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Sexual Broods and the Production of Young Queens in Two Species of Army Ants¹

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(Plates I-III; Text-figures 1 & 2)

HOW species of doryline ants produce their males and young queens is a biological enigma of long standing, toward the solution of which this paper is directed. The processes of sexual-brood production in these ants also prove to be important as prerequisites to colony division, a problem which will be considered in a further paper.

The problems of caste control and sex dimorphism have recently grown in interest for biologists (Flanders, 1939, 1950; Haydak, 1943; Whiting, 1943, 1945; Kerr, 1946; Berland, 1948). Although progress has been made, the basic processes are not well understood. The Dzierzon rule for insects, according to which males develop from unfertilized eggs and females from fertilized eggs (Newall, 1915; Wigglesworth, 1939; Grout, 1949) has much empirical standing but needs a cytological clarification (White, 1945; Whiting, 1945). The problems of polymorphism, or caste control within a sex, resist solution in terms of traditional blastogenic and trophogenic concepts used as alternatives (Goetsch, 1937; Gregg, 1942; Haskins & Enzmann, 1945). A broader and deeper range of evidence seems needed.

We believe that the circumstances concerning production of sexes and intra-sex castes in the doryline ants are sufficiently unique to repay careful study. Despite a lively speculative interest of long standing in the literature, coming to grips with this problem has been delayed by certain inherent obstacles to study (Wheeler, 1921). The mode of life of the dorylines made them an inconvenient subject for specialized observation and study, until a suitable methodology had been worked out. This was done in a series of investigations (Schneirla, 1933, 1938, 1944, 1947, 1948) which provided a necessary basis for the present work in method, evidence and theory.

Historical accounts of the early literature concerning doryline sexual individuals are available in papers by Wheeler (1921) and Schneirla (1948). Certain items considered most relevant to our present subject will be mentioned here.

From Marshall's observations, Brauns (1901) reasoned that African driver ants can establish nests only at such times as they breed new queens and males, since, he thought, the bulky larvae and pupae of these forms cannot be carried. Although this hypothesis remains untested

¹This investigation has been supported through a contract (5T, 164-468) with the Office of Naval Research, Biological Sciences Division. Laboratory studies have been supported in part by a grant from the Committee for Research in Problems of Sex, National Research Council. Through these grants, the help of Mrs. June Esserman, Miss Sarah Lichtenberg, Mrs. Rose Rizki and Dr. John Tafuri was available at various stages in the study of preserved material. The studies carried out in Panama in 1949 by Robert and Frances Brown, as well as those carried out in Trinidad in 1950 by the senior author, were subsidized by grants from the Research Fund of the Council of the Scientific Staff

of the American Museum of Natural History. Through the cooperation of Mr. James Zetek, Custodian of the Canal Zone Biological Area, arrangements for the field projects of 1946, 1948 and 1949 benefited indispensably. By his kindness in offering the hospitality of his field station at "Simla," Dr. William Beebe of the New York Zoological Society made possible the field studies of 1950 in northern Trinidad, and through aid from Trinidad Leaseholds, Ltd., with arrangements, the studies were extended to the Guayaguayare section. We are indebted to Dr. Roy Whelden, Haskins Laboratory, Union College, for histological and cytological evidence obtained in his studies on the queens of eciton.

for doryline species in the Old World, it is wrong for New World species thus far investigated. In species of *Eciton* (*Eciton*) in tropical America, the normal pattern of events involves sessile ("statory") phases at regular intervals, alternating with nomadic phases in which colony activity is maximal and colony emigration is regular (Schneirla, 1933, 1938, 1949). Nomadism and its cessation depend upon social stimulative processes introduced or removed according to the condition of developing broods, but not upon any difficulty in transporting a brood (Schneirla, 1948; Schneirla & Brown, 1950).

Brauns' idea is of interest, however, because of its implication that doryline ants produce their sexual forms under exceptional conditions. Of course, the production of sexual individuals at characteristic times of year and under more or less specialized conditions is common among social insects. Queens are produced in honey bee hives when food is especially plentiful (Grout, 1949), in bumblebee colonies late in the summer (Cumber, 1949), and in temperate-zone ants at times from spring to autumn more or less distinctive of the species (Wheeler, 1913, 1928; Talbot, 1945). As it proves, the dorylines are similar to many other social insects in this respect.

Evidence concerning the production of males accumulated slowly and in piecemeal fashion. Winged males of *Aenictus* sp. were observed in India by Wroughton (1892), and Marshall (Brauns, 1901) witnessed "large numbers" of alates issuing from the exits of a subterranean nest of *Dorylus nigricans*. Hetschko (Mayr, 1886) found "a number" of winged males of *E. (Neiv.) hetschkoi* in nests excavated at Parana, Brazil, and others since have made similar observations on various species of the subgenera *Labidus* and *Neivamyrmex* (= *Acamatus*) in the Americas. Near Austin, Texas, Wheeler (1900) saw winged males "in numbers" leaving a nest of *E. (Neiv.) schmitti* established beneath a stone. Eight days after Gallardo (1915) had dug 50 alate males from a nest of *E. (Neiv.) spegazzinii*, "numerous" males were seen taking off from the same site. "Numerous" enclosed male pupae of *E. (Neiv.) hetschkoi* at an advanced stage of development were found by Hubrich in an underground nest in the northern Argentine and were sent to Bruch (1924) for study. From a colony of *E. (Neiv.) opac. castaneus* observed by Schmidt (Borgmeier, 1948) in Brazil 65 advanced male pupae were taken, 15 of which were freshly emerged; in another, 7 male pupae were found.

Such observations suggest that doryline males appear in distinctive broods, which are fairly large (Gallardo, 1920) and are present only for

a limited time in their colonies (Bruch, 1934). This fact was established securely for two species of *Eciton* (*Eciton*) by Schneirla (1948). Unfortunately, almost no useful information can be gleaned from previous reports of doryline males observed in different parts of the world, relevant to what biological conditions may have attended the production of the respective broods.

Since doryline queens are wingless throughout life, prior evidence concerning their origin and background is very scanty. Unfortunately, the convention developed of terming eciton queens with contracted gasters virgin or young (Gallardo, 1920; Wheeler, 1921; Bruch, 1934), on the incorrect assumption that functional queens must lay eggs or be physogastric more or less continuously. Actually, the gaster of a functional colony queen becomes physogastric only at distinct intervals during the year, and is contracted during intervening periods (Schneirla, 1938, 1944, 1949). It seems to be the rule, as Wheeler (1921) surmised, that normal colonies of *Eciton* (*Eciton*) and perhaps all doryline species contain only one functional queen.

The previous literature on the American genus *Eciton* contains three records of colonies which apparently had young queens, two cases in the subgenus *Neivamyrmex* (= *Acamatus*) and one in *Eciton* (*Eciton*). In a colony of *E. (Neiv.) nigrescens* (= *schmitti*) found by Wheeler (1900) in the vicinity of Austin, Texas, two queens were found among clusters of workers under a stone. The smaller of these was judged circumstantially to be young and virgin; the larger, observed in the laboratory, laid eggs and was evidently the functional queen of the colony. A third queen, intermediate between these two in length and appearance, was found in a tight cluster of workers some days later. It is probable that she was a sister to the other young queen, present all along among the collected ants but previously overlooked in the clusters. In a presumably similar case reported by Bruch (1934), two queens were found in a colony of *E. (Neiv.) hetschkoi* var. *ogloblini* in northern Argentina, October 20, 1932. One was considered virgin because her gaster was contracted (a faulty surmise in itself), the other adult because she laid eggs. The first queen was supernumerary, we believe, and a recently emerged virgin queen (see section 7).

While the first discoveries of what presumably were young queens concerned *Neivamyrmex*, a later finding in the subgenus *Eciton* (*Eciton*) is circumstantially clearer. In a colony of *E. burchelli* encountered by Wheeler and Emerson in British Guiana on July 21, 1920, in addition to some hundreds of nearly mature male pupae in

cocoons, two "fresh-looking" queens were found moving within masses of workers smoked out from their hollow tree bivouac. Wheeler's comments (Wheeler, 1921) are interesting:

"I believe . . . that the large burchelli colony which Mr. Emerson and I were able to investigate, had already completed the production of its annual brood of workers and soldiers, and that the sexual forms constituted a later or, at any rate, a retarded brood, consisting of a large number of males, all in the same stage and destined to hatch before the end of July, or before the incidence of the dry season, and a very few females, which had hatched before any of the males."

Three of these conjectures find support in our evidence: the distinctness of sexual broods from worker broods, the common age of individuals in a sexual brood, and the presence of only a few queens in the same brood with males. Contrary to Wheeler's (1921) impression, eciton colonies do not produce just one annual worker brood but several, and at regular intervals. This fact was established by the senior author in studies on Barro Colorado I. in the rainy seasons of four different years (Schneirla, 1933, 1938, 1944). Further results show that in species of *Eciton* (*Eciton*) a similar production of worker broods occurs periodically in the dry season as well. In southern Mexico, during the dry months from December, 1944, to May, 1945, 24 colonies representing four species were found with all-worker broods (Schneirla, 1947). There was only one exception.

In early April of 1945 a colony of *E. hamatum* was found near Modelo, Oaxaca, with a brood estimated to contain nearly 2,000 large cocoons. In a sample of more than 500 of these, only male pupae were found in 400 cocoons which were opened, and the remainder were judged identical in a candling operation. However, this was not an all-male brood as reported (Schneirla, 1947), for recently in removing the remaining specimens from cocoons a single queen pupa was found among them (Plate II; Figures 5 & 6).

In a further study on Barro Colorado in the dry season of 1946 (Schneirla, 1949), 10 sexual broods and 60 worker broods were found in the 49 colonies of *E. hamatum* and *burchelli* brought under study. One colony on record for more than four months produced a series of five all-worker broods; another, in the same interval, produced a sexual brood as its second in a series of five (otherwise all-worker) broods. In all samples taken of these sexual broods, only male specimens were found. There was, however, one possible exception. This was the case of colony '46 B-I (*E. burchelli*), in which a supernumerary

queen was found during a complex series of events following the emergence of males from cocoons (Schneirla, 1949, pp. 33 f.). A later histological examination showed that this queen was virgin. Altogether, this case closely resembles that reported by Wheeler (1921), in which two "fresh-looking" queens were found among pupal males.

The production of young queens and males was clarified in our investigation of 1948, which provides the main basis for the present paper.

PROBLEM AND HYPOTHESES

We are concerned here with the conditions and processes essential to the production of sexual individuals, and with the production of new queens in particular, in two species of *Eciton* (*Eciton*).

First, we set out to test a hypothesis supported by previous results (Schneirla, 1938, 1948, 1949), namely, that sexual individuals are produced in distinct broods arising through the impact of dry-season conditions upon a functional eciton queen.

Although we expected to find young queens produced together with males in the same dry-season broods, to cover alternative possibilities our investigation extended from the last part of a rainy season through most of the following dry season.

GENERAL SCHEDULE; LOCALITIES

Field studies were carried out on the behavior and biology of eciton species, chiefly *E. hamatum* and *E. burchelli*, from November 7, 1947, to March 20, 1948. This period included the last five weeks of a rainy season and the first three months of a dry season.

The rainfall pattern during this period is represented by the data in Table 1 (see also Fig. 1, Schneirla, 1949). Although the terminal rains in November and December, 1947, were lighter than is typical for the locality, the dry period which set in after mid-December was normal in its timing, and fairly consistent except for a limited recession in January.

The principal investigation was carried out at Barro Colorado Island, C.Z., with auxiliary surveys in other areas of Panama (Fig. 1, Schneirla & Brown, 1950). There was a survey of 10 days in the Candelaria forest north of Madden Lake, at the end of the 1947 rainy season; another of two weeks in the Tuirá R. area of Darien in eastern Panama, about 50 days after the 1947 rains had ended in that area; and one of two weeks in the El Valle area west of the Canal Zone, in early March or somewhat past the middle of the dry season.

Thus, conditions during the terminal rains were studied both at Barro Colorado and one other locality; conditions of the dry season at Barro Colorado and two other localities.

METHOD AND PROCEDURES

Previous publications furnish extensive reports on methods and results of the field investigations of 1946 (Schneirla, 1949) and 1947-1948 (Schneirla & Brown, 1950). These publications are basic to this paper.

All sections of Barro Colorado Island except the southwestern part were patrolled for a maximal coverage of colonies. Colonies of both *E. hamatum* and *burchelli* were studied over considerable periods, with especial attention to colonies with sexual broods (for colony protocols, see Schneirla & Brown, 1950, pp. 276-310, also Figs. 2 and 3). Such long-term studies were aided greatly by a technique for permanently marking colony queens.

Records covered significant features of colony behavior such as the status of raiding and emigration, and of biological condition as indicated by bivouac formation, brood condition and queen's condition. Observations were extended in detail, and supplemented by appropriate tests, for colonies with sexual broods.

TABLE 1. RAINFALL RECORDS FOR BARRO COLORADO ISLAND, C. Z., FOR THE SEASONAL TRANSITIONS OF 1945-1946 AND 1947-1948

Season	Interval	Semi-monthly totals* (in inches)		
		1945-1946	1947-1948	
Rainy	September	1-15	6.29	4.99
		16-30	3.78	4.54
Rainy	October	1-15	4.37	7.00
		16-30	5.65	6.17
Rainy	November	1-30	7.42	4.33
		16-30	13.18	2.92
Rainy	December	1-15	21.04	4.99
Dry	December	16-31	3.36	0.64
Dry	January	1-15	0.43	0.78
		16-31	0.02	0.86
Dry	February	1-15	0.29	0.02
		16-28(29)	0.03	0.17
Dry	March	1-15	0.10	0.02
		16-31	1.61	0.15

* These records were obtained with a standard rain gauge located in the clearing near the main laboratory building at Barro Colorado I. They are used here through the kindness of Mr. James Zetek.

On Barro Colorado, broods of all colonies under longer study were sampled at intervals of two or three days. To minimize interference with natural events, all samples of sexual broods were held below ½%. Samples for histological study were fixed appropriately in Bouin solution, then stored in 70% alcohol.

In the Candelaria, Darien and El Valle areas, patrolling was scheduled to furnish the maximum possible number of colonies for cross-sectional studies of behavior and biological condition. As a rule, a colony was studied for only a few hours on the day of discovery. In these colonies, large randomized brood samples were taken and, in most cases, the queen was captured for preservation.

RESULTS

1. *Composition and timing of all-worker broods.* In the last weeks of the 1947 rainy season on Barro Colorado I., from November 7 to December 10, only all-worker broods were found in eciton colonies. In 14 colonies of *E. hamatum* investigated, there were 21 worker broods, and in 6 colonies of *E. burchelli*, 10 worker broods. In Candelaria, between December 10 and 19, 9 all-worker broods were found in 7 colonies of three eciton species. No sexual broods were discovered before the dry season began.

As Table 2 shows, none but all-worker broods were found in four previous rainy-season investigations on Barro Colorado (Schneirla, 1938, 1944). In these studies, a total of 103 worker broods was found in 81 eciton colonies.

All-worker broods also are produced by colonies of *E. hamatum* and *burchelli* in the dry season, as may be seen from Table 2. In 17 colonies of four species of *Eciton* (*Eciton*) studied in Mexico in the dry season of 1945, 20 broods in 21 were all-worker broods; in 51 colonies of four species studied on Barro Colorado in the dry season of 1946, 73 broods in 83 were worker broods; and in 41 colonies studied in the present investigation, 57 broods in 67 were worker broods.

