RATE OF FOOD PASSAGE AND FECAL PRODUCTION IN *CALOSOMA SAYI* (COLEOPTERA: CARABIDAE)[1]

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ABSTRACT: Adult *Calosoma sayi* beetles were allowed to feed in the laboratory on fall armyworm (FAW) (*Spodoptera frugiperda*) larvae. The interval between feeding and the first appearance of FAW material in beetle feces varied from 7.5-23 hours depending upon when feeding occurred within the diel activity cycle. The first 24 hours of fecal production was at a high level, but decreased rapidly through the fifth day post-feeding. A subsequent slow decrease in fecal production occurred until death at 24-42 days post-feeding. These findings may have significance in relation to the dissemination of entomopathogens by *C. sayi* and in developing a technique for estimating the recency of food consumption in natural populations of this predatory species.

Calosoma sayi DeJean may have an important role in the dissemination of entomopathogens to lepidopterous pests in agroecosystems (Young and Hamm 1985). By consuming diseased prey and subsequently defecating infective material for several days, *C. sayi* fulfills several requirements for a successful pathogen disseminator. An additional requirement is the production of infective feces at a time in the diel cycle when potential target hosts are active and/or when environmental conditions associated with rapid pathogen inactivation are minimal. It was unknown if *C. sayi* satisfied this requirement, because the literature on rates of food passage in carnivorous beetles is virtually non-existent (e.g., House 1974). Therefore, we initiated a laboratory investigation to determine the relative amount of fecal material produced by *C. sayi* after feeding, and the pattern of that production through time.

Considerable difficulty is usually encountered in determining when ingested food is voided in excreta (Waldbauer 1968). The usual method is to place an indicator substance in the food to be consumed and monitor its subsequent appearance in excreta. This method, however, involves several potentially complicating factors, such as the toxicity of the material and its possible absorbtion or retention by the gut (Southwood 1978). We observed during two years of maintaining colonies of *C. sayi* in the laboratory that the feces of *C. sayi* consistently changed color from brown or white to pink within 24 hours after consuming fall armyworm (FAW)

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[*Spodoptera frugiperda* J.E. Smith (Lepidoptera: Noctuidae)] larvae, and remained this color for an additional 24 hours. Other noctuid prey, though less frequently tested, usually also produced this pink color. Feeding experiments with diseased FAW as prey indicated that the pink fecal material of *C. sayi* contained infective pathogen particles within 24 hours of prey ingestion (Young and Hamm 1985). When beetles starved for 4-6 days were fed FAW larvae, the first fecal material to subsequently appear was also pink. Considering these observations, we have no doubt that the occurrence of pink fecal material is directly related to prior ingestion of FAW or other noctuid larvae, and thus can be used as a natural indicator of the passage of some types of food through the gut of *C. sayi*.

MATERIALS AND METHODS

Beetles used in these experiments were obtained on 23-24 July 1981 from a walk-in black-light trap surrounded by row crops 6 km NW of Tifton, Tift Co., Georgia. They were brought into the laboratory, placed in individual containers and subsequently maintained under the local photoperiod at ambient laboratory conditions. All beetles were not fed for the first four days after capture, and the fecal production of one group consisting of two males and two females was monitored during this period. On the fifth day after capture, members of the monitored group were each allowed to feed on two healthy fifth instar (30 mm) FAW larvae, monitored at least once daily for the next 14 days for fecal production, and subsequently on alternate days until death. Five other starved groups of beetles, consisting of two males each, were allowed to feed at different times on the fifth or sixth day post-capture and then monitored at 2-5 hour intervals until pink fecal material was detected. Previous experiments had demonstrated that *C. sayi* adults readily consumed live or dead larvae, pupae, and adults of the FAW and could survive in the laboratory on an exclusive diet of FAW larvae for more than 129 days (Young, Unpubl. Data). All beetles, when exposed to an active FAW larva, immediately attacked, captured, and consumed the prey. Total consumption time was less than 20 minutes, with only portions of the larval skin remaining.

