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LIFE HISTORY AND BEHAVIOR OF A FUNGUS BEETLE, *BOLITOTHERUS CORNUTUS* (TENEBRIONIDAE)

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THE INVESTIGATIONS of Liles (1956) on the life history of *Bolitotherus cornutus* (Panzer) suggested that there are two sympatric populations in Michigan with seasonally isolated adults. This situation, potentially of interest in speciation, was responsible for the initiation of the present study. Other aspects of the biology of this beetle have also been studied and these data are presented here along with an analysis of the seasonal life history.

LIFE HISTORY

Larvae and pupae of *B. cornutus* live inside sporophores of polyporoid fungi, most often *Ganoderma applanatum* (Persoon). During the summer, adults are usually found on or near sporophores. They feed on the tissues and spores of the fungus and mate and oviposit on or near the sporophores. Overwintering adults may be found inside sporophores or under bark of logs nearby. Only larvae and adults are known to overwinter.

Liles (1956) studied some aspects of the life history of this species in Hocking County, Ohio, and in Cheboygan County, Michigan. Sporophores of fungi she collected in Ohio in February 1954 contained third-, fourth-, and fifth-instar larvae whereas in Michigan in early November 1954 she found only second- and third-instar larvae. There were two discrete periods of egg-laying in Michigan in 1954, separated in midsummer by a period of three weeks (4 July to 26 July). No eggs were laid in the laboratory or found in the field during this period. Field-collected females laid eight to twelve eggs (at a rate of one or two per day) when brought into the laboratory and none laid eggs during both egg-laying periods.

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Based on this information and on the developmental times of different stages reared in the laboratory, Liles suggested that there are two seasonally isolated populations: that adults which overwinter are responsible for the first period of egg-laying; that the larvae from these eggs mature during the summer and overwinter as adults; and that the overwintered larvae, maturing in mid-summer, are responsible for the second brood of eggs, the larvae from which presumably overwinter and mature the following year.

I studied the seasonal life history of this species in the field and in the laboratory from 1964 to 1966. Most field observations were made in 1965 and 1966 in a wooded area along the Huron River just north of Ann Arbor, Michigan. Each adult found in this area was individually marked with paint the first time it was seen, and each time it was observed records were made of its location, its activities, and the activities of any other individuals found near it. One hundred and five adults (66 females and 39 males) were marked between 22 May and 17 September 1965. During the next summer, between 17 May and 7 September, 45 of these marked individuals (29 females and 16 males) were observed again and an additional 60 (32 females and 28 males) were seen for the first time and marked.

Only 14 of the females observed in 1965 were actually seen laying eggs that year. One female which laid an egg on 25 May 1965 was also seen laying eggs on 6 August and 12 August. This indicates that the egg-laying period of females which have (presumably) overwintered as adults is not limited to late spring and early summer, at least in Ann Arbor, and that in the field females lay eggs for more than the two-week span which would be inferred from Liles' records of oviposition in the laboratory. Another female, first seen in the field on 22 May 1965, was seen laying an egg on each of the following dates that summer: 6 June, 26 June, and 3 July. She was also seen laying an egg on 13 June 1966 after overwintering as an adult. She probably also overwintered as an adult from 1964 to 1965 since I was unable to find any pupae through 14 May 1965 (the last date sporophores were inspected that spring).

These observations show that some males and females overwinter after passing through at least part of a reproductive season, and that at least some are reproductively active in two successive seasons. The longest known adult life-span, based on times between first and last observations of marked adults in the field, is 473 days for a female (22 May 1965 to 7 September 1966) and 461 days for a male (22 May 1965 to 29 August 1966). Since nocturnal observations were made only

between 22 May 1965 and 7 September 1966, the actual life-span of these individuals was probably greater*.

