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Survivorship Advantage of Conspecific Necrophagy in Overwintering Boxelder Bugs (Heteroptera: Rhopalidae)

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ABSTRACT Adult boxelder bugs [*Leptocoris trivittatus* (Say)] (Heteroptera: Rhopalidae) were observed feeding on dead conspecifics while overwintering. Boxelder bug adults were collected in the fall of 2000 and 2001 to test the hypothesis that conspecific necrophagy provides a benefit through increased survivorship. Adult bugs were kept individually with no water or food, water only, dead boxelder bugs only, water and dead boxelder bugs, and water and boxelder (*Acer negundo* L.) seeds. Boxelder bugs kept without water, either with or without other resources, died at a significantly higher rate than bugs kept with water. Bugs provided with water and dead boxelder bugs lived significantly longer than bugs provided only with water and were seen feeding on the dead bugs for up to 2.5 h continuously. The presence of boxelder seeds did not increase survivorship beyond the water-only treatment. It was concluded that water was the most limiting factor determining boxelder bug survivorship during winter, but dead boxelder bugs provided additional resources to further increase survivorship. Conspecific necrophagy in overwintering adult boxelder bugs provides a significant survivorship advantage that could promote this trait in boxelder bug populations.

KEY WORDS boxelder bugs, *Leptocoris trivittatus*, cannibalism, conspecific necrophagy, survivorship

CANNIBALISM, FEEDING ON CONSPECIFIC individuals, has been documented in many animal populations, and particularly, in a wide range of insects (Fox 1975, Polis 1981, Elgar and Crespi 1992). Competition (Beaver 1974, Mills 1982), starvation (Banks and Macaulay 1968), nutritional enhancement (Snyder et al. 2000), reduction in parasitism (Root and Chaplin 1976), courtship (Rohwer 1978), and social interaction (Driessen et al. 1984, Webster 1987) are among the hypotheses that have been postulated to explain the occurrence of cannibalism. The development of cannibalistic behavior in predatory animals is relatively easy to understand because they normally acquire nutrition by feeding on other arthropods, including conspecifics (Duelli 1981, Mills 1982, Osawa 1992, Snyder et al. 2000). Among herbivores surrounded by their food source, such as flour beetles (Coleoptera: Tenebrionidae) and stem borers (Lepidoptera: Noctuidae), cannibalism has been explained as intraspecific competition as the food source becomes limited (Teleky 1980, Benoit et al. 1998, Chapman et al. 2000). The strong density dependence of cannibalism in flour beetle, *Tribolium confusum* Jacquelin du Val (Benoit et al. 1998), and bark beetle (Coleoptera: Scolytidae) (Beaver 1974) populations supports the intraspecific competition hypothesis. Optimal foraging theory has been applied to the development of cannibalism in

animal populations to contrast the advantages and disadvantages of cannibalism (Dong and Polis 1992). A genetic basis of cannibalism has been demonstrated, thus providing the possibility for natural selection (Gould et al. 1980, Gould 1983, Tarpley et al. 1993). Costs of cannibalism are the risk of becoming the victim of a cannibalistic encounter (Dong and Polis 1992) and that of acquiring a disease or parasite from the victim (Boots 1998).

Conspecific necrophagy, feeding on dead individuals of the same species, could be one step in the evolution of cannibalism, especially in herbivores. Development of cannibalism in some herbivorous species has been explained as a form of population regulation (Benoit et al. 1998, Chapman et al. 2000) or as a reduction in parasitoid populations within cannibalized eggs (Root and Chaplin 1976). Herbivores demonstrating a range of behavior from conspecific necrophagy to cannibalism include aphids (Homoptera: Aphididae) (Banks and Macaulay 1968), *Oncopeltus* (Heteroptera: Lygaeidae) (Root and Chaplin 1976), grasshoppers (Orthoptera: Acrididae) (Lockwood 1989), cockroaches (Dictyoptera: Blattellidae) (Gahlhoff et al. 1999), various noctuids (Lepidoptera: Noctuidae) (Gould 1983, Tarpley et al. 1993, Chapman et al. 2000), bark beetles (Coleoptera: Scolytidae) (Beaver 1974), *Tribolium* spp. (Coleoptera: Tenebrionidae) (Teleky 1980, Benoit et al. 1998), and honey bees (Hymenoptera: Apidae) (Webster 1987).

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Conspecific necrophagy was observed among overwintering populations of adult boxelder bugs, *Leptocoris trivittatus* (Say) (Heteroptera: Rhopalidae), during the winters of 1997 and 1998 in a private residence in West Virginia (M. W. B., personal observation). Occasional conspecific necrophagy among adults and cannibalism among nymphs has been reported in this species but with no suggestion as to any selective advantage (Baker and Waldvogel 1994). The boxelder bug feeds almost exclusively on boxelder, *Acer negundo* L., throughout eastern North America (Wollerman 1965), although adults can feed on unrelated hosts (e.g., Michailides et al. 1988). Adults spend winter in forest litter and other protected habitats, including buildings. In natural habitats, boxelder bugs become active during warm weather, but in buildings, they remain active until dying from apparent desiccation.

