

ECOLOGY OF THREE SYMPATRIC SPECIES OF PARASITIC INSECTS OF THE GENUS *MEGARHYSSA* (HYMENOPTERA: ICHNEUMONIDAE)

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Abstract. Three species, *Megarhyssa atrata lineata*, *M. macrurus lunator*, and *M. greeni greeni* were studied in beech-maple forests in Michigan. All are diurnal with similar activity patterns except that female *M. atrata* maintain a high degree of activity later in the day than do the others. Saturation deficits above 10 g/m³ inhibit activity whereas normal summer daytime temperatures do not. There does not seem to be a significant difference between time of emergence of females and of males in the spring, nor are there differences in seasonal occurrence of the various species except that *M. greeni* may persist slightly longer in the fall.

Insects of both sexes and of all species tend to return repeatedly to the same log or stump with but a limited amount of movement between sites.

Adults rest on the undersides of beech and maple leaves during inactive periods. Since there are more such places than individuals to use them, competition for shelter does not seem to occur. Neither do adults compete for food. The larvae of the three species are largely segregated ecologically in that they parasitize different segments of the host population. This depends on the facts that (1) the adults select a host larva at a depth in the wood so that complete insertion of the ovipositor at right angles to the surface of the wood will just reach it, (2) the ovipositors of the different species are of different lengths, and (3) the host larvae maintain themselves at about the same depth in the wood for most of their larval period.

There is succession of species on a given log but not to the extent that the three species would be ecologically segregated without the above mechanism. The sequence of species in the succession seems to depend on differences in ovipositor length.

Females are usually more abundant on logs when a species is invading a new log; males are usually more numerous in the declining phase. Adults can live at least 27 days. Predators in the area were robber flies and perhaps a chipmunk.

Incidence of parasitism of *Tremex* by *Megarhyssa* was 26.7% in part of a log which was examined.

INTRODUCTION

Townes and Townes (1960) state that "the ecological separation between *M. atrata*, *M. macrurus* and *M. greeni* has not yet been touched upon. All three of these are dependent on the same host, in the same geographic area, and frequently in the same tree or log, yet each one remains moderately common and is not eliminated by competition with its congeners." The present study was carried out on *Megarhyssa atrata lineata*, *M. macrurus lunator*, and *M. greeni greeni* during the summers of 1958, 1959, and 1960 to ascertain whether ecologic segregation occurs among them and if not, to evaluate the nature and extent of their competitive interaction. Observations relevant to other aspects of their biology were also obtained and are included here.

General Life History

The overt life histories of all three species are practically identical. All parasitize wood-boring larvae of the pigeon tremex, *Tremex columba* (Hymenoptera: Siricidae). A female *Megarhyssa* detects a host larva or pupa in a dead log

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or stump, after which she inserts her ovipositor full length into the wood and deposits an egg on the host. Upon hatching, the parasitic larva feeds on the host and finally pupates in the burrow. After metamorphosis the adult chews out of the wood. Males detect an emerging female by her chewing noises, and they aggregate at the site of her future emergence (Heatwole *et al.* 1964). Copulation takes place immediately after she emerges. Although mixed-species aggregations form at emergence sites, only males of the species corresponding to that of the emerging female attempt copulation with her (Heatwole *et al.* 1963). The inseminated female later completes the cycle by ovipositing in a log. All three species overwinter in the larval stage.

Study Areas

The study areas consisted of two mature beech-maple forests, one at Carp Lake, Emmett County, Michigan, and the other at Colonial Point, Cheboygan County, Michigan. The latter was used only for supplementary observations and for collecting specimens. At the former location, six different tremex-infested logs or stumps were numbered and used as study sites for *Megarhyssa*. A brief description of each follows, and a map of their

locations relative to each other appears in Figure 1.

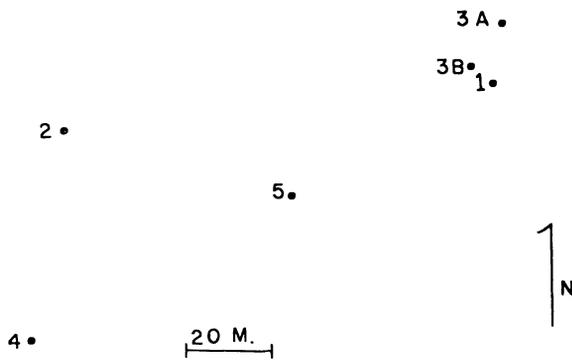


FIG. 1. Locations of the study sites in relation to each other.

Site 1. This site was a fallen dead beech log 8 m long and about 40 cm in diameter at its base. The basal end consisted of soft, highly decayed wood which was full of emergence holes; little bark remained. The opposite end was hard and undecayed and contained no emergence holes. The middle part was firm on the outside (although some of the heartwood had rotted away) and was mostly covered by bark; the fungus *Hypoxylon marginatum* was abundant. A few emergence holes were present, and all ichneumon activity occurred in this region. Of the logs containing *Megarhyssa*, this one was in the latest stage of decay. The site was well shaded most of the day.

Site 2. This site was a beech stump 55 cm tall and 41 cm in diameter at the top. The center was rotten but the rest of the wood was firm; the bark was still intact in most places. A bracket fungus of the genus *Polyporus* and a small cup fungus grew on the stump; *Collybia radicata* and another mushroom were frequently present. Moss (*Brachythecium* sp.) covered the base of the stump. An open area in the canopy exposed the stump to direct sunlight for part of the day.