Continuation of a periodic brood production throughout both seasons, with all-worker broods predominating, may be considered the rule for colonies of *Eciton* (*Eciton*). In all probability, the spacing of broods is much the same for each species, from season to season, and values obtained in the dry season are close to standard for the year. Our evidence indicates a mode of 36 or 37 days for the cycle in *E. hamatum* and of 33 to 35 days for *burchelli*, with greater variation in the latter (Schneirla & Brown, 1950,

TABLE 2. ECITON BROODS IDENTIFIED IN DRY AND RAINY SEASONS

Year and place	Species	RAINY SEASON				DRY SEASON			
		No. of Colonies	All-worker	Type of brood		No. of Colonies	All-worker	Type of brood	
				Eggs; or queen physogastric*	Sexual			Eggs; or queen physogastric*	Sexual
1932-1938 (4 seasons) Panama	<i>E. hamatum</i>	53	65	4	—				
	<i>E. burchelli</i>	28	38	2	—				
1945 Mexico	<i>E. hamatum</i>					6	6	4	1
	<i>E. burchelli</i>					8	11		
	<i>E. rogeri</i>					2	2	1	
	<i>E. vagans</i>					1	1	1	
1946 Panama	<i>E. hamatum</i>					31	47	1	4
	<i>E. burchelli</i>					18	23	2	6
	<i>E. rogeri</i>					1	1		
	<i>E. vagans</i>					1	2		
1947 Panama	<i>E. hamatum</i>	17	26		—				
	<i>E. burchelli</i>	7	12		—				
	<i>E. conquistador</i>	2	2		—				
1948 Panama	<i>E. hamatum</i>					23	33	2	6
	<i>E. burchelli</i>					18	24	2	4
1949 Panama	<i>E. hamatum</i>	6	7	1	1				
	<i>E. burchelli</i>	1	1						
1950 Trinidad	<i>E. burchelli</i>	26	36	3	1				
	<i>E. vagans</i>	1	2						
TOTALS		141	189	10	2	109	150	13	21

* Nature of brood not established.

Tables 6 and 7). With sexual broods, cycle durations are appreciably shorter in both species.

Examination of many eciton broods under a variety of conditions in both seasons indicates that worker broods tend to be much the same throughout the year. Single worker broods of *E. hamatum* may be estimated at 25,000 individuals, those of *burchelli* at close to 35,000 (Schneirla, 1944), with no evidence for substantial reductions in the dry season. Furthermore, the composition of these broods is very similar in each species throughout the year—a unimodal and continuous polymorphic series not appreciably different in the range of body sizes.

2. *Sexual broods: time of discovery and number studied.* Results for the discovery of eciton broods in the two seasons are summarized in Table 2. It is clear for the localities concerned that sexual broods are to be expected in the dry season but are very exceptional in rainy months.

Because extensive surveys have been made in

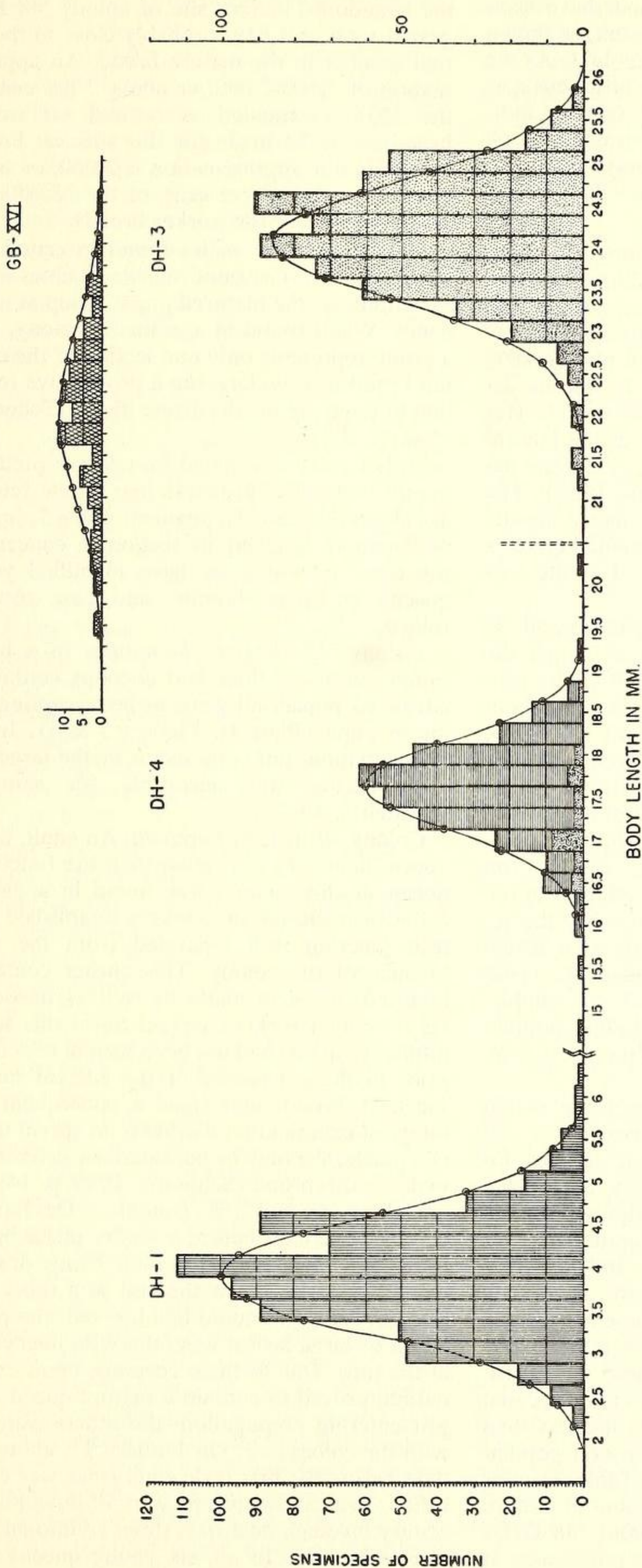
both seasons on Barro Colorado I., results for that locality may be considered basic to our point. In six different rainy seasons there, only one sexual brood was found in a total of 145 broods examined in 108 colonies; whereas in two dry seasons, 14 sexual broods were found in a total of 115 broods examined in 178 colonies. Altogether, in this and other areas in tropical America, 14 percent. of 185 broods examined in the dry season, but only 1 per cent. of 201 broods examined in the rainy season, have been sexual broods.

In the general program of investigation, 23 sexual broods have been found, 15 of them on Barro Colorado Island. In our studies, 12 sexual broods have been discovered in colonies of *E. hamatum*, and 11 in colonies of *burchelli*. Information concerning the specific times and conditions of discovery of these broods will be found in Table 3.

3. *Population characteristics of sexual broods.*

TABLE 3. SEXUAL BROODS STUDIED

Colony and species	Place	Season	Condition of brood when discovered	Period of observation	Composition of brood	
					Males	Queens discovered
'45 H-N <i>E. hamatum</i>	Coatzacoalcos R. area, Mexico	Dry	Advanced pupal stage; all enclosed	Apr. 23, 1945	Est.: 1,000- 2,000	1
'46 B-II-X <i>E. burchelli</i>	Barro Colorado Island, C. Z.	Dry	Nearly mature larvae	Mar. 19 to Feb. 20, 1946	Est.: 2,000+	?
'46 B-III <i>E. burchelli</i>	"	Dry	Callow males, 100- 200 still enclosed	Mar. 1-3, 1946	2,740+ pupa cases	?
'46 B-I <i>E. burchelli</i>	"	Dry	Early larval stage	Mar. 2, 1946	Est. 3,000	1
'46 B-IV <i>E. burchelli</i>	"	Dry	Alate males in flight condition	Mar. 6 to Apr. 3, 1946	Est. 500 remaining	?
'46 B-V <i>E. burchelli</i>	"	Dry	" "	Mar. 29 to Mar. 30, 1946	Est. 1,000 remaining	?
'46 B-VI <i>E. burchelli</i>	"	Dry	" "	Mar. 31 to Apr. 20, 1946	Est. 500 remaining	?
'46 H-J <i>E. hamatum</i>	"	Dry	Early larval stage	Apr. 3 to 4, 1946	Est. 3,000	?
'46 H-K <i>E. hamatum</i>	"	Dry	Larvae, est. two- thirds mature	Apr. 4, 1946	Est. 2,000	?
'46 H-L <i>E. hamatum</i>	"	Dry	Callow males in pre- flight condition	Apr. 9 to 10, 1946	Est. 2,000 (Probably high)	?
'46 H-M <i>E. hamatum</i>	"	Dry	Callow males in pre- flight condition	Apr. 10 to 11, 1946	Est. 2,000 (Probably high)	?
'48 H-12 <i>E. hamatum</i>	"	Dry	Newly laid eggs	Dec. 20, 1947 to Feb. 3, 1948	Est. 15,000+ as eggs; 2,000 at maturity	5
'48 B-XVII <i>E. burchelli</i>	"	Dry	Early larval stage	Jan. 23 to Mar. 2, 1948	Est. 2,500	2
'48 H-19 <i>E. hamatum</i>	"	Dry	Early larval stage	Jan. 21 to Feb. 20, 1948	Est. 2,000	?
'48 H-27 <i>E. hamatum</i>	"	Dry	Early larval stage	Feb. 11 to Mar. 19, 1948	1,619 pupa cases	3
'48 DH-1 <i>E. hamatum</i>	Darien, Panama	Dry	Early larval stage	Feb. 14, 1948	Est. 2,500	2
'48 DB-I <i>E. burchelli</i>	"	Dry	Callow males; some hundreds enclosed	Feb. 14 to 23, 1948	Est. 3,000	?
'48 DB-II <i>E. burchelli</i>	"	Dry	Alate males in flight condition	Feb. 18, 1948	Est. 2,000	?
'48 DH-3 <i>E. hamatum</i>	"	Dry	Mature larvae	Feb. 21, 1948	Counted 1,447	8
'48 DB-III <i>E. burchelli</i>	"	Dry	Mature larvae	Feb. 27, 1948	Est. 2,800	?
'48 DH-4 <i>E. hamatum</i>	"	Dry	Larvae in inter- mediate stage	Feb. 27, 1948	Est. 2,000	1
'49 H-32 <i>E. hamatum</i>	Barro Colorado Island, C. Z.	Rainy	Alate males, est. 8 days post-emergence	Aug. 4 to Sept. 5, 1949	A few hundred	?
'50 GB-XVI <i>E. burchelli</i>	Guayaguayare, Trinidad, B. W. I.	Rainy	Mature larval stage	July 10, 1950	Est. 3,000 (unenclosed)	2



TEXT-FIG. 1. Distributions of individuals in large samples representing the sexual broods of four eciton colonies, taken at distinctly different growth stages. Colonies and their samples: '49 DH-1, *E. hamatum*, early larval stage, 598 cases; '48 DH-4, *E. hamatum*, intermediate larval stage, 305 cases; '48 DH-3, *E. hamatum*, at larval maturity, 598 cases; and '49 GB-XVI, *E. burchelli*, at larval maturity, 85 cases. Note the "dwarf" cases of DH-3 (stippled) overlapped with the DH-4 distribution. The respective degrees of significance of fit to a theoretical normal population may be represented by respective acceptance levels of H_0 as follows: DH-1, acceptance at the .01 level when the two largest specimens, both queen larvae, were excluded; DH-4, acceptance at the .1 level when the largest specimen, a queen larva, was excluded; DH-3, acceptance at .05 level; GB-XVI, acceptance at the .3 level of significance.

In our investigations, sexual broods have been studied at all stages from egg to adult, as shown by the summary of records in Table 3. As we shall demonstrate, they are very distinctive as broods, composed almost entirely of male individuals, with a very few queens but no workers. Also, all individuals in a sexual brood begin and end their development within a few days of one another.

Only in one case, that of colony '48 H-12 (Schneirla & Brown, 1950, pp. 283 ff.), have we observed a sexual brood in the egg stage. The queen of this colony was taken from the statary bivouac in a condition of maximal physogastry, her gaster fully as distended as in queens delivering the eggs of eventual worker broods. Her behavior in egg-laying, observed in the laboratory, was closely similar to that of queens delivering worker broods (Schneirla, 1944). The eggs of this brood, viewed en masse in the bivouac when laying was done, seemed quite as numerous as with a worker brood at the corresponding time.

From gross observations of sexual broods at very early larval stages, we have gained the strong impression that such populations are very substantially reduced in number before about the second or third nomadic day (Text-fig. 1). More specifically, in all, 1,376 specimens were taken from this brood in samples (for preservation) obtained on December 21 and 26 from the field bivouac and from lots laid in the laboratory by the queen during her captivity on December 21. Although only a small part of the observed eggs, this number approaches the recorded population totals given below for sexual broods in this species at pupal maturity. These preliminary observations should be supplemented by further evidence including population counts at early stages, since the point is an important one.

Successive observations of the same sexual broods at times between early larval stages and pupal maturation, in taking brood samples, indicate that small reductions may take place during that time. A further although limited reduction of the sexual brood population after larval enclosure is indicated by the fact that dozens of empty pupa cases are frequently found in the statary bivouacs. These are usually taken at the border of the brood-free side of the cluster, where the functional queen is located.

Our estimates and counts of mature sexual brood populations show that they are less than 10 per cent. as large as worker brood populations in the respective species (Table 3). For *E. hamatum*, a nearly complete count of mature larvae in the sexual brood of colony '48 DH-3 gave a total of 1,447; a count of pupa cases at

the abandoned statary site of colony '48 H-27 gave a total of 1,619, probably close to the actual number in the mature brood. An approximation of 1,500-2,000, or about 7 per cent. of the 25,000 estimated as normal for worker broods, may be made for this species. For *E. burchelli*, our approximation is 3,000, or somewhat more than 8 per cent. of the 35,000 estimated as normal for worker broods.

Batches of alate males found in eciton bivouacs (Table 3) are not reliable as clues to the magnitude of the matured pupal group at emergence. When found in a nomadic colony, such a group represents only one section of the original brood now undergoing a progressive reduction through nightly departure flights (Schneirla, 1948, p. 100).

Although eciton sexual broods are predominantly male, it is probable that a few females are always present. To augment Table 3, further information is given in section 7 concerning the cases in which we have identified young queens in sexual broods, and case résumés follow.

Colony '45 H-N, *E. hamatum*. In a brood sample of more than 500 cocoons containing advanced pupae, all were males excepting one queen pupa (Plate II, Figures 5 & 6). In the field situation, only one sector of the large bivouac cluster was accessible for sampling (Schneirla, 1947).

Colony '46 B-I, *E. burchelli*. An adult, active queen, lighter in coloration than the functional queen of this colony, was found in a distinct cylindrical cluster of workers established at a trail junction well separated from the main bivouac of the colony. This cluster contained hundreds of alate males as well as masses of very young (worker) larvae. Since this supernumerary queen had not been seen in the colony prior to the emergence of the current mature (sexual) brood, and since a subsequent histological examination disclosed no sperm in her receptacle, she may be considered a sister of the males in this brood (Schneirla, 1949, p. 34).

Colony '48 H-12, *E. hamatum*. On January 8, 1948, two days before a statary phase began, four large cocoons were seen being dragged along by workers near the end of a short emigration. As far as could be observed, the population of large larvae was otherwise unenclosed at the time. One of these cocoons, upon examination, proved to contain a mature queen larva just entering prepupation—the others were left with the colony. . . . On January 27, about two days before the first male emergence was established, two callow queens were observed at the statary bivouac; next day, three additional ones were seen. . . . In all, six young queens were

identified in this brood (Schneirla & Brown, 1950, pp. 285 ff.).

