

taining a general age balance, we point out, as Dame et al. (1964) also noted, that at any particular time a relatively large percentage of the females, known to be monogamous in their mating habits, were mated and thus could not be influenced initially by the release of sterile males.

We conclude that the *A. quadrimaculatus* population in central Florida was predominantly young, continually reproducing and replenishing its numbers, and from week to week, month to month, and season to season varying only slightly in mating behavior, egg-laying capacity or viability, and physiological age distribution. Differences in the populations sampled at 2 types of stations were evident. Although the prevailing temperatures undoubtedly affected the rate of larval development and adult emergence, the only factor strongly influencing populations' size was the availability of larval breeding areas, which in turn was influenced by the water level in the area.

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The Incidence and Effect of Egg Cannibalism in First-Instar *Coleomegilla maculata lengi* (Coleoptera: Coccinellidae)¹

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ABSTRACT

In field-collected egg masses more than 21% of the eggs were destroyed by first-instar larvae from the same egg mass. Since 39.8% of these were estimated to be nonviable, the effective reduction in number of larvae owing to egg cannibalism by undispersed first-instar larvae was 12.7%. Cannibalistic behavior has been stated to have survival value, since this food supply lengthens the life and increases the chance of finding prey by otherwise nonfed larvae. Laboratory experiments showed that can-

nibalism lengthens the life span, but results also in larvae which disperse from the egg mass later and are less active than noncannibalistic larvae, so their chances of finding prey are reduced. Cannibalism might still be an advantage under low-prey-density situations were it not for the known fact that this species can maintain itself and mature on substances other than prey. Therefore, this behavior may not be advantageous to the role of larvae as natural control agents.

In many species of Coccinellidae, newly hatched larvae feed readily on unhatched eggs in their own egg masses. This special type of predation is not affected by predator or prey densities outside the egg mass, except for other predators which may feed on the coccinellid eggs or on the predispersal larvae. However, it does have a definite effect on the survival rate of the coccinellid larvae.

The extent of reduction in survival is determined by 2 factors: the number of viable eggs destroyed, and the influence of this feeding on the success of the dispersing larvae.

Banks (1956) reported that egg cannibalism in

first-instar *Adalia bipunctata* (L.) resulted in 11.8% reduction in hatching. Dixon (1959) estimated that this type of egg destruction resulted in only 2.9% reduction in *A. decempunctata* (L.), the other eggs consumed not being viable. Banks (1956) stated that infertile eggs were always destroyed, since any that were left were fed upon by larvae prior to dispersal from the egg mass. He identified infertile eggs that had been attacked by traces of yellow yolk remaining, while fertile eggs were assumed to be those with the dark remains of larvae within the egg shell. Dixon (1959) obtained an estimate of egg viability by removing newly hatched larvae and observing the remaining eggs. In half the 26 eggs which did not hatch, the embryo had already split the chorion.

Banks (1956) attributed the greater proportion of

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egg cannibalism by predispersal first-instar larvae to a larger egg-mass size and a greater variation in hatching times. Kaddou (1960) found no correlation between cannibalism and egg-mass size in *Hippodamia quinquesignata* (Kirby), but did find that 1 hour after initiation of hatching eggs were in danger of being eaten. Newly hatched larvae of *A. decempunctata* were eaten only by larvae which were considerably older and almost ready to disperse (Dixon 1959).

Feeding on unhatched eggs by first-instar larvae may well have an influence on larval survival. According to Banks (1956) and Dixon (1959), cannibalism results in an increased life span for larvae that do not encounter prey. Therefore, they are able to make a more prolonged search for prey, considerably increasing their chances of survival under low prey-density situations.

Incidence of Cannibalism.—In this study, egg masses of *Colomegilla maculata lengi* Timberlake were collected from alfalfa fields in July 1962 and July and August 1963. The egg masses were generally found on the upper surface of the alfalfa leaves and were readily visible to an observer walking through the field. In each case where hatching occurred, the larvae were found to be *C. maculata*, although the coccinellids *Hippodamia convergens* (Guérin-Méneville), *H. parenthesis* (Say), and to a lesser extent *Coccinella novemnotata* Herbst also were common in these fields. This is contrary to Girault's (1907) observation that in nature the eggs of *Colomegilla maculata* are rarely exposed to the direct rays of the sun. The egg masses had 2 to 32 eggs per mass, with mean of 11.8 for 200 masses.