Site 3a. This site was a dead beech trunk about 15 m tall with the upper 5 m lacking bark. The next 3 m had part of the bark intact; below this level all bark was intact. The shelf fungus, *Fomes fomentarius*, grew on the lower part, and *Polyporus* spp. and *Hypoxylon* were abundant.

Site 3b. This site consisted of a dead beech trunk 7 m tall which contained tight bark throughout. The heartwood had rotted but the sapwood was firm. No fungi were evident. Woodpecker drillings and emergence holes were present.

Site 4. This site was a fallen dead beech log, the main part of which was 7 m long and 23 cm in diameter. It bifurcated at one end, sending one branch vertically (1.1 m long and 18 cm in diameter) and the other as an extension of the main trunk (4 m long and 13 cm in diameter). Mosses (of which one was *Ulota crispa*), crustose lichens, and *Polyporus* spp. were scattered throughout. Direct sunlight reached the log during parts of the day.

Site 5. This site was a dead beech tree about 17 m high and with a diameter of 29 cm. It contained bark which was beginning to loosen in places.

Factors Affecting Daily Activity Cycle

These species are strictly diurnal as shown by hourly counts at sites where they were active. On one 24-hr watch at Site 2 (July 7 to 8, 1958), the insects first appeared shortly after sunrise and left at dusk (Fig. 2).

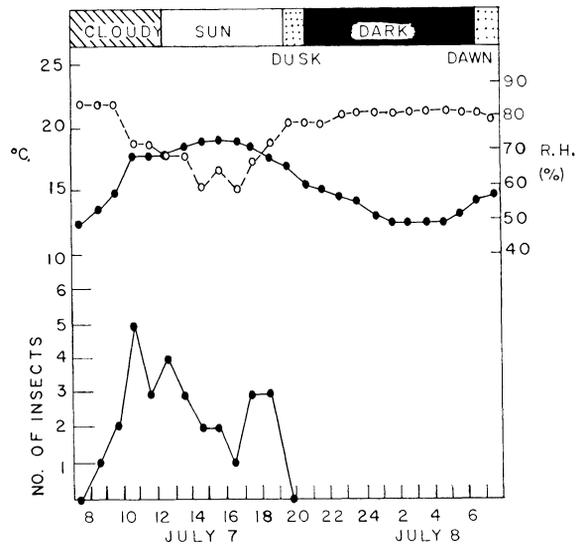


FIG. 2. Environmental conditions and activity of *Megarhyssa* at Site 2 during a 24-hr period.

During all three summers the number of insects at the various sites was frequently counted, and the results for each site were grouped according to the time the counts were made. The two sexes were treated separately. In 1958 counts were made of the total number of *Megarhyssa*; in 1959 and 1960, each species was considered separately. Counts of males aggregated at emergence sites were not included for such males are relatively unresponsive to some environmental stimuli (Heatwole *et al.* 1963). Densities of several species at some sites were too low for studies of their activity pattern. The results are summarized in Figure 3 for sites for which there were sufficient data. The same data were also plotted using mean number of individuals per observation period. The resulting histograms were practically identical to those presented in Figure 3. The period covered was 0800 to 1700 hr. Since *Megarhyssa* is active until about 2000, the entire activity period is not covered by these observations.

Site 4 in 1960 was the only situation in which sufficient data were obtained to compare adequately the patterns of different species and sexes at the same site and year. Female *M. atrata* showed maximum activity at 1600 to 1700, a time when