This study was conducted to test the hypothesis that conspecific necrophagy in overwintering boxelder bugs provides a survival advantage over bugs that do not feed on conspecifics. Such a survivorship advantage could provide a selective advantage for individuals feeding on conspecifics. Overwintering populations of boxelder bugs have few or no sources of food, other than dead conspecifics, during warm periods when they become active or in warm buildings in which they have gained access.

Materials and Methods

Adult boxelder bugs were collected in November 2000 in Jefferson County, WV, and Carroll County, MD. In November 2001, boxelder bugs were collected only from Jefferson County, WV. The bugs were held in a refrigerator, at 1–3°C, until the study was initiated. Fresh boxelder seeds were collected in November 2001 in Washington County, MD, and refrigerated until needed. Experiments were begun on 19 November 2000 and 17 November 2001, with 35 bugs per treatment being held individually in 6 cm diameter by 1.5 cm deep plastic petri dishes. In 2000–2001, the treatments were no water or food, dead bugs only, and water only. In 2001–2002, the treatments were water only, water and dead bugs, and water and boxelder seeds. Dead boxelder bugs used for the study were from the same insects collected in November of each year and killed at the beginning of the study in a household oven at 65°C for 20 min to simulate death through desiccation. Dead bugs were kept refrigerated until needed. Dead bugs were provided on the first day of the study and replaced every 2 wk in 2000–2001 and every 3 wk in 2001–2002. One boxelder seed was placed in each dish for those in the treatment with seeds in 2001–2002 and replaced every 3 wk. The experiments were done in a residence in Carroll County, MD, kept at 17–18°C in 2000–2001, and in Jefferson County, WV, kept at 18–20°C in 2001–2002. In both years, humidity was 40–60% RH. Petri dishes were examined for death of experimental bugs three times per week in 2000–2001 and every 2 d in 2001–2002. Distilled water was added to the cotton at each

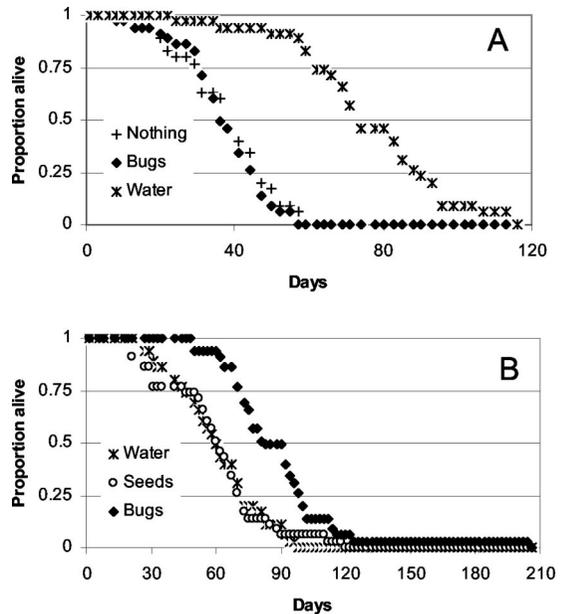


Fig. 1. Untransformed survivorship curves for experiments with individual boxelder bugs, each treatment with 35 bugs. (A) Experiments during the winter of 2000–2001: Water, provided with water only; Nothing, without food or water; Bugs, dead boxelder bugs provided but no water. (B) Experiments during the winter of 2001–2002: Water, bugs provided with water only; Seeds, water and boxelder seeds; Bugs, water and dead boxelder bugs provided.

observation, and the petri dish was cleaned with a moist tissue as needed. If the dead bug provided as food showed signs of fungal infection (which occurred infrequently and only during the third week), it was removed without replacement, and the dish was cleaned, until the scheduled time for food addition. A logistic transformation of the percentage of boxelder bugs surviving was used to linearize the data for regression analysis and normalize the residuals (Neter and Wasserman 1974). Separate regressions were done on each treatment; the two water-only treatments in each year were used as a control for differences between years. Statistical comparisons among treatments were done with 95% confidence intervals around the estimates for slope and intercept and mean 50% survivorship (Neter and Wasserman 1974).

