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ORIGINAL ARTICLE

Adult cannibalism in an oligophagous herbivore, the Colorado potato beetle

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Abstract Cannibalism, or intraspecific predation, can play a major role in changing individual fitness and population processes. In insects, cannibalism frequently occurs across life stages, with cannibals consuming a smaller or more vulnerable stage. Predation of adult insects on one another is considered to be uncommon. We investigated adult cannibalism in the Colorado potato beetle, *Leptinotarsa decemlineata* (Say), which is an oligophagous herbivore specializing on plants in family Solanaceae, and an important agricultural pest. Under laboratory conditions, starvation and crowding encouraged teneral adults to feed upon each other, which reduced their weight loss during the period of starvation. However, pupae were attacked and consumed before adults. Injured beetles had a higher probability of being cannibalized than intact beetles. Males were more frequently attacked than females, but that appeared to be a function of their smaller size rather than other gender-specific traits. Cannibalizing eggs at a larval stage did not affect beetle propensity to cannibalize adults at an adult stage. When given a choice between conspecific adults and mealworms, the beetles preferred to eat conspecifics. Cannibalistic behavior, including adult cannibalism, could be important for population persistence in this species.

Key words cannibalism; Colorado potato beetle; *Leptinotarsa decemlineata*; life boat strategy; oligophagous herbivore

Introduction

Cannibalism, or intraspecific predation, is the killing and at least partial consumption of an individual of the same species (Polis, 1981). While the role of cannibalism is often neglected when studying dynamics of natural populations, it is a regular phenomenon that can play a major role in changing both population processes and demographics (Fox, 1975). Naturally occurring cases of cannibalism have been observed in many animal species including, but not limited to: birds, mammals, fish, rotifers, snails, copepods, and arthropods (Fox, 1975). An immediate benefit of this behavior is obtaining a meal with relatively low search time. Consuming conspecifics can also provide beneficial nutrients that may not be normally obtained within the typical diet (Wissinger *et al.*, 2003; Wise, 2006). Furthermore, cannibalism can increase the relative amount of resources available to surviving individuals through the elimination of conspecific competitors (Choudhuri, 1974; Polis, 1981; Clouse, 1995; Wagner *et al.*, 1999). In addition, feeding on parasitized conspecifics has been shown to result in reduced parasite populations and improved survival (Wang & Daane, 2014).

While there are many potential benefits, cannibalism also has some potential costs. When an individual targets a conspecific of a similar or greater predatory ability, the risk of injury increases and the aggressor could become the victim (Elgar & Crepsi, 1992). Other costs may be less obvious, such as acquiring harmful parasites

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or pathogens (Pfenning *et al.*, 1998). Another cost of cannibalism is the loss of inclusive fitness that happens when an individual consumes a genetically related individual (Elgar & Crepsi, 1992).

In insects, cannibalism frequently occurs across life stages, with cannibals consuming a smaller or more vulnerable stage (Polis, 1981). In particular, oophagy is very common and involves the consumption of eggs by a more developed life stage. It has been reported in almost every major group of egg-laying animals (Polis, 1981), including every major order of insects (Richardson *et al.*, 2010), and may have originated from newly hatched larvae consuming their own egg shells (Watanabe & Oh'ura, 1997). Females of some species even lay "trophic" eggs which are infertile and are intended as an additional high protein food source for the young (White, 2011). Cannibalism of the juvenile stages is also a common occurrence, with adults and larger larvae consuming smaller larvae. To the contrary, predation of adult insects on each other appears to be a rare phenomenon, as evidenced by only few reported cases of this behavior (Richardson *et al.*, 2010).

Since cannibalism often has significant fitness effects at both the individual and population levels (Polis, 1981), we investigated this behavior in an economically important insect pest. The Colorado potato beetle, *Leptinotarsa decemlineata* (Say) (Coleoptera: Chrysomelidae), is an oligophagous herbivore that specializes on plants in the family Solanaceae. Currently, it is the most destructive insect defoliator of potatoes that can cause significant crop losses and is very difficult to control (Alyokhin *et al.*, 2013). Both adults and larvae of this species have been previously shown to consume conspecific eggs, which had an important effect on their individual fitness and on population dynamics of this insect on potato (Harcourt, 1971; Collie *et al.*, 2013). Currently, nothing is known about adult Colorado potato beetles cannibalizing other adults. Understanding what causes this shift from herbivory to predation could lead to a better understanding of the mechanisms regulating the abundance of this species, and may have implications for the long-term goal of developing sustainable management techniques.