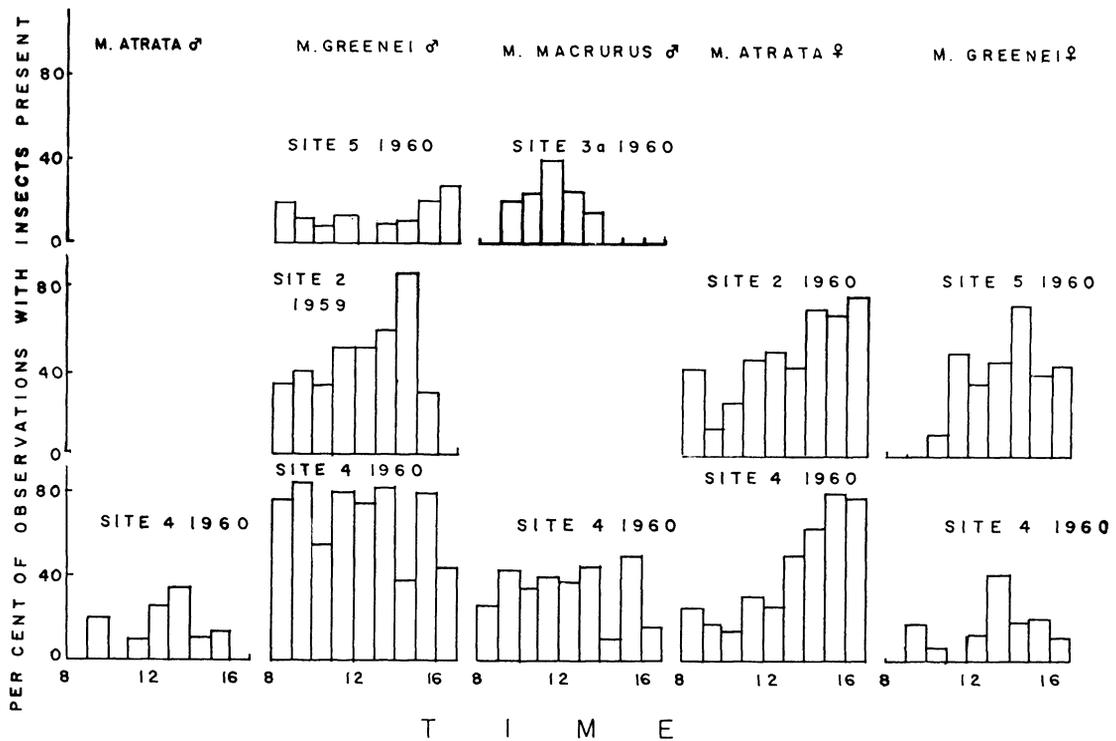


FIG. 3. Summary of activity of *Megarhyssa* at various sites during 1959 and 1960.

the activity of all other species and *M. atrata* males had already declined considerably. In males of all three species and in female *M. greenei* there was a depression of activity at 1400 to 1500. A similar depression appeared at 1000 to 1100.

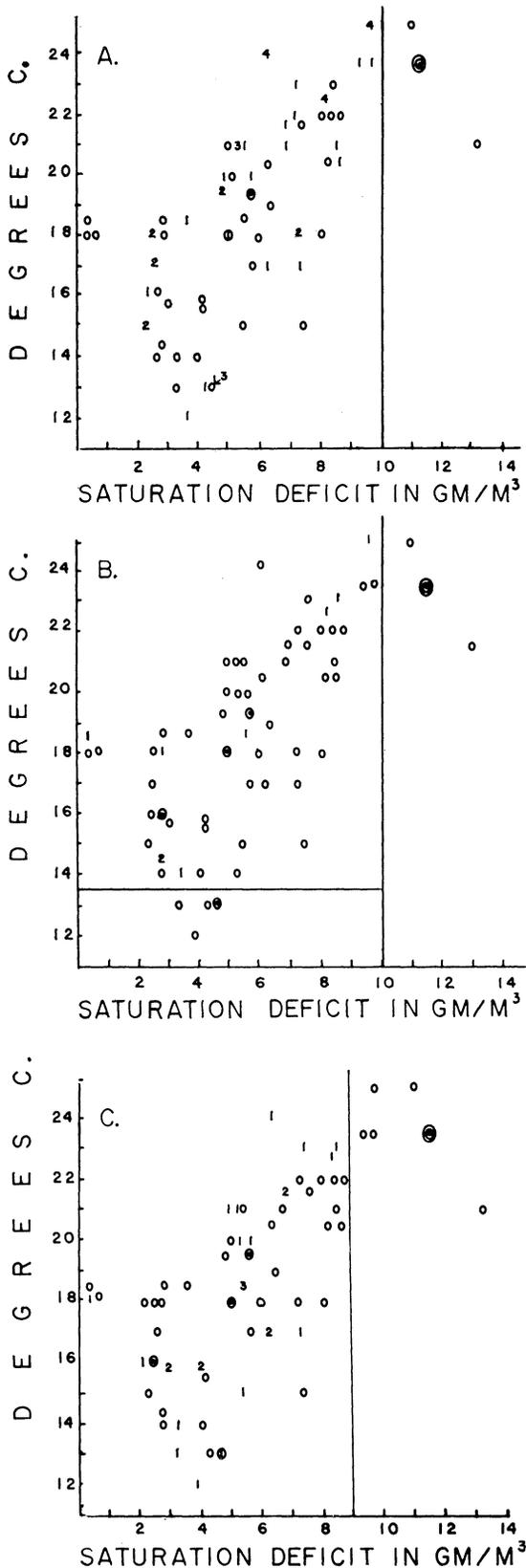
Temperatures and relative humidities, continuously recorded by a Friez-Bendix hygrothermograph from 20 June to 2 August 1960, 15 cm above the ground near Site 4, showed a relatively consistent pattern of daily change. Temperature reached its daily low (10 to 15° C) usually about midnight, after which it leveled off until after dawn when it gradually increased, reaching a high (20 to 25° C) at 1400. Relative humidity remained uniformly high (in the 80's and 90's) until about 1000 whereupon it dropped rather suddenly, reaching a low at about 1400. The value of the daily low was variable, occasionally reaching values as low as 40%. The depression in activity at 1400 at Site 4 in 1960 correlates with both the daily high in temperature and the daily low in relative humidity. The activity depression at 1000 to 1100, however, does not correlate closely with any factor measured.

Continuous weather records 15 cm above the ground from near Site 2 (2 to 25 July 1960) were similar to those from Site 4 in all pertinent features although the pattern was less regular. There was a concomitant similarity in activity

pattern of female *M. atrata*, the only group for which there were sufficient data to make comparisons between both sites that year (Fig. 3).

There was considerable variability even within the same species and sex when the different sites were compared with each other. The regimen in environmental factors is frequently different at different sites, i.e., the canopy may be such that at one place there may be direct sun on the log during the same hour that a log at another site is heavily shaded. Thus, if activity pattern is directly controlled by the environment, different patterns would be expected at different sites.

