism in *Adalia bipunctata* (Linnaeus) in the field is strongly density dependent (Mills 1982) and larval cannibalism in the same species in the laboratory decreases with increase in prey density (Agarwala and Dixon 1992). The latter, however does not conform to the output of Martini et al.'s (2009) model of the evolution of cannibalism, which indicates that cannibalism should not depend on prey density. This may be due to these authors assuming (1) that in the absence of predators, aphid populations grow logistically and (2) that they are dealing only with one patch, not with patch dynamics. It is, however, unrealistic to assume that in aphid colonies (patches) population growth is logistic (Dixon et al. 1996; Kindlmann and Dixon 1996; Dixon and Kindlmann 1998; Kindlmann et al. 2004), and patch dynamics is an important component of the population dynamics of ladybird-aphid systems (Kindlmann and Dixon 1999; Dostálková et al. 2002; Houdková and Kindlmann 2006).

An alternative explanation is that the temporal availability of vulnerable stages determines the occurrence of cannibalism in time. The most vulnerable stages are eggs/hatchlings and prepupae/pupae as irrespective of their relative size they are unable to avoid or defend themselves against active larvae. That is, the occurrence of cannibalism in time is associated with a marked asymmetry in vulnerability between the stages. The empirical evidence is not helpful in deciding whether the "*asymmetry in vulnerability*" or the "*meet and eat*" hypothesis, or some combination of these two offers the best explanation. This can only be resolved by further experiments.

Conclusions

A model that explores the effect of egg size and number on the number of surviving offspring in insect predators indicates that they can maximise their fitness by producing many small eggs rather than fewer large eggs. This often results in many eggs being laid in a patch, especially when predators are abundant relative to their prey, and because of the advantage in terms of acquiring food and reduced

competition is likely to result in high levels of cannibalism. It is the ratio of predators to prey in a patch that determines the overall level of cannibalism. Strategies have evolved enabling predators to avoid cannibalism. The most important of them is their tendency to avoid laying eggs in patches of prey where conspecific larvae are present.

Empirical data indicate that the incidence of cannibalism is greatest in the egg/hatchling and prepupal/pupal stages. The same is predicted if one assumes that the proportion of conspecifics in the diet of the larvae of predators is proportional to their relative abundance. Prey is relatively rare early and late in the development of a patch and as a consequence larvae are more likely then to encounter conspecifics ("*meet and eat hypothesis*"). Alternatively, it may be due to the occurrence in time of certain vulnerable stages. In this respect the most vulnerable stages are eggs/hatchlings and prepupae/pupae, as they are unable to avoid or defend themselves against active larvae ("*asymmetry in vulnerability hypothesis*"). Currently it is not possible to decide which hypothesis is the more likely explanation of the incidence of cannibalism in time within a patch.

Acknowledgements

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