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Aggressiveness, Territoriality, and Sexual Behavior in Field Crickets (Orthoptera: Gryllidae)

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**AGGRESSIVENESS, TERRITORIALITY, AND SEXUAL
BEHAVIOR IN FIELD CRICKETS
(ORTHOPTERA: GRILLIDAE)**

by

RICHARD D. ALEXANDER¹⁾

(Museum of Zoology and Department of Zoology,
The University of Michigan, Ann Arbor.)

(with 63 Figures)

(Rec. 25-X-1960)

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INTRODUCTION

The males in many species of crickets exhibit specialized aggressive behavior. Violent physical combat is not unusual, and LAUFER (1927) notes that the matching of fighting crickets has actually been a popular sport in the Orient for nearly a thousand years. There has been no extensive analytical or comparative study of this phenomenon, although KATO and HAYASAKA (1958) recorded a dominance order in crickets in the laboratory, and HUBER (1955) and HÖRMANN-HECK (1957) have investigated the physiological and genetic bases for aggressive and sexual behavior in the European field crickets, *Gryllus campestris* L. and *G. bimaculatus* De Geer.

Most terrestrial crickets also excavate more or less extensive burrows, and in several species, diapausing juveniles regularly pass the winter in burrows of their own construction. The burrows of adult males are usually several feet apart, and once a male has constructed a burrow he rarely becomes separated from it. Sexually responsive females are attracted to the stationary males by their loud, rhythmical stridulations, which are inevitably distinctive among naturally sympatric and synchronic species.

This study was undertaken to determine the relationship among the three activities, aggression, territoriality, and sexual behavior, and to compare their expression in different species, both closely related and in different genera and subfamilies. Special emphasis has been placed on the role of sound as a communicative mechanism. The results have shown that territorial behavior is a surprisingly complex phenomenon in field crickets. In association with the unique sexual behavior of crickets, and with complex patterns of re-

inforcement in dominance-subordinance relations, it has produced in some instances the rudiments of social behavior as elaborated in the termites, and in other instances, the rudiments of phase differences as elaborated in the migratory locusts.

The crickets treated are primarily North American species in the genus *Acheta*, of which about fifteen are known at present. All of these are either newly recognized species (ALEXANDER, 1957a; ALEXANDER and BIGELOW, 1960), or else they are among the numerous American species which remain to be described or given species rank under names synonymized by REHN and HEBARD (1915). Comparative notes are included for other Gryllinae, primarily species in the following genera: *Gryllus*, *Gryllodes*, *Anurogryllus*, *Miogryllus*, and *Scapsipedus*¹). A few comparisons are drawn with other subfamilies, chiefly Nemobiinae and Gryllotalpinae.

Since the work of FULTON (1952), there have appeared several investigations which are important in one way or another to this study, and attempts have been made to correlate data and conclusions whenever possible. In addition to the studies already mentioned, and those in which the present author has participated, COUSIN (1954, 1955) has continued her work on the inheritance of morphological characters in hybrids between various European and neotropical species of *Acheta* and *Gryllus*; KHALIFA (1949, 1950) has described the sexual behavior of the house cricket, *Acheta domesticus* L.; GABBUTT (1954, 1959) has discussed the behavior and life history of *Nemobius sylvestris* (Bosc.); SELLIER (1954) has summarized his investigations on wing polymorphism in Gryllinae and Nemobiinae; GHOURI and McFARLANE (1957, 1958a, 1958b) have investigated macropterousness in *Gryllodes sigillatus* (Walker) and demonstrated reproductive isolation between Pakistanian and Canadian house crickets which were not previously known to be different; and BIGELOW (1958, 1960) has initiated a study of developmental rate, diapause, and hybridization in various American and West Indian *Acheta* species. It is hoped that the information presented here will stimulate further syntheses and a continued interest in the field crickets. Because of their wide distribution and the ease with which they can be studied, in the laboratory as well as in the field, these insects represent excellent material for further investigation along many lines.

1) The genus *Scapsipedus* is represented in this study by specimens found in Huntsville, Alabama, during August, 1959. The origin of the colony there is unknown, though it was most likely introduced for rearing as fish bait, probably from Japan. Dr LUCIEN CHOPARD of the Museum National d'Histoire Naturelle, Paris, has concurred in its tentative identification as *S. micado* Saussure.

THE KINDS OF INTERACTIONS BETWEEN MALES

Most encounters between adult male field crickets terminate with the clear retreat of one of the two individuals so that an observer has little difficulty in deciding that one male or the other dominated the situation. However, this is not always the case, and if a series of encounters is watched, it soon becomes evident that there are several different kinds of interaction sequences in which the activities of the two individuals and the degrees or intensities

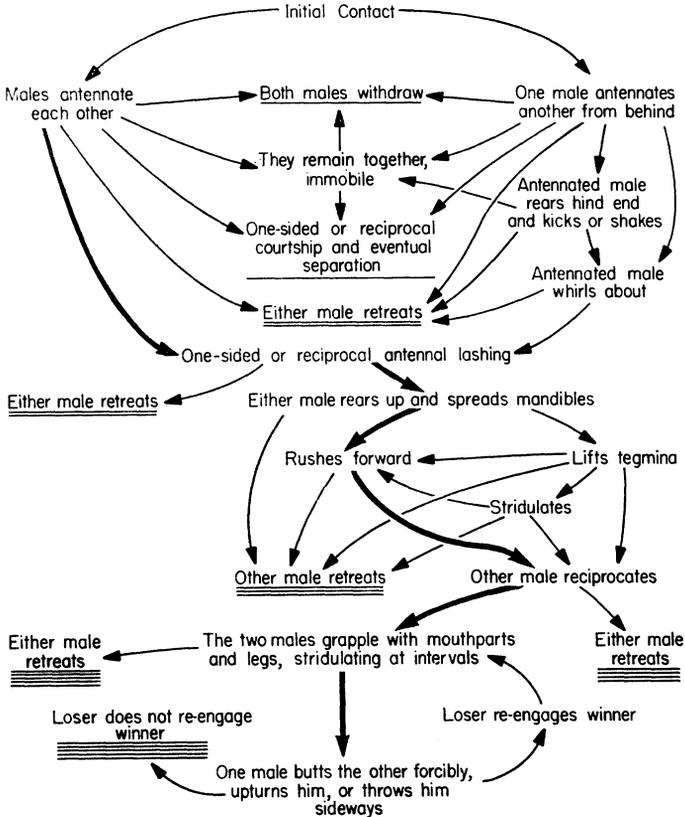


Fig. 1. A diagram of the kinds of interactions occurring between adult male field crickets. Numbers of lines drawn under terminating responses indicate the five kinds of encounters discussed in the text. Heavy line indicates the usual sequence when two aggressive males meet.

of aggression exhibited vary considerably. Fig. 1 diagrams in sequence all of the known alternatives in the actions of encountering male field crickets between the time of initial contact and the eventual termination of contact. It has been convenient in this study to refer to five "kinds" of encounters,

based upon the intensity or kind of aggression exhibited. These are indicated in the diagram by the number of lines drawn under each of the terminating responses; they may be defined as follows:

First Level. Contacts terminated without clear dominance, no apparent retreat, and no apparent aggression.

Second Level. Contacts terminated by retreat without apparent aggression.

Third Level. Contacts terminated by retreat after mild to moderate one-sided aggression or mild reciprocal aggression.

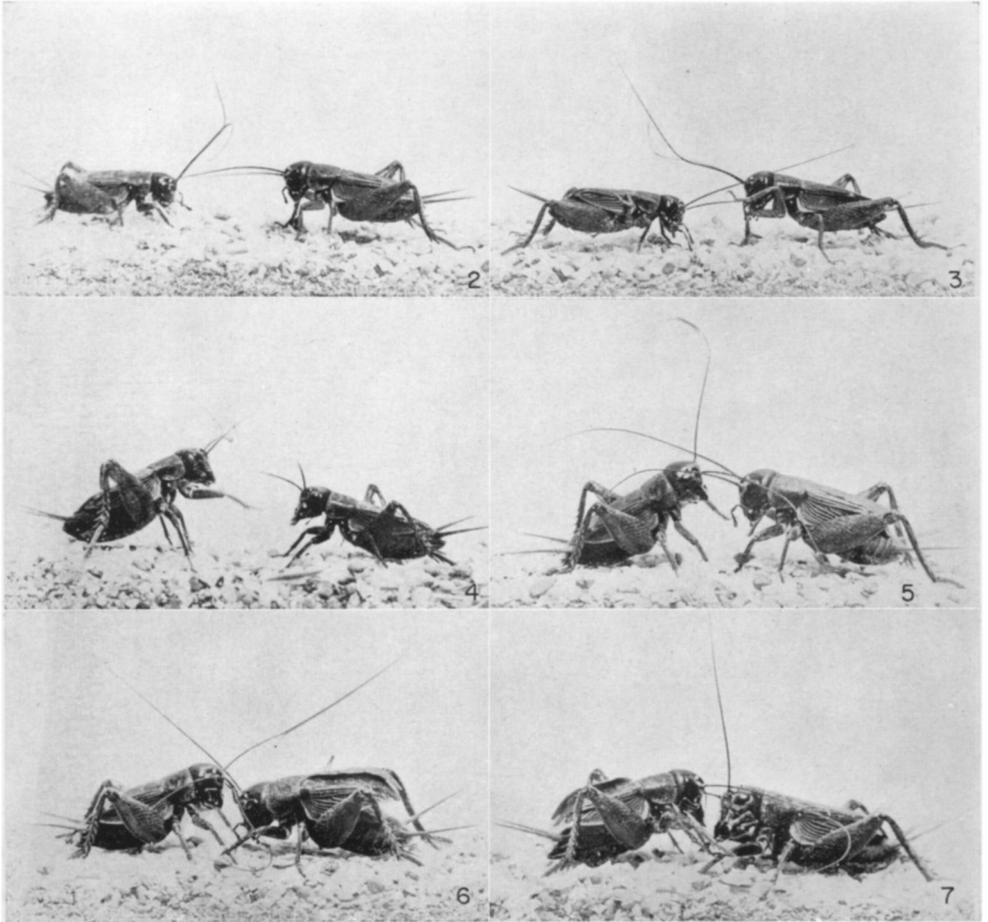
Fourth Level. Contacts terminated after moderate to intense reciprocal aggression.

Fifth Level. Contacts terminated only after sustained combat.

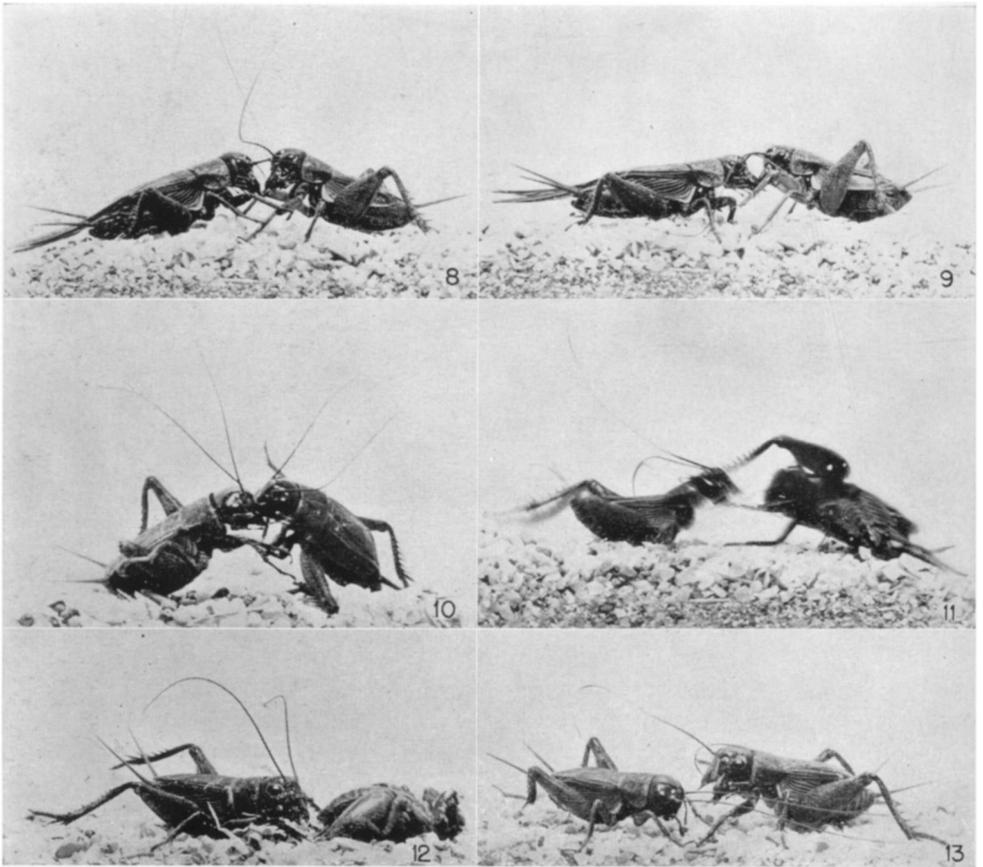
An encounter was recorded only if some part of one cricket touched some part of another. As shown in fig. 1, this usually happens in one of two different ways: the antennae of the two individuals touch, or the antennae of one individual touch the body or other appendages of the other individual. If neither individual retreats upon contact, one or both may behave aggressively or begin to court, or the two individuals may remain in contact (or barely apart) and stand immobile (or nearly so) for several minutes.

A male approached from behind, unless he is calling, most often turns quickly about and plays his antennae across the other individual. This puts the pair in about the same situation as if they had initially contacted by touching antennae together. A male approached from the rear may also shake or jerk his body, rear up his hind end, and then kick with his hind legs. These kicks sometimes repel the advancing individual, and rarely they flip an approaching male back several inches. Most often they only kick up sand and cause a temporary withdrawal by the approacher. Occasionally a male approached from the front turns about and displays these reactions, which seem best described as a mild and non-specific form of aggression. The same reaction is characteristically exhibited by encountering juvenile field crickets, and by juveniles and adults of the largely subterranean cricket, *Anurogryllus muticus* (De Geer), when substrate vibrations are caused in the vicinity of their burrows. ELLIS (1959) describes the same behavior in locusts intermediate between the migratory and non-migratory phases.