Colony '48 H-27, *E. hamatum*. On March 5 and 6, 1948, before any males had emerged, three callow queens were observed at the statory bivouac (cf. Plate III, Fig. 7). From other signs, a fourth may have been present. Two of these young queens were picked up alive at the deserted statory bivouac site when colony division was nearly finished; the third went off with one daughter colony as its queen. Collected on the eighth nomadic day, she was found to have been inseminated meanwhile (Schneirla & Brown, 1950, pp. 304 f.).

Colony '48 B-XVII, *E. burchelli*. On January 27, 1948, probing of the lower margin of the bivouac cluster brought forth two fully formed cocoons. This was before any male larvae were found enclosed, and two days before the colony definitely settled into a statory phase. Both cocoons contained developing queens (Plate I, Figure 1). One was preserved as an early prepupa; the other (Plate II, Figure 4) was raised to the late pupal stage in a laboratory nest (Schneirla & Brown, 1950, p. 306).

Colony '48 DH-1, *E. hamatum*. In a preserved sample containing an estimated one-third of this brood (see section 4 and Text-fig. 1), the two largest specimens were found to be queen larvae, all others male (Schneirla & Brown, 1950, p. 313).

Colony '48 DH-3, *E. hamatum*. During a complete examination of this brood upon its removal from the colony bivouac in the field, all larvae were found naked with the exception of 14 which had begun to spin cocoons. Eight of these were queen larvae (Schneirla & Brown, 1950, p. 315).

Colony '50 GB-XVI, *E. burchelli*. In this case (see Table 3), found in Trinidad, the bivouac cluster contained a large sexual brood nearly at larval maturity. The brood was inspected part by part as the bivouac was demolished, and all larvae were found unenclosed with two exceptions. One of these, in a complete cocoon, was found to be a queen prepupa (Plate I, Figure 2); the other, in an incomplete cocoon, was a somewhat less advanced queen prepupa.

Since we have identified young queens as members of sexual broods in eight different cases, their development in the same broods with males seems well established. No young queens at any stage of development have been taken except in connection with male broods. Young queens are very few in number, at least after an early larval stage, and easily overlooked. Our largest number of identified callow queens in a brood is five, the next largest, three; of identified

mature larvae eight, and next largest, four. How many potential queens may be present at early larval stages, prior to the second nomadic day, cannot be said at this time.

Once suitable methods had been developed, young queens were found with regularity in sexual broods, although always in very small numbers. Early queen larvae were found in large samples from the sexual broods of colonies '48 DH-1 and DH-4 by taking the largest specimens, and all others were male; they were found as mature larvae or prepupae in colonies '48 H-12, B-XVII, DH-3, and '50 GB-XVI, on the expectation that queen larvae become enclosed before males; they were found as emerged callows in colonies '48 H-12 and H-27 on the expectation that queens complete their development and leave their cocoons before males. Thus our earlier failure to find queens in certain sexual broods (Schneirla, 1949) cannot be accepted as evidence that none were present.

4. *Distribution of individuals in sexual broods.* Except for a few queens, eciton sexual broods contain only males. A useful conception of individual differences in these broods is given by three samples taken from different colonies of *E. hamatum* (Text-fig. 1) studied in Darien, R.P., in February of 1948. Each of these samples was randomized, and each very large. Fortunately, the three brood populations when found and sampled were at very different stages of larval development, as may be seen in Text-fig. 1. Circumstances indicated that colony DH-1 was in its second day of a nomadic phase when an estimated one-third of its early-stage larval brood was taken; colony DH-4 was entering the last third of a nomadic phase when an estimated one-sixth of its intermediate-stage larval brood was taken; and colony DH-3 was in its last or next to last day of a nomadic phase when nearly one-half of its mature larval brood was taken (Text-fig. 1). (Except for small Bouin-fixed lots, all three brood samples were preserved in 70 per cent. alcohol). Large samples from the sexual brood of colony '45 H-N (*E. hamatum*) at an advanced pupal stage and that of colony '50 GB-XVI (*E. burchelli*) at larval maturity have been available for comparison.

Studies of the larval samples have included measurements of total body length, body width at fifth segment and dimensions of leg buds. Measurements were made in a standardized manner with micrometer calipers under low-power magnification, with separate anterior and posterior measurements to correct for body arcing in larval specimens.

Since no evidence has been found for poly-

morphic specialization in any male population, data on body length will serve for a general comparison of these cases. The three samples of different sexual broods at early, intermediate and late stages of larval development, are represented in Text-fig. 1. The distributions of the DH-1 and DH-4 brood are unimodal and fit a theoretical normal-frequency distribution curve to a fairly good approximation (see legend, Text-fig. 1). In contrast to these distributions, that of the DH-3 sample is somewhat skewed and exhibits a distinct although minor bimodality. Since no other sexual brood closely observed at larval maturity (e.g., H-12, H-27) has departed from a unimodal pattern, we are considering DH-3 a special case. This judgment is supported by the fact that the samples of sexual broods from both colony '50 GB-XVI, taken at a stage of larval maturity (see Text-fig. 1) and '45 H-N, taken at an advanced pupal stage, closely approximate a normal-frequency pattern.

We have found only two deviations from the normal-frequency pattern in sexual brood populations sampled after an early larval stage has been reached (i.e., after their colonies have passed the second nomadic day). The first is a limited departure, theoretically expected in all eciton sexual broods. It occurs at the upper extreme of the size distribution, involving the young queens. In the DH-1 sample the two queens found were the longest, and in the DH-4 sample the one queen found was the longest in the series. With these omitted, the normal-frequency fit is a closer one in each case. (The DH-3 sample cannot be considered a randomized sample with respect to the upper extreme, since, as mentioned in section 3, 14 specimens were removed which had begun to spin. Eight of these were queens, the others probably among the largest of the male larvae.² It seems probable that the male populations of eciton sexual broods, considered after they have passed an early larval stage, tend to approximate a smoothly graduated normal-frequency distribution.

The DH-3 male distribution clearly deviates from the others in two particulars. Not only is the principal bulk of the curve definitely skewed upward, but there is also a cluster of small individuals well separated from the main body of the population. All of these last individuals were seen at the time of collection, but more than a dozen of them were quickly bundled away by

workers. A randomized sample of the remaining smallest members of the population is represented in Text-fig. 1, where it falls within the size range of the DH-4 sample. Clearly, the case of colony DH-3 calls for separate study.

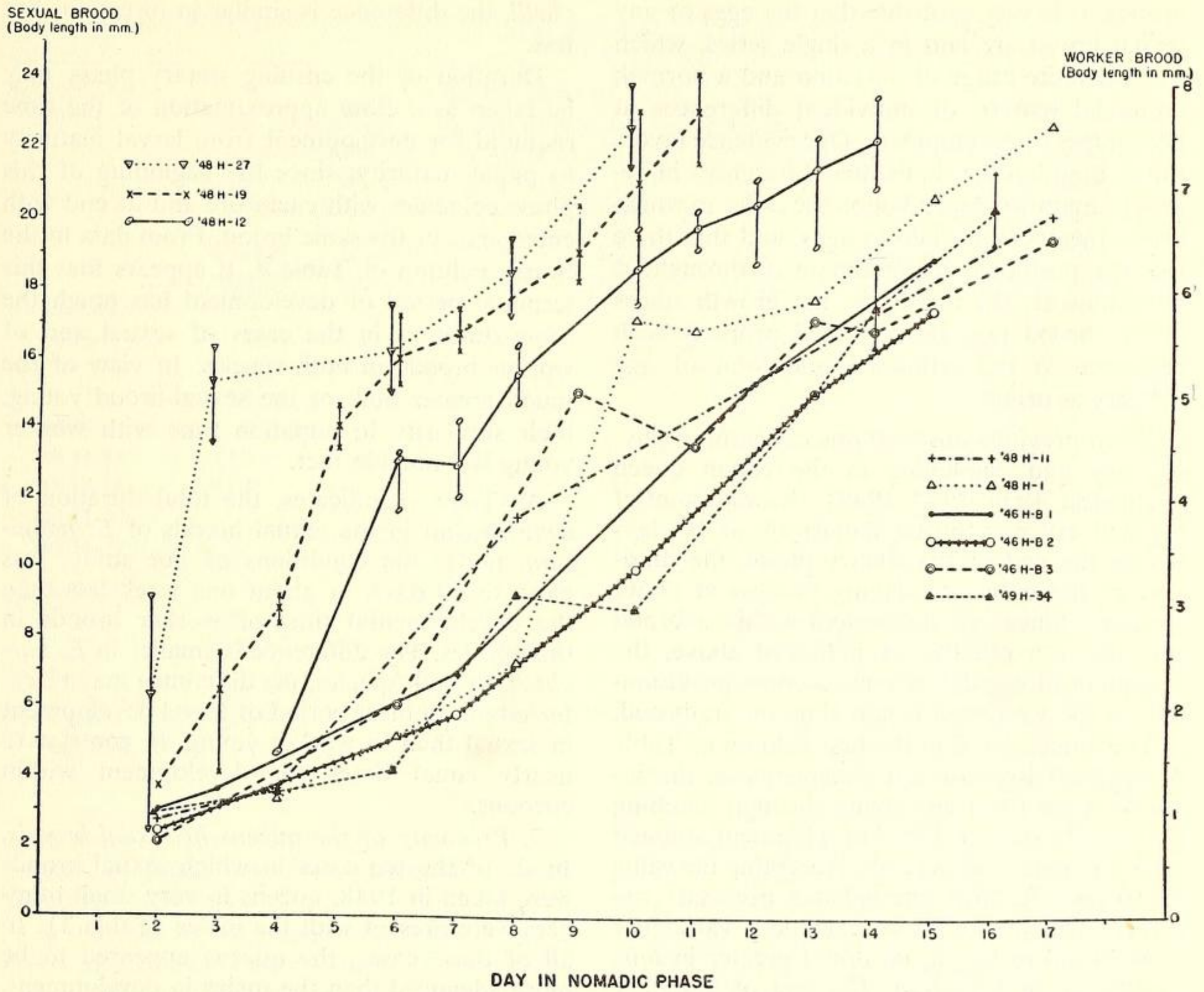
5. *Course of larval development.* The sexual broods of three colonies of *E. hamatum* and two of *burchelli* investigated on Barro Colorado were sampled periodically through the principal part of their larval development, on alternate days when possible. As a rule not more than 12 specimens were taken in a sample. The three sexual broods of *E. hamatum* are represented in Text-fig. 2 in terms of the means and ranges of over-all body lengths in the respective samples. For purposes of comparison, mean body-length curves obtained from larval worker broods of various colonies of *E. hamatum* are also presented in Text-fig. 2. It should be noted that each curve begins at the nomadic day on which the represented brood was first sampled—for example, the H-27 brood was first sampled on the second nomadic day and H-12 on the fourth day. All curves end with the last sample taken before larval maturity.

In the developmental curves for the three sexual broods, an early marked acceleration of growth is notable, followed by a more gradual approach to maturity. The initial acceleration is seen first in H-27, next in H-19 and last in H-12. It occurs in the H-27 brood from the second to the third nomadic day, roughly, but in the H-12 brood not until the fourth day of the phase. In the records for the two sampled *burchelli* broods, an abrupt rise of similar nature begins about the third nomadic day in both cases (cf. '46 B-I, Schneirla, 1948, 1949).

In the slow trend of these sexual broods toward maturity, after the initial stage of rapid growth, brood differences are indicated in Text-fig. 2. Although the terminal phases are gradual in all three cases, and similar in slope on the whole, progress in the H-12 brood seems to have slowed somewhat toward the end, especially as compared with H-27.

From the results represented in Text-fig. 2, it may be seen that the trend of development is distinctively different in sexual broods as compared with all-worker broods of *E. hamatum*. During the first third of the nomadic phase the larval worker broods exhibit a low rate of development, in contrast to the early spurt of larval sexual broods. The curves also indicate that when an increase appears in the rate of larval-worker development, it is considerably slower than the earlier increase in sexual larvae. It appears that larval development is accomplished in a different course and more rapidly in sexual broods than in worker broods.

² An effort was made to raise these for preservation at respectively different advanced stages, as with the specimens taken from colony '48 B-XVII on Barro Colorado. Unfortunately, kept under the variable conditions of field travel, all died without pupating.



TEXT-FIG. 2. Growth rate of three larval sexual broods (upper left) and six larval all-worker broods (lower right) of *Eciton hamatum*, represented by curves for average over-all body lengths in successive samples taken in the nomadic phase. Ordinate scales of the curves are approximated for equivalence in height at the point of larval maturity of sexual and worker broods. Colony identifications for sexual broods are given at the upper left; colony identifications for all-worker broods at the lower right of the figure. Individual samples ranged in magnitude from 10 to 30 individuals in the sexual broods (for which the ranges of body lengths are shown by vertical lines), and from 500 to 1,500 in the all-worker broods, in which, for clarity, expressions of variability are omitted except for the σ 's of the last two samples of the H-34 brood.

Although we are not well equipped with evidence concerning early larval development in sexual broods, it is apparent from the figure that by the second nomadic day sexual larvae approximate a body size close to the average size of worker larvae at maturity (i.e., at nomadic days 15-17). In section 4 we noted that size differences among male larvae are not absolute but relative at this time, since a normal-frequency distribution is approximated (e.g., in the brood of colony DH-1, Text-fig. 1). Also, such relative differences evidently are maintained throughout larval development, since similar distributions are obtained at various later stages. The magnitude of the difference at larval ma-

turity may be expressed in the following way: a randomized sample of 341 mature male larvae (alcohol preserved) of *E. hamatum* (DH-3) displaced 71 cc. of water, but a randomized sample of 341 mature worker larvae displaced only 4 cc. At maturity, therefore, male larvae have roughly 17.8 times the body volume of worker larvae, presumably a crude indication of the ratio of their tissue bulks. According to calculations based on this ratio, in *hamatum* a brood of 25,000 mature worker larvae would have the same bulk as 1,405 mature male larvae. Actually, a total of 1,447 larvae was counted in the sexual brood of colony DH-3.

6. Duration of developmental stages in sexual

broods. It is very probable that the eggs of any sexual brood are laid in a single series, which has a definite range of variation and a normal, unimodal pattern of individual differences at later stages of development. Our evidence favors the assumption that individual differences in degree of maturity depend upon the order in which brood members are laid as eggs, and that these relative positions are maintained throughout development. On this basis, the growth stages in any brood may be described properly with reference to the estimated mid-point of egg delivery as origin.

From previous observations concerning physo-gastry and egg-laying in the eciton queen (Schneirla, 1938, 1944, 1949), the mid-point of egg-delivery may be set tentatively at 10 days before the end of the stary phase, the duration of the entire egg-laying process at about six days. Since age differences within a brood probably are relative, as indicated above, the mid-point of egg-delivery is accepted provisionally as the expressed origin time of the brood.

The values given in the first column of Table 4 represent hypothetical statements of the inclusive time from egg-laying through hatching to the early stage of larval development attained when the stary phase ends. Accepting the value of 10 days for this interval is a necessary expedient which should not exclude a variability from brood to brood, no doubt greater in *burchelli* than in *hamatum*. The end of a stary phase is conditioned upon the emergence of a mature pupal brood, an occurrence more delimited in time for colonies of the latter species (Schneirla, 1938). Successive broods are not exactly synchronized even in *hamatum*, and in some cases nomadism may begin after a shorter post-hatching interval than in others. Thus, when nomadism began, the H-12 and H-19 sexual broods were less advanced than that of H-27 (Text-fig. 2), possibly for this reason.