In addition to the above-mentioned weather records taken near the various sites, a number of readings of temperature and saturation deficit were taken directly at a log or stump immediately after counts of the active insects had been made. Males of *M. greenei* and *M. macrurus* were found at logs at all levels of temperature encountered during the day (12 to 25° C) (Fig. 4), although they were somewhat torpid at 12 to 13° C. Male *M. atrata* were found at all temperatures except those below 14° C. However, temperatures between 12 and 14° C were encountered so infrequently that absence of *M. atrata* males in this range is probably due to chance. Thus it seems that temperature within the normal range of daytime summer conditions does not influence the



activity of *Megarhyssa* males. Females were not encountered within the entire range of naturally occurring temperatures, although the lower number of females at logs when direct measurements of weather were made prevents evaluation of the data.

No individual of any sex or species was present at the logs when the saturation deficit exceeded 10 g H₂O/m³ air, although male *M. greenei* and *M. atrata* were active at values between 9 and 10 g/m³, and a *M. macrurus* male was active at 8.3 g/m³. No females were active above 7.2 g/m³. The low number of females prohibited any decision as to whether this difference between the sexes is significant or simply due to chance.

The lowest value of saturation deficit encountered (the most humid condition) was 0.3 g/m³. When this measurement was made, male *M. atrata* and *M. macrurus* were active despite a light rain. Males of *M. greenei* were active at saturation deficits as low as 2 g/m³. Again the number of females is too low to permit evaluation of the data. In summary, it seems that males are active at all levels of saturation deficit up to 10 g/m³, above which the drier conditions inhibit their activity. This result, in conjunction with the occurrence of active insects at all levels of temperature encountered, suggests that the depression of activity at 1400 hr is related to the dryness of the air at that time rather than the high temperature. This is in line with the general dependency of ichneumonids upon moisture mentioned by Townes (1958).

Seasonal Cycle

Males will ordinarily copulate only with an emerging or very recently emerged female (Harrington 1887; Abbott 1934) and hence any female emerging in the spring is lost from the reproductive resources of the population unless males are already on hand to mate with her. Consequently, some mechanism causing earlier emergence of males than females in the spring might be expected. To test this we grouped the data from 634 museum specimens (not considering specimens reared in the laboratory from wood) according to locality and date of capture. There was no consistent tendency for first captures of the season from a given area to contain only males; thus a seasonal difference in initiation of emergence between the sexes was not demon-

FIG. 4. Number of male *Megarhyssa* active at different temperatures and saturation deficits. Number of concentric circles indicate number of zero readings at that point. A.—*M. greenei*, B.—*M. atrata*, C.—*M. macrurus*.

strated although an analysis of this sort cannot prove that it does not occur.

Of the nine geographical areas with sufficient data and in which two of the species were present, the month of first occurrence was the same for all species present with the single exception of Canada where *M. atrata* was first collected in May and *M. greenei* first collected in June. Of the four areas in which there were sufficient data on *M. greenei* and *M. macrurus* together, the last month of the year in which specimens were taken was the same for both species in two areas; in two others *M. greenei* was collected during the month following the last collections of *M. macrurus*. In all five areas for which there were adequate data for *M. greenei* and *M. atrata* together, the month of last occurrence of *M. greenei* was the month following that of the last occurrence of *M. atrata*. Thus there seems to be little, if any, seasonal separation of

the species although *M. greenei* may persist longer in the fall than the other two.

Local Movements

Abbott (1936) marked male *M. lunator* (= *macrurus*) and found that some returned on several different days to the place of their original capture. However, he obtained no information on females or other species and did not attempt to ascertain the extent to which males visited logs other than the one at which they were marked. We extended his observations by marking insects with dots of paint on the dorsal surface of the thorax and/or abdomen. By use of different colors of paint and marking different combinations of body segments, each insect could be recognized individually at long distances with the aid of 7 x 50-power binoculars. After being marked and released all insects left the log on which they were captured.

TABLE I. Movements of *Megarhyssa* during the summer of 1959 in a beech-maple forest

Species	Sex	No.	No. of times observed ^a	Time between first and last records	Greatest distance between locations
<i>M. greenei</i>	♀	1	1	13 days	0
		2	0	—	—
		3	0	—	—
	♂	4	4	7 days	0
		5	2	4 days	0
		6	1	3 days	0
		7	5	11 days	0
		8	1	1 day	0
		9	1	1 hour	0
<i>M. macrurus</i>	♀	10	0	—	—
		11	0	—	—
		12	0	—	—
		13	2	14 days	0
		14	1	6 days	0
		15	1	1 hour	0
	♂	16	3	3 days	0
		17	0	—	—
		18	1	6 days	0
		19	3	6 hours	50m
		20	3	14 days	0
		21	2	3 days	0
		22	0	—	—
		23	1	1 hour	0
		24	0	—	—
		25	0	—	—
		26	1	3 days	101m
		27	1	1 day	50m
28	0	—	—		
<i>M. atrata</i>	♀	29	0	—	—
		30	2	1 day	0
	♂	31	0	—	—
		32	1	2½ hours	0
		33	0	—	—
		34	2	4 days	0
		35	0	—	—

^aNot including original capture

In 1959, 35 insects were marked, of which three were female *M. greenei*, six were male *M. greenei*, six female *M. macrurus*, 13 male *M. macrurus*, two female *M. atrata*, and five male *M. atrata* (Table I). Of these, 14 (40%) were never seen again after the original marking. The remaining 60% were observed again one to five times within periods ranging from an hour to two weeks after marking. With three exceptions (all males of *M. macrurus*), the insects were always observed on the same log or stump as their original capture (indicated by 0's in Table I). One male *M. macrurus* which was observed at two different locations (No. 19), was originally captured and marked at Site 2 at 1012 hours, 26 June. It flew into the forest, but returned within a few minutes; it was again present at the same log at 1550 of the same day. At 1610, 20 min later, it was observed at Site 4, a distance 50 m away. Another male *M. macrurus* (No. 27) was marked at Site 4 on 2 July and was observed the following day exploring Site 2, again a distance of 50 m. The third male *M. macrurus* (No. 26) which was observed at more than one site was marked 26 June at Site 1 and observed three days later at Site 2, a distance of 101 m.

