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Filial cannibalism in burying beetles

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Summary. Infanticide is a common phenomenon in many animal groups, but filial cannibalism, the deliberate killing and consumption by parents of their own young, is extremely unusual. The burying beetle *Nicrophorus vespilloides* Herbst has a limited food supply, in the form of a buried corpse, on which to raise its young. On corpses weighing 10–15 g, clutch size in the lab is such that complete hatching success will produce more larvae than the corpse can support without severe reduction in the individual weights of final instars. The parents reduce the brood by killing and eating almost half of the first stage larvae. It is suggested that, in the field, predation of eggs and newly hatched larvae may be heavy, and that the excess eggs are laid as an insurance. If survival is then unusually high, superfluous young are killed by the parents before competition for food can occur.

Introduction

Few cases of filial infanticide have been reported. Brood reduction through siblicide or starvation is common among birds (O'Connor 1978) and may occur in some marsupials (Wooler et al. 1981) but the parents in these cases do not directly kill their young. Direct infanticide may be accidental, as when the coral reef fish *Acanthochromis polyacanthus* kills some of its young in the process of driving an early-season brood from its own territory, apparently to be fostered by neighbouring adults (Thresher 1985), or when coot chicks are killed during behaviour used to regulate food allocation to the brood (Horsfall 1984). It may be a response to unusual circumstances, as when queens in colonies of social insects use eggs or young larvae as food during a time of shortage in the colony (Wilson 1971; Masuko 1986). In the case of *N. vespilloides,* brood reduction is shown here to be caused by adults killing and eating their own young during the normal raising of a brood. It is suggested that the consequent brood reduction can be interpreted as a means of optimising the eventual ratio of larvae to available carrion food.

Beetles of the genus *Nicrophorus* (Coleoptera; Silphidae) bury the corpses of vertebrates and use them as a food source for their larvae. *N. vespilloides,* the species used here, creates a burial chamber or crypt around the buried corpse and scatters its eggs up to several centimetres away. The hatched larvae make their way to the crypt, and there develop through three instars before returning to the soil to pupate. The larvae eat the corpse, and are also fed regurgitated carrion by their parents. Both adults are normally present throughout larval development, feeding the young, repairing any damage to the chamber, and driving off insects which trespass on the crypt.

The number of *Nicrophorus* larvae a corpse can support increases with corpse size (Easton 1979; Wilson and Fudge 1984). However, the North American species *N. orbicollis* was found not to adjust its clutch size according to corpse size and to lay more eggs on a 15 g corpse than the corpse could support (Wilson and Fudge 1984). The purpose of this study was to compare the behaviour of *N. vespilloides,* a smaller species than *N. orbicollis* and the most common in Britain, and to examine the mechanism of any brood reduction that might take place.

Methods

Beetles were trapped near Edinburgh and a breeding population maintained in the lab for several months. They were kept at a room temperature of 21° C with a 16 h:8 h light:dark cycle. The corpses used were of lab mice (*Mus musculus*). The mice were frozen within an hour of death and thawed before use in experiments. Each pair of beetles was bred in a plastic container 225 mm × 120 mm × 90 mm three-quarters filled with potting compost. Once burial was complete the soil above the crypt was removed and replaced by a beech leaf. This could then be lifted away for observations into the crypt. Three sets of experiments were done.

a) Variation in brood survival with corpse size

The success of broods was compared on 15 g and 30 g mice to see if there was any difference in the number of eggs laid and the number of larvae developing on the different sizes of corpse. Thirty-six adults were given a 15 g mouse and allowed to bury it and lay eggs. For 12 of the pairs the number of eggs laid was counted by removing all the soil from the breeding-box and picking out the eggs. For a further twelve pairs the eggs were not disturbed before hatching and the number of first stage larvae reaching the corpse was counted by inspecting the corpse every 2 or 3 h and removing the larvae as they arrived. The final twelve pairs were left undisturbed until the third stage larvae dispersed from the corpse and the number of larvae dispersing was counted. A further 36 pairs of adults were bred on 30 g mice and divided into three groups of twelve, treated as above.