Termination of the nomadic phase is taken as a rough indication of larval maturity in sexual as in worker broods, since it coincides with the prevalence of cocoon-spinning in both cases. In sexual broods, the beginning of nomadism, as well, is a turning point for the larval brood, since then or shortly thereafter this brood undergoes a sharp increase in rate of development not seen in worker broods (Text-fig. 2). With this interval added, the values in the first two columns of Table 4 give 18-19 days as a rough statement of developmental time from egg-laying to larval maturity in the sexual brood of *E. hamatum*. It appears, then, that this interval is from 7 to 10 days shorter for sexual broods in this species than for worker broods. In *bur-*

chelli, the difference is similar in direction, but less.

Duration of the ensuing stary phase may be taken as a close approximation of the time required for development from larval maturity to pupal maturity, since the beginning of this phase coincides with enclosure and its end with emergence of the same brood. From data in the fourth column of Table 4, it appears that this terminal period of development has much the same duration in the cases of sexual and of worker broods in both species. In view of the much greater bulk of the sexual-brood young, their similarity in pupation time with worker young is a notable fact.

As Table 4 indicates, the total duration of development in the sexual broods of *E. hamatum*, under the conditions of our study, was close to 40 days, or about one week less than the developmental time of worker broods in this species. The difference is smaller in *E. burchelli*. In both species, the difference may be referred to a shorter period of larval development in sexual than in worker young, in contrast to nearly equal times for development within cocoons.

7. *Precocity of the queens in sexual broods.* In six of the ten cases in which sexual broods were taken in 1948, queens in very small numbers were present with the males (Table 3). In all of these cases, the queens appeared to be more advanced than the males in development. In the early-stage larval brood of colony DH-1, the two queen larvae found were larger than any males; and in the intermediate-stage larval brood of colony DH-4, the only queen larva found was larger than any male. In colonies DH-3, H-12 and B-XVII studied in Panama in 1948, as well as in GB-XVI found in Trinidad in 1950, one or more queens reached larval maturity and became enclosed ahead of the males. In colonies H-12 and H-27, three or more queens had emerged as callows before any callow males were found. A precocious development of queens in sexual broods is indicated.

Instances in which young queens have been found in this program are summarized briefly in section 3. In the case of colony '48 H-12, a contrast of queens and males is possible at two well separated times in development. First, at a time when all male larvae evidently were still unenclosed, four similar dark cocoons were observed. One of these, when opened, was found to contain a queen prepupa which had completed its larval maturation in advance of the males. This, no doubt, was also true of the three uncollected specimens. Later, just before the stary phase ended, four active callow queens

TABLE 4. DURATION (IN DAYS) OF DEVELOPMENTAL STAGES IN WORKER AND SEXUAL BROODS

Species and colony	Developmental stage							
	Mid-point of egg-laying to early larval stage (i.e., to end statary phase)		Early larval stage to maturity and enclosure (i.e., through nomadic phase)		Prepupal and pupal development (i.e., statary phase)		Total developmental time	
	Worker broods	Sexual broods	Worker broods	Sexual broods	Worker broods	Sexual broods	Worker broods	Sexual broods
<i>E. hamatum</i>								
'46 H-B	(10)*		16		21		47	
" "	(10)*		17		20		47	
" "	(10)*		16		20		46	
'48 H-11	(10)*		17		18		45	
'48 H-15	(10)*		17		20		47	
'48 H-18	(10)*		18		19		47	
'48 H-12		(10)*		13		21		44
'48 H-27		(10)*		12		21		43
<i>E. burchelli</i>								
'46 B-I	(10)*		10		20		40	
" "	(10)*		10		21		41	
" "		(10)*		8		21		39

* Inferred value.

were seen in this colony before any evidence could be found of male emergence from cocoons.

A study of brood samples from colonies '48 DH-1 and DH-4, taken in Darien, suggests that queen precocity holds from an early stage of larval development. In each of these instances, queen larvae were largest in a sample otherwise composed of hundreds of male larvae. Three further cases point to queen priority in reaching larval maturity. In an examination of the brood of colony DH-3 as the bivouac was demolished literally strand by strand, 14 larvae were found which had begun to spin. (Unfortunately, a plan to keep most of these specimens alive for preservation at further stages was unsuccessful). Eight queen prepupae were identified among them. At the time these individuals were already well advanced in making their cocoons, virtually all of the male larvae were still active and unenclosed. The males, although naked, were nearly ready to spin, as indicated by the expulsion of a large wad of viscid fluid from each when plunged into hot water.

On the assumption of queen precocity we were able to capture the first larval specimens of queens ever taken in *E. burchelli* (Schneirla & Brown, 1950). When colony '48 B-XVII was in its next to last nomadic day with a larval sexual brood, probings into the cluster brought forth only naked male larvae, with two exceptions. Intrusions into the lower border of the

bivouac at length disclosed two complete cocoons, each within a tight bolus of workers. One of these cocoons, opened soon afterward at the laboratory, yielded a queen in the prepupal stage (Plate I, Figure 1). The second was placed with workers in an artificial nest, where the workers clustered over it closely or lugged it about intermittently in their circular column. When opened nine days after it was collected, this cocoon contained a well-formed queen pupa (Plate II, Figure 4). Thus, both of the enclosed specimens were queens, and both were more advanced in development than any observed male larvae in the same brood.

Similar evidence was obtained in colony GB-XVI, *E. burchelli urichi*, studied by the senior author in Trinidad. When found in late afternoon, this colony was engaged in a vigorous raid based on a large cluster within the broken shell of a hollow log. When a sexual brood close to larval maturity was found within the bivouac, steps were taken to look for enclosed specimens. In a brood estimated to contain 3,000 larvae, all of those observed were naked with the exception of two enclosed specimens, each within its own compact bolus of workers. One had completed the spinning of a cocoon closely similar to those of the two prepupae of colony '48 B-XVII, and on removal was found to be a queen prepupa. The other, within a thinner case evidently still incomplete, also was a queen prepupa. As may be seen in Plate I, Figure 2, the

latter was smaller and evidently less mature than the specimen in the completed cocoon. Both of these specimens evidently were ahead of the males in development, since all males observed in this brood were still naked, active and unstraightened.

In three instances, fully emerged young queens have been found in broods of still enclosed male pupae. In the colony of *E. burchelli* observed by Wheeler and Emerson (Wheeler, 1921), two active ("fresh looking") queens were found, doubtless both callows which had emerged before any of the nearly mature male pupae. In our study, the earlier eclosion of queens was established clearly in two colonies of *E. hamatum*, and was suggested by circumstantial evidence in colony '46 B-I, *E. burchelli*.

Detailed records are available from two colonies of *hamatum*. When colony H-12 was passing its 18th day (January 27) of a statary phase with an enclosed sexual brood, a fully emerged, active young queen was seen within a cluster of workers close to the main bivouac. She was removed for preservation. On the evening of the same day, two further callow queens were seen in the bivouac vicinity, one outside the cluster but near it, and another in the bivouac wall. A fourth was observed later the same evening, in a cluster at some distance from the main bivouac. These queens were all readily identified as callows by their light orange-yellow coloration. All four moved about freely and vigorously, except as restrained by workers clustered about them or following them closely, at a time when no emerged males could be found in the bivouac. Next morning (January 28) small numbers of eclosed alate males were observed; male emergence accelerated during the day, continued on January 29 and reached its virtual completion late in the evening. In this case, the first queen seems to have emerged about two days before any males, and all of the later queens evidently preceded all except a few initial male eclosions.

In colony H-27, the first callow queen (Plate III, Figure 7) was observed on the evening of March 5, the 17th day of the statary phase, in a small cluster near the bivouac; the second on the following day, at noon, also in a small separate cluster of workers; the third a few hours later, exposed in the center of a thick group of workers. The first signs of male emergence were not observed until late afternoon on March 7. Male eclosion continued at an accelerated rate to its completion on March 10th, when the colony moved from the site in the evening. In this case, not only the first callow queen to be

observed, but evidently one or both of the others as well, reached pupal maturity and emerged from their cocoons before any of their brother males.

8. *Conditions of production of sexual broods.* In studies on Barro Colorado during the rainy months of six different years, in a total of 108 colonies, 153 broods were identified, and only one of these was a sexual brood. In the forested areas of the Caribbean region, where annual rainy and dry seasons were well differentiated, production of all-worker broods seems almost invariable in colonies of *Eciton* (*Eciton*) during the rainy season.

Results stated in section 1 show that a regular production of worker broods is the basic pattern of the dry season as well; however, in dry months the succession is interrupted in some of the colonies by the appearance of a bisexual brood (Table 2). During the final rainy weeks of 1947 preceding the onset of dry weather, 24 colonies of *E. hamatum* and *burchelli* were studied on Barro Colorado and in the Pequeni area of Panama, with a total of 38 all-worker broods but no sexual broods discovered. But subsequently, in 41 colonies studied in the 1947-1948 dry season, 11 sexual broods were found in addition to 59 worker broods, on Barro Colorado and in Darien. And on Barro Colorado during the dry months of 1946, 49 colonies of the two species had a total of 71 all-worker broods and 10 sexual broods. In the areas of study, with limited exceptions to be considered, sexual broods evidently are specific to the dry season.

The connection of sexual broods with dry weather has a striking illustration in the case of colony H-12. During November and early December of 1947, this colony was studied during the time it produced two successive all-worker broods. These were the last weeks of the 1947 rainy season (Table 1), and on December 10 (when we left the Island for another area) ground moisture was plentiful. When we returned on December 20 the situation was sharply different: rainfall had stopped abruptly about one week before, lower vegetation was dry, and the forest floor had lost moisture to the extent that ground cracks were widespread.

On December 22, or about ten days after dry weather had set in (see Table 1), colony H-12 was rediscovered, then in a statary bivouac within the blind hollow of a large open log shell, in a dry hillside clearing exposed to the south. From the developmental status of the pupal worker brood, the colony was judged to have spent about two weeks at this site before its discovery. This estimate agrees with previous

phases of the colony (Schneirla & Brown, 1950), and would allow for a statary phase of 20 days before a new nomadic phase began on December 28.

In the December statary phase a sexual brood was initiated. The H-12 queen was physogastric when taken from the bivouac on December 22, but had evidently finished delivering the main part of her current batch of eggs. In one sample of nearly 100 eggs taken from the mass already laid, many well-advanced embryos and some minute larvae were found, which with graduated signs of development in the remainder indicated that egg-laying must have been going on for a few days. This queen, as observed during a captivity of three hours in the laboratory, was similar in egg-laying and related behavior to other queens of this species studied in the last stages of an egg-delivery episode (Schneirla, 1944).

On December 26 when the bivouac was next examined, from the queen's behavior and from the reduced size of her gaster, together with the size of the large brood mass, it was apparent that delivery of eggs must have ended. Nomadism began on December 28 when, after carrying out a three-system raid during the day, the colony completed an emigration early in the night (with a large, newly emerged brood of callow workers). On December 31, when this colony was rediscovered (and identified by means of the queen's mark), its young brood was at once seen to be a sexual brood.

From all the circumstances, this colony must have entered a statary phase about December 8, or only two or three days before dry weather began in the general locality. Thus it is highly probable that during the principal time of physogastry and egg-delivery, colony H-12 and its queen were subject to conditions of marked heat and drought in the known bivouac location, sharply in contrast to circumstances prevalent in the microclimate during the final weeks of rains, when this colony initiated two successive worker broods.

For reasons to be clarified in the discussion, we propose that the first half of a statary phase is the critical time for events determining whether a brood is to be sexual or all-worker in make-up. In the light of this assumption, let us examine our evidence on sexual broods found in the dry seasons of 1946 and 1948.

In Table 3 there is a general record of the cases in which sexual broods were found in the 1946 and 1948 dry seasons. In each case, a judgment has been made of the developmental status of the brood at the time of discovery, based on a comparison of the brood sample with evidence

from continuous studies of brood development in the species (cf. Text-figs. 1 & 2). From these considerations in relation to evidence on the duration of development presented in section 6, each brood has been traced inferentially to the time of its initiation. The estimated times of inception for the respective sexual broods discovered in the two dry seasons are given in Table 5.

The investigation in the 1946 dry season (Schneirla, 1948, 1949) began early in February. As may be seen in Table 3, 10 sexual broods were found between February and early April, but none thereafter to mid-June. Of these cases, six were in colonies of *burchelli* and four in *hamatum*. It is interesting to note in Table 5 that the critical brood-initiation times (according to our hypothesis) fall before February 3 in all six *burchelli* broods, but after that date in all *hamatum* broods. This may be a true species difference, dependent upon conditions in the particular season and year.

It seems relevant here that *burchelli* colonies when statary often bivouac in hollow trees at considerable distances from the ground, whereas *hamatum* colonies usually remain on or close to the ground. In the 1946 dry season, of 27 recorded statary bivouacs in *burchelli*, 10 were at ground level, 6 within one meter, and 11 at heights between one and ten meters from the ground; of 36 recorded statary bivouacs in *hamatum*, 25 were at ground level, 10 within one meter, and 1 at two meters. Atmospheric conditions affecting the statary bivouacs of these two species must have been very different, as a result. On Barro Colorado in late 1945, rainfall was exceptionally heavy, as indicated by a December total more than twice the average of a 15-year record for that month (Schneirla, 1949, Fig. 1). In January and February of 1946, however, rainfall was sparse, accounting for a persistent atmospheric dryness in the forest during the daytime. On the other hand, in most parts of the island, retention of ground moisture was excellent even to the middle of February. In the first two weeks of the 1946 season, *burchelli* colonies in their elevated statary sites may have been more effectively exposed to drought than *hamatum* colonies in their sites close to the ground.

In 1946, rains continued into early January, then stopped abruptly on Barro Colorado. From the estimated times of brood initiation in Table 5 it is evident that colonies B-I, B-II, B-III and B-IV (*E. burchelli*) must have initiated their sexual broods before January 20. Thus, in four of six colonies of this species found with sexual broods in that season, the event had its inception within three weeks after intensive dry weather

TABLE 5. INFERRED TIMES OF INITIATION OF ECITON SEXUAL BROODS STUDIED DURING TWO DIFFERENT DRY SEASONS

(H—colony of *E. hamatum*; B—colony of *E. burchelli*)

Season	Time interval						
	Dec. 16-31	Jan. 1-15	Jan. 16-31	Feb. 1-15	Feb. 16- 28 (29)	Mar. 1-15	Mar. 16-31
1945-1946		B-IV	B-III B-II-X	B-VI B-V B-I	H-K	H-J	
Total		1	2	3	1	1	
1947-1948	H-12 DB-II	H-19 B-XVII DB-I	H-27 DH-3 DH-1	DH-4 DB-III			
Total	2	3	3	2			

began. Comparably, in 1948 the sexual brood of colony H-12 was initiated during the first three weeks of dry weather, and the sexual broods of colonies H-19 and B-XVII evidently were initiated not long thereafter, in early January.

We propose that some, if not all, of the conditions for sexual-brood initiation are met when a colony enters its first stary phase after dry weather has begun. From this hypothesis, when a drought begins suddenly and is maintained, more eciton colonies should produce sexual broods than when dry weather begins gradually and continues brokenly. It seems significant that in 1948 only four eciton colonies with sexual broods were found, as compared with ten in 1946, although nearly equal totals of more than 50 colonies of the two species were studied on Barro Colorado in these two dry periods. Somewhat more variable environmental conditions during the first half of the dry season in 1948 than in 1946 may have been responsible.