Materials and methods

Study insects

The Colorado potato beetle colony used for the following experiments were the subsequent generations of a native field population collected in nontreated potato plots on Aroostook Research Farm in Presque Isle, ME, in July of 2013. Foliage containing beetle eggs was cut and incubated in Petri dishes (55 × 12 mm) in a growth chamber at 22 °C and a 16 L : 8 D (Percival Scientific, Perry, IA, USA). Within 24 h from hatching, larvae were transferred into cages built of large wooden-frame panels of fine mesh screening (50 cm × 50 cm × 90 cm). Throughout larval development cages were supplied with *ad libitum* potato plants grown from tubers in plastic pots (20 cm in diameter). Pots were filled with Fafard Growing Mix # 2 (Fafard Corporation, Agawam, MA, USA) that had been mixed with 150 mL of 14-14-14 NPK fertilizer per 28 L of soil in a stand mixer. Cages remained in the University of Maine greenhouse in Orono at 25 ± 5 °C and under a combination of natural and artificial light at 18 L : 6 D. When larvae burrowed into the soil to pupate, foliage was clipped and removed from the cage. Unless stated otherwise, the experiments were conducted with newly emerged teneral beetles that had no feeding experience as adults. Upon emergence, the beetles were removed from their cages and isolated within individual Petri dishes (90 mm × 12 mm) for 48 h prior to experimentation. During both the starvation period and the subsequent trials, the beetles remained in a growth chamber at 22 °C and a 16 L : 8 D (Percival Scientific). Their sex was determined under a dissecting microscope based on distinct indentation on the last abdominal sternite (Rivnay, 1928).

General testing protocol

Unless stated otherwise, trials were run for 72 h in Petri dishes (55 mm × 12 mm). Each dish contained 2 male and 2 female beetles. All the beetles were weighed to the nearest milligram using a microbalance (Ohaus Corporation, Parsippany, NJ, USA), at the start and end of the trials. In order to identify beetles throughout the experiment, we developed a recognition technique based on the number of black spots naturally occurring on their pronotae. Every individual was provided with a 2-digit score, with each digit of the score coinciding with the number of nonconnecting dots on the left and right side, respectively. The resulting scores were unique to each beetle in each trial.

Surviving beetles were examined under the dissecting microscope for visible signs of external damage. Signs of cannibalism ranged from completely consumed abdomen, elytra, and thorax to chewed and missing edges of elytra. Noncannibalized beetles were reweighed as described above. Beetles reaching the end of the trials were again isolated in individual Petri dishes. After 48 h, beetle frass was removed from the dishes and examined under the dissecting microscope for the remnants of cannibalized beetles.

Unless specified otherwise, statistical analyses were conducted using R (RStudio, Boston, MA, 2014). In most cases, data were analyzed using a Pearson's Chi-square test. Fisher's exact tests were used when 1 or more of the values in the contingency tables were lower than 5. Effects of several different factors on cannibalistic behavior were tested as described below.

Food deprivation

For each trial, three 90 mm × 12 mm Petri dishes were set up with 1 of 3 different treatments: 1 dry cotton ball, 1 moist cotton ball, or 1 moist cotton ball and daily replenished potato foliage. Three male and 3 female beetles were added to each dish. The experiment was replicated 9 times. For each dish, the number of individuals consumed after 3 d was recorded. Pearson's Chi-square tests were used to test for differences between the numbers of individuals cannibalized among the 3 treatments. A Fisher Exact test was used to test for differences among the treatments in the number of trials where incidences of cannibalism occurred.