In 1960, a total of 39 individuals was marked (6 male *M. macrurus*, 5 female *M. macrurus*, 9 male *M. greenei*, 7 female *M. greenei*, and 12 female *M. atrata*). Of these, 15 (38.9%) were not subsequently observed. Three individuals were observed at sites other than the one at which they were marked. One of these was a male *M. greenei* originally marked 23 June at Site 5. It was subsequently observed on Site 4 (a distance of 72 m) on 27 and 28 June. On 5 July it was found back at Site 5. A female *M. greenei* originally marked at Site 2 on 16 July and which returned to that site later the same day, was observed on Site 4 (50 m away) on 19 July. Finally, a female *M. macrurus* originally marked at Site 5 on 2 July was observed at Site 4 on 11 July. The remaining 21 individuals were encountered two to twelve times each during intervals from one to 27 days between the first and last observations (Table II). None of these was observed anywhere but at the original capture site.

These data indicate that insects of both sexes tend to come back repeatedly to the same log or stump where they carry out exploring activity (females searching for host larvae and males searching for mates) and thus can be said to have a home range. Some of the females were observed to oviposit at almost every visit; one *M.*

atrata oviposited at least twice the same day. The factors involved in site recognition are not known although the antennae do not seem to be important, since some of the males which Abbott (1936) observed to return to a specific site had been antennectomized at their original capture. It is not known whether the animals tend to return to the log from which they emerged or not.

ECOLOGIC SEGREGATION

There are at least three possible sources of interspecific competition. These are: (1) competition for shelter or resting sites, (2) competition for food among adults, and (3) competition for host larvae.

No individuals were ever encountered in the field except at logs or stumps where they were exploring. However, insects leaving such sites were followed on several occasions. Female and male *M. atrata* and female *M. macrurus* were followed to their shelter sites; *M. greenei* were hard to follow and were invariably lost. All successful attempts to follow insects gave the same result; the ichneumons flew up in a tree and came to rest on a beech or maple leaf two to ten m above the ground. Usually they would land on the underside of the leaf and hang upside down, although sometimes they would land on the upper surface and then crawl to the lower one. Captive individuals would spend the night upside down beneath leaves in their cage. Thus, shelter sites of adults appear to be the underside of leaves. Since the number of such leaves in a beech-maple forest during the summer is much greater than the total number of *Megarhyssa*, competition for shelter sites by adults does not seem to exist.

Competition for food among adults also seems to be nonexistent as Townes (personal communication) indicates that *Megarhyssa* do not feed in the adult stage unless perhaps they take in some food (nectar) in the droplets of water they drink from the surfaces of leaves and flowers.

Competition for host larvae might be expected to be keen since all three species are restricted to the same host and occur together. However, several factors of importance which must be considered are the oviposition behavior of *Megarhyssa* and the burrowing behavior of the host larvae. In regard to the first, Heatwole *et al.* (1964) have shown the following: (1) females detect the location and depth of the host larvae and direct their ovipositors to them; (2) they select only those larvae which are at a depth in the wood so that the ovipositor just reaches them when fully inserted and directed at right angles to

TABLE II. Movements of *Megarhyssa* during the summer of 1960 in beech-maple forest

Species	Sex	No.	No. of times observed*	Time between first and last records	Greatest distance between locations	
<i>M. greenei</i>	♀	1	2	21 days	0	
		2	0	—	—	
		3	0	—	—	
		4	0	—	—	
		5	1	15 days	0	
		6	2	3 days	50m	
		7	0	—	—	
	♂	1	2	6 days	0	
		2	3	12 days	72m	
		3	3	5 days	0	
		4	0	—	—	
		5	1	2 days	0	
		6	9	27 days	0	
		7	1	1 day	0	
		8	2	4 days	0	
		9	0	—	—	
	<i>M. macrurus</i>	♀	1	0	—	—
			2	1	9 days	72m
3			0	—	—	
4			2	3 days	0	
5			0	—	—	
♂		1	1	2 days	0	
		2	0	—	—	
		3	7	21 days	0	
		4	3	10 days	0	
		5	2	2 days	0	
		6	4	5 days	0	
		7	0	—	—	
<i>M. atrata</i>	♀	1	4	10 days	0	
		2	4	6 days	0	
		3	0	—	—	
		4	11	15 days	0	
		5	0	—	—	
		6	0	—	—	
		7	1	6 days	0	
		8	0	—	—	
		9	0	—	—	
		10	2	4 days	0	
		11	5	10 days	0	
		12	2	7 days	0	

*Not including original capture.

the surface of the wood—all ovipositions result in complete insertions of the ovipositor. Thus if the ovipositors of the three species are of different lengths and the host larvae do not change their depth from the surface during their tunneling in the log, the *Megarhyssa* would essentially be parasitizing different populations of the host species.