In an area presenting a variety of microclimatic conditions, as does Barro Colorado with its many ravines and hills, chance differences in stary locations may be critical for sex control in broods. In 1948, although colony H-19 initiated a sexual brood during a stary phase which began on January 31, colony H-18, which began a stary phase at nearly the same time, had a worker brood instead. And colony H-23, which must have begun a stary phase in December, 1947, not long after H-12, initiated a worker brood while the latter colony had a sexual brood. It seems important that whereas both colonies

H-12 and H-19 passed these stary phases in distinctly dry forest glades well exposed to air currents, colonies H-18 and H-23 were located in more humid and better sheltered places. In *burchelli*, colonies B-XII and B-XVII had coincident stary phases early in January; however B-XII was situated in a deep and moist inter-butress niche where it initiated an all-worker brood, whereas B-XVII had a more exposed cluster three meters from the ground in a broken tree trunk, where it initiated a sexual brood. Our records contain other contrasts of this type, but no contradictory instances.

In Table 5 it is seen that most of the sexual broods found on Barro Colorado in 1946 and all of those found in 1948 were initiated before the end of February, or during the first third of the dry season. In 1946, a routine search for colonies continued from early February to mid-June; in 1948, a similar search continued nearly to the end of March. If sexual broods were initiated to any extent in the last weeks of the dry season, it seems also that evidences of them should have been found in the investigations of four different years when routine searching was carried out during May and June. The one trace of a late dry-season inception in *Eciton* (*Eciton*), a dealate male found in a colony of *E. hamatum* on June 10, 1932, must have developed in a brood initiated before the end of April, i.e., before the end of the dry season.

Our Darien survey of 1948 was scheduled on the assumption that in an area where the dry season begins abruptly with persistent drought thereafter, initiation of eciton sexual broods is

confined largely to the early weeks.³ The dry season in lowland Darien typically begins late in December and is continuous until late April, and 1948 was a typical year. Our survey was carried out during the last two weeks of February when, according to the above hypothesis, a maximum of colonies should have sexual broods in advanced stages of development. Results fully justified this expectation, since in a total of eight discovered colonies, six colonies had sexual broods. These broods ranged from an early larval to a post-pupal stage, and, as Table 5 indicates, must have been initiated after the beginning of dry weather in late December. Although a repetition of the survey in March or April, desirable as a control, unfortunately was not possible, results for Barro Colorado Island (Table 5) indicate the probable outcome.

9. *Exceptional (rainy-season) sexual broods.* As Table 2 shows, our records cover a total of 191 identified broods in five species of *Eciton* (*Eciton*) studied during various rainy seasons in Panama and other areas. In this long series only two cases, or 1 per cent., were sexual broods. In contrast, in a total of 172 broods of four species studied in the regular dry season, 22 broods (i.e., about 13%) were sexual. In a tropical area with well-differentiated seasons, it appears that sexual broods are produced only exceptionally in the regular season of rains.

There are two apparent exceptions in our records, to which in all probability the case discovered by Wheeler and Emerson (Wheeler, 1921) should be added. The first of our special cases was the *hamatum* colony ('49 H-32) found with a presumably remnant alate male brood at Barro Colorado Island on August 4, 1949, by Robert and Frances Brown (Table 3). This colony terminated a nomadic phase on August 12, which provides a basis for inferring the developmental stages of the sexual brood. With July 26 taken as the approximate date of emergence of the sexual brood, from considerations outlined in section 6, the statary phase in which this brood was initiated may be presumed to have fallen roughly from June 7 to 27, with egg-laying about June 13 to 21. Normally the rainy season begins during May in this locality (Schneirla, 1949, Fig. 1). In the 1949 rainfall records for Barro Colorado, precipitation was regular and normal in amount from early May

to the end of the rainy season in December, with the exception of early June. From the records reproduced in Table 6, it may be seen that in the intervals June 3 to 7 and June 14 to 18, rainfall was sparse in the daytime hours. It therefore is possible that an interval of hot, dry weather may have affected colony and queen at the time postulated as critical for brood initiation.

Our second special case, as described previously, was colony GB-XVI (*E. burchelli urichi*) found in southeastern Trinidad on July 10, 1950, during a nominal rainy season. From the fact that this sexual brood was then only about one day short of larval maturity, the statary phase of its production may be inferred as from about June 10 to 30, and the duration of egg-laying roughly established as from June 17 to 23. Fortunately, rainfall records were available from a locality only about 10 miles from where this colony was found, and close to the heavy forest.⁴ Precipitation was somewhat irregular but appreciable in amount through May, but a significant change came after the first days of June, as represented in Table 7. After June 9 there ensued an interval of more than three weeks in which days were almost altogether rainless, hot and clear, with rainfall restricted to scattered light showers at night. It is possible, as the table indicates, that the sexual brood later found in colony GB-XVI was initiated within this dry interval.

The sexual brood found by Wheeler and Emerson in a *burchelli* colony at Kartabo, British Guiana, was close to pupal maturity on July 21, 1920, near the end of a short semi-annual rainy period. From considerations presented in section 6 and summarized in Table 4, it seems probable that this brood was initiated during the first three weeks of June. In the absence of published data, Dr. William Beebe was asked about precipitation in the Kartabo area during the months of May through July in 1920, when he was in continuous residence at the station. His reply, based on his notes for that season, was that after an irregular but appreciable rainfall through May, the month of June and especially its first half had been very dry and clear, followed by consistent rains until near the end of July. Thus, the interval of sexual-brood inception in the recorded colony may have coincided with a distinct dry period following a series of rains.

³ A comparison of the daily march of atmospheric changes at Yavisa in Darien, as reported by Breder (1946), with conditions at Barro Colorado, shows that at Yavisa air temperature rises more rapidly in the morning and reaches a considerably higher peak at mid-day with a lower trough in humidity, and drops more slowly in the afternoon than at Barro Colorado.

⁴ These records were obtained with a standard funnel-type rain gauge operated at the Beach Field station of Trinidad Leaseholds, Ltd., and are used here through the courtesy of Mr. Peter Highgate, Chief Engineer at the station.

TABLE 6. RAINFALL RECORDS FOR BARRO COLORADO I., C. Z., FROM MAY 15 TO JUNE 30, 1949, WITH ESTIMATED TIMES OF SEXUAL BROOD INITIATION IN COLONY '49 H-32, *E. hamatum*

Date	Rainfall in inches				Inferred colony events
	12 P.M. to 6 A.M.	6 A.M. to 12 A.M.	12 A.M. to 6 P.M.	6 P.M. to 12 P.M.	
May 15		.01	1.78	.16	
16		.01	.06	.06	
17			1.28	.01	
18	.01		.01		
19					
20			.48	.07	
21	.28	.01	.06	.02	
22	.02	.22		.10	
23	.10		.32		
24		.01			
25	.12		.25	.04	
26			.01	.02	
27	.06		.81	.03	
28			.22	.05	
29		.01	1.06		
30			.17	.01	
31	.01				
June 1		.01	.19	.14	
2	.01	.04	1.52	.03	
3	.01				
4					
5		* .07		.03	
6	.09	* .21			
7					
8	.02	.01	.91		(Statory phase inferred, June 8-27)
9			.11	.02	"
10	.01	† 1.10	‡ .75	.03	"
11	.21	.19			"
12		.01	.89		"
13			‡ 2.24	.27	"
14	.10			.15	" (Egg-laying inferred, June 14-21)
15			.05		"
16					"
17	.01			.34	"
18	.01	† .05		.01	"
19	.04	* .46	‡ .09	.01	"
20			.06		"
21		.01		.18	"
22	.01				"
23	.04		.01		"
24	.01				"
25				.02	"
26			.38		"
27	.01	.19	.20		"
28		.01	.44		
29			.41	.94	
30	.01		.62		

* All before 8:00 A.M.

† Mainly before 8:00 A.M.

‡ After 2:00 P.M.

It is probably no accident that in all three of our ostensibly exceptional cases, in which an eciton colony produced a sexual brood during a period of nominally rainy weather, dry periods of appreciable duration occurred at about the time when brood initiation may be inferred. It seems possible that these were not actually exceptional cases, but really equivalent to the case of colony H-12, in which egg-production and laying were established in close coincidence with the first two weeks of a regular dry season.

DISCUSSION

In these eciton species the pattern of life is much the same throughout the year, in that great all-worker broods are produced at regular intervals and colony behavior oscillates synchronously between the nomadic and stately conditions. In the dry season, neither more arduous environmental conditions nor difficulties in getting an adequate haul of booty prevent a continuation of this pattern. The most striking reaction of *Eciton* to the dry season involves the production of fertile individuals and the colony sequels to this event.

In American tropical areas with well-marked seasons, in which our results have been obtained, broods appear periodically in rainy months with large populations of workers alone but no reproductive individuals whatever (section 1). This is also the case in the dry season, with the exception of a single bisexual brood in some of the colonies (section 2). Under the conditions of our study, production of sexual broods in eciton is an event specific to the dry months. Our findings provide a basis for understanding how these exceptional broods are produced, not only in tropical areas having distinct seasons (sections 2 and 8), but also in regions without well-defined seasons (section 9).

For the two terrestrial species of *Eciton* (*Eciton*) we have studied, a sexual brood is a distinct population of young developing from eggs laid by the same queen, which contains a small number of potential wingless queens and a large number of potential winged males (section 3). Briefly summarized, the demonstrated characteristics of this event are: seasonal timing (sections 2, 8, and 9); apparent restriction to one such brood per colony per season (sections 2 and 8); a dimorphic makeup, with few females and many males (sections 3 and 4); a fractional population size as compared with all-worker broods, fairly constant for the species (section 3); a precocious development and emergence of queens (sections 4 and 7); a distinctly shorter period of larval development, with a different time rate of change, than in worker broods

(sections 5 and 6); and graduated individual differences in size approximating a normal-frequency distribution (sections 3 and 4). To account adequately for these characteristics, it seems necessary to postulate factors concerning egg-production and egg-delivery in the queen as well as factors in colony behavior affecting brood development, distinct from conditions in the population of worker broods.

Our evidence favors the hypothesis (Schneirla, 1948) that the initial impact of dry-season conditions upon colony and queen specifically causes sexual broods. In the first place, such broods tend to appear early in the dry season (sections 2 and 8), each one as a single episode in a regular series (otherwise of all-worker broods), and furthermore, it is probable that no colony has more than one such brood in a season. The critical time in the cycle for this effect seems to be roughly the first half of a stately phase, when the queen becomes gravid and delivers a single large batch of eggs (section 8). During this interval the queen may be susceptible to extrinsic conditions which somehow determine the sex of this brood.

Evidence presented in sections 8 and 9 indicates that specific environmental conditions as well as a colony susceptibility are involved. The chances that many colonies in an area will be exposed to the necessary extrinsic conditions within a theoretical time limit after the onset of dry weather evidently depend upon what colonies may settle into stately phases at nesting sites where dry-weather conditions prevail. Thus colony '48 H-12 on Barro Colorado, after producing two successive all-worker broods during the last rains in 1947, almost coincidentally with

TABLE 7. RAINFALL RECORDS FOR BEACH FIELD, GUAYAGUAYARE, TRINIDAD, FROM JUNE 1 TO JULY 12, 1950, WITH ESTIMATED TIMES OF SEXUAL BROOD INITIATION IN COLONY GB-XVI, *E. burchelli*

Period	Total rainfall in inches	Developmental stage of brood
June 2- 5	3.83	
" 6- 9	3.02	(Stately phase inferred, June 10-30)
" 10-13	0.25	
" 14	0.30	
" 15-18	1.15	(Egg-laying inferred, June 17-23)
" 19-22	2.00	
" 23-26	0.85	
" 27-30	0.85	
July 1- 4	0.55	
" 5- 8	0.90	Larvae mature, July 10-11
" 9-12	0.70	

the onset of dry weather entered a statary phase at a site where drought conditions soon prevailed. This colony seems to have been maximally exposed when susceptible, and a sexual brood resulted. Certainly, the *general* prevalence of dry weather in an area does not *alone* condition such broods in all colonies. Other colonies, which became statary at nearly the same time as colonies producing sexual broods, but which entered more humid and better sheltered sites, produced all-worker broods.

A greater coincidence of eciton sexual broods was expected in the Darien lowlands, where dry weather begins almost coincidentally with Barro Colorado but is more intensive. In Darien, most of the eciton colonies discovered in the last two weeks of February had sexual broods, doubtless initiated within the first month of the dry season (Table 5). On Barro Colorado more than 50 colonies of two species were discovered in the same season, but only four had sexual broods. There, with a more variable microclimate and rainfall pattern, chances evidently were considerably less than in Darien that any one colony would meet the necessary conditions in its first statary phase after dry weather began. These considerations suggest a somewhat different pattern of inter-colony mating in eciton colonies of these species, according to the conditions of terrain and climate in the area.

The abruptness with which dry weather begins and the uniformity with which it dominates the microclimates of an area seem critical for the occurrence of sexual broods there. Conditions on Barro Colorado in the dry season of 1946 would appear to have been more favorable than in 1948 in this respect, for 10 sexual broods were found in 1946 but only four in 1948, in comparable surveys. A related question concerns why six sexual broods of *E. burchelli* found in the 1946 dry season evidently were all initiated before any of the recorded cases in *hamatum*. The answer apparently depends upon a species difference, whereby *burchelli* when statary tends to occupy elevated sites far more frequently than *hamatum*. Under the climatic conditions prevalent in this area in 1946, with the ground moister than usual but with a very dry daytime atmosphere, early in the dry season *burchelli* colonies must have been more frequently and fully exposed to dry conditions than *hamatum* colonies (section 8). In 1948, with the forest floor much drier from the start of dry weather, no species difference of this kind was obtained.

Apparently, eciton sexual broods may be produced at any time of year, provided a suscep-

tible colony encounters the necessary extrinsic conditions. Three cases have come to light in which sexual broods were produced outside the regular dry season of the locality (section 9). In each of these cases, a distinct period of dry weather may have coincided with the time when a colony presumably became statary and initiated a sexual brood.

Specifically, a sexual brood may be expected when a colony with functional queen, acclimated to rainy-season conditions, is subject to persistent dry-weather conditions in the first half of a statary phase. In our study, sexual broods were initiated most frequently in the early part of the regular tropical dry season (section 8). We find indications that relatively few colonies have sexual broods after the first third of the dry season has passed, and that some colonies have only worker broods in given dry seasons. Hence it is possible that through a variable or a gradual introduction to dry-season conditions, a queen and colony may become acclimated by degrees early in the season and thereby protected in some manner from maximal dry-weather effects encountered later on. Or, on the other hand, once the effective extrinsic conditions have accounted for production of an exceptional brood, an inhibitory effect of some kind may oppose a repetition in the same season. We have many records in which sexual broods were preceded and followed by worker broods, but none of two successive sexual broods in the same colony, or of two from the same colony in the same season.

A considerable precision in this event in *Eciton*, with stable properties according to species, is indicated by the manner in which sexual broods occur and by their population characteristics (sections 2, 3, 4, and 7). *Eciton* seems to have far greater precision than most other insects, both in the ratios of dimorphic individuals produced at one time by any one colony and in the manner of their appearance. In most other insects, protandry (i.e., prior appearance of males) is the rule, usually somewhat variable, as in *Trigona* (Schwarz, 1948). The opposite condition, queen precocity, is relatively rare and seldom as precise as in *Eciton*. In *Eciton*, so far as we know, queens never appear in the same brood with workers, but always as a precocious minority in a brood otherwise containing only males.