In determining the amount of cannibalism, egg masses were left on the alfalfa leaflets and placed either in a pint ice cream carton lid with a petri dish cover, or in a stoppered homeopathic vial. Counts were made on the number of eggs present prior to the initiation of hatching and the number of larvae present at the completion of hatching. All larvae were determined to species.

The apparent mortality within 141 egg masses caused by cannibalism by undispersed first-instar larvae and nonviability is shown in Table 1. The undispersed first-instar larvae fed upon 21.1% of the eggs in their own masses (2.8 eggs per mass). Cannibalized eggs included both slower-developing and nonviable eggs. In 3 egg masses, containing 1.7% of the total eggs, no eggs were viable. Larvae emerged from 77.2% of the eggs (10.1 eggs per mass).

In August 1963, 30 egg masses were collected and the eggs separated either into separate depressions of spot plates and covered with plastic, or placed individually in micro-shell vials, to determine the viability of *C. maculata* eggs. The eggs or larvae were examined within 24 hours after initiation of hatching in that egg mass. This gave an estimate of viability uninfluenced by cannibalism. Generally, all nonviable eggs are eaten by first-instar larvae in egg masses in which some hatching occurs. Of the eggs which did not hatch, 52.2% remained yellow, 46.3% had darkened, and 1.5% died in the process of hatching. *C.*

maculata eggs are bright yellow-orange until 2–3 hours prior to hatching, when they turn gray as pigmentation of the embryo takes place.

It is possible, by extrapolation, to obtain an estimate of the percent of nonviable eggs in masses in which some hatching occurs and which would normally be consumed along with the slower developing, viable eggs. Table 1 shows the actual causes of mortality, excluding outside sources. The 12.7% are eggs which would have hatched in the absence of cannibalistic behavior, and represent a loss in the number of larvae available to act as natural control agents. The eggs (8.4%) which were not viable but were consumed by first-instar larvae represent the utilization of a suitable food source.

Effect of Egg Cannibalism on Life Span.—Reports of the normal length of the first larval stadium range from 4.6 days (Garman and Jewett 1914) to 7 days (McGregor and McDonough 1917). The influence of cannibalism on the life span of first-instar larvae is shown in Table 2. Individuals given neither food nor water lived about 70 hours. This span was shorter than the 3.2 days (77 hours) that Smith (1961) reported. The longevity of unfed larvae provided only with water (89 hours; Smith 1961) corresponded closely to that obtained for larvae provided 1 egg each. The 25% increase in life span owing to cannibalism was not so great as that obtained by Banks (1956), who found that consumption of a single egg almost doubled the life span of *A. bipunctata*. He reported also that first-instar *A. bipunctata* molted after feeding on only 3 eggs. In this study, first-instar *C. maculata* molted before dispersing from the egg mass if 3 or more eggs were eaten. One larva was observed to destroy 9 eggs. Less than 1% of the larvae molted prior to dispersal from the egg mass. Both Banks (1956) and Tan (1934), the latter working with *Coccinella axiridis* (Pallas), found that cannibalism did not affect the length of the stadia.

Effect on Predatory Activity.—The larvae from field-collected egg masses were placed in groups, depending on the amount of cannibalism occurring in their egg mass. Cannibalism in group A ranged from 0.27 to 0.33 eggs per larva, in group B from 0.11 to 0.12, and in group C no eggs were eaten. This does not mean that each larva in groups A and B had fed. Hatching occurred over a 6-hour period.

Five larvae, approximately 1 day old, were placed

Table 1.—Percent survival and mortality within *Colomegilla maculata* egg masses.