When two aggressive males meet head-on and neither retreats with the initial antennal contact, each then begins to "lash" his antennae rapidly upon the other. This is generally associated with (1) rearing the forebody, (2) drawing the palpi up and back, (3) spreading the mandibles, and (4) stepping forward (figs 2-3). The antennal lashing is interpreted here as



Figs 2-7. Photographs of male field crickets in early stages of aggressive encounters (not in sequence); Figs 2-3, right male behaving aggressively, left male still examining; Figs 4-5, two males sparring at long range; Figs 6-7, two males at close range, stridulating and grappling with the legs.



Figs 8-13. Photographs of male field crickets in late stages of aggressive encounters (not in sequence); Figs 8-9, two males engaging the mouthparts; Fig. 10, two males wrestling with mouthparts locked together; Figs 11-12, one male flipping another; Fig. 13, a non-aggressive male avoiding an aggressive male.

the initial act of aggression in head-on encounters. If two males are not closely matched, the contact is usually terminated at this point (fig. 13). If the males are closely matched, or if the normally subordinate individual (1) is behaving territorially, (2) has just copulated, (3) has just been in isolation, or (4) has just won an intense battle, then neither male retreats at this point, and one or both individuals may lift the tegmina and stridulate distinctively, jerk or shake the body, rear up further, or dash forward. Activity at this point is very rapid and difficult to interpret visually, but apparently any sequence or combination of these four kinds of activity can occur in either or both individuals. Such pronounced aggression is followed by retreat or by at least temporary reciprocation on the part of the other individual. If neither individual retreats, the antennae are pressed together as the two crickets move forward (figs 6-9), and the two males begin "sparring" with the forelegs. This seems to consist of each individual striking forward with his forelegs and then jerking them back, continually placing them on top of the other male's legs and hooking at his appendages with the tarsal claws (figs 6-9). During such sparring, either male may flip the other off-balance or butt him back with the head (figs 11-12). The two may stand head-to-head and battle in this manner for several minutes (fig. 9). If neither individual retreats, the mandibles are eventually locked together and there is a sort of wrestling activity (fig. 10) in which either male or both can be flipped or thrown sideways. This usually causes quick retreat, but it may also end with one male throwing the other backward up to several inches, flipping him up into the air (fig. 11), or turning him completely over on his back (fig. 12). Sometimes both males leap into the air and come down several inches apart or some distance from their original location. Occasionally the males wrestle with locked mandibles for several seconds before one is bested. Such violent combat usually ends the fight, but if the weaker individual is fighting near his crevice or burrow or has just copulated, he may re-engage the other male repeatedly, and rarely, cause him to retreat through this repeated attacking (fig. 60). The most violent and prolonged fights observed in this study lasted about two minutes.

When either male stridulates during prolonged combat (figs 6-7), the other usually stridulates immediately afterward. Stridulation while fighting is accompanied by a slight squatting and withdrawal, but this does not seem to place a male at a disadvantage, and stridulation nearly always occurs during combat. Although the crickets move too quickly for the situation to be very clearly analyzed without high-speed moving pictures, it seems as if they pause together for a moment whenever either stridulates, as if a male is inhibited both from fighting and from stridulating during the time that he

can hear his opponent's stridulation. It is common for the subordinate male to stridulate once or twice during an intense encounter, then retreat, this followed by the dominant male stridulating several times. In fourth and fifth level encounters, both individuals usually (but not always) stridulate during the encounter, the winner almost always stridulates afterwards, and the loser almost never stridulates afterward. The causes and effects of aggressive stridulation will be treated in detail later.

A male is more likely to court a male which approaches him from behind than he is to court a male met head-on. When two males meet head-on, courtship is rarely initiated unless one of the males displays the passivity or immobility characteristic of antennated females. When one of two crickets in an encounter is aggressive and the other begins to court, a curious situation results. An aggressive male rears up and dashes at the other male with spread mandibles, nipping at him or butting him with his head. In ordinary circumstances an aggressor encounters another head with spread mandibles, extended antennae, and striking forelegs; or he encounters nothing because the other male has retreated. However, a courting male always orients his abdomen toward such a touch, and this means that the aggressor runs into the soft, yielding, lowered abdomen of the courting individual. The contact of the aggressor, moreover, often causes the courting male to lower his abdomen still more, flattening against the substrate and backing toward the aggressor just as he would if contacted by a female from behind. If the aggressor backs off and approaches again from a side angle, the courting male re-orientes so that his rear end is again directed toward the head of the aggressor. Such a situation occasionally continues for some time, the aggressor making short runs and sometimes partially mounting the courting male, chewing at his cerci, hind legs, or tegmina. Rarely the presumed aggressor behaves exactly like a responsive female, mounting the courting male and standing immobile over him. If this happens, the courting male orients his abdomen with his cerci, vibrating them down the sides of the other male's abdomen, then brings a spermatophore into view and begins to probe with the tip of his abdomen along the underside of the other male's abdomen. This finally causes the other male to dismount. In such fashion, a male can repeatedly perform every part of the courtship sequence but the actual transference of the spermatophore through contact with other males. As HUBER (1955) pointed out for *Gryllus campestris*, this appears to be an example of bisexual or reciprocated homosexual behavior; on a lesser scale, immobility in a male upon being antennated by another male—a situation which often leads to homosexual courtship—might be similarly interpreted.

Encounters involving courtship by one male and aggression by the other

terminate when the aggressor stops behaving aggressively and backs or turns away, when the courting male is nipped or butted and runs away, or when the two males become oriented so that they meet head-on. In the last case, the dominant male, regardless of whether he happened to be the courter or the aggressor, repels the other. If the aggressor leaves without the other male ever turning to face him, the courting male may continue his courtship for up to several minutes, sometimes backing against an object in the cage or against the side of the cage. Eventually he stops courting, turns around, and after antennating the area which was immediately behind him and usually stridulating in a fashion similar to aggressive stridulation, he goes on to other activities.

In a few cases, lone males have been seen courting. In micropterous males the stimulus was probably accidental cercal contact with the side of the cage or with an object in the cage while calling. Such a lone male often strokes his cerci with the hind tarsi at intervals; this action definitely prolongs courtship and seems also to increase its vigor. Macropterous males frequently begin to court while vibrating the hind wings in the manner which precedes flight. The tegmina are lifted slightly and the hind wings are then whirred rapidly. The whirring of the wings against the cerci initiates courtship, and in two cases observed, the wing whirring and courtship continued together until the male eventually deposited a spermatophore on the screen surface of the cage. Climbing a vertical surface at night seems to initiate wing-whirring, and some species do this continually when caged in the dark. Other objects in cages are also climbed, the cricket leaping from the highest point reached, with wings vibrating as in flight. Macropterous individuals of *Acheta assimilis* Fabricius which have flown to lights take off in flight by leaping from horizontal surfaces, even when disturbed, and even in daylight. Undisturbed micropterous crickets sometimes climb objects, slowly crouch, and leap off in a very characteristic fashion, but without lifting the tegmina or spreading or vibrating the reduced hind wings; otherwise, jumping has not been observed in undisturbed crickets. Wing-whirring prior to flight occurs in other Orthoptera, and LOHER (1959) describes a wing-whirring in *Schistocerca gregaria* Forskal which he believes has acoustical significance in sexual behavior.

It is interesting that aggressive encounters have also been divided into four or five "kinds" in *Polistes* wasps (PARDI, 1948a), *Sphecius* wasps (Mr NORMAN LIN, personal communication), and crayfish (BOVBJERG, 1953; LOWE, 1956). Encounters corresponding to those labelled "first level" in this study, or the kind of contact which terminates without aggression or retreat on the part of either individual, are usually omitted; otherwise the

terminology in all these cases, derived independently for each group, is remarkably similar. BOVBJERG indicates that crayfish individuals always meet in "tension contacts," implying that there is always retreat. He suggests that even the copulatory sequence is a "tension contact," and that male crayfish react to other males and to females in exactly the same way, at least early in the encounter. Male crickets sometimes react to one another in the same way that they react to females, as already noted, and isolated, inexperienced males usually behave aggressively toward females in several encounters before beginning to court, unless approached and touched from behind while calling. Otherwise, the courtship sequence diverges early and is easily distinguishable from aggressive contacts.

The close similarity between crayfish encounters and cricket encounters is further evident in Table I, which compares the levels and percentages

TABLE I

A comparison of kinds of encounters in cricket and crayfish hierarchies (the latter from BOVBJERG, 1953).

Term used		Percentages of encounters at each level	
Crickets	Crayfish	Crickets	Crayfish
1st level	—	7	—
2nd level	avoidance	26	23
3rd level	threat	56	39
4th level	strike	7	32
5th level	fight	4	6

of each type of encounter occurring in 4000 encounters between BOVBJERG's crayfish and in the 1042 encounters between male crickets recorded during the first four days of a study of a hierarchy of five individuals (Tables II-VIII), before apparent territoriality became involved. These data suggest similar reductions of stress in aggressive encounters in these two rather widely different kinds of animals.

HIERARCHICAL RELATIONS AMONG MALES

INTRODUCTION

Hierarchical behavior in vertebrate animals is a widely investigated and discussed phenomenon (see ALLEE, 1952; TINBERGEN, 1953; COLLIAS, 1944, for summaries and bibliographies). Its interplay with territoriality on the one hand and with division of labor or leadership and followership on the other hand have been documented for several different species. Among vertebrates it is not unusual to find all three of these characteristics

prominently interwoven in the social organization of a single species (ALLEE, 1952).

Analytical studies of dominance and subordination, and the relationship of these phenomena to other kinds of interactions among individuals, are almost completely lacking for invertebrate animals. There are a few notable exceptions: the studies of BOVBJERG (1953, 1956) and LOWE (1956) on dominance hierarchies in crayfish, the study of CRANE (1958) on social organization in fiddler crabs, and the studies of PARDI (1948a, 1948b) on social dominance and division of labor in *Polistes* wasps. These investigators found that the animals they studied exhibit dominance-subordination interactions which play important roles in their particular modes of life, and which are in some respects comparable to situations found among vertebrates.

Probably the greatest value of the investigation of hierarchical relations to the present study has been that it has given a quantitative index to the aggressiveness of individual males, so that when a change was effected by one means or another, it was immediately obvious. In addition, detailed analysis of the structure of cricket hierarchies (Tables II-XXXI) has afforded clues as to the bases for the different kinds of interactions occurring among males. It is unlikely that the labile nature of aggressiveness in male crickets would have been discovered had this study not begun with observations on hierarchical relations in a confined group.

In 1954, seven males of *Acheta veletis* Alexander and Bigelow were collected in the field as late juveniles and allowed to mature together in a small terrarium. Five of the males matured over a period of a few days, and during the days following it was noted that some individuals were consistently dominant over others. The males were marked, and intermittently over a period of 12 days the winners of specific encounters were recorded. The sixth male matured on the first of these 12 days, and another male which had been kept in isolation as a juvenile and young adult was introduced briefly into the terrarium on the 12th day. Records of 198 encounters were accumulated and a linear dominance hierarchy seemed to prevail. Of the 168 encounters recorded among the six males which were caged together as adults continually during the 12 days, 40, or about 24 per cent, were inconsistent with the apparent dominance order. Of these, two were recorded with a question; one was followed by an immediate, decisive reversal; 16 were parts of continuous "sprees" by males which had just copulated with two females which were in the terrarium during most of the observations; six were parts of spreeds by two males which for unknown reasons dominated six or more encounters in succession; and the remaining 15 could not be correlated with any special circumstances. Eight of these 15 involved the

cricket at the bottom of the hierarchy, specifically in victories over the fifth, third, second, and first males in the hierarchy.

The youngest male had no significant encounters with the other males until he had molted to adulthood. All but one of the five encounters he dominated occurred on the last day of the test. The isolate made only eight contacts during his brief stay in the terrarium, encountering all but the third male in the hierarchy; although he was younger than any other male in the group, he dominated every encounter.

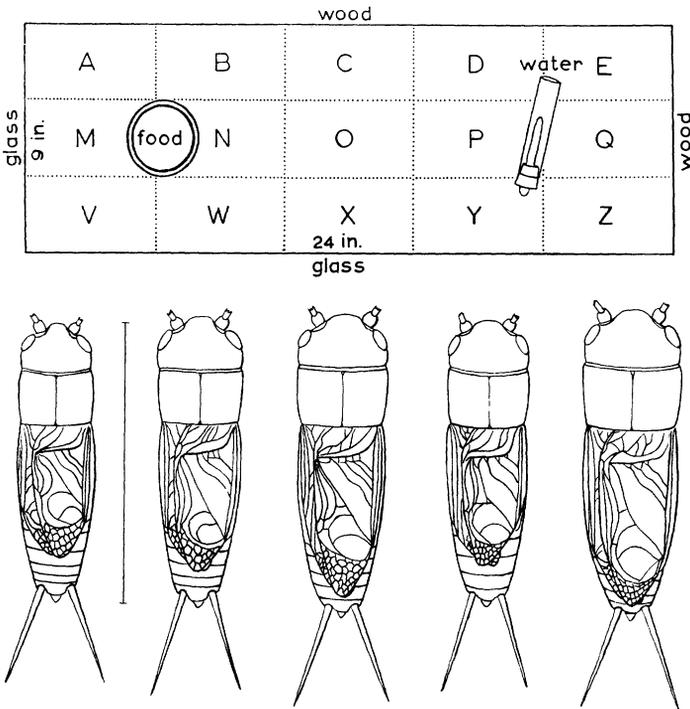


Fig. 14. Top: The terrarium used in the principal hierarchical tests; dotted lines indicate compartments visualized for recording location of encounters; compartments identified by letters in the text; Bottom: The relative sizes and body conformations of the five males used in the principal hierarchical studies. Line equals one cm. L-R: #1-#5.

Relationships of the different males with the two females in the terrarium were recorded during the 12 days, but without any special attention. Neither the location nor the intensity of the encounters between males was recorded. By the end of the observation period it was evident that these things might have been involved in certain inconsistencies in the results obtained.