Crowding

Cannibalism was compared in Petri dishes containing 2, 4, or 6 beetles. The experiment consisted of 18 replicates. In order to test for differences in the numbers of individuals cannibalized among crowding levels, a Pearson's Chi-square test was used. A Fisher Exact test was used to test for differences across crowding levels in the number of trials where incidences of cannibalism occurred.

Initial weights from the remaining beetles that were determined to be cannibalistic using frass observations were compared with the initial weights of beetles that were cannibalized using two-way ANOVA, with beetle sex treated as the second main factor. Data was tested for normality using a Shapiro–Wilk Test. Weight changes were calculated for both cannibalistic and noncannibalistic beetles by subtracting the posttrial weights from the initial weights. Differences in weight change between those 2 groups were analyzed using two-way ANOVA.

Injury

Male beetles were carefully selected and paired to have similar weights within 1 mg of each other. For the first experiment, 1 male was randomly selected from each pair and the lower half of the right-hand side elytra was clipped using a pair of microdissection scissors ($n = 22$). For the second experiment, the randomly chosen male had each of its elytra pierced with a #4 (39 mm × 0.55 mm) insect pin ($n = 24$). No females were injured in either experiment. The dishes were monitored on a daily basis for 3 consecutive days to compare cannibalism of injured and intact males. A Pearson's Chi-square test was used to test for significance.

Beetle age

Two teneral and 2 mature beetles were confined in Petri dishes. Teneral beetles were collected and maintained as described above. Mature beetles were also collected as newly emerged beetles, but were allowed to feed on 4-week-old potted potato plants for 5 d before a 2-d starvation and isolation period. During the feeding period, beetles were housed in the same type of mesh-screened wooden cages as outlined above. Cages were moved to the laboratory and kept at 21 ± 3 °C and under a combination of natural and artificial light at 18 L : 6 D ($n = 22$). A Fisher's Exact test was used to test for differences between the number of teneral and mature beetles consumed. Additionally, 10 trials were conducted to investigate cannibalism frequencies in groups of beetles where all 4 beetles were allowed to feed on foliage for 5 d.

Structural refuges

Two clear plastic 30-mm C-shape tunnels, with a 9 mm × 4 mm entrance dimensions, were cut and glued together to form an "X" pattern. All 4 ends of the structure were open to allow easy entrance for beetles. Each trial contained 2 dishes, 1 of which was the typical standard arena and the other included the aforementioned plastic structure placed directly in the middle of the dish ($n = 20$). All other methods were as outlined in the previously described cannibalism protocol. A Pearson's Chi-square was used to test for differences between the numbers of individuals cannibalized in each treatment and between the numbers of trials where incidences of cannibalism occurred.

Prior egg cannibalism experience

Colorado potato beetles egg masses were collected from the greenhouse colony, and individually placed into 40 mm × 12 mm Petri dishes using a camel hair paintbrush. Eggs were checked daily and when 30 or more eggs hatched, they were separated into 3 treatment groups. The treatment groups were as follows: Foliage, Egg/Foliage, and Egg. During the first day the Foliage group larvae were provided fresh potato foliage. The Egg/Foliage group larvae received fresh potato foliage and 3 eggs from a recently laid clutch. The larvae in the Egg group received only 3 recently laid Colorado potato beetle eggs. During the second day, the Foliage and Egg/Foliage groups both received a fresh potato leaflet, and the Egg group was given 2 additional Colorado potato beetle eggs. On the third day, larvae were removed from their individual dishes and placed into larger bucket cages.

Each cage was constructed from 2 plastic 19 L buckets placed on top of one another. The sides and tops of each of the buckets had large rectangular panels removed and fitted with fine mesh screening to allow light in. Larvae were placed on 4-week-old potted potato plants with other individuals from the same treatment group. Larvae were provided foliage *ad libitum* and allowed to complete development under greenhouse conditions. Once all larvae had burrowed into the soil, foliage was clipped and removed. When adults emerged from their respective treatment pots, they were isolated and starved as outlined above. Each trial contained 1 male and 1 female from the same treatment group that were randomly matched against 1 male and 1 female from another group. A Chi-square test was used to test for differences in the proportion of adults cannibalized per treatment.