To estimate crudely the relative amount of fecal material produced by adult *C. sayi* under experimental conditions, the following procedure was employed. Each beetle was placed in a 17 x 12 x 6 cm plastic container with a tight-fitting lid. A piece of white filter paper (Whatman No. 3) was cut to fit the bottom of the container and saturated with water. Much of this moisture evaporated into the atmosphere of the cage within one hour, after which more water was added. An attempt was made to keep the substrate

moist throughout the experiment to minimize variations in the degree of absorption of the feces, to maintain high humidity in the container, and to provide consumable water for the beetle. Because the fecal material produced by *C. sayi* was in a liquid form, a single defecation produced a spot on the filter paper of varying size. This spot ranged in color from pink to beige to black and was easily detectable. At no time was a beetle observed to defecate on the container substrate without the fecal spot being subsequently detected. Each sheet of filter paper was periodically removed from the container and the circular fecal spots and the entire sheet measured to determine respective surface areas. Overlapping spots were each assumed to be circular and measured accordingly, as were spots at the edge of the paper. The total surface area of fecal spots was then expressed as a percentage of the surface area of that particular sheet. These percentages were then used to compare the relative amount of feces produced by the various test groups through time. This general procedure should be considered inadequate as an absolute measure of the amount of fecal material produced by each beetle per unit time. However, when used as a relative measure it has the virtues of simple design and ease of execution, as well as avoiding the critical assumptions that would be necessary for its use as an absolute measure.

RESULTS

There was a rapid decline in fecal production for the first four days when wild *C. sayi* adults were retained in the laboratory without food (Fig. 1). Fecal production from starved beetles increased at least four-fold on the first day post-feeding, then decreased rapidly over a four-day period (rate of decrease per day = 33.8%, range = 8-61%). Fecal production in male *C. sayi* reached a plateau at five days post-feeding that remained relatively constant for the next seven days, then decreased to a lower level which was maintained until death. Fecal production by female *C. sayi* also decreased rapidly in the period 2-5 days post-feeding, but subsequent production fluctuated more than for males. Sexual differences were not significant, however, thus the data is combined in Fig. 1. The presentation of these results as average daily values also obscured the fact that once low levels of fecal production occurred ($\geq$ five days post-feeding), some individual beetles defecated less than once daily.

The rate of passage of ingested FAW larvae through the digestive tract of adult *C. sayi* appeared to be influenced by the time of consumption in the diel cycle (Table 1). If larvae were consumed in the early (0530 hrs) or mid-morning (0930 hrs), the first defecation of that material occurred the same evening. When feeding occurred in the afternoon (1430 hrs) or evening (1930 hrs), defecation of that material began late the same night or