On February 2, 1959, the terrarium shown in Fig. 14 was set up, and five marked males of the F₁ generation from a cross between a Grand

Isle, Louisiana, *Acheta firmus* (Scudder) male, and a female of an undescribed species (?) of *Acheta* (pale brown with a striped head¹) from the same locality, were placed in the terrarium. These males were reared together from eggs as a group of nymphs with no adults present. They were numbered in their order of maturation, and these numbers were used to identify them all through subsequent tests. Each male was deliberately placed in a situation different from that of every other male within 24 hours of his molt to adulthood. The observations made on this group of crickets formed the basis for a number of hypotheses and for subsequent experimentation, some of which has already been mentioned in the description of aggressive behavior. Consequently, most of the observations on this group are reproduced in Tables II-XXXI. Detailed analyses will be found in the various discussions which follow.

The males were identified as follows:

Male #1. Matured January 8; left antenna abbreviated by about one-half; placed with a female of a California species of *Acheta*, with which he did not mate, but which he courted for long periods of time.

Male #2. Matured January 12; right antenna abbreviated by about one-half; placed with a female of the same history with which he mated many times.

Male #3. Matured January 21; red mark on pronotum, otherwise a perfect specimen; placed in isolation.

Male #4. Matured January 28; hind tarsi missing; red mark on tegmina; left with the group of nymphs with which he was reared.

Male #5. Matured February 1; red mark on right hind femur; otherwise a perfect specimen; placed immediately into the test arena.

The mutilations of males #1, #2, and #4 were not purposely imposed, but had happened through unknown causes prior to the tests. No mutilations occurred during the tests as a result of fighting. The red marks on males #3 and #4 disappeared after a few days, but by that time all males could be readily identified so no other marks were used. All of the males but #5 were brown in color; #5 was almost black. All but #5 produced normal sounds; #5's chirps were always comparatively soft and creaky. The five males ranked in size as follows: #5 (largest), #3, #2, #4, #1. Fig. 14 shows their relative sizes and body conformations.

Contacts among the males in this group were recorded continuously during irregularly spaced periods of time varying in length from a half hour to four hours. The males involved in each encounter, which one dominated, the kind of encounter, its location in the arena, and its approximate time were all recorded by the use of graph paper. The arena was imagined to be divided into 15 different compartments (Fig. 14), and the letters designating these compartments were written at the heads of columns on the

1) This female is still unidentified because no males with these markings were successfully reared from the few nymphs collected with *Acheta firmus* in the first or second instar. The "hybrids" used here looked, stridulated, and otherwise behaved exactly like *A. firmus*.

page. Each encounter was recorded on a separate horizontal line. The time was written at the left as often as it could be noted. This system provided room for extra notes on the page and allowed quick scanning of the data for analysis later.

Because the nomenclature for different kinds of encounters was still being formulated during the first three hours after the crickets were put together (Table II), the levels of aggression recorded during this time are probably not exactly comparable with those recorded later. Although there may have been some actual change in the percentages of different kinds of encounters after this period, it is probable that many of the encounters recorded in Table II as second level aggression would have been recorded as third level if they had occurred during subsequent observations, and many of those recorded as first level would have been recorded as second level later. Otherwise, it is believed that the different kinds of encounters recorded throughout the tests can be compared with considerable validity.

During the first three days, eight hours of watching were completed (Tables II-VIII). An average of 130 contacts per hour occurred, with a range of 83-219 per hour, and a total of 1042 contacts for the eight hours. If these data are considered as a single unit, a hierarchy closely resembling those demonstrated by BOVBJERG (1953) and LOWE (1956) for crayfish is indicated. Even cricket #5, always lowest in the order during this period, dominated four of 268 encounters. But during the actual times that observations were being recorded, the hierarchy seemed much more consistent than this would suggest. Furthermore, when observations were resumed after a break of a few hours or overnight, it often seemed that a change had taken place in the order during that time. During the second set of observations (Tables III-IV), such a change occurred in the middle of the observation period. Thus, #4 dominated all eight of his encounters with #3 between 8:24 and 9:00 p.m., then he lost seven encounters straight during the next half hour. There was no see-sawing.

Because fluctuations were occurring in the order, the data for different times of observation were separated into different tables. This made the observed hierarchies 95% consistent. Of the few inconsistent encounters recorded (*cf.* Table II-IX), many were either 2nd level or they were recorded with a question, indicating that they were either inconclusive or unclear to the observer at the time.

BOVBJERG noted that he did not tabulate his data for several days in an effort to avoid the introduction of bias into his observations. Cricket encounters are generally so clear-cut that this would not be likely to happen. In addition, the dominance order is usually obvious within a few minutes

after beginning to make observations, even to someone who has never watched crickets before, making it impossible to exclude this kind of bias if it is going to affect the decisions made.

In Tables II-XXXI, the data are arranged so that the dominance order corresponds to the order of the numerators in the fractions in the left-hand column which indicate encounters and dominance-subordination relations; the lowest individual in the hierarchy does not appear in the numerator of any of these fractions. The denominators, indicating the losers in each encounter, are also arranged in order of dominance for each successive numerator or dominant individual. In this manner, the encounters between the two individuals at the top of the hierarchy appear first, then the encounters of the dominant male with the other males in the group in order of their dominance. Then all the encounters of the second male with the males subordinate to him follow, and so on. In the right side of each table the fractions are reversed, showing for each kind of encounter how many times the other male won. Thus, the encounters inconsistent with the suggested dominance order all appear on the right side of the table. The kinds of encounters, as defined earlier, are indicated in the columns marked, "Encounters at Each Level." In the lower part of each table are shown the total number of encounters recorded during the period, and the numbers won and lost by each male, in order of dominance.

TABLE II

354 Encounters, 2:15-3:15 p.m., 2 Feb. Just after the males were placed together; 3 previously isolated; 5 only one day adult.

Males Dom/Sub	Encounters at Each Level					Males Dom/Sub	Encounters at Each Level				
	1st	2nd	3rd	4th	5th		1st	2nd	3rd	4th	5th
3/2	1	60	9	4	5	2/3					
3/1		43	2	2	3	1/3					
3/4			53			4/3					
3/5			41			5/3					
2/1	22	29				1/2	8				
2/4	8	16				4/2					
2/5	3	16				5/2					
1/4	5	5				4/1					
1/5	4	9				5/1					
4/5	4	2				5/4					
Totals	47	180	105	6	8		0	8	0	0	0

Summary of Encounters of Individuals

Male	Total	Won	Lost	No-Decision
3	223	222	0	1
2	181	61	86	34
1	132	22	79	31
4	93	2	74	17
5	79	0	68	11

TABLE III

127 Encounters, 8:24-9:00 p.m., 2 Feb.

Males Dom/Sub	Encounters at Each Level					Males Dom/Sub	Encounters at Each Level				
	1st	2nd	3rd	4th	5th		1st	2nd	3rd	4th	5th
2/1		16	3	6	4	1/2					
2/4		4	11	3		4/2					
2/3		3	3	4		3/2					
2/5		6	7	1		5/2					
1/4		2	7			4/1					
1/3	1	4	5	1		3/1			1		
1/5		4	8			5/1					
4/3	2	4	2			3/4					
4/5	4	5	2			5/4					
3/5	1	3				5/3					
Totals	8	51	48	15	4		0	0	1	0	0

Summary of Encounters of Individuals

Male	Total	Won	Lost	No-Decision
2	71	71	0	0
1	62	31	30	1
4	46	13	27	6
3	34	4	26	4
5	41	0	36	5

TABLE IV

68 Encounters, 9:00-9:30 p.m., 2 Feb.

Males Dom/Sub	Encounters at Each Level					Males Dom/Sub	Encounters at Each Level				
	1st	2nd	3rd	4th	5th		1st	2nd	3rd	4th	5th
2/1		1	1	4	3	1/2					
2/3			2	4		3/2					
2/4		2	6	2		4/2					
2/5			10			5/2					
1/3			7	2		3/1			1		1
1/4			3			4/1					
1/5		3	4			5/1					
3/4		1	3	3		4/3					
3/5		3	1	1		5/3					
4/5						5/4					
Totals	0	10	37	16	3		0	0	1	0	1

Summary of Encounters of Individuals

Male	Total	Won	Lost	No-Decision
2	35	35	0	0
1	30	19	11	0
3	29	14	15	0
4	20	0	20	0
5	22	0	22	0

TABLE V

219 Encounters, 8:00-9:00 a.m., 3 Feb.

Males Dom/Sub	Encounters at Each Level					Males Dom/Sub	Encounters at Each Level				
	1st	2nd	3rd	4th	5th		1st	2nd	3rd	4th	5th
2/3		1	14	9	6	3/2			5		
2/1		8	32	2		1/2			1		
2/4			22			4/2					
2/5		2	27			5/2					
3/1			18			1/3		1	3		
3/4			18			4/3					
3/5			12			5/2					
1/4	3	2	8			4/1		1	1		
1/5	2	1	10			5/1		2	1		
4/5	2		3	1		5/4		1			
Totals	7	14	164	12	6		0	5	11	0	0

Summary of Encounters of Individuals

Male	Total	Won	Lost	No-Decision
2	129	123	6	0
3	87	53	34	0
1	96	26	65	5
4	66	7	54	5
5	60	4	52	4

TABLE VI

90 Encounters, 4:00-5:00 p.m., 3 Feb.

Males Dom/Sub	Encounters at Each Level					Males Dom/Sub	Encounters at Each Level				
	1st	2nd	3rd	4th	5th		1st	2nd	3rd	4th	5th
2/3				4	3	3/2					
2/1			12	3		1/2					
2/4			18			4/2					
2/5			4			5/2					
3/1			5			1/3			6		
3/4	1	2	13	1		4/3					
3/5			3			5/3					
1/4			6			4/1			1		
1/5			5			5/1					
4/5			3			5/4					
Totals	1	2	69	8	3		0	0	7	0	0

Summary of Encounters of Individuals

Male	Total	Won	Lost	No-Decision
2	44	44	0	0
3	38	24	13	1
1	38	17	21	0
4	45	4	40	1
5	15	0	15	0

TABLE VII

83 Encounters, 9:00-10:00 a.m., 4 Feb.

Males Dom/Sub	Encounters at Each Level					Males Dom/Sub	Encounters at Each Level				
	1st	2nd	3rd	4th	5th		1st	2nd	3rd	4th	5th
2/3			3	3	2	3/2					
2/1			11		1	1/2					
2/4			15	1		4/2					
2/5			14			5/2					
3/1			7			1/3			1		
3/4	1		4			4/3					
3/5	1		4			5/3					
1/4			7			4/1					
1/5	1	1	2			5/1					
4/5	5		2			5/4					
Totals	3	1	71	4	3		0	0	1	0	0

Summary of Encounters of Individuals

Male	Total	Won	Lost	No-Decision
2	50	50	0	0
3	26	15	9	2
1	32	12	19	1
4	32	4	27	1
5	27	0	25	2

TABLE VIII

101 Encounters, 8:30-9:30 a.m., 5 Feb.

Males Dom/Sub	Encounters at Each Level					Males Dom/Sub	Encounters at Each Level				
	1st	2nd	3rd	4th	5th		1st	2nd	3rd	4th	5th
2/3			2	4	7	3/2					
2/1			3		2	1/2					
2/4	3	1	14	1	5	4/2			2		
2/5			11			5/2					
3/1			9			1/3		1	2		
3/4	1		5			4/3			1	1	
3/5			4			5/3					
1/4			9			4/1			4		
1/5			2			5/1					
4/5	5		2			5/4					
Totals	9	1	61	5	14		0	1	9	1	0

Summary of Encounters of Individuals

Male	Total	Won	Lost	No-Decision
2	55	50	2	3
3	37	18	18	1
1	32	14	18	0
4	54	10	35	9
5	24	0	19	5

TABLE IX

39 Encounters, 1:45-2:45 p.m., 10 Feb. Male #3 is out in isolation.

Males		Encounters at Each Level					Males		Encounters at Each Level				
Dom/Sub	1st	2nd	3rd	4th	5th	Dom/Sub	1st	2nd	3rd	4th	5th		
2/1			1	3		1/2							
2/4			2	1	4	4/1							
2/5	2		5			5/2							
1/4						4/1			9				
1/5	2	2	1			5/1							
4/5	4		3			5/4							
Totals	8	2	12	4	4		0	0	9	0	0		

Summary of Encounters of Individuals

Male	Total	Won	Lost	No-Decision
2	18	18	0	0
4	23	12	7	4
1	19	3	13	3
5	17	0	9	8

TABLE X

79 Encounters, 3:24-3:47 p.m., 10 Feb. Male #3 just placed back in the group following four days of isolation, except for 15 minutes on 8 Feb.

Males		Encounters at Each Level					Males		Encounters at Each Level				
Dom/Sub	1st	2nd	3rd	4th	5th	Dom/Sub	1st	2nd	3rd	4th	5th		
3/2			5		6	2/3							
3/4			15	4		4/3							
3/1			5			1/3							
3/5			13			5/3							
2/4			5		1	4/2			1				
2/1			3			1/2							
2/5			4			5/2							
4/1			9			1/4							
4/5			5			5/4							
1/5	1		1			5/1			1				
Totals	1	0	65	4	7		0	0	2	0	0		

Summary of Encounters of Individuals

Male	Total	Won	Lost	No-Decision
3	48	48	0	0
2	25	13	12	0
4	40	15	25	0
1	20	1	18	1
5	25	1	23	1

TABLE XI

90 Encounters, 8:23-8:52 a.m., 11 Feb. Male #2 now occupying his burrow under the water vial (P), after first showing special attention to the spot during the last observation period (Table X).