Cannibalism of pupae

Four adult beetles and 1 pupa were confined in a Petri dish for 72 h. Newly formed pupae were selected in order to avoid an adult beetle's eclosing before the trial ended. The number of trials with incidences of pupal cannibalism was recorded ($n = 19$).

Predation on mealworms

Predation trials were setup as outlined above. The only difference was an addition of a single larva of the mealworm beetle, *Tenebrio molitor* L., to each of the 19 arenas. Mealworms were purchased from a local retailer and kept in a growth chamber (Percival Scientific) at 22 °C and a 16 L : 8 D photoperiod before being used in the experiment. After 72 h in Petri dishes, the mealworms were investigated under a dissecting microscope for signs of predation (visible bleeding and/or chewing damage).

Beetle gender

The overall numbers of male and female beetles cannibalized were compared by pooling results of the food deprivation, crowding, predation, structural refuges, pupal cannibalism, beetle age, and predation on mealworms trials. Cannibalized beetles from the injury trials were not included because of an obvious treatment effect. Data were analyzed using a logistic regression (PROC LOGISTIC, SAS Institute 2014).

Results

Food deprivation

None of the beetles from the control treatment that included potato foliage were consumed. Eighteen beetles in the dry cotton ball treatment trials were consumed, and 6 beetles in the arenas with the wet cotton ball were consumed. This difference was highly significant ($\chi^2 = 21$, df = 2, $P < 0.0001$). The percentage of trials showing incidences of cannibalism were 0% for the control group, 88.9% of the dry cotton treatment, and 55.6% of the wet cotton treatment. This difference was also significantly different ($P = 0.0003$).

Crowding

In all the trials containing 2 Colorado potato beetles, only 4 beetles (11.11% of the individuals) were cannibalized, and 22.2% of the trials showed at least 1 instance of cannibalism. The arenas containing 4 and 6 beetles per dish had 29 and 41 (40.27% and 37.96%) of the total number of individuals cannibalized, and both had 83.3% of the trials that showed at least 1 instance of cannibalism. Both the difference in the number of individuals cannibalized ($\chi^2 = 10.3807$, df = 2, $P = 0.0056$) and the number of trials where incidences of cannibalism occurred ($P = 0.0003$) were significant among the crowding levels. With the initial weight of 97.3 ± 2.3 mg, females were significantly larger than males that weighed, on average, 82.0 ± 2.5 mg (df = 1,109, $F = 9.876$, $P = 0.0022$). Initial weight of cannibalistic beetles was 101.2 ± 2.7 mg, which was significantly larger than the initial weight of 83.0 ± 2.0 mg of the consumed beetles (df = 1,109, $F = 30.137$, $P < 0.0001$). Since there was no significant interaction between beetle sex and cannibalism (df = 1,109, $F = 0.995$, $P = 0.3206$), we can conclude that both smaller males and smaller females are more likely to be targeted. Cannibalistic beetles also lost less mass (6.2 ± 1.7 mg vs. 13.2 ± 1.3 mg) during the trials than beetles that were not cannibalistic (df = 1,88, $F = 10.667$, $P = 0.00156$).

Injury

Twenty beetles that had their elytra clipped and ten intact males were consumed by the end of the experiment. This difference was significant ($\chi^2 = 5.6146$, df = 1, $P = 0.0178$). Furthermore, of the clipped males that were cannibalized, all but one was fed upon within the first 24 h (Fig. 1).

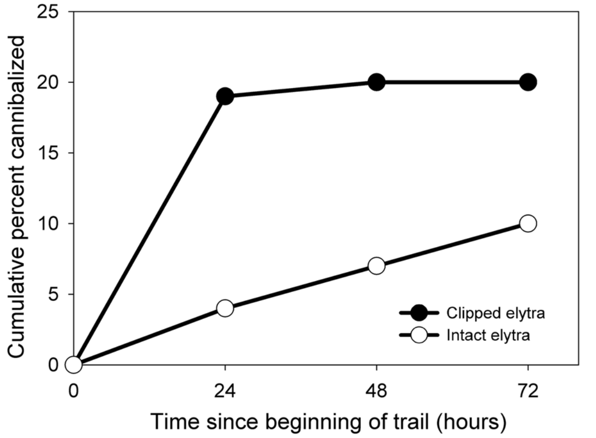

Fig. 1 Cannibalism of adult male Colorado potato beetles that had the lower half of the right-hand side elytra clipped compared to the intact control beetles ($n = 22$).