To test the first of these conditions, the ovipositors of insects captured in the field were measured as well as unbroken ones of specimens in the University of Michigan Museum of Zoology. Only the subspecies studied in the present report were used, and in order not to introduce error through possible geographic variation in ovipositor length, only specimens from Michigan were measured.

As indicated by Figure 5, *M. atrata* has longer

ovipositors than *M. macrurus*. In fact the ranges of ovipositor length of these two species did not overlap in the sample studied, if one abnormally small individual is excluded. Even including this dwarf in calculating the mean and standard error, the differences between the two species are significant as indicated by failure of the rectangles representing twice the standard error on each side of the means in Figure 5 to overlap (Dice and Leraas 1936). Townes (personal communication) has indicated that such dwarf individuals occur in many species of the family. He suspects that they are sexually sterile.

To test the second condition, tremex-infested logs were opened and examined. The path which one *Tremex* larva followed was traced through the wood. After hatching near the surface of the log, it burrowed in at about 45° and then leveled

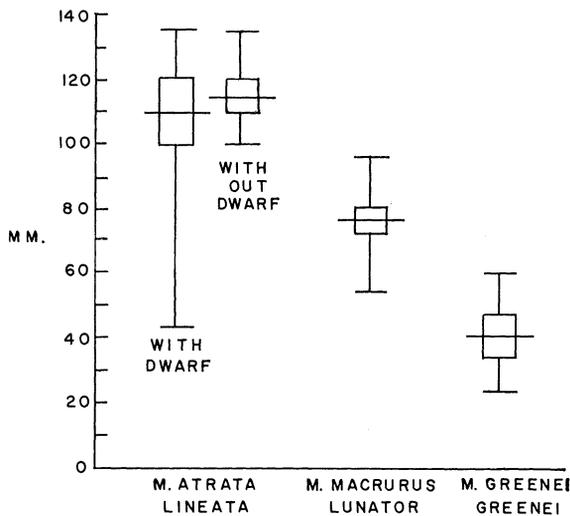


FIG. 5. Comparison of ovipositor lengths of three species of *Megarhyssa*. Vertical lines indicate ranges; rectangles represent twice the standard error on each side of the mean which is represented by included horizontal line. $N = 50$ for *M. macrurus*, 18 for *M. greenei* and 16 for *M. atrata* (including dwarf).

out and followed the grain of the wood. Logs sawed in cross-sections showed tremex larvae and burrows scattered at various depths in both the heartwood and sapwood. All followed the grain of the wood except the very smallest. Thus the pattern of burrowing noted above seems to be general, with the tremex larvae leveling off at variable depths. Once this has taken place, the larvae appear to maintain a relatively constant depth in the wood until they are ready to emerge.

Thus the conditions for ecologic segregation of the three species of *Megarhyssa* are met, and the parasites do not appear to compete for host larvae except perhaps to a limited extent owing to the small overlap in ovipositor length between *M. macrurus* and *M. greenei*.

A further test to check the spatial separation of the three species would be to open logs and identify the parasite larvae at different depths. Unfortunately all three species are practically identical in the larval stage, and we could not distinguish them. Attempts to culture host larvae with their attendant parasites in sawdust and in blocks of wood were not successful, and all *Megarhyssa* died.

Although differences in ovipositor length largely isolate the three parasites to different parts of the host population, it was considered pertinent to make a study of different logs to ascertain whether there were differences in ratios of the different species in either space or time which might enhance their ecological separation.

Each time the periodic counts discussed above were made, all sites were visited within a half-hour period. These counts may therefore serve as a basis for comparing the sites. The mean number of insects of each species and sex per observation period is plotted in Figure 6.

Three stages were noted in the succession of *Megarhyssa* species on the logs. Stage I occurred at Sites 3b and 5 which were the two firmest pieces of wood studied. In 1959 they did not have any *Megarhyssa*. In 1960 the parasites were beginning to appear with *M. greenei* predominating.

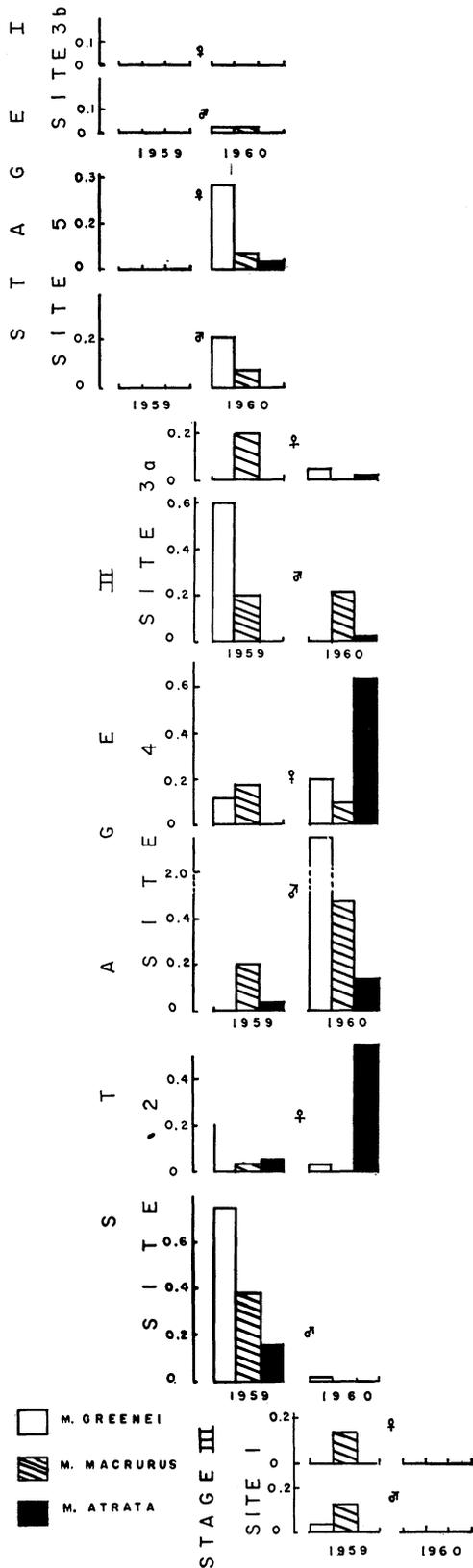
Stage II is a shift in numerical dominance from *M. greenei* through *M. macrurus* to *M. atrata* and is represented in various substages by Sites 2, 3a, and 4, all of which were decaying and were characterized by presence of fruiting fungi.