Cause	Apparent (%)	Actual (%)
Eggs hatching normally	77.2	77.2
Nonviable eggs, no hatching in the mass	1.7	1.7
Cannibalism by first-instar larvae	21.1	12.7
Nonviable eggs in masses with some hatching	—	8.4

Table 2.—Average life span of first-instar *Coleomegilla maculata* without water or food except eggs.

Food	Number of individuals	Time (hours)	% increase
No food	13	70.5	—
1 egg per 2 larvae	16	85.4	21.1
1 egg per larva	9	88.1	25.0

in a petri dish with 5 apterous adult or late-instar clover aphids, *Anuraphis bakeri* (Cowen). This experiment was replicated 4 times for each of the 3 groups. Seven observations were made periodically over a 2¾-hour period on the number of larvae attacking aphids. Table 3 shows the percent of larvae that were observed attacking aphids. It shows also the number of aphids killed after 2¾ hours. The data in Table 3 indicate that larvae which had not fed are more active and successful in finding prey, but may not be so successful in killing this prey after being starved for 24 hours. The aphids had all been consumed 1 day after exposure.

Observations were made on the 3-day- and 4-day-old larvae to determine their activity. It is noteworthy that their activity increased both with increase of time since feeding and with the decrease in number of eggs eaten previously, even though they had fed on aphids.

In another test on the effect of egg cannibalism on the predatory efficiency of first-instar *C. maculata*, 24 larvae were removed from the egg mass while in a teneral state and placed individually in the lids of pint ice cream cartons with Saran Wrap^a covers. Twelve of these larvae were placed in contact with an unhatched coccinellid egg, and half were unfed. Approximately 6 hours after eclosion, 3 first-instar pea aphids, *Acyrtosiphon pisum* (Harris), were placed in each container. Comparative activity and feeding were noted 18, 36, and 54 hours after hatching. Each time they were checked, the aphids which were dead but had not been fed upon were replaced.

Larvae which were not provided eggs dispersed earlier, remained more active, and killed a greater number of aphids than those provided with eggs (Table 4). Movement from the original position after 18 hours was significantly heterogeneous when tested by an adjusted chi-square. Activity of fed and non-fed larvae was not heterogeneous when tested individually at the different times, but activity when tested as a whole was significantly different. The difference in aphid kill after 36 hours was not significant.

DISCUSSION

In the evaluation of the effects of egg cannibalism by undispersed first-instar larvae, the proportion of viable eggs destroyed must be compared with the proportion of nonviable eggs consumed, and the effects on the surviving larvae from this early and accessible food supply. Of the eggs which were fed upon, 60.2%

Table 3.—Influence of egg consumption on the predatory efficiency of first-instar *Coleomegilla maculata*.^a

Group	A	B	C
Average number eggs eaten per larva	0.30	0.11	0.0
Number observed attacking	34%b	36%b	51%a
Final aphid kill	40%a	55%a	45%a
Active, 3 days	20%b	34%ab	46%a
Active, 4 days	38%a	44%a	67%a

^a Values in a row followed by the same letter are not significantly different as determined by Duncan's multiple range test. Number observed attacking were determined at both 95% and 99% and all others at 95% level. Data analyzed using arc sin $\sqrt{\%}$ transformation.

were viable (12.7% = 60.2% of 21.1%) (Table 1). In the absence of cannibalism these eggs would have contributed to the larval population. Cannibalistic behavior, therefore, results in an increased food supply and a reduced larval population density.

Generally, less than 50% of the hatched larvae feed on eggs prior to dispersal from the egg mass. This conclusion is based on the observations that seldom do more than 2 larvae feed on a single egg, and that 21.1% of the eggs are fed upon. If we assumed that only 1 larva fed on each egg, then $(21.1/77.2 = 0.273)$ 27.3% of the larvae would have fed. If 2 larvae had fed on each egg then 54.7% would have fed. The actual figure is between the two.

Cannibalism extends the interval of time between eclosion and dispersal, and results in larvae which are less active after leaving the egg mass. Cannibalistic larvae are probably stronger and, if subsequently not fed, will live longer than those which did not feed on eggs. In the temporary absence of food, cannibalism would increase larval survival. It would tend to reduce their efficiency as predators if aphids or other food were available. Smith (1961) gave the opinion that water encountered in the field probably contains substances that may increase survival to a greater degree than the 5% sucrose solution, which he showed kept first instar *C. maculata* alive for 15 days. Thus the polyphagous nature of this insect appears to negate many of the apparent advantages of limited egg cannibalism.