b) Timing of mortality on small corpses

Once mortality of the brood on 15 g corpses had been established it was necessary to know at what stage the larvae disappeared. Fifteen broods with a mean of thirty first stage larvae (to match the brood size found in the previous experiment) were created on 15 g mice by pooling the hatchlings of several families and dividing them between the mice. Each brood was attended by the male and female which had buried the corpse on which it was placed. Previous experience suggested that adult *N. vespilloides* cannot recognise their own larvae and will raise a foster-brood, but as a control for abandonment of foster-broods clutches laid around a set of 10 g mice were taken from the soil just before hatching and the larvae that hatched returned to their own corpse. The adults on the 10 g mice therefore had broods of their own larvae and the survival of these broods could be compared with the artificial broods on the 15 g mice. Availability of different corpse sizes meant that 10 g rather than 15 g mice had to be used for the control experiment. The size difference has no effect on the principle being tested. All broods were counted as the number surviving to second instar, to third instar and to dispersal from the corpse.

c) Cause of larval mortality

The cause of the observed larval mortality was studied by watching broods on 15 g mice. Pairs of adults were allowed to bury corpses and the crypt roof was replaced with a leaf as described above. The brood was not disturbed for counting and so the initial brood sizes were not known. The broods were watched until the movements of the parents in the crypt turned the larvae out of sight, giving a different period of observation for each brood (Table 2). The number of larvae surviving to second instar was counted and this number compared with that for broods on 15 g corpses which had not been watched.

d) Larval weight at dispersal in relation to brood size on 15 g mice

The effect of brood size on larval weight and so the significance of brood reduction in terms of weight of the dispersing larvae was tested in the laboratory on 15 g mice. Pairs of adults were allowed to bury mice and lay eggs, eggs were removed from the soil just before hatching and different numbers of first-stage larvae placed on the corpse. The number surviving to second instar was counted and the number and mean weight of the larvae at dispersal recorded.

Results

a) Brood survival on 15 g and 30 g mice

Clutch size on 30 g mice is not significantly different from clutch size on 15 g mice, but subsequent survival of the brood is very different (Table 1). On 30 g mice there are no significant differences in the numbers at the egg stage, first instar and larvae at dispersal. On this size of corpse hatching success is high and as many larvae as reach the corpse are likely to disperse from it. On 15 g mice there is no significant difference between the mean number of eggs laid and the mean number of first stage larvae reaching the mouse but the difference between the mean number of first stage larvae and the mean number of larvae at dispersal shows that only about half of the larvae which reach a 15 g corpse are likely to complete development. These results are similar to those for *N. orbicollis* (Wilson and Fudge 1984) and suggest that the clutch size laid around 15 g mice is such that normal hatching success produces more larvae than can complete development on the corpse.

b) Timing of mortality on small corpses

No experimental broods on 15 g mice or control broods on 10 g mice were abandoned, suggesting that the parents on the 15 g mice did not recognise

Table 1. Success of broods on 15 g and 30 g mice. Natural clutch sizes, number of first stage larvae and number of dispersing larvae in three independent sub-groups of twelve on each of two mouse sizes

Clutch size	First stage larvae	Dispersing larvae
a) 15 g mice: means ± 95% CL		
29.69 ± 3.31 (n = 12)	30.21 ± 1.88 (n = 12)	16.16 ± 1.68 (n = 12)
b) 30 g mice: means ± 95% CL		
30.92 ± 2.80 (n = 12)	33.92 ± 2.06 (n = 12)	30.08 ± 2.34 (n = 12)