Males Dom/Sub	Encounters at Each Level					Males Dom/Sub	Encounters at Each Level				
	1st	2nd	3rd	4th	5th		1st	2nd	3rd	4th	5th
2/4			7	2	6	4/2			1		
2/3			4	2		3/2					
2/1			7	1		1/2					
2/5	2		11			5/2					
4/3			5		1	3/4					
4/1			8		2	1/4		1			
4/5	1		7			5/4					
3/1	1	1	6	2		1/3		1			
3/5			4		1	5/3					
1/5	2	1	3			5/1					
Totals	6	2	62	7	10		0	2	1	0	0

Summary of Encounters of Individuals

Male	Total	Won	Lost	No-Decision
2	43	40	1	2
4	41	24	16	1
3	28	14	13	1
1	36	6	27	3
5	32	0	27	5

TABLE XII

73 Encounters, 8:52-9:23 a.m., 11 Feb. Male #3 occupying his burrow at P.

Males Dom/Sub	Encounters at Each Level					Males Dom/Sub	Encounters at Each Level				
	1st	2nd	3rd	4th	5th		1st	2nd	3rd	4th	5th
2/3			3		1	3/2					
2/4			7	3	2	4/2					
2/1	1		6	1		1/2					
2/5	2		13			5/2					
3/4	1	2	3	2	1	4/3				1	
3/1	1		4			1/3					
3/5			1	1		5/3					
4/1			3	2		1/4			1		
4/5			5	2		5/4					
1/5	3		1			5/1					
Totals	8	2	46	11	4		0	0	1	1	0

Summary of Encounters of Individuals

Male	Total	Won	Lost	No-Decision
2	39	36	0	3
3	21	14	5	2
4	35	13	21	1
1	22	1	16	5
5	28	0	23	5

TABLE XIII

47 Encounters, 11:00-11:30 a.m., 11 Feb. Male #3 occupying his burrow at P.

Males Dom/Sub	Encounters at Each Level					Males Dom/Sub	Encounters at Each Level				
	1st	2nd	3rd	4th	5th		1st	2nd	3rd	4th	5th
2/3			5	1	4	3/2					
2/4			2	2	3	4/2					
2/1				1		1/2					
2/5	3		7			5/2					
3/4			1	2		4/3					
3/1			1	1		1/3					
3/5	1		2			5/3					
4/1			5	1		1/4					
4/5			3			5/4					
1/5	1		1			5/1					
Totals	5	0	27	8	7		0	0	0	0	0

Summary of Encounters of Individuals

Male	Total	Won	Lost	No-Decision
2	28	25	0	3
3	18	7	10	1
4	19	9	10	0
1	11	1	9	1
5	17	0	12	5

TABLE XIV

112 Encounters, 3:40-4:40 p.m., 11 Feb. Artificial crevice just introduced at M.

Males Dom/Sub	Encounters at Each Level					Males Dom/Sub	Encounters at Each Level				
	1st	2nd	3rd	4th	5th		1st	2nd	3rd	4th	5th
2/3	1		3		5	3/4				1	
2/4			10	1	1	4/2					
2/5	7		13	2		5/2					
2/1	2		13	1		1/2					
3/4			5		1	4/3					
3/5			3			5/3					
3/1			13	1		1/3			1		
4/5			4		1	1/4			2		
4/1	1		7			5/4			3		
5/1	1		7			1/5		1	1		
Totals	12	0	78	5	8		0	1	7	1	0

Summary of Encounters of Individuals

Male	Total	Won	Lost	No-Decision
2	60	49	1	10
3	34	23	10	1
4	36	12	23	1
5	42	9	25	8
1	52	6	42	4

TABLE XV

29 Encounters, 5:05-5:35 p.m., 11 Feb. Male #2 occupying burrow at P, male #3 occupying the introduced crevice at M.

Males Dom/Sub	Encounters at Each Level					Males Dom/Sub	Encounters at Each Level				
	1st	2nd	3rd	4th	5th		1st	2nd	3rd	4th	5th
3/2				2	3	2/3					1
3/4			3			4/3					
3/1			2			1/3					
3/5			2	2		5/3					
2/4			2		4	4/2					
2/1	1		1			1/2					
2/5	2		1			2/5					
4/1				2		1/4					
4/5						5/4					
1/5			1			5/1					
Totals	3	0	12	6	7		0	0	0	0	1

Summary of Encounters of Individuals

Male	Total	Won	Lost	No-Decision
3	15	14	1	0
2	17	9	5	3
4	11	2	9	0
1	7	1	5	1
5	8	0	6	2

TABLE XVI

38 Encounters, 8:07-9:30 p.m., 11 Feb. Males #2 and #3 still occupying crevices at P and M, respectively.

Males Dom/Sub	Encounters at Each Level					Males Dom/Sub	Encounters at Each Level				
	1st	2nd	3rd	4th	5th		1st	2nd	3rd	4th	5th
3/2	3				3	2/3			1		
3/4	1		2	1		4/3			1		
3/5	6		5			5/3					
3/1	1		2	1	2	1/3					
2/4			1			4/2					
2/5	1		4			5/2					
2/1		1	1			1/2					
4/5						5/4					
4/1			1			1/4					
5/1						1/5					
Totals	12	1	16	2	5		0	0	2	0	0

Summary of Encounters of Individuals

Male	Total	Won	Lost	No-Decision
3	29	16	2	11
2	15	8	3	4
4	7	2	4	1
5	16	0	9	7
1	9	0	8	1

TABLE XVII

87 Encounters, 9:03-10:03 a.m., 12 Feb. Males #2 and #3 still occupying crevices at P and M, respectively.

Males Dom/Sub	Encounters at Each Level					Males Dom/Sub	Encounters at Each Level				
	1st	2nd	3rd	4th	5th		1st	2nd	3rd	4th	5th
2/3					3	3/2					
2/4			4	5	8	4/2					
2/5	3	1	10	4		5/2					
2/1			1	9	1	1/2					
3/4			1	1	7	4/3					
3/5			3	1		5/3					
3/1		1	7	3		1/3					
4/5			7	1		5/4					
4/1				2		1/4			1		
5/1			2						1		
Totals	3	2	35	26	19		0	0	2	0	0

Summary of Encounters of Individuals

Male	Total	Won	Lost	No-Decision
2	49	46	0	3
3	27	24	3	0
4	37	10	27	0
5	33	2	28	3
1	27	1	26	0

TABLE XVIII

Ten Encounters, 4:30-5:00 p.m., 12 Feb. Male #2 occupying burrow at P; #1 held crevice at M briefly after entering while #3 was outside.

Males Dom/Sub	Encounters at Each Level					Males Dom/Sub	Encounters at Each Level				
	1st	2nd	3rd	4th	5th		1st	2nd	3rd	4th	5th
2/3						3/2					
2/4				1	3	4/2					
2/5						5/2					
2/1						1/2					
3/4						4/3					
3/5						5/3					
3/1			1		1	1/3			1	1	
4/5			2			5/4					
4/1						1/4					
5/1						1/5					
Totals	0	0	3	1	4		0	0	0	1	1

Summary of Encounters of Individuals

Male	Total	Won	Lost	No-Decision
2	4	4	0	0
3	4	2	2	0
4	6	2	4	0
5	2	0	2	0
1	4	2	2	0

TABLE XIX

91 Encounters, 8:15-9:05 a.m., 13 Feb. Male #2 still occupying his burrow at P; #3 and #4 alternately occupying the crevice at M.

Males Dom/Sub	Encounters at Each Level					Males Dom/Sub	Encounters at Each Level				
	1st	2nd	3rd	4th	5th		1st	2nd	3rd	4th	5th
2/3			3	1		3/2			1		
2/4			3	1	7	4/2					
2/1	1		7	2	1	1/2					
2/5	2		7	5		5/2			1	1	
3/4			1	1	4	4/3			4	2	
3/1		1	5			1/3				1	
3/5			3	2		5/3				1	
4/1			8			1/4					
4/5			5	1	1	5/4					
1/5			3		2	1/5			3		
Totals	3	1	45	13	15		0	0	9	3	2

Summary of Encounters of Individuals

Male	Total	Won	Lost	No-Decision
2	43	37	3	3
3	30	18	12	0
4	38	21	17	0
1	34	6	27	1
5	37	6	29	2

TABLE XX

132 Encounters, 12:08-2:45 p.m., 13 Feb. Male #2 occupying his burrow at P; #3 and #4 alternating in occupation of pillbox at M. A female which had copulated only with #1 in from 12:35 to 2:45; she landed and stayed in #2's territory, copulating only with him, though mounting #1 and #5 without spermatophore transfer.

Males Dom/Sub	Encounters at Each Level					Males Dom/Sub	Encounters at Each Level				
	1st	2nd	3rd	4th	5th		1st	2nd	3rd	4th	5th
2/3	2		11	10	9	3/2				1	
2/4			1	1	1	4/2					
2/1			8	3	7	1/2			1	1	
2/5	1		2	1		5/2					
3/4	1			2	4	4/3			7	7	5
3/1			6	2	1	1/3			2	2	4
3/5	2		6			5/3					
4/1			6	1	2	1/4				3	
4/5			2	1		5/4					
1/5	1		4	1		5/1					
Totals	7	0	46	22	24		0	0	10	13	10

Summary of Encounters of Individuals

Male	Total	Won	Lost	No-Decision
2	60	54	3	3
4	44	31	12	1
3	90	22	57	5
1	55	18	36	1
5	21	0	17	4

TABLE XXI

31 Encounters, 3:54-4:24 p.m., 13 Feb. Male #2 occupying his burrow at P; #5 occupying the pillbox at M.

Males Dom/Sub	Encounters at Each Level					Males Dom/Sub	Encounters at Each Level				
	1st	2nd	3rd	4th	5th		1st	2nd	3rd	4th	5th
5/2	1			1		2/5					
5/3	2			1	2	3/5					
5/4			1	1		4/5					
5/1			8			1/5					
2/3					1	3/2				1	
2/4				5		4/2					
2/1			3	1	1	1/2					
3/4	1		1			4/3			1		
3/1			1			1/3					
4/1				1		1/4				1	
Totals	4	0	10	10	4		0	0	1	2	0

Summary of Encounters of Individuals

Male	Total	Won	Lost	No-Decision
5	13	10	0	3
2	13	10	2	1
3	11	3	5	3
4	12	2	9	1
1	12	1	11	0

TABLE XXII

113 Encounters, 11:00-12:32 a.m., 14 Feb. Male #2 occupying his burrow at P; #5 occupying the pillbox at M.

Males Dom/Sub	Encounters at Each Level					Males Dom/Sub	Encounters at Each Level				
	1st	2nd	3rd	4th	5th		1st	2nd	3rd	4th	5th
5/2			2		9	2/5					1
5/3			1	3	3	3/5					
5/1			10	2	1	1/5					
5/4	1		2	4	2	4/5					
2/3	1		8	7	3	3/2					
2/1	1		12	1	5	1/2		1			
2/4			4	5	1	4/2					
3/1	1		3			1/3			1		
3/4	1		2	2	2	4/3					1
1/4		1	4	1		4/1			2	2	
Totals	5	1	48	25	26		0	1	3	2	2

Summary of Encounters of Individuals

Male	Total	Won	Lost	No-Decision
5	41	39	1	1
2	61	47	12	2
3	39	9	27	3
1	48	8	38	2
4	36	5	29	2

TABLE XXIII

35 Encounters, 1:45-2:45 p.m., 14 Feb. Male #2 occupying his burrow at P; #5 occupying the pillbox at M most of the time, #4 occupying it briefly.

Males Dom/Sub	Encounters at Each Level					Males Dom/Sub	Encounters at Each Level				
	1st	2nd	3rd	4th	5th		1st	2nd	3rd	4th	5th
5/2						2/5					
5/3			1	1	4	3/5					
5/4			1			4/5					
5/1			8			1/5					
2/3			1			3/2					
2/4			6	1	5	4/2					
2/1			2			1/2					
3/4			1			4/3				1	
3/1						1/3					
4/1			3			1/4					
Totals	0	0	23	2	9		0	0	0	1	0

Summary of Encounters of Individuals

Male	Total	Won	Lost	No-Decision
5	15	15	0	0
2	15	15	0	0
3	19	1	18	0
4	18	4	14	0
1	13	0	13	0

TABLE XXIV

42 Encounters, 8:42-9:12 a.m., 16 Feb. Male #2 occupying his burrow at P; #1 isolated by partitioning off the pillbox at M.

Males Dom/Sub	Encounters at Each Level					Males Dom/Sub	Encounters at Each Level				
	1st	2nd	3rd	4th	5th		1st	2nd	3rd	4th	5th
2/3			2	2	3	3/2					1
2/4			2	4	6	4/2					
2/5	1		2	2		5/2					
3/4			5		3	4/3					1
3/5			3	1		5/3					1
4/5			3			5/4					
Totals	1	0	17	9	12		0	0	0	0	3

Summary of Encounters of Individuals

Male	Total	Won	Lost	No-Decision
2	25	23	1	1
3	22	13	9	0
4	24	4	20	0
5	13	1	11	1

TABLE XXV

41 Encounters, 9:14-9:54 a.m., 16 Feb. The partition separating #1 from the other males was just removed; #2's burrow at P appears to be filled in.

Males Dom/Sub	Encounters at Each Level					Males Dom/Sub	Encounters at Each Level				
	1st	2nd	3rd	4th	5th		1st	2nd	3rd	4th	5th
5/3					1	3/5					
5/2			2		2	2/5					1
5/4			2		4	4/5					
5/1			2	1		1/5					
3/2					2	2/3			2		1
3/4	2			4	2	4/3					
3/1			5		2	1/3					
2/4			1			4/2					
2/1			3			1/2					
4/1			2			1/4					
Totals	2	0	17	5	13		0	0	2	0	2

Summary of Encounters of Individuals

Male	Total	Won	Lost	No-Decision
5	15	14	1	0
3	22	16	4	2
2	13	7	6	0
4	17	2	13	2
1	14	0	14	0

TABLE XXVI

54 Encounters, 10:10-10:40 a.m., and 11:00-11:30 a.m., 16 Feb. Three pillboxes introduced at M, C, and Q; last vestiges of #2's burrow removed; all males occupying intermittently, #1 least of all.