The eggs of *Bolitotherus cornutus* are laid singly, usually on the top surfaces of sporophores of host fungi, but sometimes on nearby wood and on the lower surfaces of sporophores when they are not sporulating. After laying an egg, the female covers it with a capsule of dark material. Since the capsule remains even after the egg has hatched and the larva emerged, it is possible to record the amount of egg-laying activity on individual sporophores without actually witnessing oviposition. Cumulative records of all eggs laid on three sporophores in 1965 are shown in Figure 1. These records, combined with observations of egg-laying by females on all fungi in the area (lower curve, Fig. 1), indicate that there was no gap in egg-laying in Ann Arbor in 1965 such as Liles (1956) found in northern Michigan in 1954.

Sporophores of *G. applanatum* collected near Ann Arbor, Michigan, in February 1964 and in April and November 1965 contained larvae with head capsules of all sizes found (and presumably, therefore, of all instars) (Table 1). All sporophores, however, do not necessarily contain all sizes of larvae. None of the largest class of larvae were found in sporophores collected in March 1964. Some were found earlier that winter in other sporophores, however, and, since no pupae were found, the absence of large larvae probably reflects the fact that not all sporophores have egg-laying females on them throughout the reproductive season.

Cumulative egg-laying records for sporophore 1 are shown in Figure 2. When this sporophore was collected, on 1 November 1965, the larvae in it were small, probably in the first instar (Fig. 3). They were kept in a shaded location on the roof of the University of Michigan Museum of Zoology in a plastic container with small pieces of that sporophore from November 1965 to October 1966. On 26 July 1966 three of the 15 larvae that successfully overwintered had matured. Two of these

* On 19 June 1967, while this paper was in press, I checked the study area and found 14 adults, six of which (3 males and 3 females) were marked in 1965. One of the six, a male, was only six feet from the fungus on which he was marked on 19 July 1965. The other five were 15–80 feet from where they originally were marked, but not on the same logs. One female, marked 17 September 1965, was seen ovipositing in both 1966 and 1967. These observations increase the known adult life span to 725 days for a male and 759 days for a female. They also indicate that my observations are still inadequate to describe adult longevity: one female seen the last night of observation in 1967 was marked on the first night of observation in 1965, and the 1965 date was sufficiently early in the season to suggest strongly that she had already overwintered once as an adult.

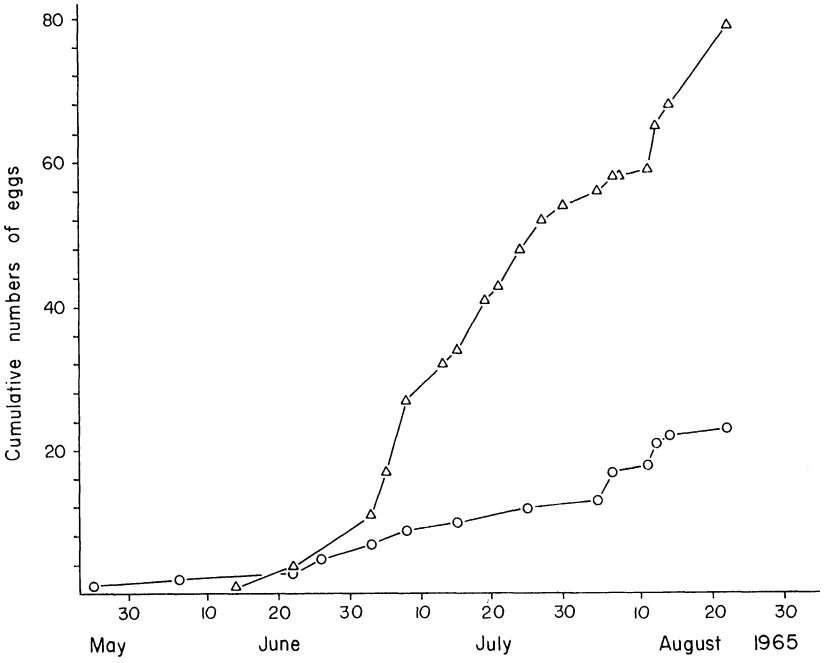


FIG. 1. Triangles show cumulative numbers of eggs found on sporophores 1–3 in the study area in 1965. Circles indicate cumulative numbers of eggs seen being laid on all sporophores in the area. These data indicate that there was no mid-summer gap in egg-laying in 1965.

adults were not yet dark. By 12 September seven more had matured; one larva was found dead and two others, not found, were presumed dead. Only two of the individuals remaining alive had not matured; those were still larvae in October.