Results and Discussion

In the 2000–2001 experiment, boxelder bugs provided with water survived longer than bugs in either treatment without water (Fig. 1A; Table 1). The survivorship regression had a significantly higher intercept, indicating that water increased average survivorship over the other treatments. A slope significantly closer to zero also indicated a decreased rate of mortality over bugs that were not provided with water. Clearly, the bugs in this trial were limited by water, with the bugs that were provided with water having a mean 50% survivorship twice that of bugs

Table 1. Regression statistics and mean 50% survivorship for boxelder bug conspecific necrophagy study

| Provision (year) | Slope | Intercept | r^2 | 50% survivorship (95% CI, days) |
|-------------------------|--------|-----------|-------|---------------------------------|
| None (2001) | -0.13b | 4.69b | 0.988 | 28–36 |
| Water (2001) | -0.08a | 6.16c | 0.979 | 63–78 |
| Dead bug (2001) | -0.14c | 5.11d | 0.980 | 28–38 |
| Water (2002) | -0.04a | 2.41a | 0.766 | 38–58 |
| Water + seed (2002) | -0.04a | 2.35a | 0.813 | 36–56 |
| Water + dead bug (2002) | -0.05b | 4.76b | 0.828 | 70–100 |

Logistic transformation ($\log([1 - P]/P)$, where P = probability of surviving) of survivorship data. Regression estimates within a column and year followed by different letters are significantly different with 95% confidence intervals.

without water (Table 1). Although bugs provided with dead bugs as food had a significantly higher slope than bugs without food or water (Table 1), the small magnitude of the difference and similarity in survivorship curve (Fig. 1A) indicates no real biological significance.

In the 2001–2002 experiment, all treatments were provided with water. The survivorship regressions for the bugs provided with just water were significantly different between years, with longer survivorship in 2000–2001 than in 2001–2002 (Table 1), likely because of differences in rearing conditions. Providing fresh dead bugs every 3 wk did significantly increase survivorship over bugs provided with only water (Fig. 1B), with twice the mean 50% survivorship than treatments lacking dead bugs on which to feed (Table 1). The first bug in the treatment with dead bugs died 29 d after the first mortality event in either of the other two treatments. One boxelder bug in the treatment with dead bugs survived 88 d after the last bug died in the other treatments (this last surviving bug, however, was omitted from the analysis as a statistical outlier). The intercept of the survivorship regression for the treatment with dead bugs was significantly higher than the control provided with just water, but the slopes, while statistically significant, show no biological differences. This indicates that the average survivorship was increased (higher intercept) through conspecific necrophagy, but once mortality began, the rate of mortality (equal slopes) was not very different from the bugs provided with only water. The survivorship regression for boxelder bugs provided with water and boxelder seeds was not significantly different from bugs provided with only water, indicating the boxelder seeds provided nothing to increase survivorship.

Numerous incidences of conspecific necrophagy were seen during the 2001–2002 experiment during random observations. Twenty-four of the 35 bugs in the treatment with dead bugs were observed feeding on dead boxelder bugs, often more than once. Frequently, the bugs were observed feeding on newly provided dead boxelder bugs within 2 min of being introduced into the petri dish. Continuous feeding was observed to occur for as long as 2.5 h. Feeding occurred at nearly any place on the body of the dead bug.

There did seem to be a cost of conspecific necrophagy after about the first 2 mo of the experiment in

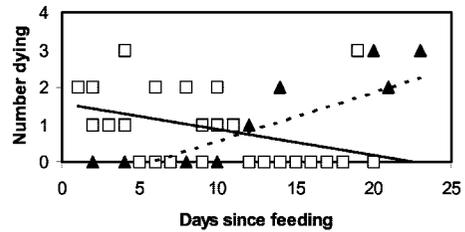


Fig. 2. Boxelder bug mortality, including only bugs provided with water and dead boxelder bugs in 2001–2002, correlated with days since most recent addition of fresh dead bugs. Dashed line and solid triangles indicate the trend during the first 73 d of the study ($r = 0.73$, $P < 0.01$), and the solid line and open squares indicate the trend after day 73 ($r = -0.37$, $P < 0.05$).

2001–2002. After day 73 of the study, there was a significantly negative correlation ($r = -0.37$, $P < 0.05$) between mortality events in the bugs provided with dead bugs and number of days since a new dead boxelder bug was added (Fig. 2). This indicates that the probability of death was higher closer to the addition of a dead bug than later. Before day 73 of the study, there was a significantly positive correlation ($r = 0.73$, $P < 0.01$) between day since feeding and mortality events. Early in winter acts of conspecific necrophagy seem to be beneficial for survivorship, but after ≈ 10 wk, there was a potential cost of feeding on dead conspecifics. Heat treating and refrigeration of the dead bugs reduced the possibility of the corpses containing live parasites, but there was some change in the suitability of dead bugs as food after 10 wk.

The results of this study demonstrate a survivorship advantage of conspecific necrophagy in a stenophagous herbivore by providing additional resources during the winter months. The ability of boxelder bugs to feed on dead conspecific individuals increases survivorship during the winter by providing some nutritional input. Conspecific necrophagy has only been observed in heated houses, but it may occur under natural conditions during warm winter days. The ability to feed on dead conspecifics would increase the probability of those living individuals to survive until host plants become available without reducing the probability of survivorship for other individuals. Through the winter, there are many warm days when these bugs become active, especially in the southern portions of their range (Wollerman 1965), providing the opportunity for conspecific necrophagy.

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