Males Dom/Sub	Encounters at Each Level					Males Dom/Sub	Encounters at Each Level				
	1st	2nd	3rd	4th	5th		1st	2nd	3rd	4th	5th
3/5			1	1	1	5/3			1		
3/2	1		1	1	1	2/3					1
3/4	1				3	4/3					
3/1			2		3	1/3					3
5/2	1	1			2	2/5					1
5/4			2	5	1	4/5					
5/1			5			1/5					
2/4					5	4/2					
2/1	1		1			1/2					
4/1	1		5			1/4			1	1	
Totals	5	1	17	7	16		0	0	2	1	5

Summary of Encounters of Individuals

Male	Total	Won	Lost	No-Decision
3	21	14	5	2
5	22	17	4	1
2	17	8	6	3
4	25	5	18	2
1	23	5	16	2

TABLE XXVII

79 Encounters, 1:00-2:52 p.m., 16 Feb. Three pillboxes available, at M, C, and Q; Males #2, #4, and #3 usually occupying; #3 briefly.

Males Dom/Sub	Encounters at Each Level					Males Dom/Sub	Encounters at Each Level				
	1st	2nd	3rd	4th	5th		1st	2nd	3rd	4th	5th
3/2					1	2/3					1
3/4	1		1	1		4/3					
3/5	1		1	2	3	5/3					
3/1			12	1	2	1/3					
2/4	1		7	2	2	4/2					
2/5	2			2	6	5/2					
2/1				1		1/2					
4/5	1		2	1	2	5/4					3
4/1			10	4		1/4			1		
5/1			4		1	1/5					
Totals	6	0	37	14	17		0	0	1	0	4

Summary of Encounters of Individuals

Male	Total	Won	Lost	No-Decision
3	27	24	1	2
2	25	21	1	3
4	39	19	17	3
5	31	8	19	4
1	36	1	35	0

TABLE XXVIII

57 Encounters, 2:52-3:51 p.m., 16 Feb. Three pillboxes available at M, C, and Q; males #2, #1, #3 occupying.

Males Dom/Sub	Encounters at Each Level					Males Dom/Sub	Encounters at Each Level				
	1st	2nd	3rd	4th	5th		1st	2nd	3rd	4th	5th
2/3				1	1	3/2					
2/1						1/2					
2/4			3	5	1	4/2					
2/5	5		1	7		5/2					
3/1				1		1/3					
3/4	2		6	2	5	4/3					
3/5			2		1	5/3					
1/4			1	2	8	4/1					
1/5					1	5/1					
4/5			1	1		5/4					
Totals	7	0	14	19	17		0	0	0	0	0

Summary of Encounters of Individuals

Male	Total	Won	Lost	No-Decision
2	24	19	0	5
3	21	17	2	2
1	13	12	1	0
4	37	2	33	2
5	19	0	14	5

TABLE XXIX

55 Encounters, 3:51-5:00 p.m., 16 Feb. Three pillboxes available, at M, C, and Q; males #3, #2, #5 occupying most of the time, #4 and #1 briefly.

Males Dom/Sub	Encounters at Each Level					Males Dom/Sub	Encounters at Each Level				
	1st	2nd	3rd	4th	5th		1st	2nd	3rd	4th	5th
5/3						3/5					
5/2			1		1	2/5				1	
5/4	1		1	3	2	4/5		1			
5/1	1		5	1	1	1/5				1	1
3/2	3			2	4	2/3			1		1
3/4						4/3					
3/1				1		1/3					
2/4	2		4	6	4	4/2				1	
2/1				3		1/2					
4/1				2		1/4					
Totals	7	0	17	12	12		0	0	2	3	2

Summary of Encounters of Individuals

Male	Total	Won	Lost	No-Decision
5	21	15	4	2
3	12	7	2	3
2	34	20	9	5
4	27	4	20	3
1	16	2	13	1

TABLE XXX

116 Encounters, 8:40-9:40, 10:00-10:12 a.m., 18 Feb. All crevices removed.

Males Dom/Sub	Encounters at Each Level					Males Dom/Sub	Encounters at Each Level				
	1st	2nd	3rd	4th	5th		1st	2nd	3rd	4th	5th
5/2	1		1		4	2/5			2		
5/3	3		8	3	11	3/5			1		1
5/4	3		9	2	2	4/5					
5/1					12	1/5					
2/3	4		1	4	4	3/2			1		
2/4	2		7	3		4/2					
2/1			2	2		1/2				1	
3/4	1		5	2	3	4/3			1		
3/1				1		1/3					
4/1	1		7	1		1/4					
Totals	15	0	53	17	24		0	0	6	0	1

Summary of Encounters of Individuals

Male	Total	Won	Lost	No-Decision
5	63	52	4	7
2	38	25	7	7
3	54	14	32	8
4	49	9	33	7
1	27	1	25	1

TABLE XXXI

12 Encounters, 4:31-5:35 p.m., 18 Feb. Male #1 removed; four pillbox crevices provided, one for each male.

Males		Encounters at Each Level					Males		Encounters at Each Level				
Dom/Sub		1st	2nd	3rd	4th	5th	Dom/Sub		1st	2nd	3rd	4th	5th
5/4							4/5						
5/2			1	1		3	2/5						
5/3						3	5/3						
4/2							2/4						
4/3				2	1		3/4						
2/3					1		3/2						
Totals		0	1	3	2	6		0	0	0	0	0	0

Summary of Encounters of Individuals

Male	Total	Won	Lost	No-Decision
5	8	8	0	0
4	3	3	0	0
2	6	1	5	0
3	7	0	7	0

In each table it is evident that a consistent order of dominance persisted during the time for which encounters are recorded, based upon the following three considerations:

1. Each individual won all or nearly all of his fights with males below him in the order, and lost all or nearly all of his fights with males above him in the order.
2. The intensity of aggression exhibited during encounters decreased toward the bottom of the hierarchy.
3. The total number of encounters by each male decreased gradually toward the bottom of the hierarchy.

All of these characteristics were generally consistent, shifting together when the dominance order changed. Thus, when the group was first put together, #3 was dominant, and all 5th level contacts were between this male and the next two males in the order, #2 and #1 (Table II). But five hours later, when #3 had dropped to fourth place and #2 was dominant with #1 second, all of the 5th level encounters were between #2 and #1 (Table III). Likewise, the number of fights involving #3 had dropped, in this particular case to even less than for #5, the most subordinate male.

SENSORY CAPACITIES AND DOMINANCE-SUBORDINANCE RELATIONS

The activities of crickets, both confined and in the field, suggest that three senses are most important in their reactions to each other. At long range, sound is probably the only important stimulus. At close range, hearing, vision, and the tactile (mechanical and chemical) senses primarily centered in the antennae, cerci, and palpi are all important in interactions among individuals (HUBER, 1955). The two outside disturbances to which crickets seem most sensitive are substrate vibrations and quick motions, especially of large objects.

The antennae of a cricket are probably its most important sensory apparatus in dealing with objects at close range. The long, slender antennae of a locomoting cricket are in constant motion, playing over and curling about every object and every surface in its path. At the same time the palpi probe continually at the surface over which the cricket is moving. These three sets of appendages—the legs, antennae, and palpi—almost give an impression of being mechanically interconnected, so that when the legs begin to operate so invariably do the antennae and the palpi.

Following the period covered in Tables II-XXXI, #2's antennae were removed except for the basal three-eighths of an inch. This did not change his position in the dominance order, even briefly. The following day the remainders of his antennae were removed and he immediately dropped below male #4 with which he had just previously been having 4th and 5th level encounters. He did not again become dominant over #4, although he continued to dominate #1, which had contacted him previously only in 3rd level encounters. Male #2 behaved peculiarly after complete removal of his antennae, extending his palpi far out in front and running headlong against other males in fights.

There is evidence that crickets respond visually to one another at close range. Thus, one individual often turns toward another a few inches away or flips his antennae toward him, even when the two are separated by a glass partition. This usually happens only if there is movement involved. When an object of large size is moved near a group of crickets, all activity ceases and all antennae extend toward the object. This always happened in the present tests when someone leaned over the glass-covered terrarium used. Sudden motion or sudden and violent vibration of the substrate always caused the crickets to dash about and pile together in the darkest corner or in the corner farthest from the disturbance. However, there is a great deal of accommodation to long-continued disturbances of this sort.

Vision probably plays little part in dominance-subordinance relations other than in a simple response to moving objects. KHALIFA (1950) found

that house crickets court and copulate in total darkness, apparently without delay. Covering the eyes of #4 with dark fingernail lacquer did not change his dominance status, though he failed to respond to movements nearby, and he produced the calling song continually for long periods of time during the day, which was unusual for these particular crickets.

In an attempt to see if a cricket's shape or size is important in establishing his place in the dominance order, a subordinate cricket (#1) was fitted with a vertical black piece of cardboard glued to his pronotum. It extended upward about a half inch and spread to a width of a half inch at the top. Although it greatly altered the side and shape of this male, especially from a front view, there seemed to be no effect upon his behavior. His rank in the hierarchy did not change during the hour before this "crest" broke off when he entered a crevice, and the only evidence of an effect upon the crickets he encountered was that they always examined the cardboard in great detail with the antennae.

It is interesting that neither removal of the antennae nor blinding alone completely destroyed the males' ability to fight or altered their special responses to artificial crevices. BOVBJERG (1953) found that neither removal of the antennae nor blinding alone destroyed the ability of crayfish to establish hierarchies, but removal of the antennae and blinding together did. The latter test was not performed in this study.

INDIVIDUAL PECULIARITIES AND INDIVIDUAL RECOGNITION

Individual peculiarities in specific situations were noticed in the different crickets used in the tests, as follows:

1. Male #1 often paused, then squeezed quickly past a dominant male he met while walking around the terrarium, instead of turning 60° to 180° and retreating (Fig. 13) as the other males characteristically did in this situation. This usually had a peculiar effect on the dominant male, causing him to jerk back at first, then to dash forward and act very aggressive, more so than he likely would have if #1 had retreated instead. This "squeezing past" behavior was noticed in six encounters on February 16 alone. It was not seen in any other male.

2. Male #3 sometimes turned away from a male he was fighting and "ambled" slowly away, just as though he had suddenly lost interest in the whole affair. This reaction occurred in encounters with all of the other males, even those over which he was quite dominant when he stood and fought. It did not appear to be a retreat or an act of subordination in the usual sense.

3. Male #5 sometimes allowed a very aggressive male, either dominant or subordinate to him at the time, to push him around and nip at him for extended periods of time without retaliation or retreat. He simply stood passively, turned partway away from the other male, sometimes beginning courtship after this had been going on for a while. This behavior may have been associated with #5's introduction into the terrarium with the other older males directly after maturation; it undoubtedly was responsible for the tendency of other males to start courting #5. The situation usually ended in one of the following ways: (1) with #5 beginning courtship and the other male eventually doing so too, (2) with the other male nipping and pushing for a while, then "uncertainly" moving away—occasionally returning for a last nip or shove, or (3) with #5 eventually beginning to fight and repelling the other male. Male #5 was stronger than any of the other males, and late in the tests he dominated all of the fights in which he persisted, but he never showed a clear, consistent dominance.

When each individual in a group responds in a specific fashion to each other individual, it may be difficult to determine whether or not learning or "recognition" in the usual sense is involved. Such a group could easily be arranged in a social species of ant, for example, by including only one individual each of different worker and soldier castes, a queen and a male. Here the individuals would be quite different from one another. A less obvious but similar arrangement might be one in which the different individuals were grossly different in size, so that they reacted individually to one another on that account. BOVBJERG (1956) indicated that some sort of "recognition" is necessary for crayfish to react as they did in his tests, and the same would seem to be true of crickets. Here, however, the situation seems more complicated, for a cricket often retreats upon contact with a dominant so that no fight can occur, then just a few seconds later engages an individual slightly subordinate to him in violent combat.

It was found that the dominance status of two male crickets can be reversed over and over again, apparently indefinitely, by "defeating" the dominant at any particular time through causing aggression to be directed against a device which simulated antennal lashing by another cricket (Fig. 61) while simultaneously playing electronically-produced imitations of the aggressive sound of the species. This caused the male to retreat sooner in subsequent encounters with the other male, and perhaps effected some more subtle change in his behavior upon contact which caused the other male to react more aggressively than usual. This observation suggests that the only "recognition" in crickets must be response to specific actions—thus, a recognition of aggressive "state," which can change from time to time

in the same individual or be approximately the same in different individuals, rather than recognition of any other individual characteristics. The failure of the intensity of aggression exhibited in specific encounters to decrease gradually with time (Tables II-IX) further suggests that individual recognition by any ordinary definition was not involved. The special characteristics listed above which distinguished the behavior of certain individuals to the observer seem unlikely to have played any part in causing specific reactions by other crickets to the individuals possessing them, except in direct association with the particular activity. We can conclude that crickets do not retain information from encounters which causes them to respond differently in subsequent encounters with the same individual.

COURTSHIP BEHAVIOR

No courtship was noticed among the males until February 5, and then during the period shown in Table VIII there were seven courtships, all by #4. Subsequently there was a general, steady increase in the number of courtships noticed and in the amount of time spent in courtship by each individual male.

Early in the tests, as courtship was just beginning to be noticed, nearly all cases involved the two males which were at the bottom of the hierarchy. These two males generally had more encounters in which they remained immobile without separating and without displaying aggression than did any of the others. As mentioned earlier, the female's first distinctive response to a male she meets by chance is immobility upon antennal contact, and continued contact without aggression promotes courtship even when no female is involved. The general increase in amount of courtship during these tests was probably due to an increase in time spent in contact without aggression, and possibly also to some sort of cumulative physiological change associated with failure to copulate.

AGGRESSIVE STRIDULATION

As the tests progressed there was an increase in the amount of stridulation occurring during encounters. After the appearance of territorial behavior (Tables XI-XXXI), this could be associated with the more violent encounters taking place, but during the early part of the test the chief factor involved seemed to be that each individual was more likely to chirp during an encounter if he had chirped at least once during a previous encounter. During the first three hours (Table II) male #3, previously isolated and strongly dominant, was with one exception the only male to chirp. The

exception occurred at 4:46 p.m. when male #2 chirped once during a 5th level encounter with #3. This fight lasted about a minute and was the most violent encounter recorded during this three-hour period; #2 became the dominant male sometime during the next three hours and 38 minutes (Table III).