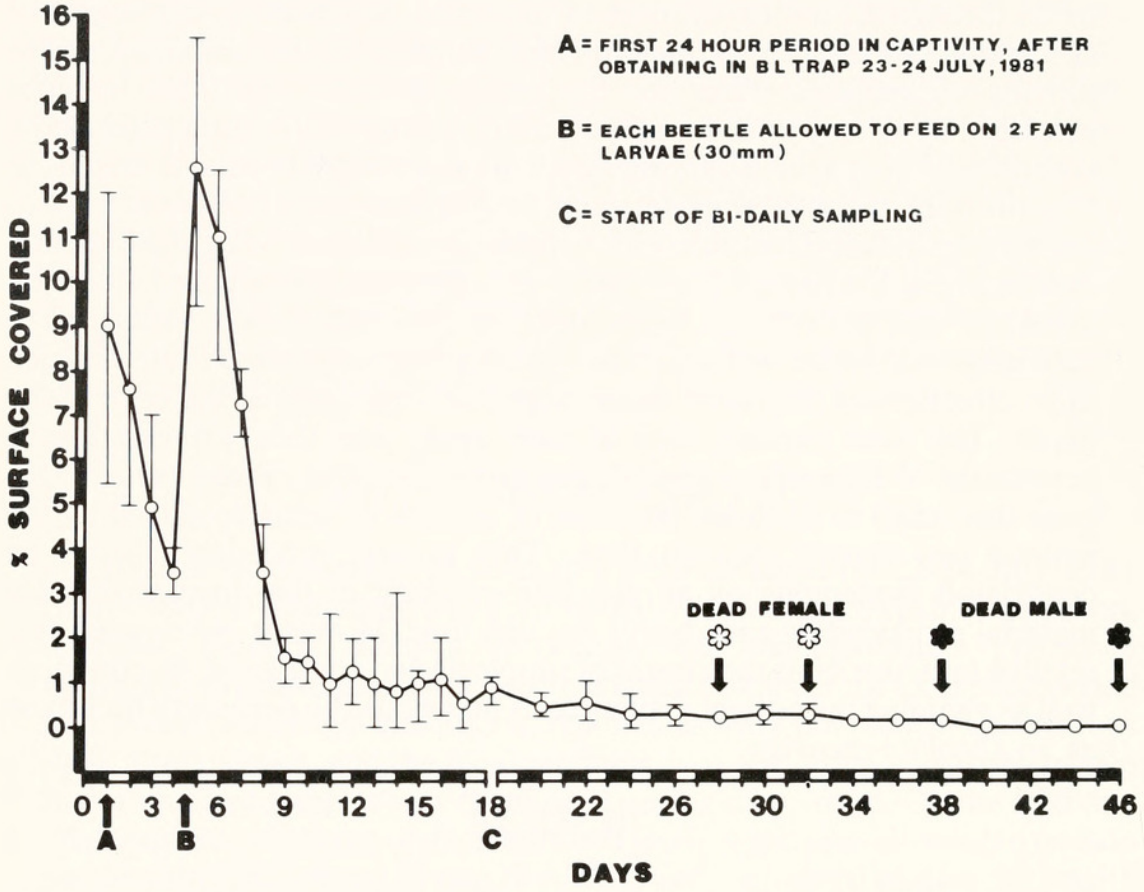

Figure 1. Relative daily amount of fecal material produced by two male and two female *C. sayi,* expressed as percent surface area of cage floor covered by fecal spots.

Table 1. Passage rate of FAW larvae through digestive tract of *Calosoma sayi.*

Feeding time	*Beetle No.*	*First defecation w/FAW material*	*Interval-post feeding*
0930 hrs*	1	1700 - 1900 hrs	7.5 - 9.5 hrs
	2	1900 - 2100	9.5 - 11.5
1430	3	0030 - 0530	10 - 15
	4	0030 - 0530	10 - 15
1930	5	0530 - 0930	10 - 14
	6	0530 - 0930	10 - 14
0030	7	1430 - 1930	14 - 19
	8	1930 - 2330	19 - 23
0530	9	1430 - 1930	9 - 14
	10	1930 - 2330	14 - 18

*Each of two male beetles allowed to feed on two FAW larvae (30 mm). Beetles starved for the four previous days.

early the next morning. Feeding that occurred in the middle of the night (0030 hrs) generated feces late in the next afternoon or early evening. The first appearance of FAW material in beetle feces may thus range from 7.5 to 23 hours after consumption. These data are consistent with the available information indicating that *C. sayi* adults are crepuscular-nocturnally active (Price and Shepard 1978b) and that defecation should occur at the start of an activity period after long periods of inactivity (Wigglesworth 1972).