TABLE 1

SIZE RANGES OF LARVAE COLLECTED ON VARIOUS DATES IN 1964 AND 1965 IN ANN ARBOR, MICHIGAN

Only small larvae are likely to be overlooked

Approximate width of head capsule (mm)	1964			1965	
	February	March	April	April	November
1	4	26	0	12	11*
1½	10	42	3	25	5
2	8	14	4	18	5
2½	2	8	1	14	20
3	11	0	2	10	8

* There were more, but they were not all counted.

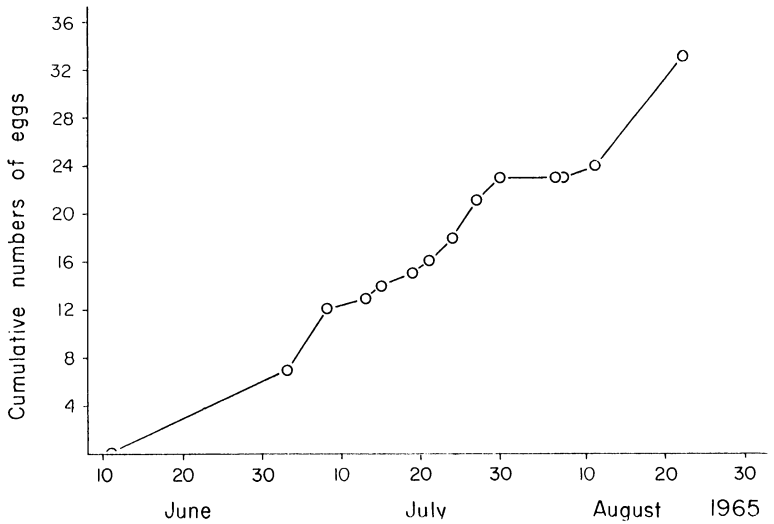


FIG. 2. Cumulative numbers of eggs found on sporophore 1 during 1965. Figures 1, 2, and 4 show that egg-laying does not occur throughout the summer on all sporophores.

Sporophore 4, observed in the same area during 1965, had as many as eight adults on it early in the summer (Fig. 4). I saw no females laying eggs on this sporophore after 8 July 1965. Five days later I noticed the lower surface was not producing spores. Between 8 July and 25 July no more than two adults were seen on the sporophore. No adults were seen on it after 25 July, except one on 6 August. On 1 November this sporophore was lying on the ground beside the log; it contained two unmarked adult females and larvae of all sizes, though most had head capsules 2.5 mm wide (Fig. 3). There were nine adult emergence holes in the lower surface.

Most overwintering larvae, especially those overwintering in later instars, probably mature before fall; some, however, may overwinter a second time, either as larvae or as adults, before reproducing. Larvae from eggs laid in early summer possibly do not mature until the following summer.

Activity records of females seen only in 1965 and of females seen in both 1965 and 1966 (Fig. 5) show that females observed both years were mounted by males relatively more often in 1965 than those seen only that year. On the other hand, females observed in 1965 but not in 1966 oviposited relatively more frequently in 1965 than females seen both years, especially later in the year. Figure 6 compares the same kind of information for 1965 and 1966 for females seen both years.