During the first three hours, #3 chirped in connection with all of his 223 encounters except the single no-decision encounter recorded with #2; he dominated all of these 222 encounters. In the next 223 encounters involving #3, of which he won 115 while ranking 4th, 3rd, and 2nd in the hierarchy at different times, he chirped during only 77 encounters. While #3 was fourth in the hierarchy during this period, he chirped in connection with only two of 30 encounters; both were encounters which he lost, and he did not chirp in connection with any of his four wins during this time. During 29 encounters while he was third in the hierarchy, #3 chirped in five winning contacts and five losing contacts. During 197 encounters as the second male in the hierarchy, he chirped in 26 of 111 winning contacts and in 20 of 74 losing contacts. Nearly all of the latter were 4th and 5th level encounters with the alpha (most dominant) male, #2.

During the five hours involving Tables III-VIII there were 688 encounters; aggressive chirps were produced in connection with 157 of these. In 28 cases both males chirped, and these were of course all 4th and 5th level encounters. In 115 cases, only the winning male chirped, and in 14 instances the losing male was the only one to chirp. Analysis of these 14 cases showed that 11 of them involved the previous dominant, #3, chirping after losing encounters with #1 and #2, and the remaining three involved #4 chirping after encounters he lost to #1. This was the period during which #3 was moving up in the hierarchy from 4th place to 2nd place after a drop from 1st place which he held for the first few hours when the group was put together. Likewise, Table IX shows that a few hours after this period, #4 moved up to 3rd place in the hierarchy, above #1, the male with which he had had the three encounters in which he chirped although losing. These data suggest that an encounter in which the retreating male is the only one to chirp constitute an indication of impending change in the relationship of the two males.

In the first 1042 encounters recorded (Tables II-VIII), there were 379 in which aggressive chirps were produced. Only 54 of these chirping encounters (14.3%) did not involve the alpha male, and only 12 (3.2%) involved neither the alpha nor the beta male; likewise, only 12 (3.2%) involved the epsilon (most subordinate) male, and he himself chirped only twice during this entire period. The winners of encounters chirped 365

times, while the losers chirped 41 times. Fig. 15 shows the distribution in the dominance order of the 157 encounters which involved the production of aggressive chirps during the six hours covered in Tables III-VIII. From these data it can be concluded that dominant males chirp more than subordinate males, and that this forms a more or less linear order, with the exception that males near each other in the hierarchy are more likely to chirp during encounters with one another than males which are separated by two or more ranks. These correlations are due in part to the different levels of aggression displayed in these different kinds of encounters (that is, encounters between males high in the hierarchy are usually more violent and extended than encounters between males low in the hierarchy); there is

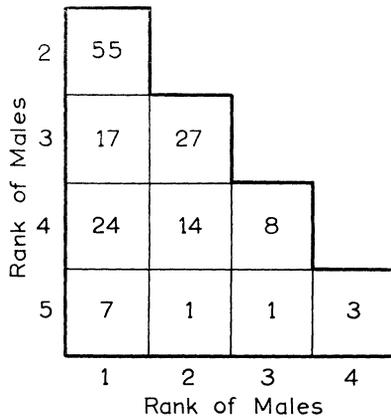


Fig. 15. The arrangement of all encounters involving stridulation by one or both males, according to the ranks of the males involved.

also a correlation between the amount of chirping and the winning or losing of encounters, as already pointed out.

Aggressive chirps may be produced either during an encounter or after contact has been lost through retreat. Nearly every case in which a losing male was the only one to chirp was an instance in which the loser chirped during the encounter. The loser practically never chirped after contact was lost following an encounter, while the winner almost invariably did so in 3rd, 4th, and 5th level encounters. Only two exceptions were noted during the period covered by Tables III-VIII, and these were instances in which #3 chirped after retreating from #1, prior to his later domination of #1. Thus, chirping by a male after he retreats is an even more positive indication that his status with respect to the male to which he has just lost will change in the near future.

Aggressive chirping is definitely an indication of a male's aggressive state. Tests were designed to determine (1) if aggressive chirping alone can induce aggressive behavior, and (2) if aggressive chirping can change the outcome of specific encounters or enhance the effect of domination upon a subordinated male.

Two sets of observations first suggested that aggressive chirping has specific effects upon the activity of individuals within hearing range:

1. When male #3 was re-introduced into the terrarium after being out in solitary for five days (Table X), he contacted three males (#1, #4, and #5) almost simultaneously less than a minute after his introduction into the Z corner of the terrarium. He delivered one long, aggressive chirp during this multiple encounter, and the alpha male, #2, who was alone several inches away at P and out of sight behind the water vial, immediately whirled about, produced a long, aggressive chirp, then dashed forward in several short runs in different directions, eventually becoming motionless again as he had been when this happened. Less than a minute later, #3 contacted another subordinate male in the Z corner and again produced one long chirp. Again #2 dashed about and stridulated. This response of #2 occurred both times within about one-tenth of a second of the time of #3's aggressive chirp.

2. A second observation involved individuals of four presently unrecognized species of *Acheta* from Utah. These will be designated here as species A, B, C, and D. Originally, a male of A and a male of B were caged with two females of C. The A male courted both females intermittently, produced the calling song when out of contact with the females, and chirped aggressively in contacts with the B male, which A seemed to dominate. The B male displayed no aggressive or courtship behavior during this time and made no sounds. A and B were both small and about the same size. Then, A was removed and a male of species D, much larger than either A or B, was introduced. D began to court one of the females, and instantly male B, completely out of sight and several inches away, scrambled toward the pair, chirping aggressively. Upon reaching them he chased male D around the cage several times, biting at him and chirping continually. Finally they separated and B stopped chirping and became immobile. This entire sequence was repeated several times during the next half hour, and when another large D male was introduced, he too was chased by the small B male each time that he began courting one of the females or chirped when encountering the other D male. Male B did not court or call during any of this time.

In attempts to test further the effects of aggressive chirps upon individ-

uals which hear them, tape recordings of single, eights-pulse chirps produced by a male in a fight were played back to males in various situations, with the results indicated below. All of the reactions described took place less than a half second from the time of the playback, and in all cases playbacks were made only when the tested male had been motionless for 15 seconds or more. Intensity of the sound was approximately 75 decibels at the location of the cricket, with one exception noted. All playbacks produced some reaction, and all are described. No reaction persisted longer than indicated, though in all cases except the last the playbacks were repeated several more times.

1. Chirps were played to male #4 while he was occupying an inverted pillbox crevice and was caged with two subordinate males with which he had just been involved in courtship and fights. Four times in succession he produced two to four aggressive chirps immediately after a playback of a single eight-pulse chirp. Each time there was temporary movement of the antennae, and twice he took a few steps forward.

2. Chirps were played to male #1 while he was caged with two males dominant to him and with which he had just been involved in courtship and in fighting. Four times in succession he dashed forward and stopped without evidence of aggressive behavior ("retreat?").

3. Chirps were played to males #4 and #5 while each was caged alone occupying a pillbox crevice; they had been in this situation for the previous ten days. Neither cricket had been out of its crevice for two hours when the sounds were played. Slight motion of the antennae was noticed: five, four, four, and three times in succession on different occasions. Once, #4, who had been facing into his crevice for two hours previous to the test, turned about and extended his antennae outside the crevice after playback of a single chirp. On four separate occasions a male walked immediately out of his crevice after the playback, then turned and went back in. When the intensity was increased to about 120 decibels, #5's antennae vibrated each time that the chirp was played, at what seemed to be the pulse rate within the chirp, but he showed no other reaction. Male #4 retreated into his crevice, withdrew his antennae, and turned about each of four times that chirps were played at this intensity while he was immobile facing outward from his crevice.

Several other attempts were made to elicit aggressive behavior in other situations and under different arrangements of the auditory stimuli, but none gave conclusive evidence of response.

The above observations and tests established that at certain times and in certain situations, auditory stimuli alone can evoke the entire repertoire

of aggressive activities in a male cricket. But our inability to reproduce positive results with a high degree of consistency and predictability indicated that unknown factors were still involved. The fact that only the alpha male responded when the newly introduced male (#3) chirped suggested that whether or not auditory stimuli alone can induce aggressive behavior depends upon the aggressive "state" of the individual. Similarly, only a very subordinate male (#1 above) responded by rapid locomotion suggesting retreat. The fact that the Utah male (B) reacted aggressively to the sounds of one species but not to the sounds of another shows that qualitative differences can affect the adequacy of auditory stimuli in aggressive situations; because he reacted to courtship and calling sounds of the other species as well as aggressive sounds, some basic parameter such as pulse rate must have been the determining factor.

Eventually it was discovered that aggressive sounds can be elicited consistently and repeatedly by auditory stimuli alone when these stimuli are presented to a male which has just won a severe fight, and that aggressive sounds re-inforce the subordination of a male which has just lost a severe fight; these tests are discussed below under the heading, "The Effects of Previous Wins and Losses."

SHIFTS IN THE DOMINANCE ORDER INDEPENDENT OF TERRITORIALITY

Aside from changes in the ability of particular males to dominate particular encounters when they were occupying niches or behaving territorially, two major shifts occurred in the dominance order shown in Tables II-XXXI: (1) male #3 moved both up and down in the order in association with his isolation from other crickets on two occasions, and (2) males #4 and #5 moved up in the order after having been adult 10-13 days. All other changes were associated with one or the other of these two major shifts.

The Effects of Isolation.

The increased aggressiveness of isolated males had already been noticed in the 1954 hierarchy of *Acheta veletis* males, and in the extreme dominance of an isolated male of *A. assimilis* Fabricius over several males with which he was placed after isolation. This effect has since been demonstrated in males of several different species. It is especially interesting because no such situation has been demonstrated in any vertebrate animal, where only the opposite effect seems to occur, and because it enhances the ability of a male to retain possession of a crevice or burrow and thus helps to explain the field behavior of crickets. Along with the tendency of males to attach

themselves to and modify particular niches and crevices, enhanced aggressiveness due to isolation largely explains the permanence of location of males in the field and the stability of structure in colonies. A permanently located male is a more effective signaller, and the spacing of males as a result of aggressive contacts and acoustical repellence promotes the development of a continuous acoustical field of maximal size, and one in which each signaller is both close enough to his neighbors to be stimulated into song by their calling and far enough away to reduce to a minimum, disturbing contacts which would disrupt the re-inforcing effect of auditory feedback once he had begun to sing.

A further interesting aspect of this increase in aggressiveness and dominating ability as a result of isolation is its disappearance when the male is caged again with a group. As shown in Tables II-XII, #3 was only dominant during the first few hours after he had been placed back with the group subsequent to isolation. Then he dropped in rank down to third or fourth place, and only moved back to second place which he then held more or less permanently (prior to #5 becoming dominant). The upward adjustment in rank did not take place as quickly as the earlier drop in rank either time, but involved several hours during which #3 became dominant over the males above him one at a time. This downward and then upward shift in dominance rank, and the apparent difference in the rate and manner of shifting, suggest that more than a single mechanism is involved. It would seem that the dominance achieved after being in the group a while is more comparable to that studied in vertebrate animals, with some sort of conditioning involved. With this in mind, further tests were performed with the results given below.

The Effects of Previous Wins and Losses.

The first indication that some sort of conditioning takes place in cricket hierarchies appeared when male #3 radically changed his behavior after his first loss to #2. For a while he lost most of his fights because he retreated with little or no reciprocation of aggression. This sort of change had been noticed previously when two aggressive males were placed together for the first time. The first fight or the first few fights were 5th level, severe combat, then a sudden change appeared in the loser, and subsequent encounters terminated with this male retreating before an intense fight could take place. There seemed to be an opposite effect upon the winner; he displayed more aggression than previously.

Following the above suggestion, experiments were performed on a group of four males of *Acheta pennsylvanicus* (Burmeister) which when placed

together ordinarily produced a hierarchy. A/B/C/D. Males A and B were placed in one arena overnight, and males C and D in another. In this situation, male B lost all of his encounters, while C won all of his encounters. When the four males were placed back together, the new order was A/C/B/D. This effect was then reversed by separating A and C together and B and D together. When the four were again caged together, the original order, A/B/C/D, reappeared. Next, the males were paired overnight, A with B, C with D. The following morning B was placed with C and D, and the order was C/B/D. A was then placed into the arena and he dominated all the other males severely for 15 minutes. Then A was removed and placed in an arena with another male which severely dominated him. He was left there for 67 minutes, then replaced with the other three males. Six minutes later he was defeated twice in succession by C, but A chirped after the latter of these two encounters, and continued chirping for a while. Four minutes later he defeated C and was again dominant in the group which was now A/B/C/D, as it had been originally. This was the only way the strongly dominant A male could be made subordinate to any of the other three crickets, and his conditioned subordination to them was extremely brief. Males B and C, on the other hand, were closely matched and could be reversed easily. This kind of information is important in using dominance rank to evaluate changes in aggressiveness.

At this point it seemed that some sort of conditioning or "priming" might be involved in evoking the aggressive sequence as well as in determining dominance status. Aggressive behavior had been evoked by auditory stimuli alone (above) and also by lashing a male cricket with simulated antennae (Fig. 61), but both auditory and tactile stimuli had given erratic results when used alone; only rarely did a male chirp as well as rush forward and "spar" with the artificial antennae. Then males were lashed at the same time that aggressive chirps were being played, and either aggression or what seemed to be specific retreat was elicited every time. Because of the enhanced aggressiveness of males which had recently won a fight, elicitation of aggression by auditory stimuli alone and tactile stimuli alone was attempted only within a few seconds after a male had won an encounter, and this proved successful every time. Then an attempt was made to change the dominance status of two males by "defeating" the dominant repeatedly, using a combination of the artificial lasher and playbacks of aggressive chirps. After several such defeats (during which time it should be noted that the subordinate male was also being subjected to the aggressive stridulation but not to the lashing), the two males were reversed in dominance status; the previous dominant now retreated before the encounter went

beyond the 3rd level. Then the order was again reversed by defeating the new dominant a few times, and the entire process was repeated. This experiment was repeated several times without failure. When the auditory stimulus was deleted, it was very difficult to secure a definite retreat in the lashed male, and only once in several attempts did it seem as though a change in dominance order had been secured.