DISCUSSION

In situations where entomopathogens are decimating a prey population, predators such as *C. sayi* may consume a high proportion of diseased prey and the abundance of that prey may decline rapidly. To survive under those conditions, *C. sayi* must (A) be unaffected by pathogens infecting their prey or be able to detect and avoid diseased individuals if the pathogens do have an effect, and (B) (1) be able to survive long periods without food, (2) switch to alternative prey, and/or (3) disperse to areas with more abundant food. Previous research has demonstrated that the longevity of *C. sayi* individuals is unaffected by consumption of at least two entomopathogens associated with lepidopterous larval prey, and that diseased prey are not avoided (Young and Hamm 1985). *Calosoma sayi* also appears to be capable of utilizing all three strategies for coping with a decline in its preferred food items. Rapid colonization of areas with abundant food has been demonstrated (Price and Shepard 1978a), and *C. sayi* is known to consume a wide variety of lepidopterous larvae as well as other soft-bodied living and dead prey (Burgess and Collins 1917, Young 1984). The data presented herein document the capability of *C. sayi* to withstand long periods of starvation (>23 days). This period of time would permit either considerable dispersal to abundant food supplies or a recovery of local prey populations to adequate densities and may be an important component of the feeding strategy for this species.

The rate of passage of food through the alimentary tract of *Calosoma* species apparently has not been previously investigated (e.g. Thiele 1977). For other carnivorous carabids the rate of passage has been estimated at approximately 24 hours (Kullmann and Nawabi 1971). The data presented here indicate that passage in *C. sayi* may occur as rapidly as 7.5 hours and can be influenced by the time of consumption relative to the diel activity pattern of the individual. This has significant implications for the possible role of *C. sayi* in disseminating entomopathogens (Young and Hamm 1985). If a *C. sayi* individual consumed a FAW larva infected with nuclear polyhedrosis virus (NPV) at dawn, by sunset the feces produced by that individual would contain infective NPV polyhedra. Fall armyworm larvae

are active in the early evening (Leppla et al. 1979), and could consume foliage contaminated with *C. sayi* feces. NPV polyhedra are relatively stable when protected from sunlight (Couch and Ignoffo 1981); thus they would remain potentially infective for FAW larvae for a considerable period of time, if they were deposited on leaf surfaces in the early evening. However, if NPV-infected FAW larvae are consumed by *C. sayi* in the early evening, infective feces would be produced at the next dawn. This would result in the subsequent rapid inactivation of the virus by sunlight and minimal consumption by FAW larvae. The absence of data on the relative foraging rate of *C. sayi* at dawn and dusk prevents a determination of which situation is more likely to occur.

One unanticipated byproduct of these experiments is the discovery of a possible method of estimating the time interval between feeding and trap capture in predatory *Calosoma* species. The beetles represented in Fig. 1 were captured in a large walk-in light trap sometime during the night of 23-24 July 1981. During their stay in the trap (removed 0830 hrs, 24 July), they probably defecated and may have consumed some prey. When placed in cages on paper at 0930 hrs, 24 July, their fecal production declined over the next four days in a pattern very similar to that demonstrated after feeding on 28 July (Fig. 1). It can be estimated, by superimposing the pre- and post-feeding patterns, that the four beetles had fed on the night of capture or the previous night. If this is a consistent pattern - four days of decreasing fecal production before reaching a low-level plateau on the fifth day - then a very simple technique is now available for indirectly estimating the recency of food consumption for a local population. It is easy to envisage situations where, due to environmental disturbances such as prolonged rain, drought, or selective control applications for prey species, predators such as *C. sayi* may be faced with a shortage of food. A sampling of individuals at those times may indicate that many are at the lower end of the fecal production curve, i.e., four or more days post-feeding. In more normal times, few if any individuals would be expected to occur in that range. By placing beetles in individual cages and depriving them of food for five days while monitoring relative fecal production, then providing food with subsequent deprivation and fecal monitoring for 7-10 days, considerable information could be obtained relevant to levels of food consumption through time and space in a population or its subgroups.

Investigations that deal with the relation of a predator species with its food supply usually attempt to estimate the availability of prey by direct monitoring of the prey population (e.g., Holling 1966). However, the predator could also provide this information, since the amount and frequency of food obtained by a predator is a function of the availability of food. Thus, the non-lethal, inexpensive, and technically simple method

herein described may be of particular value to research on relatively host-specific predators of lepidopterous larvae. Testing of more prey taxa and predators, and refinements in technique, may permit this method to be applied more widely in insect ecology.

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