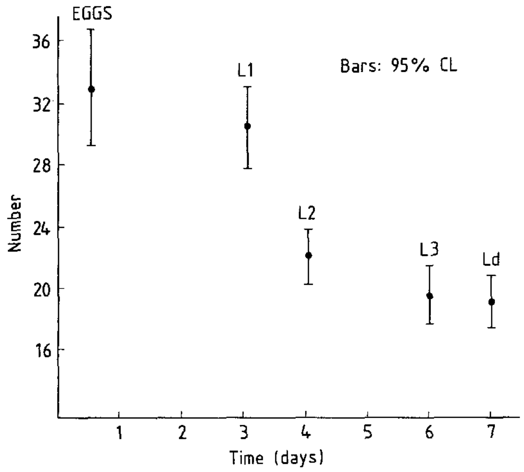

Fig. 1. Survival of artificial broods on 15 g mice. Using the broods of 25 females, 15 broods of first stage larvae (L1) were made, with a mean brood size of 30. These were then introduced to 15 g mice previously buried and tended by a pair of adults. The figure shows the numbers of larvae surviving 24 h, 72 h and 96 h later, as second stage larvae (L2), third stage larvae (L3) and dispersing third stage larvae (Ld)

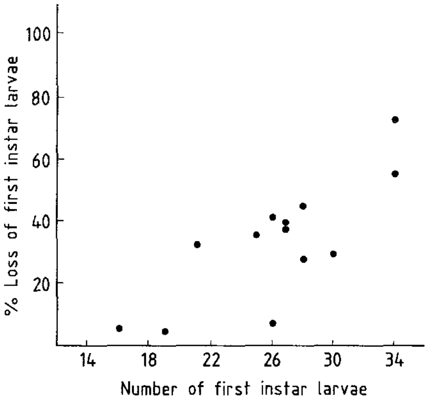

Fig. 2. Mortality among natural broods on 10 g mice. The percentage survival to the second instar is shown for broods on 10 g mice. The broods were made by removing clutches of eggs from the soil and putting the first stage larvae back on their corpse as they hatched

the larvae they were given as strange. The artificial broods of thirty first stage larvae created on a set of 15 g mice showed a significant fall in larval numbers between first and second instars but no significant mortality between second and third instars and up to dispersal (Fig. 1). The control broods on 10 g mice were of variable size because of differences in numbers of eggs laid. There was no mortality between first and second instars if the brood size was below about 15, but for broods larger than this numbers dropped sharply in the first 24 h on the mouse, which is the period of the first instar (Fig. 2). On both 15 g and 10 g mice, therefore, using artificial or natural broods, reduction of excessive numbers of larvae is found to happen on the first day of larval development.

c) Cause of mortality

In all the broods set up for observation the parents were seen to kill and eat first stage larvae (Table 2). This had also been seen in three other broods in earlier experiments and could explain the brood reduction found in the experiments above. The main period of larval mortality on 10 g and 15 g corpses is at the first instar, during the first 24 h after the larvae have reached the corpse. It is most unlikely that food is limiting at this time since only a small hole has been eaten in the skin of the mouse and the larvae have not begun to penetrate the body. Table 2 shows that if broods can be watched for long enough, sufficient larvae will be eaten to account for the 50% or 60% brood reductions that the earlier experiments recorded.

There was no significant difference between the number of second stage larvae on the mice used for observation and on the mice buried at the same time but not watched (Table 2).

Discussion

The infanticide described in these experiments is of an unusual kind. These are not trophic eggs which are eaten but viable larvae. They are not killed by mistake nor in response to suddenly

Table 2. Broods were watched until the hole in the corpse where the brood fed was turned out of sight by the movements of the adults in the crypt. The number of second stage larvae in these broods is similar in each case to the mean number of second stage larvae in the controls, broods set up at the same time on the same size of mice (15 g) but not watched during the first larval instar

Brood	Hours in view	Larvae seen killed	Parent responsible	Mean L2 (exp't) ($n=5$)	Mean L2 (control) ($n=11$)
1	1	1	Female		
2	2	3	Female		
3	15	14	Male	18.00	17.65
4	10	16	Male + female	±2.10	±2.05
5	4	7	Male		

stressed or altered conditions but are deliberately lifted from the brood and eaten as part of a normal breeding attempt in which their surviving siblings continue to be fed and defended.