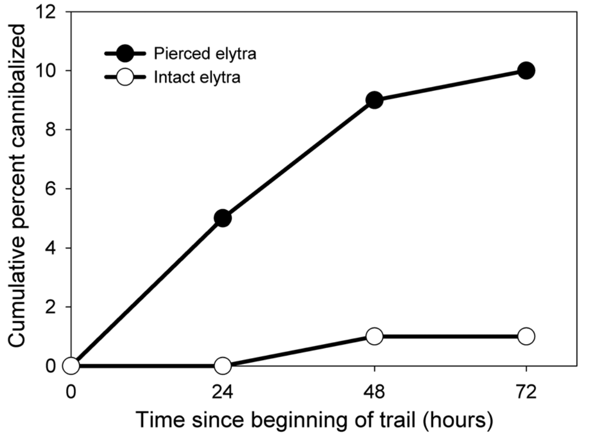

Fig. 2 Cannibalism of adult male Colorado potato beetles that had each of its elytra pierced with a #4 insect pin compared to the intact control beetles ($n = 24$).

Ten pierced males were cannibalized, which was significantly more than the 1 intact male beetle that was consumed in the control group ($\chi^2 = 7.5479$, df = 1, $P = 0.0060$). Of the pierced beetles that were cannibalized, most were attacked and fed upon within the first 48 h (Fig. 2).

Beetle age

Within the 22 trials, 46.7% of the arenas had incidences of cannibalism. Seven teneral beetles were consumed, which was not significantly different from the 2 mature beetles that were consumed ($P = 0.1567$). No signs of cannibalism were observed in any of the arenas that contained 4 mature beetles.

Structural refuges

Incidences of cannibalism occurred in 45% of the dishes that contained the plastic structure and in 40% of the dishes that did not have the structure. The difference was not significant ($\chi^2 = 0.294$, df = 1, $P = 0.5876$). There was also no significant difference in the number of adult Colorado potato beetles consumed, with 14 cannibalized in the dishes with the structures, and 13 cannibalized in the control dishes ($\chi^2 = 0$, df = 1, $P < 1.0$).

Prior egg cannibalism experience

There was no significant difference between the proportion of individuals cannibalized from each treatment group ($\chi^2 = 1.881$, df = 2, $P = 0.3904$). Only 13.75% of individuals from the Foliage group, 16.67% of the Egg treatment group, and 14.44% of the Egg/Foliage group were cannibalized.

Cannibalism of pupae

Not only were all the pupae tested in this experiment completely consumed, but they also were cannibalized before any adult beetle. Once the pupae were gone, a total of 16 adult beetles were also eaten, with 58.3% of the Petri dishes having incidences of adult cannibalism.

Predation on mealworms

Only 1 mealworm was consumed throughout the trials. In the same time, cannibalism still occurred quite frequently between the Colorado potato beetles, with 38.1% of trials having incidences of cannibalism.

Beetle gender

Within the pooled trials, a total of 162 beetles were cannibalized. Of those beetles, 73.4% were male and only 29.6% were female. This difference was highly significant ($\chi^2 = 33.697$, df = 1, $P < 0.0001$).

Discussion

Removing food and water and limiting dispersal resulted in frequent occurrences of cannibalism among adult Colorado potato beetles under laboratory conditions. One possible reason for this behavior is often referred to as “the life boat strategy.” During periods of very limited food availability and difficult environmental conditions resorting to cannibalism has been shown to prolong survival and prevent population extinctions (Polis, 1981). This life history strategy offers individuals a last-effort opportunity to avoid starvation and withstand suboptimal conditions in an attempt to hold-out until better conditions become available. For example, Ullyett (1950) examined how life history habits of 4 different carrion-feeding blowflies impact survival. He found that larvae of *Chrysomya albiceps* (Weidemann) (Diptera: Calliphoridae), which was frequently a predacious and cannibalistic species, were better suited than noncannibalistic species to survive periods of limited food availability by resorting to intraspecific predation.