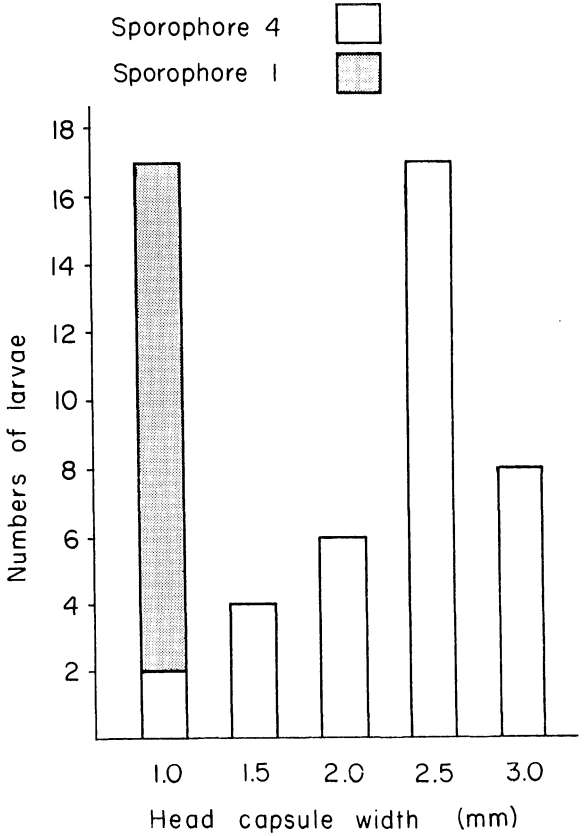


FIG. 3. Head capsule widths (mm) of larvae in sporophores 1 and 4 on 1 November 1965. All larvae in sporophore 1 came from eggs laid after 10 June 1965 (see Fig. 2). In addition to the larvae in sporophore 4 there were two unmarked adults and nine adult emergence holes. Most of the individuals in this sporophore probably came from eggs laid before 10 July 1965 (see Fig. 4).

Records of mating activity and aggression for males seen only in 1965 and for those seen in 1965 and 1966 (Fig. 7) show no similarly striking change in the activities of (presumably) older males, although there is a suggestion that younger males were reproductively active slightly earlier in 1965 and spent relatively more time mating and fighting than older males.

DISCUSSION OF ADULT LONGEVITY

Adults of temperate insects are usually thought to have relatively short reproductive lives and to reproduce only during one season. The only commonly noted exceptions are among some of the social insects

(termites, bees, and ants) in which some individuals may have very long reproductive lives. Norris (1964), however, states that "many beetles reproduce during more than one season . . . ." Only two of the three papers she cites support this statement. Based on a 25–30 per cent mortality per year in groups of adult dytiscids collected at all seasons, Joly (1945) concluded that the adult life of some kinds of dytiscid beetles is probably three to four years. Reproductive activity in all years was presumed. Waloff and Richards (1958) found that at least a few females of a chrysomelid beetle, *Phytodecta olivacea* (Forster), oviposited in two successive years and entered a third winter. De Wilde (1954) says that during warm summers a "small number of [second generation *Leptinotarsa decemlineata* (Say.)] . . . starts oviposition." Norris evidently presumes that these beetles enter diapause and oviposit the following spring, which is probable, but no evidence to this effect was presented by de Wilde.

I know of only two similar examples among beetles, besides *Bolitotherus cornutus,* in which the individuals observed were kept as nearly as possible under field conditions. Field observations of marked individuals of a subsocial passalid, *Popilius disjunctus* (Illiger), showed