Considering the high degree of uniformity which evidently prevails throughout colonies of a species in *Eciton*, the pattern is indeed a striking one. For example, it is probable that a functional queen of *E. hamatum* normally produces about nine successive all-worker broods

before a sexual brood may interrupt the annual series. On the Dzierzon assumption that female-producing eggs are fertilized eggs, this queen must therefore produce a rough total of 200,000 or more fertilized eggs, in separate lots at 36-day intervals, before a break to a dimorphic brood occurs. On the same assumption, the major part of a sexual brood, namely the males, might be considered the result of some major interruption in the fertilization of matured eggs. This would be a time-limited change, from which a queen normally recovers fully to the condition in which fertilized eggs once more are produced invariably in each great brood of the series.

At first sight the sexual-brood event might seem attributable to a depletion of sperms in a queen, with a possible recovery through refertilization. It is true that male-producing eggs are laid intermittently with an increasing frequency by elderly queens in certain ants (Goetsch & Käthner, 1937) as well as by honey-bee queens when over-aged (Grout, 1949) or low in sperms (Laidlaw & Eckert, 1950). This hypothesis does not seem to fit *Eciton*, since it would lead us to expect sexual broods of variable makeup produced at almost any time of year, and not seasonally conditioned broods of a consistent dimorphic population pattern, preceded by full-sized all-worker broods. Moreover, all functional eciton queens thus far examined histologically, whatever the season of capture, have been found with ample supplies of sperms in their receptacles. From our evidence, it would appear that any functional eciton queen may produce a sexual brood, provided the necessary extrinsic conditions are effective when queen and colony are susceptible.

The state of affairs in *Eciton* in this respect is not unrelated to conditions in other insects. It is well known that reproductive variations, including changes in the sex ratio, may occur in many insects under the influence of extrinsic conditions (Wigglesworth, 1939; Flanders, 1939). A seasonal production of fertile individuals is common in insects, although its mechanism is poorly understood. In ants, males and queens are ordinarily produced at times characteristic of the species, early in the temperate-zone summer in some and later in others (Wheeler, 1913; Talbot, 1945); male-producing eggs are usually laid by honey bee queens in the autumn (Vandel, 1931), the season when males and fertile females ordinarily are produced by bumblebees (Cumber, 1949). Insect metabolic processes are known to be delicately responsive to changes in environmental temperature and humidity in particular (Uvarov,

1931; Chapman, 1931; Mellanby, 1935; Ludwig, 1945), and the reproductive processes of many are very sensitively affected by ecological conditions (Alpatov, 1932; Wigglesworth, 1939). Specifically, the ovaries in queens of numerous ant species have been found to vary in function according to relatively slight changes in individual metabolic conditions (Wheeler, 1913; Ezikov, 1923). It is not surprising that reproductive processes in doryline queens show a sensitivity to seasonal extrinsic changes.

Theoretically, we may characterize the extrinsic effect in the case of *Eciton* as an adequate dry-season impact, its terminal organic result a temporarily sustained inhibition of egg-fertilization in the functional queen. This relationship is undoubtedly less direct and plastic than in some of the solitary Hymenoptera, in which a comparable process occurs promptly by reflex response to specific extrinsic stimuli (e.g., size of host), or in the honey bee queen, in which contact with a large comb cell typically elicits the laying of an unfertilized egg, a small comb cell a fertilized egg. However, the mechanism in *Eciton* may not be dissimilar to that outlined theoretically by Flanders (1939, 1950) specifically for the honey bee.

What intervening variables may be set into play by seasonal extrinsic factors to cause exceptional reproductive changes in the eciton queen? We are limited to speculation. The phenomenon may involve a rather direct and reflex-like process set up by the action of specific atmospheric changes upon the queen; it may be an outcome of more subtle metabolic changes (e.g., water reduction) attributable to extrinsic conditions; or it may be even more indirect, with the inclusion of social factors. To illustrate the last hypothesis, one possibility is that the critical extrinsic conditions may first act upon the general population, perhaps by lethargizing the workers sufficiently to reduce trophallactic stimulation for the queen below the level essential for facilitation of insemination processes.

Whatever its *modus operandi*, the phenomenon has certain general properties which may be inferred from our findings. Properties of stability and perhaps of complexity are suggested by an apparent latency in onset which would seem to impose a precise limitation on fertilization at the beginning of each exceptional series. A process with a definite threshold is indicated by the all-or-none manner in which insemination apparently stops. A process of more than simple reflex characteristics, but with a stable and persistent organic mechanism, is indicated by the continuation of the non-fertilization condition once it is in force. A metabolic

sustaining condition of a temporary and all-or-none character, opposed by conditions normal to the nomad-statory cycle, is suggested by evidence for a seasonal adaptation against a repetition of the episode. In all of these respects the phenomenon occurs in a markedly precise way, indicating great stability of the causal factors in the species.

Because the first-laid eggs are presumably fertilized, they develop into females; also, through their prior emergence in the colony, they have a certain advantage for competition in the colony trophic situation. There is at present no reason to believe, however, that these first-delivered members of the potential sexual brood are different genetically or in nutrient resources from the corresponding members of a potential all-worker series. In both cases, the initial eggs evidently are fertilized, hence develop into females. However, we have no evidence for different rates of egg-production in the two broods, hence no apparent basis for a differential absorption of nutrient material, as postulated by Flanders (1946) to account for queen-worker specialization in other social insects. If no differences exist in the nutrient content of initial members in the two egg series, the development of queens in the one case and major workers in the other must be attributable to trophic processes in the colony situation, effective after laying. A genetic differentiation seems unlikely here.

Interesting consequences follow from the postulation of potential sexual- and worker-brood series which are equivalent in timing and in number at delivery into the colony. Dimorphic differences within the sexual brood presumably are due to the non-fertilization of all but an introductory part of that egg series. At the moment of fertilization, however, similar graded differences presumably exist through each series, perhaps in the nutrient content of eggs as dependent upon their order of maturation. This condition, suggested by the absorption theory of Flanders (1945), would establish a basis for the graduated differences arising within each type of population. A stable basis of this sort for individual differences is suggested by the high degree of similarity we have found in the unimodal bisexual populations from an early larval stage, and by a comparable situation in all-worker broods. Graduated differences of such a description, established prior to laying and later amplified trophically through development in the colony, may furnish a basis for degrees of variation among individuals in both series. It is presumed that genetic factors effective through fertilization admit polymorphic differences among females up to a limit de-

pendent upon the trophic advantages available to each individual. It is also presumed that non-fertilization excludes such differences in the male series.

Very different potentialities for colony reaction appear to exist in all-fertilized and mainly-unfertilized series of eciton eggs produced in separate broods. Between the time of laying and our first glimpses of the larval broods at the start of nomadism, some catastrophic change must be imposed upon the potential bisexual brood to which the entire all-worker brood seems to be immune. The apparent result is that the sexual-brood population is reduced to a small fraction of its number at laying, a fact of greatest importance for the eventual character of the sexual brood.

To account for this reduction, two alternative hypotheses may be offered. The first is that unfertilized eggs may be inferior in viability to fertilized eggs, so that most of them fail to pass some critical stage of early development (e.g. hatching). An alternative hypothesis concerns the possibility of an extensive cannibalism by workers based on specific chemotactic properties of unfertilized eggs. Some shortcoming in odorous properties, such as a deficiency in surface fluids, might cause unfertilized eggs to be treated like booty. Or on the other hand, some discriminable property of unfertilized eggs might cause workers to lick and handle them excessively, and thereby consume many of them in the process. This might indirectly increase the casualties among potential queens in particular. That the trophallactic reactions of licking and handling, when intense and exaggerated, can readily become transformed into feeding, has been made plausible by Wheeler (1928). Under given trophic conditions eciton workers readily consume the brood, as we find when whole colonies are kept in the laboratory with insufficient food.

Whatever the processes of brood-reduction may be in this instance, it is clear that they must operate on a chance basis through the population, since close approximations of a normal-frequency pattern are obtained with the survivors (Text-fig. 1). Susceptibility to the eliminative processes therefore would appear to have a chance relationship to position in the brood series. Furthermore, these processes must operate in a comparable manner and to much the same extent in all potential sexual-brood populations of a species, since we find that the magnitude of finally matured populations is characteristic of the species.

The elimination of the greatest part of the potential bisexual brood, which apparently occurs in *Eciton*, seems to be critically important

for shaping the condition of the eventual brood. Through the postulated reduction processes the number of potential food-competing individuals is brought to a relatively low and relatively constant magnitude and thereby a predictable over-feeding of all survivors is insured. Perhaps the organic matter made available as a by-product of this process contributes part of the diet of the survivors in the early stages of larval development. An early over-feeding, which may be augmented from this source, must account for the distinctive growth superiority of a sexual brood as compared with a potential worker brood at the beginning of nomadism.

The queen larvae, with the remaining survivors of the eciton sexual brood, exhibit a remarkable early spurt in development not seen in the case of worker broods (section 5). As a result of such differences and the constant individual over-feeding on which they must depend, members of the sexual brood reach larval maturity within about one week less than the time required by worker larvae. At that stage they have more than twice the body length and nearly 20 times the body volume of the largest worker larvae at maturity. The mature queen larvae are not only much larger, but are clearly differentiated from worker larvae in both their external and internal morphology.⁵

The potential queens, as compared with their counterparts (i.e., individuals developing from first-laid eggs) in the potential worker brood, thus enjoy a considerable advantage. It is safe to say that the few potential queens leading a sexual brood series are enormously over-fed (and probably also hyperstimulated) throughout their development in comparison with the relatively low food limit which must be imposed upon the corresponding (soldier-producing) members of a potential worker brood. In contrast to the queen, the worker or neuter-female social insect is generally considered a product of chronic inanition during development, a "starvation form" (Wheeler, 1928). In its general outlines the eciton situation appears to resemble that of the honey bee, for which there is evidence (Rhein, 1933; Melampy, et al., 1940; Haydak, 1943; Kuwabara, 1948) that genetically equivalent fertilized eggs may produce workers or queens, depending upon whether food supplied during post-hatching development is sufficient to bring the larva to the

queen threshold. Evidence bearing upon the importance of over-feeding for production of queens as against workers has been reported for ants by Wesson (1940), and for *Trigona* and *Lestrimelitta* species among stingless bees by Kerr (1946, 1950).

A sexual brood must be considered an interactive agent in the functioning of its colony, basically similar to a worker brood in this respect (Schneirla, 1938). With both types of brood in the early larval stage, a great batch of newly emerged callows sets off a nomadic phase (Schneirla, 1948, 1949). These callow adults feed voraciously for a few days, and must furnish a heavy food competition to the young larval brood. In the case of worker broods, this factor must play a large part in holding down the growth rate during the first few nomadic days while the callows retain heavy appetites. It is probably no accident that an initial slow growth rate in the larval worker brood (see Text-fig. 2) coincides with a period of maximal intra-bivouac activity and feeding in the callows. Matters are different for the sexual-brood larvae, which accelerate strikingly in growth rate during the period of callow-worker maturation and feeding. These larvae are already rather large at the start of nomadism, and plainly more attractive to workers than are worker larvae at that stage, hence are individually more successful than worker larvae in the food competition. Also, since by that time the sexual brood has been reduced to a fraction of the size of a worker brood, large-scale feeding can proceed among its members despite the competition of voracious callows.

It seems clear that the distinctly shorter time required for larval development in a sexual brood is attributable to a high growth rate sustained by maximal feeding, as compared with underfeeding in worker larvae. It is probable that, during a larval stage only about two-thirds as long as with worker broods, a sexual brood consumes roughly the same total of food as does a worker brood of far greater numbers. These very different broods are roughly the same in their total tissue bulks at larval maturity, although the population of a sexual brood then is considerably less than 10 per cent. as large as that of a worker brood. This would suggest that in these two types of broods approximately the same amount of food is distributed among very different numbers of growing individuals.

Studies both under field and laboratory conditions indicate that at most stages of development a more extensive and intensive trophalactic relationship holds between workers and sexual brood than with a worker brood. This

⁵ Although nearly 2,000 ovarioles have been found by Dr. Roy Whelden in a queen prepupa of *E. burchelli*, and 1,200 by Dr. Harold Hagan in a functional queen of this species, few or no homologous structures are found in worker larvae of the species (see also Holliday, 1904).

difference is revealed in a variety of ways. For example, getting brood samples from a bivouac usually is more difficult with a sexual brood, because of a greater reactivity of workers to these larvae and a greater tenacity in clinging to them than to worker larvae. In the bivouac, each of the large male larvae is held within a group of workers, the center of a distinct zone of stimulation and activity. The intensity of this relationship undoubtedly is greatly magnified with queen larvae. Observed in laboratory nests, the workers are found much more responsive to male larvae than to worker larvae of about the same size. They cluster more tenaciously about sexual larvae, spend more time licking, touching and shifting them about, and drop food upon them more frequently than with worker larvae. During the colony emigration at night, the complexity and high pitch of activity in transporting the bulky male larvae emphasize the strong energizing effect of this brood upon the colony. This is exemplified in the formulation of living "ant roadways" which become more prominent in the colony movements as a sexual brood advances in larval development (Schneirla, 1948). Correspondingly, daily raids show a striking increase in scope and in numbers of participants as the nomadic phase wears on.

Evidence on the developmental status of queen larvae (sections 4, 5, and 7), indicates that from an early stage they must enjoy a relative advantage over the male larvae in their stimulative potency for workers. Direct observations support this conception of the young queens as dominant trophallactic agents. Even when the queen larvae have become enclosed in cocoons, they are individually the centers of greater commotion among the workers than are any of the male larvae. Actually, their trophallactic advantage over the males appears to increase in time, very possibly with the advent of distinctive processes (e.g., secretory) augmenting their attraction for workers. There is no question that any one of the newly emerged queens is a far more powerful attractive and excitatory agent among the workers than is any one male (Schneirla & Brown, 1950).

The emergence of most or all of the young queens from their cocoons before the males, evidently typical in the ecitons, is a fact of the greatest importance for the final outcome. Also very significant for the colony reaction is the existence of gradations in behavioral status among the young queens, with a clearly superior attraction for workers exerted by the most precocious of this small group. These and other principal aspects of the eciton sexual brood

serve as stable prerequisites to the occurrence of colony division and related events.

Although the trophallactic relationship of a sexual brood to its colony is basically similar to that of a worker brood, it differs from the latter in important ways. A sexual brood exerts a general excitatory effect upon workers which promotes nomad-statory processes essentially as does a worker brood (Schneirla, 1938, 1944, 1949). Each type of brood exerts a total excitatory effect adequate to maintain nomadic function while it is in the larval stage of development. With sexual broods this phase is shorter in both investigated species than with worker broods, which have a longer stage of larval development. The statory phase, on the other hand, shows no reliable difference with the two types of brood, which are nearly the same in the duration of their post-larval development. In both cases, the emergence of a mature pupal brood raises colony excitation to the threshold of nomadism. With sexual broods, however, colony excitation is definitely higher at this time than with worker broods. This high level of arousal proves crucial for the manner in which the first emigration and its unique related events take place.