Differences in weight change between cannibalistic beetles and noncannibalistic beetles could support "the life boat" strategy because cannibalistic beetles lost less weight than noncannibalistic beetles after the 3-d starvation period. Despite a small overall average loss in mass, some cannibalistic individuals actually managed to gain weight after consuming conspecifics. While we did not monitor survival after the starvation period, if changes in weight were representative of overall beetle health, partaking in cannibalism could have improved beetle fitness.

Many of our other experimental results confirmed the general predictions about cannibalism suggested by both Fox (1975) and Polis (1981), especially regarding crowding, size differences, and age. As expected, crowding increased cannibalism frequency as evidenced by more cannibalism occurring in dishes with both 4 and 6 individuals. These findings are consistent with the review by Polis (1981), who notes 65 other studies reporting similar results. Reasons for this increase in frequency could be due to the frequency of individuals violating the critical minimum individual distance, which has been suggested to promote cannibalism (Polis, 1981).

Although male beetles were more likely to be eaten than female beetles, it was likely a result of their smaller size rather than from other gender-specific traits. Both smaller males and smaller females were cannibalized more often during the trials, which is consistent with many other cases of cannibalism in arthropods (Richardson, 2010). Noronha and Cloutier (1998) conducted a study that looked at how beetle mass effected digging ability in prediapause Colorado potato beetles. They found that the beetle mass was directly related to the individuals capacity for digging and its energy reserves. Weight differences of 1 mg resulted in an additional day of digging. If beetle size is representative of its capacity for work, this could be representative of a beetle's ability to fend off or overcome an opponent.

Age also had a major impact on the results of our experiment. For most trials where cannibalism occurred, beetles that had just eclosed from pupae were used. No cannibalism was observed when all the beetles confined in a dish were allowed to feed for a week before the beginning of the experiment. Newly emerged beetles go through a 3–5 d period during which the exoskeleton stabilizes and hardens (Arakane *et al.*, 2012). Once hardened, the skeletorized elytra act as a shield from physical and environmental stressors (Arakane *et al.*, 2012). Stevens (1992) argued that the rarity of cannibalism at the adult stage in order Coleoptera is likely due to beetles being sclerotized, which protects them from conspecific attacks. Other reported cases of adult beetle cannibalism also involved consumption of a teneral individual (Stevens, 1992). However, we did observe 2 instances in which previously fed beetles with hardened exoskeletons were cannibalized when confined with teneral beetles. Therefore, it is possible that previously fed beetles are reluctant to initiate potentially risky cannibalistic behaviors because they have already accumulated sufficient resources to survive a period of starvation.

Results of the experiments looking at pupal predation were again consistent with predictions by Polis (1981), and Richardson (2010), who suggested that conspecifics are more likely to target individuals from inactive developmental stages. Pupal cannibalism in noncarnivorous beetle species accounted for almost a quarter of reported cases (Richardson *et al.*, 2010). In our experiment, all pupae were cannibalized before other adults. Similarly, Tschinkel (1981) found that pupal cannibalism in a naturally occurring population of giant mealworm beetles, *Zophobas atratus* (Fabricius) (Coleoptera: Tenebrionidae) is a major contributing factor for promoting prepupal larval dispersal. In a portion of the experiment, Tschinkel (1981) noted pupal cannibalism resulting in as high as 92% mortality.