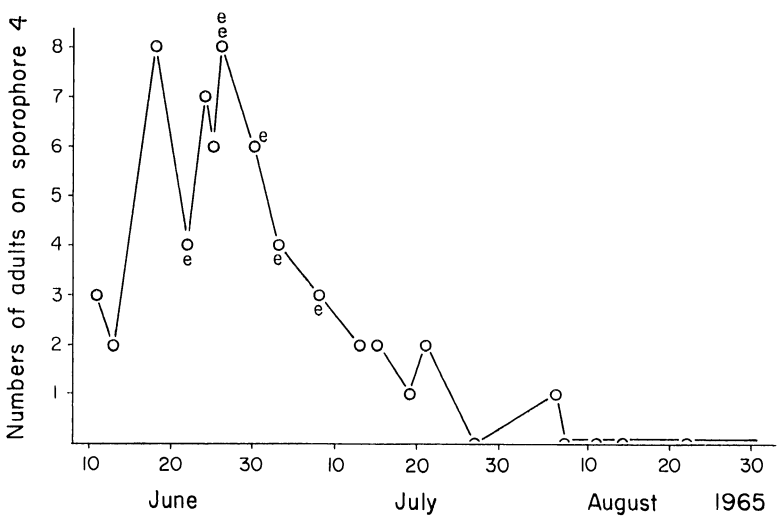
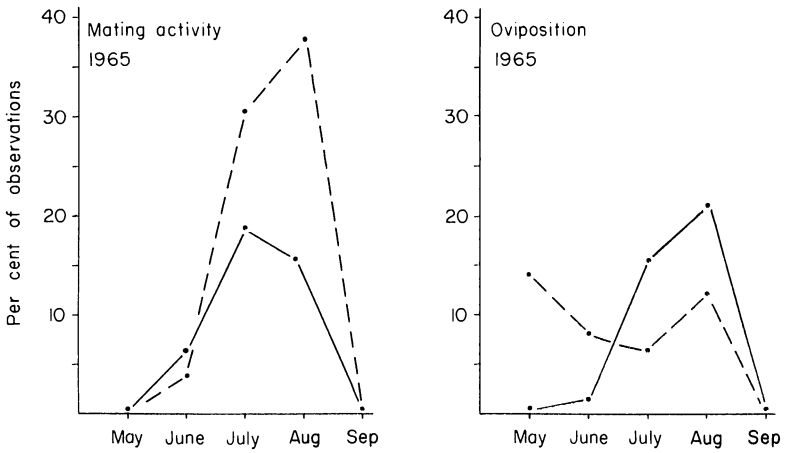


FIG. 4. Open circles indicate the number of adults found on sporophore 4 during 1965. Each "e" indicates a female seen laying an egg. Most oviposition on this sporophore probably occurred before 10 July 1965. Sporophore 4 probably died during the summer. On 13 July it was not shedding spores and on 1 November was lying on the ground beside the log.



	May	June	July	Aug	Sep	
females seen in 1965 and 1966	7	50	46	58	35	no. of observations
	5	9	12	16	22	no. of individuals
females seen in 1965 only	12	78	32	19	8	no. of observations
	8	21	8	9	6	no. of individuals

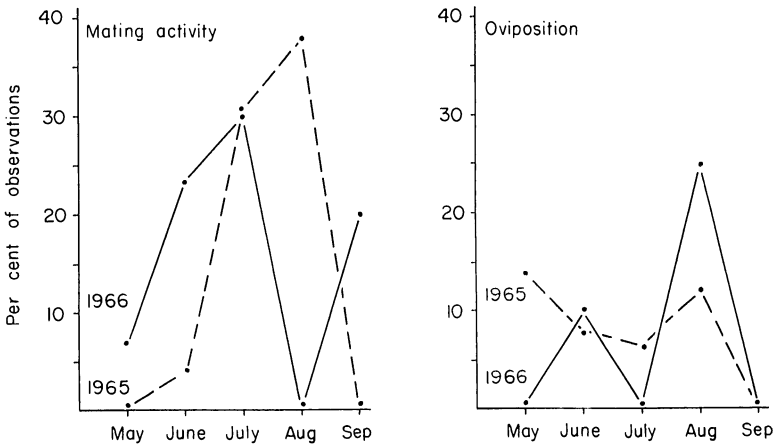
FIG. 5. Relative amount of mating activity and oviposition during 1965 by two groups of females: those seen only in 1965 (solid line); and those seen both in 1965 and 1966 (dashed line). The number of observations of females in every month for each group of females is given as the numerator below that month in the graph; the actual number of female individuals seen is given as the denominator. Per cent of observations of mating activity and oviposition are based on the total number of observations for each month.

that some adults live for two and possibly three years in North Carolina (Gray, 1946). Putman (1955) recorded oviposition of isolated individuals of a coccinellid beetle, *Stethorus punctillum* Weise, in an insectary and found the longest adult life of any individual under these conditions was 449 days. Of 11 females which matured in mid-summer 1951 and laid eggs that year, seven oviposited again in 1952. Five of these females died before October and the other two died during the winter of 1952 to 1953.