Hence, there is an important qualitative difference in the colony reaction to these two types of broods. An accentuated attraction of workers to the sexual brood may be in force from the egg stage, with a consequent intensification of brood and colony relationships. The composite effect of this type of brood in the colony is different in nature from that of a worker brood, judging from a contrast in the bivouac situation of these broods. From an early larval stage the placement of a sexual brood suggests a nascent split in the worker population, in that many workers, through a persistent affiliation with the brood, tend to avoid the functional queen and workers associated with her. Through this expanding process of counter-attraction, there arises a complex state of affairs which reaches a head only with the emergence of the sexual brood. In this entire process, the developing queens may be considered nuclear.

In a forthcoming paper, a further consideration of these events will demonstrate that the seasonally conditioned appearance of eciton sexual broods has reproductive consequences not only in the production of fertile individuals, but also in the rise of new colonies.

RÉSUMÉ AND CONCLUSIONS

In the two investigated species of *Eciton* (*Eciton*), fertile individuals are produced in distinctive annual broods which typically are

initiated early in the dry season. The apparent cause is an impact of dry weather upon queen and colony, which in some direct or indirect manner may effect a temporary inhibition of fertilization during a periodic episode of egg-production and delivery.

Acclimation to the dry-season impact seems possible, either insulating the queen against a repetition of the sexual-brood episode in the same season, or preventing the occurrence of this episode if exposure has been gradual.

Possibly a slight initial latency in the action of extrinsic factors on the queen's reproductive processes may account for the laying of a few fertilized eggs to start each series, with queens developing from these eggs through a consistent overfeeding in the colony. These queens are precocious with respect to their brother males at all stages of development.

In *E. hamatum*, a mature sexual brood contains only about six new queens together with 1,500-2,000 males; in *E. burchelli* there are likewise only a few new queens with as many as 3,000 males. Either a relatively low viability of unfertilized eggs, or cannibalistic inroads of workers against these broods, reduces them to fractional proportions at an early stage of development.

A radical reduction of total numbers in a sexual brood at an early stage permits the overfeeding of all survivors. Consequently in this brood there is a marked early spurt in larval development not shown in worker broods, and the larval stage is appreciably shorter than in worker broods. The time required for post-larval development is nearly the same in the two types of brood. Total developmental time in *E. hamatum* is about 40 days with bisexual broods, in contrast with about 47 days required by an all-worker brood.

That a stable set of conditions governs the production and development of any sexual brood is indicated by the fact that large randomized samples taken from early larval stages of development tend to approximate a normal-frequency pattern. Since the total tissue bulk of a sexual brood at larval maturity approximates that of a worker brood at the same stage, the influence of rigid limiting factors governing colony food-economy may be suspected.

A more intensive trophallactic relationship holds between the worker population and a sexual brood than when an all-worker brood is present. The developing queens have a central role in a process whereby a nascent division arises in the colony, a process developing through the maturation of a sexual brood. This paper therefore is preliminary to a further study

on the processes of colony division in these army-ant species.

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EXPLANATION OF THE PLATES

PLATE I

FIG. 1. Specimens of mature larvae from the sexual brood of *Eciton burchelli*, colony '48 B-XVII (see Table 3). *From the left:* (1) cocoon (approximate length, 24.3 mm.) containing a mature queen larva, from which, 10 days later, the pupa represented in Plate II, Figure 4, was removed; (2) a mature queen larva removed from a cocoon nearly identical with that of '1'; (3 and 4) male larvae taken at the same time, still unenclosed.

FIG. 2. Lateral view of specimens from a sexual brood of *E. burchelli* (colony '50 GB-XVI—see Table 3) taken at the mature larval stage. *From the left:* the first and third specimens are queen larvae (approximate lengths, 24.6 and 23.7 mm.), the former completely enclosed at capture, the latter partially enclosed. The other specimens, both mature male larvae, were naked at capture (approximate lengths, 24.2 and 23.7 mm.).

FIG. 3. Below: ventral view of the two queen larvae. (N.b.: Coloration modified as result of fixing in Bouin's solution).

PLATE II

FIG. 4. *From the left:* dorsal, lateral, and ventral views of a pupal queen of *Eciton burchelli* (colony '48 B-XVII—see Table 3). This specimen was originally taken as a mature larva which had completed its enclosure and was entering the prepupal stage (see Plate I, Figure 1). It was kept with workers in the laboratory for 9 days, during which it developed into the pupa shown in this figure (approximate length, 19.6 mm.).

FIG. 5. Dorsal view of pupal queen of *Eciton hamatum* (center, over-all length, 18.6 mm.) with two male pupae from the same brood (over-all lengths, 17.5 and 16.3 mm.).

FIG. 6. Ventral views of the same specimens (colony '45 H-N—see Table 3).

PLATE III

FIG. 7. Virgin queen (left) and callow male of *Eciton hamatum* (colony '48 H-27—see Table 3). When this photo was taken, the queen was at six days and the male roughly at three days post-emergence. Over-all length of queen (less antennae), 19.6 mm.

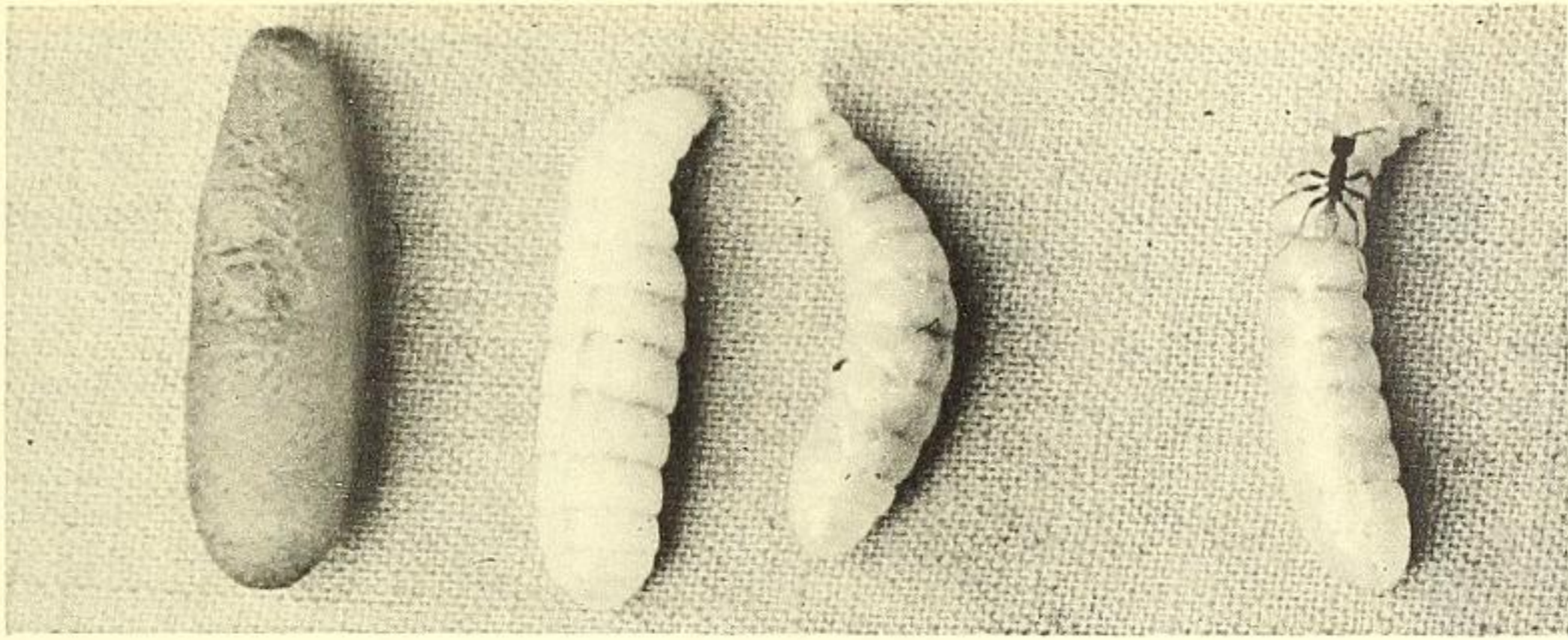


FIG. 1.

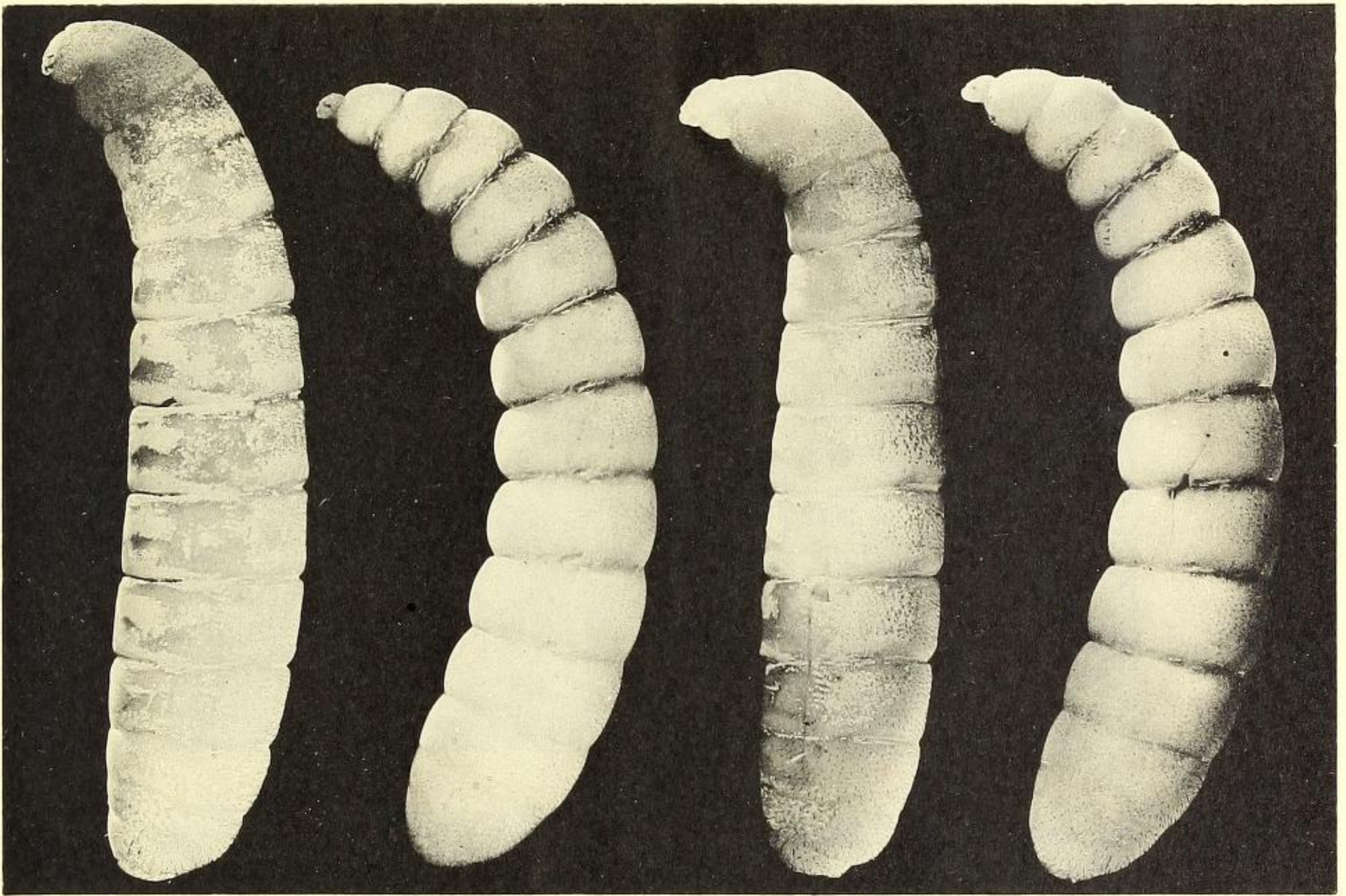


FIG. 2.

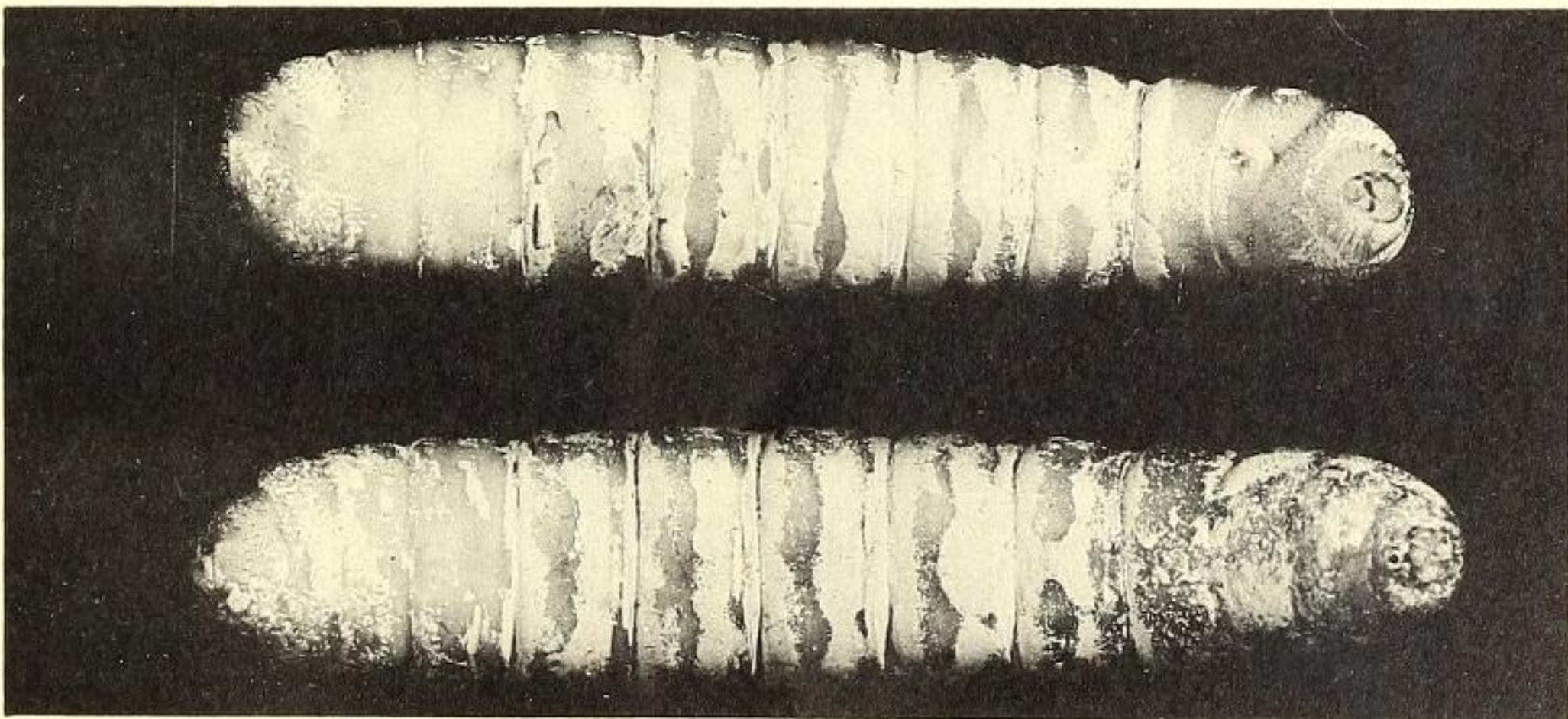


FIG. 3.

SEXUAL BROODS AND THE PRODUCTION OF YOUNG QUEENS
IN TWO SPECIES OF ARMY ANTS.