Injury was also one of the factors promoting cannibalism. To the best of our knowledge, this was the first study investigating the effects of injury on cannibalism. Previously, effects of injury on prey susceptibility have been only studied for interspecific predation. Semlitsch (1990) suggested that susceptibility of injured prey depended on the nature of the injury and the foraging mode used by the predator. For example, in cases where the injury limits mobility, the injured prey would be easier to obtain and therefore more likely targeted by actively foraging predators. However, it will likely be a less common prey for sit-and-wait predators. Based on our results, injured beetles were targeted more often than intact beetles. Pierced elytra did not cause any visible changes in mobility. However, they likely affected the overall vulnerability of the beetle. Clipped elytra removed a large portion of the protective shielding, making the membranous hind wing and other relatively soft body portions more exposed and relatively easier a target. Pierced elytra likely had a similar, but smaller, effect because piercings still created an additional opportunity for the cutting edge of the mandibles to penetrate, but did not leave beetles as exposed as clipped sections.

When given a choice, Colorado potato beetles attacked conspecifics more frequently than they attacked mealworms. A similar situation has been observed in natural systems for several arthropod species. When prey was ranked based on biomass, conspecifics were the number 1 diet item of desert scorpions, *Paruroctonus mesaensis* (Stahnke) (Scorpionida: Vaejovidae) (Polis, 1980). Similar results have also been documented in species of wolf spiders, *Lycosa lugubris* (Walckenaer) (Araneae: Lycosidae) (Edgar, 1969), and green lynx spiders, *Peucetia viridans* (Hentz) (Araneae: Oxyopidae) (Turner, 1979). This preference could be based on a higher nutritional benefit achieved from conspecifics than other species. Alternatively, herbivores that are limited in host plant availability could be expected to consume prey that resembles the odor or taste of the host plant (Coll & Guershon, 2002). In our experiment, mealworms were reared on wheat bran, while the Colorado potato beetles were reared on potato foliage. As a result, Colorado potato beetles likely contained the host plant cues and thus were targeted for predation. However, a significantly larger number of species of potential insect prey needs to be tested before making more definite comparisons between cannibalism and heterospecific predation. Mealworms were selected because of their seemingly (to a human observer) higher vulnerability to predation, in particular lack of heavily sclerotized integument. In the same time, they are obviously very different morphologically from adult Colorado potato beetles, which may have affected their propensity of being attacked.

Arenas containing structural refuges did not result in decreased levels of cannibalism compared to the arenas without structures. These results were unexpected, since we had predicted that additional hiding places would likely limit number of conspecific encounters. It should be noted that clear tunnels were used. That allowed us to observe the beetles at all times, but likely allowed the conspecifics to see through the structure as well. Also, our arenas remained rather simple even with the refuges, while more complex structures could have provided a better protection.

While all of the aforementioned results demonstrate how Colorado potato beetle adult cannibalism can occur under laboratory conditions, predicting the possibility of this behavior under field conditions is complicated. Our experiments were designed to augment this behavior and utilized Petri dish arenas that did not allow the beetles to easily evade one another. Higher mobility under the field conditions would likely reduce the frequency of cannibalism.

Although it may seem unnatural for the Colorado potato beetles to be exposed to overcrowding with limited resources, in fact they often encounter situations where host plants are absent (Gui & Boiteau, 2010). For example, during the spring, when beetles emerge from diapause, they are often located in the overwintering grounds along the edges of forested areas away from crop plants. Summer generations can encounter food-limited environments through emergence in areas of severe or complete defoliation, as well as in areas where vines have been killed for early harvest. Additionally, dispersal flights can often end in nonhost fields. In all cases, beetles must decide whether to wait for crops to emerge or continue dispersing (Gui & Boiteau, 2010).

Colorado potato beetles are occasionally exposed to these conditions and, as a result, they have developed a remarkable ability to survive long periods of starvation. MacQuarrie and Boiteau (2003) reported beetles surviving starvation periods of over 30 d. However, there are critical points in the beetle's life where starvation is much less tolerable. Beetles first emerging from diapause require water, and beetles which are newly eclosed from pupae need access to food in order to survive (MacQuarrie & Boiteau, 2003).

Pest management and agricultural practices could also create field conditions that favor cannibalistic behavior in the Colorado potato beetle. For example, push–pull strategies, trap cropping, and crop rotation could all result in environments with limited food availability and high population densities. In these cases, better understanding cannibalism as it relates to the "life boat strategy" could be important for better understanding population persistence in this species.

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