Finally in Stage III, there is a disappearance of *Megarhyssa* from the log. This is represented by Site 1 which had both *M. greenei* and *M. macrurus* in 1959 but no *Megarhyssa* in 1960. As indicated earlier, much of the log at Site 1 was in a late stage of decay.

The succession of *M. greenei* to *M. macrurus* to *M. atrata* seems to be related to ovipositor length. In most cases, firm newly fallen logs would begin to be broken down by fungi beginning on the outer surface and proceeding inward. Thus conditions would first become favorable for *Tremex* in the more superficial areas, i.e., those in the ovipositor range of *M. greenei*. Later, when the log had decayed in the deeper areas, *M. macrurus* could come in, and eventually conditions would be favorable for *M. atrata*. The outer regions would become unsuitable because of advanced decay before deeper ones, and hence the numbers of *M. greenei* would decline before reduction of the *M. atrata* population begins. This is perhaps the mechanism behind the observed succession.

Stage III as depicted in Figure 6 is not according to expectation for the last species inhabiting the log was *M. macrurus* rather than *M. atrata*. This is accounted for by the fact that the log had suffered a rot of the heartwood and was hollow in the section on which there were *Megarhyssa*. Thus the part of the log available to *M. atrata* was already badly decayed before the study began. Other hollow logs or stumps had only a small region of the center badly decayed and the firmer part was thick enough to accommodate the long ovipositor of *M. atrata*.

Stage II undoubtedly lasts for several years and hence there is a long period of time in which



all three species may be present together. They can therefore not be considered as completely separated on the basis of their temporal sequence of occupancy of a log. Rather, differences in ovipositor length seem to be responsible both for ecologic segregation and succession of species.

Sex ratios at a given site varied widely from one year to the next. Usually females predominated if the species was first beginning to invade a log, whereas males predominated if the species was declining. Early in the cycle, hosts would be present but not emerging females. Thus more females than males would be expected to be active on the log. Later, when few suitable unparasitized hosts remain but emerging females are still present, the greater proportion of males which were observed would be expected.

Mortality and Longevity

As indicated by records of marked insects, the adult stage can have a rather long existence. The longest interval during which an individual adult was known to survive was 27 days (Table II). This was a male *M. greenei*, originally captured and marked 26 June 1960 and last observed 23 July 1960.

During the study two dead insects were found near logs where exploring activity had been taking place. One (an unmarked male *M. macrurus*) was found on the leaf litter beside Site 4. The second was a *M. macrurus* male found dead at Site 2 on 13 July 1959. It had been marked 29 June 1959. In both cases cause of death was unknown.

Predation was a known cause of mortality at Site 4 during mid-June of 1959. A total of three ovipositors were found protruding from the log, 26 June. At the same site on 2 July 1959, a freshly killed female *M. greenei* was found with her ovipositor inserted in the wood. Her abdomen was still moving and the detached legs were kicking. Part of the head and thorax had been eaten. A chipmunk, *Tamias striatus*, had a burrow under the log and is believed to have been the predator for no further evidence of predation was found subsequent to its disappearance from the area.

Ovipositing females are at a disadvantage because they are unable to fly away when their ovipositors are inserted. *M. atrata* usually requires more than one hour for complete oviposition (Heatwole *et al.* 1963) and is therefore quite vulnerable to predation. The time is shorter in

FIG. 6. Mean number of insects per observation period for various sites and years.

M. macrurus (12 min) and even less in *M. greenei* (about 7 min), the species with the shortest ovipositor. From the standpoint of predation, selection would seem to favor short ovipositors. However, there is also a selective advantage in the opposite direction in that it permits successful coexistence with species having shorter ovipositors.

Predation upon flying insects was also observed. On two occasions a robber fly (family Asilidae) was observed attacking *Megarhyssa*. Once, near Site 2, a fly hit a male *M. macrurus* in mid-air knocking it to the ground. A similar attack was also made on an individual of an unidentified species of *Megarhyssa*.

Mortality during the short period between metamorphosis and emergence is apparently high since a number of adults was found dead and moldy in their burrows.