In the humid tropics, where there is presumably little or no seasonal restriction in the availability of resources, increases in adult longevity are probably frequently favored because they would usually result in increased reproduction. In temperate regions, on the other hand, even if there is no seasonal restriction in resource availability, increases in adult longevity would presumably be favored only when the additional offspring entered winter in an appropriate stage. In these regions

selection should favor a maximization of egg-laying during that restricted part of the growing season which would result in a maximum number of offspring entering winter in a favorable stage. If there is seasonal restriction in the availability of resources, or if only one or a few stages can overwinter, only those increases in adult longevity great enough to get reproducing adults into another reproductive season could be favored. Slight increases in longevity would probably not be advantageous.

When suitable resources are available throughout the year (a perennial fungus sporophore in this case), the existence of multiple overwintering stages (as in *Bolitotherus cornutus*) increases the proportion of the growing season favorable for egg-laying. Presumably this would increase the chances that advantageous lengthening of adult life could occur. In turn, the chances of adults surviving from one egg-laying period to the next, and thus reproducing in successive seasons, should increase. In some combination, these factors have probably been responsible for producing the present life cycle of *B. cornutus*.



	May	June	July	Aug	Sep	
1965	7	50	46	58	35	no. of observations
	5	9	12	16	22	no. of individuals
1966	29	30	3	4	5	no. of observations
	18	18	3	4	5	no. of individuals

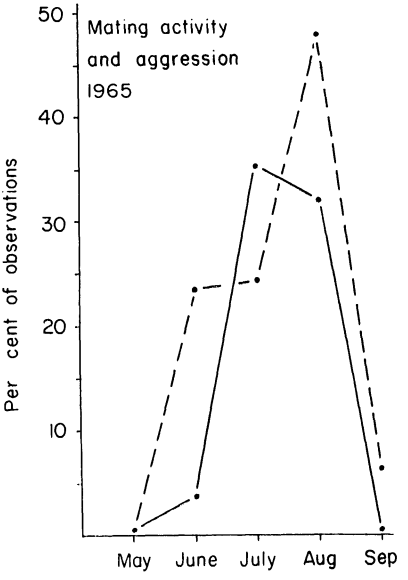
FIG. 6. Relative amount of mating activity and oviposition in 1965 (dashed line) and 1966 (solid line) by that group of females seen both years. The numbers of observations and individuals in each month for both years are given below the graph.

BEHAVIOR

This species is primarily nocturnal and, as Liles (1956) and Park *et al.* (1931) have noted, most activity occurs between about 8 P.M. and 4 A.M. The earliest activity noted by Park *et al.* was at 7:02 P.M. and the last individual they observed was at 6:27 A.M. Although most of my field observations were made between 9 P.M. and 3 A.M., (Eastern Standard Time) I saw oviposition as early as 3 P.M. and as late as 3:40 A.M., mating behavior between 2 P.M. and 5:30 A.M., and adults feeding in the middle of the day.

Behavior associated with mating has been briefly described by Liles (1956):

> Prior to mating, the male beetle clasped the female in such a manner that the ventral surface of his abdomen rested on the dorsal surface of her thorax, and the



	May	June	July	Aug	Sep	
males seen in 1965 and 1966	3	34	54	48	16	no. of observations
	2	7	11	14	11	no. of individuals
males seen in 1965 only	10	54	37	25	3	no. of observations
	5	16	8	9	2	no. of individuals

FIG. 7. Relative amount of mating activity and aggression (considered together as indicators of the total amount of reproductive activity) during 1965 in two groups of males: those seen only in 1965 (solid line); and those seen both in 1965 and 1966 (dashed line). The numbers of observations and individuals for both groups of males are given below the graph for each month observations were made in 1965.