Courtship, like aggression, appears to require more specific tactile stimuli for its elicitation than for its continuance once started, unless the male is either calling or has just stopped courting because of cessation of contact with the female. On one occasion a male which had escaped from our cages was found calling from a pile of papers; a light touch with the device in Fig. 61 started this male courting at once. He backed on to the observer's hand and was carried about, courting continually. Eventually a touch of the observer's finger was sufficient to re-initiate courtship, even after the male had fallen several feet to a concrete floor. After about fifteen minutes of continual courtship this male was dropped into a cage containing several females from a height of about three feet. He continued courting almost uninterruptedly upon alighting, and copulated with one of the females in less than a minute.

As HUBER (1955) indicates, there does not seem to be a close relationship between priming for courtship and priming for aggression; a calling male does not show increased aggressiveness. The duration of priming is uncertain in either case, though it is obviously temporary unless continually re-inforced. Some indication of the time involved is shown by the time lapses while male #3 was regaining second place in the hierarchy after losing to #2 subsequent to his re-introduction into the cage after isolation (Tables II-V, X-XII). However, the situation is greatly complicated by concurrent conditioning of the other males in the group. Furthermore, there appear to be quantitative differences which must be understood before retention can be evaluated.

The physiological basis for changes of the above nature is unknown. The reversible nature of the change in aggressiveness suggests that some kind of neural change is involved, perhaps in the suboesophageal ganglion, described by HUBER (1955) as a "center of excitation." Further aspects of aggressive "priming" will be discussed later in connection with copulation and territoriality.

The Effect of Age.

Both juveniles and adult females exhibit aggressive behavior, but juveniles of the species studied here have never become involved in more than third

level encounters, and adult females have fought with only slightly more intensity. All of the tests performed, involving several different species, indicate that a male reaches his peak dominance after being adult 10-14 days, with little or no loss in his fighting ability or dominance status as a result of age until the actual onset of physical disability, which is the first indication of a sort of slow death that characteristically occurs in healthy adult crickets after about two or three months.

HÖRMANN-HECK (1957) indicates that juveniles of *G. campestris* in the last two instars before adulthood fight any conspecific upon contact, apparently requiring even less specific stimulation than adult males. The females in this species are also hyper-aggressive.

The Effect of Size.

Size is undoubtedly a factor in determining which of two very aggressive and persistent males will dominate an encounter. However, it is rare that there is a direct correlation between size and rank in a hierarchy, and small males often defeat large males with identical histories in 5th level encounters. Furthermore, the various conditioning or priming factors discussed here can overcome size differences to the point that a male can defeat in a 5th level encounter a male that is several times his size (Fig. 60).

The Effect of General Fighting Ability.

This concept is mentioned only because it has been used as a common "catch-all" for dominance of undetermined origin in studies of this sort. We might, for example, refer to a particular male as being a "better fighter" than another if he was consistently dominant over that male for unknown reasons, or when all known factors were eliminated. Actually we do not know what is involved in such situations, and events in the nymphal history of the two individuals which have little to do with "fighting ability" could be involved; for example, effects similar to the "conditioning" observed here might be permanently fixed. Some males are probably able to move faster or spar more effectively than others, but differences of this sort have so far not been analyzed, and we do not even know if they would affect the outcome of encounters. In this connection, male #5, as already noted, won all of the fights in which he persisted during the last part of the observation period on the five male hierarchy. This male's manner of fighting was so distinctive that the photographer and other persons who only occasionally watched the crickets in encounters noticed it. He had an unusually large head (Fig. 14), and in 5th level encounters he reared up less than the other males and simply pushed forward, inevitably forcing the other

male backward until he retreated. However, there is little doubt that even this male could have eventually been forced to retreat if his opponent had just copulated (see below) or was behaving territorially. As pointed out earlier, in all but 5th level combat the encounter is terminated by one cricket retreating before physical superiority can be established, and even 5th level fights terminate before mutilation occurs.

The Effect of Copulation.

In the 1954 observations on a group of seven *A. veletis* males caged with two females, six copulations were noticed, five of them by other than the alpha male. In every case the male which had just copulated became very aggressive and was able to dominate every other male in the group for a short time. In subsequent observations on a pair of California field cricket males caged with a single female for three weeks, seven of eight copulations seen were performed by the dominant male, and the subordinate won only one of 39 encounters, this taking place a few seconds after his only copulation with the female. Additional experiments were set up, each using two *A. pennsylvanicus* males and a single female. The results will be discussed in connection with interactions between males and females; in every case the dominant monopolized the female unless the subordinate was allowed to copulate first, whereupon the post-copulatory rise in aggressiveness reversed the dominance status of the two males until the normally subordinate male's contact with the female was terminated through her failure to continue copulating without ovipositing.

TERRITORIAL BEHAVIOR

INTRODUCTION

The nature of territoriality in invertebrate animals is a subject of some dispute. CARPENTER (1958) completely excluded the invertebrates from a discussion of territoriality, apparently because of the paucity of investigations which would allow adequate comparisons with the phenomenon as it is known in vertebrate animals.

Four phenomena are associated to produce most of the various kinds or degrees of territoriality in different animals. The first two of these are:

1. displays of aggressive behavior in encounters between individuals.
2. a tendency on the part of individuals to remain in unusually restricted localities (the home range) or to consistently return to specific spots (crevice, burrow, nest, marker), or both of these tendencies.

These two characteristics exist in a wide variety of arthropods, among

insects in both social and non-social species. When they occur together, they result in a simple sort of territoriality in which the location of individual animals can be predicted at particular times, and in which the location of aggressive encounters between particular individuals can also be predicted, but in which the outcomes of particular encounters do not necessarily bear a relationship to their location. 1)

In many vertebrate animals, one or two additional phenomena have been found to occur.

3. the domination by an individual of encounters within its home range which it would have lost anywhere else and/or the exhibition of aggression by an individual within its home range in situations in which it would not have exhibited aggression elsewhere.

4. a gradual decrease in ability to dominate particular encounters and/or a gradual decrease in the number of situations in which aggression is exhibited with an increase in the distance from the center or focal point (crevice, nest, burrow, marker) of the home range. Extremes of elaboration in this direction could result in (a) reduction and eventual elimination of physical contact, with aggressive behavior becoming simply a "threat" expressed only by individuals approached at their nests or within their "home ranges" and rarely or never reciprocated, and (b) total avoidance so that each individual always remains within his own range and never trespasses upon those of his neighbors, even when behavioral interactions resulting from population density are the prime factors limiting the size of the home range.

Apparently, neither of the last two phenomena listed above (3 and 4) has previously been clearly demonstrated in a non-social invertebrate animal, though JACOBS (1955) and KORMONDY (1959) have presented evidence that male dragonflies incorporate a degree of geographic significance in their aggressive behavior. 2).

1) Although widely used, NOBLE'S (1939) definition of territory as "any defended area" is difficult to apply, especially to insects; because of problems in determining what constitutes "defense," it eventually comes to mean that territoriality exists in any animal which fights or displays aggression, and that an animal's "territory" is therefore any place in which it fights. It seems clearer to specifically reserve the term "territoriality" for the evolutionary stage characterized by association with a particular area, and the first indication of this is when the individuals of a species are not only aggressive but also restrict their movements (or their aggressiveness) in some special fashion, thereby affording a degree of predictability as to where they will have most or all of their fights.

2) MOORE (1952) states that PUKOWSKI (1933) has demonstrated "undoubted territorial behavior" in carrion beetles (*Necrophorus* sp.); PUKOWSKI'S paper was not available during preparation of this manuscript.

It seems logical that in any species in which the individuals occupy crevices or burrows for brief or extended periods of time, the mere entering of such a niche would provide a degree of invulnerability, allowing animals to resist aggression by individuals which would always dominate them in encounters in the open. However, most aggressive encounters in crayfish and crickets terminate without the sort of combat whereby the subordinate is routed through sheer force of physical strength, and this might have a bearing on how often such presumed invulnerability would actually affect the outcome of specific encounters. Even if the mere entering of a crevice increases an individual's ability to dominate or to resist aggression by others, there is still the question of whether the change is due to (1) an effect upon the inhabitant of the crevice, (2) an effect upon the individual who encounters another ensconced in a shelter, or (3) effects upon both individuals.

Many different sorts of special relationships to particular localities exist in different kinds of insects. For example, homing may be based primarily upon alteration of a locality, such as by odor trails in ants (MACGREGOR, 1948); primarily upon configurational characteristics of a locality or upon marker objects, such as in digger wasps (BAERENDS, 1941); or upon complex combinations of reactions to distance, direction, and configuration, such as in honey bees (VON FRISCH, 1952). In social insects there are factors complicating analysis of territoriality, such as the fact that individuals may perform differently within the locality of the hive or nest as compared with outside this locality primarily because of factors associated with the presence or absence of other members of the colony.

As already noted, adult male field crickets of many species are characteristically found spaced at well-worn burrows; careful observation night after night shows that each male is remaining in the same location. The laboratory experiments described below have given a more complete picture as to how field populations develop and maintain their characteristic spatial arrangements.

TERRITORIALITY IN CAGED MALE FIELD CRICKETS

When the five crickets used in the principal hierarchical studies were initially introduced into the terrarium there were no niches or crevices available. For seven days there was no evidence that any cricket was restricting his movements around the terrarium more than any other. Fig. 16 shows the location of 1096 encounters recorded during 9½ hours of observation on these days. All of the crickets spent more time and had more encounters at the EQZ end of the terrarium (Fig. 14) than at the AMV end. Two

factors, the location of the water vial and the lower light intensity caused by the two wooden walls, A-E and E-Z, were probably involved.

On the ninth day of the test (Feb. 10), the dominant male (#2) was noticed to be resting alongside the water vial at P more than usual. Then it was seen that a small depression had been hollowed out there, and #2 later dug and kicked at the sand in the bottom of the depression, gradually

Before Male No. 2's Territoriality (590 min.)					During Male No. 2's Territoriality (90 min.)				
Encounters Involving Male No. 2									
4.7	6.6	8.3	11.4	12.4	0	0	0	24.3	11.8
2.2	1.1	2.7	10.2	11.1	0	0	1.8	30.6	10.8
1.8	4.4	8.3	12.0	9.3	0	0	0	10.8	10.0
totals 585					111				
Encounters Not Involving Male No. 2									
2.1	4.1	7.9	11.9	9.5	1.0	3.0	6.1	20.4	7.1
1.5	3.0	3.9	10.3	5.2	0	1.0	0	7.1	1.0
1.2	3.7	12.3	13.7	9.5	2.0	4.1	11.2	24.5	11.2
totals 511					98				
All Encounters									
3.5	5.0	7.9	11.7	11.0	0.5	1.5	2.9	22.6	9.6
1.9	2.0	3.4	10.2	5.0	0	0.5	0.9	19.2	6.3
1.6	4.0	10.1	12.7	10.0	0.9	2.0	5.3	17.3	10.5
totals 1096					209				

Fig. 16. The percentages of encounters occurring in different parts of the terrarium before and after male #2 had begun to behave territorially with regard to his burrow under the water vial (arrow).

enlarging it until a day later it was big enough that he could squeeze completely under the water vial and come out on the other side. On the morning of the tenth day, #2 remained motionless or nearly so for long periods of time (up to 10-15 minutes) in the depression under the water vial, returned to it after encounters with males nearby, and was not observed

to go beyond the middle of the terrarium all day long (four separate hours of continual observation and intermittent observations all through the day). Repeatedly he walked down the wall of the terrarium to near the midpoint, then turned at about the same place each time and went back to his burrow. Subsequently, the same behavior was exhibited by all the other males as each occupied inverted rectangular pillboxes open at both ends which were introduced into the terrarium.

Before Feb. 10, encounters involving #2 occurred at different locations in the terrarium with about the same frequency as encounters which did not involve him, while after Feb. 10, nearly all of his encounters were within the four compartments at the EQZ end of the terrarium (Fig. 16). In P and Q, the compartments located precisely at the entrances to #2's crevice, #2 had 21.3 % of his encounters before Feb. 10 and 41.4 % after Feb. 10, while of all other encounters, 15.5 % occurred in these compartments before Feb. 10 and 8.1 % afterward. When #2 repelled a male in compartments P or Q, the dominated individual frequently stopped retreating at D or Y, this accounting for the increase in encounters not involving #2 at these locations. D seemed more an integral part of #2's territory than Y, for he spent much more time in that area and had more encounters there.

The nature and effect of #2's attachment to his burrow at P can be summarized as follows:

1. He spent long periods of time nestled immobile in the burrow, repeatedly examined, explored, and moved about, in, and out of it, and made unusually direct returns to it after encounters.

2. He made distinctive "sallies" or "patrols" out of the burrow, these consisting of him suddenly walking out after a long period of immobility — without external stimuli apparent — walking directly away from the burrow to about the midpoint of the terrarium, then turning about and walking directly back to the burrow (not meandering along the wall of the terrarium as was usual) and beginning another period of immobility nestled inside it. His behavior during these sallies was recognized as distinctive — and aggressive — even by persons who had never seen it before. He stalked in a quick, positive fashion, reared high on his forelegs, with the maxillary palpi drawn up and back in the same position as during fighting (*cf.* right male, Fig. 2, for a similar position).

3. He was never absent from the burrow for very long, and he failed to travel as far away from it at any time as he had done frequently prior to his occupation of it.

4. There was a definite shift in the location of encounters, with #2 monopolizing the area around his burrow.

These characteristics appeared in what seemed to be identical form whenever crevice occupation began. It was easy to recognize territorial behavior, and no male acted this way except when he was occupying a crevice or burrow. If a male was going to begin territorial behavior, it could usually be perceived when he entered a crevice, by the characteristic way that he examined it and then settled himself inside. Several times subordinate males began to behave in this fashion upon entering a crevice temporarily vacated, but then were routed so quickly that further elements of territoriality did not appear. CRANE (1958) found that fiddler crabs occupy burrows intermittently, apparently in association with cycles of physiological change. The temporary absence of a hungry or thirsty male cricket from a burrow might produce a similar effect, and through such temporary absence a male might lose the hyper-aggressiveness associated with burrow occupation, though retaining sufficient association with the burrow to successfully return to it (*cf.* figs 18, 19). Lone males caged with a single crevice available are rarely seen outside except at night, and in the present tests the frequent failure of subordinant males to occupy temporarily vacated burrows may have been due to their continual domination by the other males with which they were forced to come into contact rather frequently.