Relation to Host

Part of a beech log taken from Colonial Point was gradually dissected into small pieces. All host and parasite larvae were collected and preserved. Of the total of 86 host larvae which were thus obtained, 23 (26.7%) were parasitized. There were no cases of more than one parasite on a given host, suggesting that the female can detect whether or not a larva has been previously parasitized when her ovipositor reaches it. Heatwole *et al.* (1964) have shown that she does not receive this information *before* she inserts her ovipositor.

Host larvae ranged from 3.8 to 36.1 mm. Those containing parasites ranged from 7.1 to 31.7 mm. One *Tremex* pupa had a parasite on it. All parasites except two were just behind the host in the burrow and unattached to it. One exception was near the head, and the other was attached to the host just behind the head and was actively feeding. One parasite was found with the empty skin of its host larva.

DISCUSSION

Recently a number of investigators have doubted the validity of universally applying the competitive exclusion principle and have suggested that two closely related species may coexist (Ross 1957, 1958; Cole 1960; Saville 1960). In view of the controversy this has stimulated, it becomes of considerable importance to study carefully any suspected cases of violation of this principle in nature. In the present example, which initially appeared to us to be a clear-cut case of coexistence without ecologic segregation, the three species were found to be almost completely separated by the combination of different ovipositor lengths and

selection of hosts at a depth in the wood equal to the length of the ovipositor. The effectiveness of the mechanism separating the species depends also on the burrowing behavior of the host larvae. Thus the segregation of the *Megarhyssa* depends on three rather subtle factors, none of which is readily evident and none of which would be effective alone or even in conjunction with only one of the other factors.

Although the results we obtained do not in any way indicate that exceptions to Gause's Rule cannot be found in nature, it is clear that one presumed example of coexistence without ecologic segregation did not hold up when analyzed. Other such suspected violations of the principle of competitive exclusion should perhaps be viewed with extreme skepticism unless very carefully studied. Certainly, up to the present time, very few demonstrations of violations of the principle are definitely known. Furthermore, demonstration of lack of ecologic segregation at a given time does not necessarily mean that it does not occur at another time when something becomes scarce. For example Lack (1946) has shown that several birds of prey feed on the vole when it is abundant but that when it is scarce they turn to alternate foods.

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THE ABERT SQUIRREL AND ITS DEPENDENCE ON PONDEROSA PINE

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Abstract. The Abert squirrel (*Sciurus aberti aberti*) occurs throughout the ponderosa pine belt in central Arizona where it appears to have become ecologically dependent on ponderosa pine. Studies of the squirrels and their relationship to ponderosa pine were conducted at the Fort Valley Experimental Forest and adjacent areas on the Coconino National Forest near Flagstaff, Arizona, between October 1953 and June 1955.

Adult squirrels molt twice each year, and their summer and winter pelages are somewhat different in color shade and pattern. In a sample of 313 adult squirrels, males weighed an average of 589 g; females, 602 g. Body measurements are similar between sexes, except that females apparently have longer tails. The squirrels obtain most of their food from ponderosa pine. The inner bark of terminal twigs is the principal food during winter, and ovulate cones are preferred in summer. Staminate flowers and apical buds of pine are also important foods. Other foods include fleshy fungi, carrion, and bones.

The home range of squirrels was determined in summer by trapping and in winter by mapping areas of activity in snow. On the average, squirrels ranged over about 18 acres during summer and five acres in winter. Squirrels are strictly diurnal and in 1954 were active and fed each day even in inclement weather.

Abert squirrels build nests in the branches of ponderosa pine. These nests, composed of pine twigs, have an outside diameter of about one and one-half feet and an inside diameter of six inches. Squirrels do not prefer any particular site in the tree for their nest. They may occupy several nests during a year.

In 1954 squirrels bred only in May at Fort Valley. The gestation period was estimated at about 40 days, and young squirrels were born between June 10 and July 12. Litter size varied from two to five and averaged 3.4.

Of 729 squirrels collected during six different years, 57% were male and 43% were female. Young squirrels had thick ear tufts in September, but on adults tufts were absent or very thin at that time. This difference is the best available criterion of age. The obvious causes of mortality did not appear to be responsible for the considerable losses that evidently occurred during the winter of 1953-54; other factors must have reduced squirrel densities.

The number of feeding sites evident after fresh snows is a reliable indicator of squirrel density. Counts of the total number of twigs clipped by squirrels during winter appear to be related to population densities and differences between years should indicate trends in populations.

In central Arizona squirrels are now apparently less numerous than at the turn of the century. This is probably due to the deterioration of squirrel habitat caused by logging and lack of adequate pine regeneration. Short-term fluctuations in population are believed to be caused by variations in quality and quantity of food supply which in turn may be related to the reproductive cycle of ponderosa pine. Intensive forest management should result in larger and more stable populations of the Abert squirrel.

INTRODUCTION

In the extensive ponderosa pine forests of the Southwest there exists a group of tree squirrels that are among the most handsome of North American mammals. Squirrels of this group belong to the subgenus *Otosciurus*; two species have been described, the Abert squirrel (*Sciurus aberti*) and the Kaibab squirrel (*S. kaibabensis*). Eight sub-

species of the Abert squirrel have been recognized. The different forms of these squirrels vary somewhat in coloration but are similar in size and general appearance. These animals, commonly known as the tassel-eared squirrels, are confined to the Colorado plateau and the southern Rocky Mountains of Colorado, Utah, Arizona, and New Mexico in the United States, and to the