> ventral surface of his thorax rested on the dorsal surface of her abdomen. When in this [reverse] position, the male rubbed the ventral surface of his abdomen across the two prominent tubercles which projected from the female's thorax. This produced a distinct rasping sound audible at a distance of six to eight feet from the fungus.

During 1965 I saw 60 pairs in the reverse position. In 18 of these the male turned around and attempted copulation with the female. Nine times the male returned to the reverse position after attempting copulation. In ten cases the male, when first seen, was mounted on the female in either the copulatory position or with both individuals facing the same direction but with their bodies parallel. One of these males later turned to the reverse position. Although I have watched males approach and mount females only a few times, in all cases the male assumed the reverse position before attempting copulation.

Park *et al.* (1931) describe seeing two females in the reverse position. It is probable, however, that the upper individual in each of the cases observed was a small male rather than a female. Very small males have disproportionately smaller horns on the thorax than larger males. These horns may lack the hairs which are present on the under surface of the horns of the larger males. For this reason the small males resemble females, which have only blunt tubercles not covered with hairs. I have not seen females in the reverse position, though I have mistaken small males for females before looking at them carefully.

Adult males are sometimes aggressive toward other males. I have not seen aggressive females or males showing aggressive behavior toward females. Aggression consists of butting or nudging another male with forward and upward movements of the head, sometimes with the mandibles open. The other male may reciprocate with the same kind of movements, remain in place without returning the blows, or move away. I have seen aggression only in the field.

Six of eight closely observed cases involved aggression toward males mounted on females in either the reverse or the copulatory position. In two of these six cases the aggressive male dislodged the mounted male from the female. One of these successful males immediately mounted the female. The displaced male walked away. In the other case the successful male antennated the female but did not mount her. He went toward the displaced male (which had stopped about two inches away) and again butted and nudged this individual, following him across the top of the fungus, once turning him on his back. The pursued male righted himself and walked rapidly away from the aggressor which followed him about an inch, nudged the fleeing beetle again, and then

returned to his original position (before the encounter) on top of the fungus. The female did not move away, but the male did not seem to pay any further attention to her. This encounter occurred on 14 August 1965 on sporophore 5. Territoriality is suggested since this aggressive male was seen in two other aggressive encounters on 25 July and on 7 August in the same place.

In the other four cases the mounted male was not dislodged by the aggressive male. In one case the mounted male was in the copulatory position. The two males butted each other and opened their mandibles. The female began to walk away and the male mounted on her turned around to the reverse position and began sound production. I watched these beetles 20 minutes more then left the area and returned after about 40 minutes. During the following 55 minutes the mounted male did not mate with the female. At the end of this period, while the male was mounted in the reverse position, the aggressive male butted him again, but still did not dislodge him from the female.

In two of the other three cases the aggressive male remained next to the pair. In the third case the aggressive male mounted another female less than 15 minutes after his last unsuccessful encounter.

During two cases of aggression neither male was courting a female. One of these cases seemed to involve a particular hole in a log. There were several exchanges between the two males and each one was followed by one of the males leaving the hole and stopping about one or two inches away. Once, the male which had left the hole and stopped about two inches away was followed by the other male and nudged again. This time the male did not return the blows, but simply walked farther away. The pursuing male then returned to the hole. During these exchanges this male once approached a nearby female, but otherwise neither of the males apparently paid any attention to her.

The second case involved the male subsequently observed in aggressive encounters on 7 August and on 14 August. In this case he butted another male head-on. This male turned, was butted again, and then moved away. In about five minutes he had moved off the sporophore and was about ten inches from the aggressive male. Thirty minutes later he had mounted a female and was about two or three feet away from the sporophore. Nearly three and one-half hours after leaving the sporophore he still had not mated with the female. The aggressive male was on top of the sporophore and had not pursued this male beyond its surface.