In the field there is a gradation in amount of cannibalism in different egg masses, ranging from those

Table 4.—Influence of artificial larval feeding (1 egg per larva) on activity and predation.

Type of activity	Hours after eclosion		
	18	36	54
Moved from original position—fed	36%	100%	100%
unfed	92%	100%	100%
Visibly active—fed	0%	28%	64%
unfed	17%	50%	92%
Average no. aphids killed—fed	0	1.6	3
unfed	0.1	2.5	3

^a Dow Chemical Co., Midland, Michigan.

with none to those in which the emerged larvae may enter the second instar prior to dispersal from the egg mass. This fact provides a certain inherent variability in the population which under certain periods of stress, may have survival value.

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Ecological Studies of Mites Found in Sheep and Cattle Pastures. I. Distribution Patterns of Oribatid Mites¹

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ABSTRACT

Data which approximated the Negative Binomial model were obtained in a sampling program designed to investigate the distribution of oribatid mites in a sheep pasture and a cattle pasture in Kentucky during the summer months. The sheep pasture had higher population densities, but fewer mite species, than the cattle pasture; *Scheloribates lacvigatus* (Koch) was the dominant species in the sheep pasture, *Eupelops*, n. sp., in the cattle pasture. A relatively abrupt increase in mite density in the grass zone of the sheep pasture in July and August contrasted with a more stable but lesser density in this zone of the cattle pasture. Mite densities in the grass zone were highest in the early morning and declined

somewhat during the day, but this phenomenon was not marked. Appreciable populations of mites, including such potential hosts of anoplocephalid cestodes as *Scheloribates lacvigatus* and *Galumna* cf. *virginiensis* Jacot, were present in the grass zone throughout the day. This indicates that diurnal fluctuations in the vertical distribution patterns of potential intermediate hosts cannot be used in controlling infection of sheep and cattle by anoplocephalid tapeworms. The results of this study agree generally with those of a previous, preliminary investigation, although some discrepancies were evident; these are discussed in some detail.

As a part of our ecological studies on the macrochelid mites we expanded work that was initiated the previous season on the ecology of mites inhabiting pastures (Wallwork and Rodriguez 1961). The objectives in the continuing study were: (1) to study the characteristics of aggregation in the populations of a sheep and a beef cattle pasture of the Kentucky Agricultural Experiment Station near Lexington, (2) to compare the species composition in the 2 pastures, and (3) to investigate the diurnal and seasonal fluctuations in spatial distributions of species populations.

In the previous preliminary study referred to, we found that the oribatid and mesostigmatid mites comprised virtually all of the acarine forms extracted from 3 distinct vertical zones; namely, grass, the turf plug, and from soil to a depth of 2 in.

Studies on the distribution of oribatid mites in

sheep and cattle pastures take on significance because at least 30 species of oribatid mites have been implicated in the life histories of 9 species of anoplocephalid cestodes that infest mammals, particularly sheep and cattle (Rajski 1959).

METHODS AND PROCEDURES

Sampling and Extraction.—The sheep and cattle pastures were of 4 and 3 acres, respectively, both were seeded to Kentucky Bluegrass, *Poa pratensis*, and this grass was well established. There was, however, a small amount of orchard grass, *Dactylis glomerata*. The sheep pasture was divided into 82 quadrats of equal size plus a loafing area of 0.12 acre that was divided into 70 small quadrats. The loafing area was virtually devoid of grass but it was still rich in organic matter and this was the location of the watering troughs. The cattle pasture was divided into 40 quadrats. These pastures were situated within 1000 feet of each other.

Sampling was at approximately 10-day intervals throughout the summer, weather permitting, beginning in July and terminating in early October. Samples were taken at 3 distinct times on each sampling date, namely, 8 AM, 1 PM, and 5 PM.

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