Brood reduction is best known in birds (O'Connor 1978). It has been argued that reduction is practised in response to uncertain food availability; when food is scarce the last of an asynchronous brood to hatch is allowed to starve, whereas all offspring are fed when food is plentiful. This explanation is unlikely to appyl to *Nicrophorus,* for which the food supply, once secured for breeding, is assured. Clark and Wilson (1981) proposed alternative explanations for asynchronous hatching in birds: the nest failure hypothesis, where incubation begins as early as possible in order to offset the risk of predation, and the insurance hypothesis (Dorward 1962; Stinson 1979), where only one young is raised and the one or two additional eggs serve only as insurance against the failure of the first. Variable mortality of eggs or of hatchlings making their way to the corpse may explain why *Nicrophorus* lays many more eggs than are raised around a small corpse. A staphylinid *Philonthus decorus,* often found at corpses, has been seen to kill the young of *Nicophorus* (Easton 1979) and will eat as many as half the larvae of an untended brood in the lab whilst failing to kill any of the larvae where parents are present (pers. obs.).

Fungal infection, or predators such as *Philonthus* which a corpse attracts in large numbers, could cause the unpredictable mortality proposed here. An alternative explanation for the high number of eggs laid is that the beetles fail to assess accurately the capacity of the corpse or are bound by a physiological constraint such that they must lay a minimum clutch which is greater than the capacity of a small corpse. In the laboratory *N. vespilloides* will lay 46.83±5.86 eggs on a 75 g corpse ($n = 18$) and 18.44±2.05 eggs on a 5 g corpse ($n = 27$), showing that some adjustment of egg number with clutch size is possible and that it is physiologically possible to lay a clutch smaller than the capacity of a 15 g corpse.

The raptors discussed by Stinson (1979) do not raise the hatchlings of their 'extra' eggs; these are killed by their older sibling or starve in competition with it. The adults can only bring enough food to raise one young. Similar constraints make the clutch laid by *Nicrophorus* on small mice excessive. The strong relationship between brood size and mean larval weight at dispersal (Fig. 3) is found even over a range of brood sizes less than that at which culling would be expected to occur. At higher densities, without culling, there might be insufficient food for all larvae to complete development and emerging adults would certainly be very much smaller than the products of less crowded crypts. Intraspecific competition over corpses, the result of which is largely determined by body size (Wilson and Fudge 1984), means that small beetles have a greatly reduced chance of breeding. Small size also restricts the number of eggs a female can lay, both in a single episode on a large corpse and over several breeding attempts on a sequence of corpses (pers.obs.).

Fig. 3. Mean larval weight at dispersal: broods size at dispersal. First stage larvae were placed on the 10 g corpse around which they had been born such that 19 broods of between 5 and 20 larvae were created. In all cases survival of the brood was >90%. The regression line is plotted; slope is significantly different from 0 ($P < 0.001$)

Brood reduction in *Nicrophorus* is therefore a phenomenon which probably occurs in response to a shortfall of food relative to the requirements of the larvae arriving at the corpse. The laying of an excessive number of eggs is more likely to reflect uncertainty about the number of larvae successfully reaching the corpse than about how much food will be available and would, if this is true, conform to the 'insurance' hypothesis discussed by Clark and Wilson (1981). The situation differs from that in birds in that laryae can feed themselves as well as receiving regurgitated carrion from their parents. The adults cannot afford to let the members of an excessively large brood compete amongst themselves for the corpse and they therefore reduce the number by culling rather than by allowing some to starve. They cull the brood at the earliest stage: the larvae are feeding on a fixed resource and the sooner the brood is reduced the more food will remain for those which survive. Direct and early action, the most unusual features of *Nicrophorus* infanticide, are a consequence of their particular biology.

The experiments described here did not examine the question of how *Nicrophorus* adjusts the number of larvae that are culled. The simplest hypothesis was that adults allowed a certain number of hatchlings to reach the corpse and killed all subsequent arrivals, but culling was found to occur whether larvae were allowed the reach the corpse naturally or added in a single batch. It is hoped in future experiments to test whether larvae are killed at random or selected on the basis of size or sex (Horsfall 1984). If filial cannibalism is to benefit *Nicrophorus* parents, then their total number of grandchildren must be greater, through the increased reproductive success of their surviving offspring, than it would have been through a larger brood of individually smaller young. The high costs of small size in an animal which must fight for the chance to breed on a rare resource argue that the behaviour is likely to have this effect.

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