Several of these observations suggest that adult male *Bolitotherus cornutus* are sometimes territorial. The aggressive male in the last

encounter above was first seen on sporophore 5 the night of the encounter (25 July) and was seen within approximately eight inches of this place every time observations were made (except for a one-hour period on 30 July) from 25 July to 17 September 1965. Sporophore 5 was shedding many spores throughout this period. Until 13 July I had seen this male only on sporophore 4, but between that night and 21 July I saw him three times at other places on the same log and only twice on that particular sporophore. Sporophore 4 was probably dead before 13 July. It shed no spores after that date and fell to the ground before November 1965. This male was never seen in aggressive encounters on sporophore 4, but was subsequently seen in three aggressive encounters on sporophore 5. Since large numbers of spores occur only near healthy growing sporophores (suitable oviposition sites), and, since adults feed on spores when they are available, presence of spores may be the principal stimulus determining where adults are found and where males establish territories.

Adults of *Bolitotherus cornutus,* like those of some other tenebrionids, have abdominal glands which are exposed when the individual is disturbed. The substance produced has a pungent odor. It burns when it touches the inside of the mouth and is bitter tasting and nauseating. Some effect is still noticeable about half an hour after tasting. Exposure of the abdominal glands is not readily elicited by mechanical stimulation (poking, prodding, etc.). In these cases the animal gives a characteristic death feint, bringing its legs close to its body and then becoming immobile. As a result it usually rolls off any but a flat surface. The "defensive reaction," which involves exposing the glands with the abdomen raised in the air as in *Eleodes* (Eisner and Meinwald, 1966), is readily elicited by blowing gently on the beetle. Sometimes an individual continues to walk with these glands exposed, touching the tip of the abdomen to the stubstrate at intervals and leaving a visible trail. Eisner (1960) shows a photograph of another tenebrionid, *Diaperis maculata* Oliver, doing the same thing.

PREDATORS AND PARASITES

Larvae of *B. cornutus* are probably preyed upon by birds: I have found sporophores with holes in the top resembling those made by wood-pecking birds. Once I saw an ant chew open an egg capsule and carry away the anterior part of the larva that was beneath it; it might have removed the entire animal if I had not disturbed it. I once saw an adult female eating an egg which was probably her own since there was no evidence of a capsule near it.

TABLE 2

BRACONID PARASITES EMERGED FROM LARVAE COLLECTED IN MID-APRIL 1965

The total number of larvae collected is given in Table 1

Head capsule width of larvae (mm) when collected	Larval length (mm)	Number of parasites	
		Male	Female
1	—	2	0
1.5	10 or more	3	0
1.5	less than 10	2	1
2	—	0	4
2.5	—	0	0
3	—	0	0

Larvae are parasitized by a braconid wasp (*Eubadizon* sp.). Overwintering larvae, collected in mid-April 1965, were sorted by sizes, placed in separate screen-topped gallon jars on autoclaved sporophores, and kept outside in a shaded place on the roof of the University of Michigan Museum of Zoology until the following spring. No parasites emerged from the largest larvae. Female parasites generally emerged from larger larvae than males (Table 2). All wasps emerged between 24 May and 31 May 1965, and all were dead by 6 June 1965. No adult wasps have been seen in the field, and it is not known whether the degree of synchrony in emergence observed here is characteristic of the species as a whole.

SUMMARY

Larvae and pupae live inside sporophores of *Ganoderma applanatum*. Eggs are laid from May to September in southern Michigan, usually on the tops of sporophores, and eggs laid early in the year may mature before winter. Adults and all sizes of larvae overwinter. Observations of marked adults in the field during two summers showed that many males and females overwinter after passing through part of a reproductive season, and that at least some of these are reproductively active both years.

Adult males are sometimes aggressive, usually toward males mounted on females and, as a result, sometimes dislodge and replace these mounted males. They may also be territorial since some aggressive males were found in the same place night after night and chased other males away.

Gentle puffs of air elicit a "defensive reaction" from adults, involving exposure of abdominal glands; other mechanical stimuli usually elicit a death feint.

ACKNOWLEDGMENTS

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