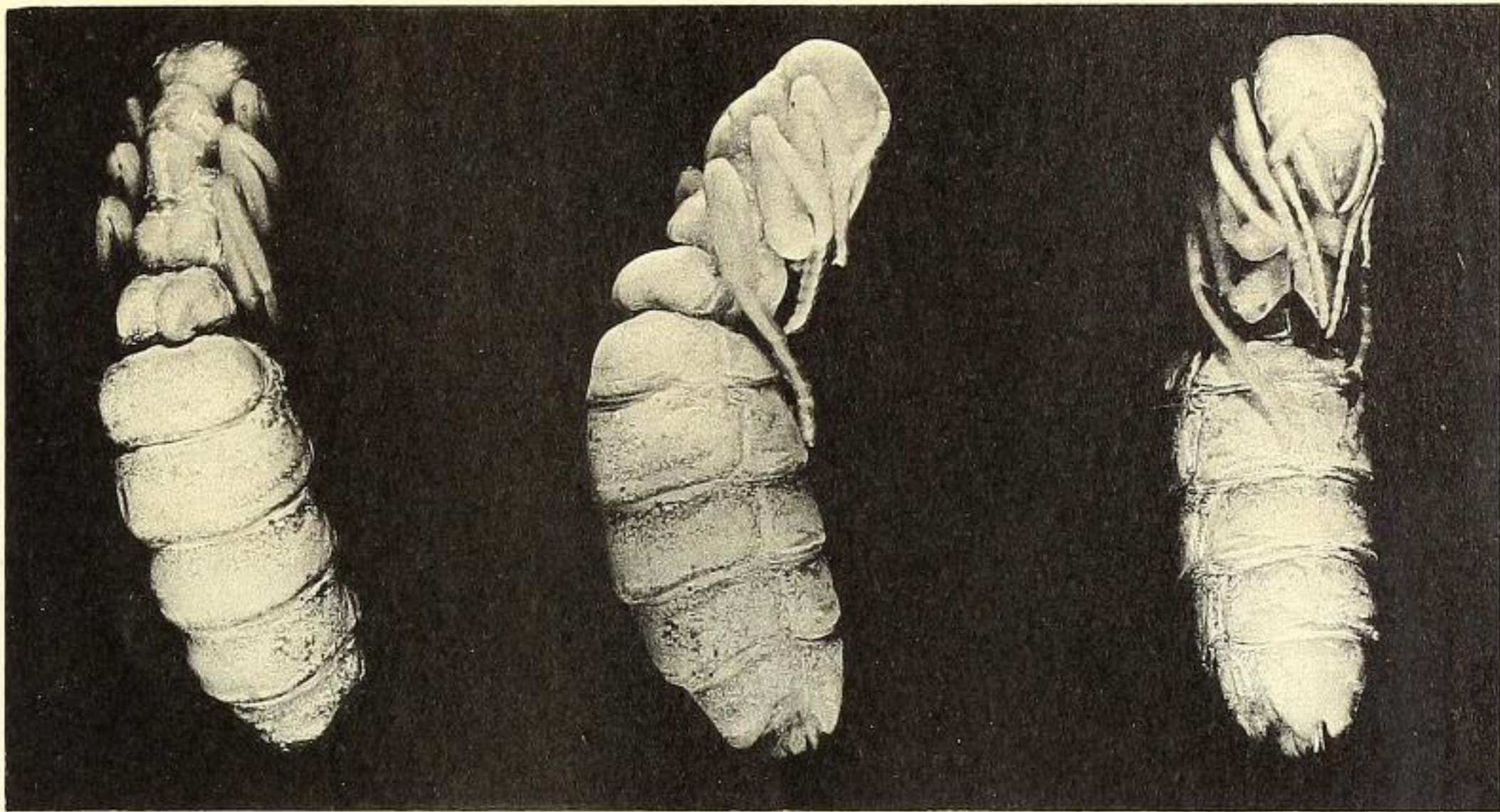


FIG. 4.

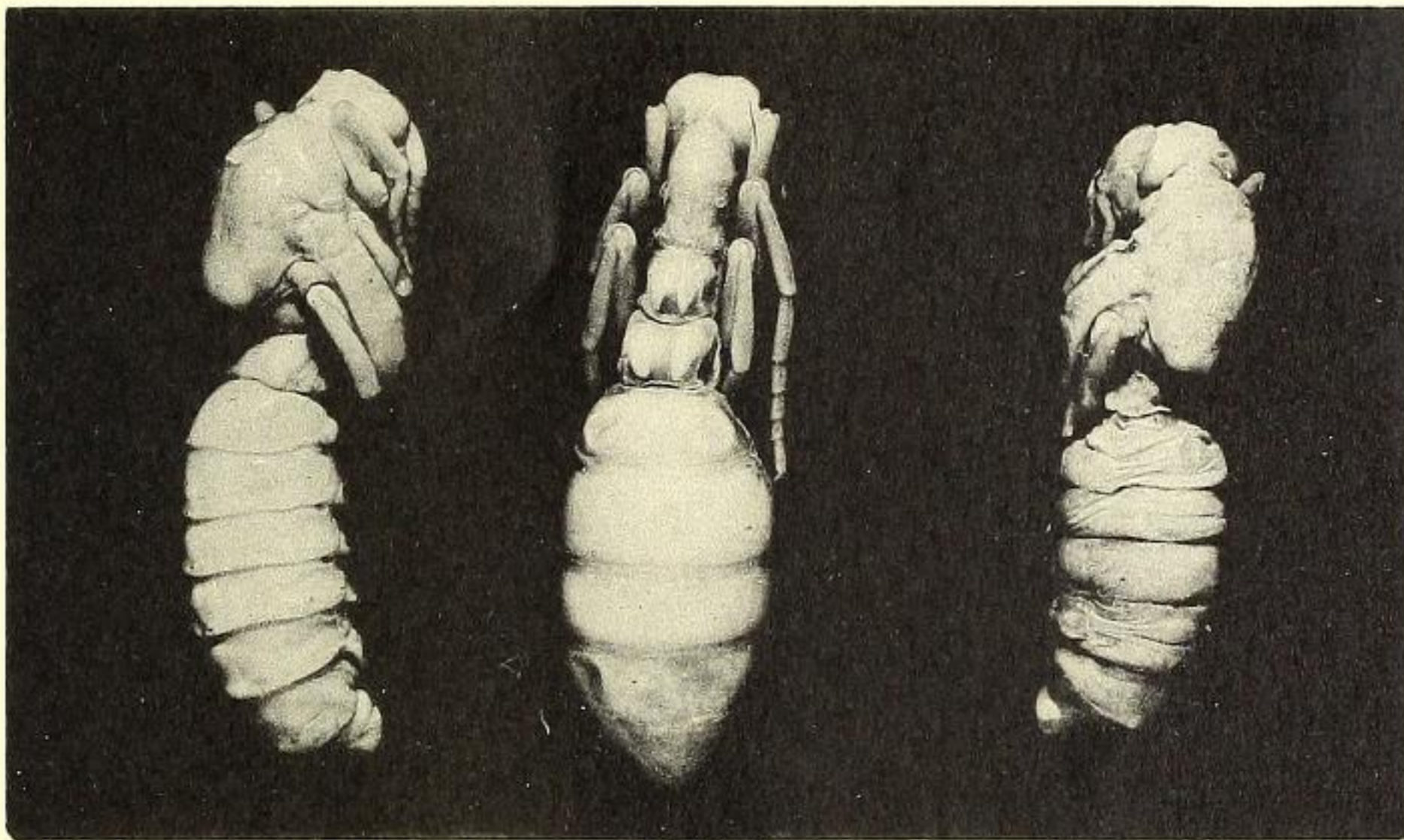


FIG. 5.

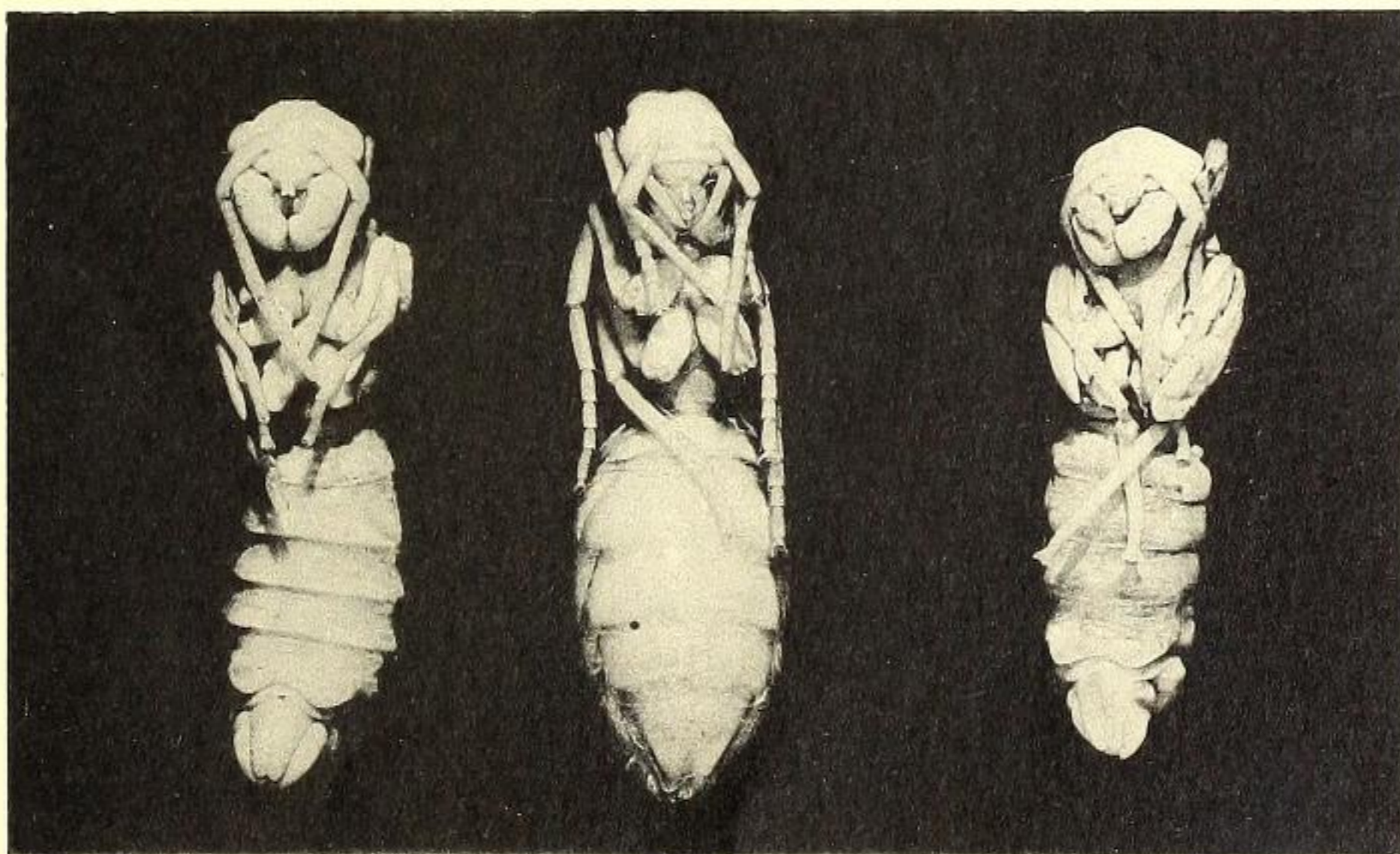


FIG. 6.

SEXUAL BROODS AND THE PRODUCTION OF YOUNG QUEENS
IN TWO SPECIES OF ARMY ANTS.

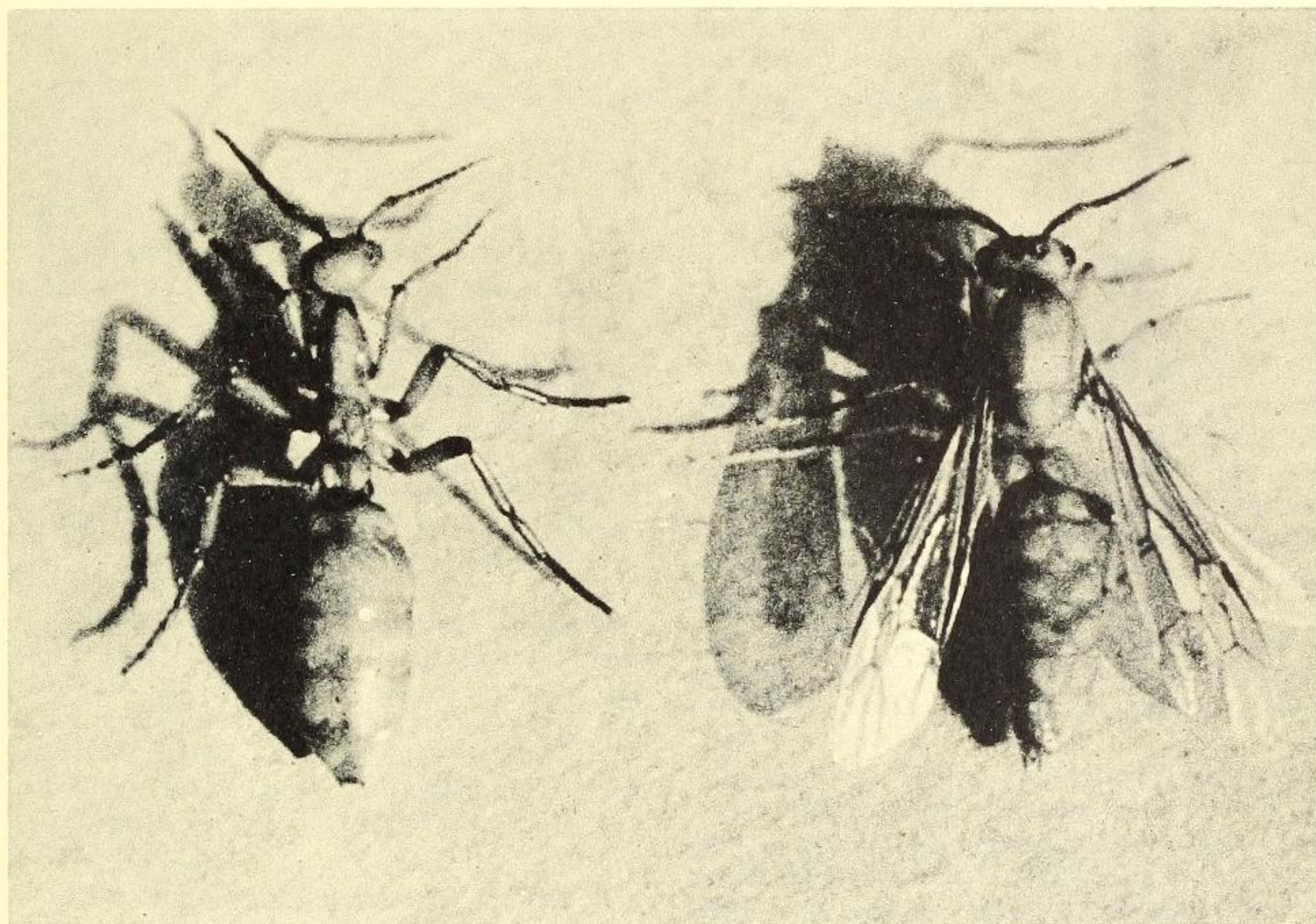


FIG. 7.

SEXUAL BROODS AND THE PRODUCTION OF YOUNG QUEENS
IN TWO SPECIES OF ARMY ANTS.