It appears to be significant that male #2 actually "created" the crevice at P; until this burrow was destroyed, he did not occupy introduced crevices (inverted rectangular pillboxes open at both ends), although he entered them several times and routed subordinate males (Tables XI-XXIII). No male ever took over #2's burrow, even after others had become temporarily dominant over him (Tables XV, XVI, XXI-XXIII), and even though the artificial crevices introduced before #2's burrow was destroyed changed occupants several times.

At 3:40 p.m. on Feb. 11, about a day after #2 was noticed behaving territorially with respect to the crevice at P, an inverted pillbox was introduced into the terrarium at M, providing a second crevice (Table XIV). At this time the dominance order was fairly stable at #2|#3|#4|#1|#5. Male #3 entered the new niche about a minute after it was introduced and repelled #1 from it a moment later. Then #4 entered, and shortly afterward #3 left, without aggression being exhibited between #3 and #4. Male #4 remained in the niche, repelling #1 about five minutes later, and #5 at 3:50 p.m. In the next five minutes, #4 repelled #1 twice more and #3 once when the latter approached and turned away without combat. At 4:00 p.m., #3 met #4 head-on at one end of the niche and repelled him decisively in a 4th level encounter. In the next hour, #3 had 12 encounters, repelling #1, #4, and #5, six, four, and two times, respectively. Between

encounters he stayed in the niche, motionless or nearly so. During this time he was spending such an unusual amount of time immobile that the observer noted that his occupation of the niche was having almost the same effect as if he had been isolated into another cage. Then, at 5 : 05 p.m., after a brief quiet period following a scuffle and courtship with #1, #3 walked abruptly out of his niche in the "patrolling" attitude and went directly up the middle of the terrarium to Y where he decisively dominated #2 (Fig. 18). Male #2 had been dominant to #3 since sometime before observations had started on this day; during nine hours he had won all of their 21 encounters. After his domination of #2, #3, turned and walked down the middle of the terrarium directly toward and into the niche at M and became immobile again. This was one of the most distinctive examples of "sallying" behavior observed during the tests. Ten minutes later #3 again walked

Winner	Niche-Occupying Male		
	Neither	No.1	No.4
No.1	0	13	0
No.4	4	1	15

Fig. 17. The outcomes of 33 encounters between two closely matched males (#1 and #4) during times when neither or only one was occupying a crevice.

out, encountered #2 at P, and repelled him after a very violent encounter. Male #3 remained out then for five more minutes, dominating #2, #1, #4, and #5 in that order at C and E. Then he met #2 at C again, and after a 5th level encounter he was decisively dominated and retreated toward P. Although #2 was out of contact with #3, he walked down the CBA side of the terrarium for the first time all day and encountered #3 at #3's niche, where #3 dominated him in a 5th level encounter—this only 15 seconds after the encounter dominated by #2 at C! Male #2 then retreated to D, and five minutes later, #3 sallied out again and dominated #2 at D in a 5th level encounter, and again walked quickly and directly back to his niche and entered it. Ten minutes later, #3 began producing the calling song while inside his niche. The last six in this series of encounters are diagrammed in Fig. 18.

The above sequence of events, and the fact that a male which remains

immobile inside a burrow or crevice for extended periods of time is effectively isolated from other males in the immediate vicinity, indicates that occupation of a niche and its peculiar associated behavior changes a male's ability to win specific encounters. Because a male occupying a niche rarely leaves its vicinity, the effect is that males displaying territorial behavior

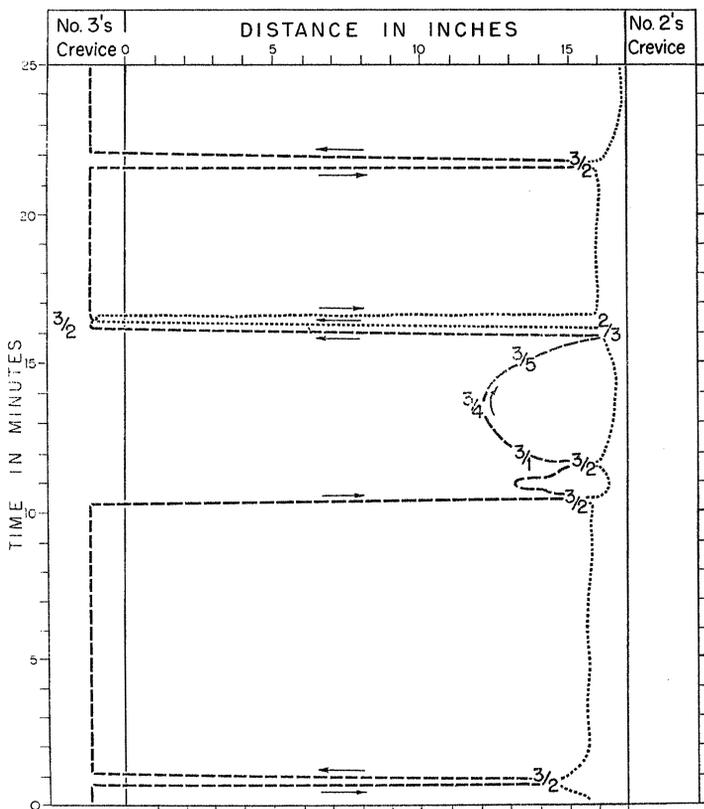


Fig. 18. An account of six encounters between two closely matched males (#2 and #3) during a time when #2 was continually occupying an inverted pillbox and #3 was remaining near (but perhaps not strictly "occupying?") his burrow under the water vial, 17 inches from #3's crevice.

dominate a much higher percentage of their encounters than they would otherwise. Although the mechanism is quite different, the effect is very similar to that produced in vertebrate animals when a complex association with a particular area enables an individual to defend it against intruders which could defeat the defender in combat in any other locality.

Fig. 17 confirms that the mere occupancy of a niche goes along with a slight adjustment in dominance, or an ability to dominate males which without the complication of niches and territories are slightly dominant to the niche occupant. Male #1's single loss while "occupying" a niche in this series occurred just after he had entered a niche, and before he had time to show any special reaction toward it.

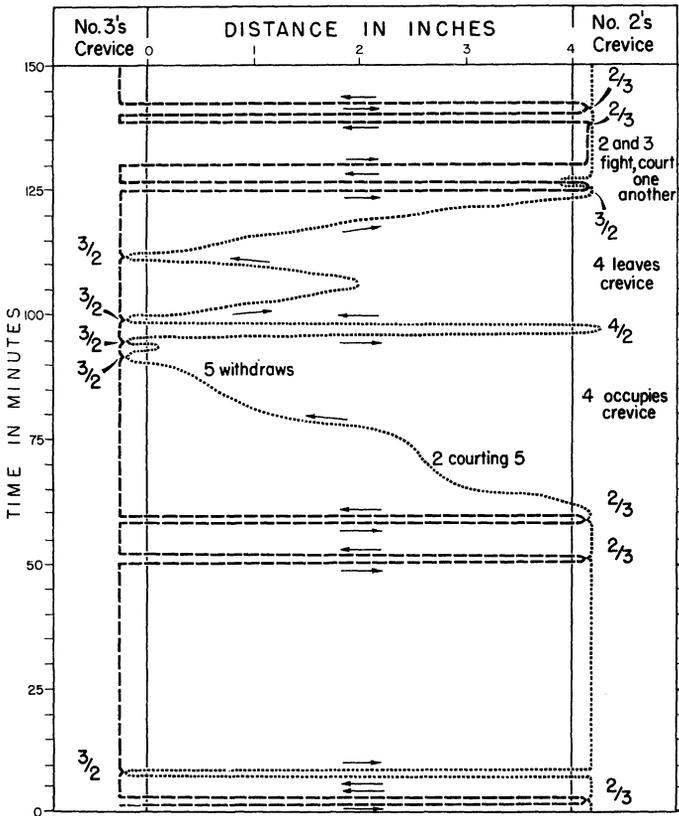


Fig. 19. An account of eleven encounters between two closely matched males (#2 and #3) during a time when they were simultaneously occupying identical inverted pillboxes only four inches apart.

The question still remains as to whether a male's attachment to a particular niche affects where he can dominate particular individuals. This question can best be answered in analyses of encounters between closely matched males which are simultaneously occupying neighboring niches which are close enough together that the two males occasionally encounter one

another during their "sallies." If the males only encounter when one (or both) may have temporarily lost contact with his niche (as may have happened in Fig. 18), then the encounters have little significance for this particular question.

The above conditions were most completely satisfied on a single occasion during the present tests when the two closely matched males, #2 and #3, simultaneously occupied niches at Q and C, respectively, four inches apart, for several hours on Feb. 16. The location and outcome of encounters during this time are shown in Fig. 19. The sallying male was almost inevitably defeated at the entrance of the other male's niche, and then—regardless of how brief an interval had elapsed when they next met near the other niche—dominance was reversed. Most of the fights took place with both crickets either inside or outside the niche, eliminating any great significance for relative invulnerability for the occupying male. In one case, the sallying male actually slipped into the other male's niche while the latter was temporarily outside engaged in a fight with another intruder. Nevertheless, he was defeated when the occupant re-entered. The continued attachment of the males to their own niches is shown by direct returns to the niches after encounters. Of further interest are the encounters following the gradual shifting of #2 across the terrarium while he was continually courting #5 over a period of about ten minutes, an unusually long time for an occupying male to be out of his niche. Male #2 had just sidled alongside #3's niche when #5 turned away and left. When #2 stopped courting, he turned and entered #3's niche, walking straight in and immediately attacking #3 in a very aggressive fashion. The fight that followed lasted two minutes, with #3 forcibly throwing #2 back several times and #2 re-engaging in an unusually tenacious manner each time. This kind of fight usually happens only when a male is attacked by an ordinarily superior male in his own niche. Up to this time #2 had in fact given to the observer the impression that he was behaving as if #3's niche were his own, although just what this implies is not clear. However, #2 did not return to his original niche after being forcibly ejected from #3's niche, but circled #3's niche directly and re-engaged him almost immediately at the other end, losing again. When #2 lost this second encounter with #3, he turned around and immediately lost an encounter with a male he had dominated all day previously. Then he moved slowly across the terrarium—not at all in the direct fashion of an occupying male—to his old niche, where he was repulsed without fighting back by #5 who had taken over the niche in #2's long absence. Returning to #3's niche, #2 began to court #3, later entering #3's niche during mutual courtship. Finally he

was expelled again by #3, returned to his old niche which was temporarily vacant, and entered it. A few seconds later he was ejected by #3 who was on a typical sally. Male #3 remained in this niche then, courting #2. Later, after two hard fights with both males inside the niche, each fight terminating with the two males gradually beginning to court one another, #2 finally expelled #3, and #3 returned directly to his old niche. After an antennal examination, he turned away without entering it, and returned to #2's niche. This time #2 repelled him, and #3 walked directly back to his old niche and entered it. Both males then began characteristic occupying behavior, did not again encounter, and were still occupying the same niches 45 minutes later when observations were terminated.

The above interactions further confirm that a male is able to win some fights within his home range or near his burrow entrance which he would lose elsewhere, and they indicate that a male reacts with unusual aggressiveness when approached by another male at his home niche. Thus, #2 entered his home niche and expelled #3 even when the latter was already inside, and even though #3 could expel #2 from his (#3's) niche. The peculiar reaction of #2 following termination of his courtship of #5 not only suggested that he had been responding to #3's burrow as if it were his own, but also that he responded afterward as if he had been ejected from his own niche. Later, after being inside his own niche a while courting #3 (who apparently never became "attached" to #2's niche), #2 successfully expelled #3. If #2 actually was reacting to #3's niche as if it were his own, then the success of #3 in ousting him from it, even though only after a very long and fierce fight, and the subsequent loss of #3 to #2 in #2's original niche, suggest that some rather complex interaction with the niche is involved.

Tables XI-XXXI illustrate the effects of territorial behavior upon a confined group and corroborate the evidence and conclusions presented above. As might be expected, the number of encounters per minute through this period fluctuated in an inverse relationship to the number of crevices available: Tables II-X (no crevices), one encounter per 0.49 min.; Tables XI-XIII (one crevice), one encounter per 0.43 min.; Tables XIV-XXIII (two crevices), one encounter per 0.87 min.; Tables XXVI-XXIX (three crevices), one encounter per 1.6 min.; Table XXX (no crevices, four males), one encounter per 0.6 min.; and Table XXXI (four crevices, four males), one encounter per 5.3 min. With steady occupancy of the available crevices by the same males, stability prevailed in the hierarchy (Tables XV-XVII); when occupancy was continually changing, the hierarchy was less consistent (Tables XVIII-XX). Proportions of 5th level encounters among subordinate

males and encounters inconsistent with any dominance ranking both increased when crevices were added. When crevices were provided for all males, scarcely enough encounters could be recorded to establish any kind of hierarchy.

The occupation of a crevice or burrow by a male cricket functions in still another, more indirect fashion, in increasing the likelihood of production of the calling song. A male producing aggressive chirps after repelling another male from his crevice often does not stop chirping, but continues, gradually changing to the calling song rhythm and then sometimes keeping this up for long periods of time. Through the advertisement of calling, a male is more likely to attract and copulate with a female, this again raising his dominance temporarily. A territorial male's isolation is undoubtedly enhanced by his calling, due to the similarity of this sound to the aggressive sounds, and its functioning as a mildly aggressive stimulus. Finally, the calling of one territorial male must frequently stimulate calling in neighboring individuals, as it does in other *Tettigonioidea* (ALEXANDER, 1960).

THE KINDS OF INTERACTIONS BETWEEN MALES AND FEMALES

In times of high population density, sexually responsive adult male and female field crickets may often come into contact accidentally, but in low-density populations, a high percentage of male-female contacts result from the locomotion of the sexually responsive female toward the stationary, stridulating male, as a result of hearing his calling sound. The two auditory organs of the female operate together as a highly directional apparatus because of their separated location upon her front tibiae; additionally, in most species the cavity containing the tympanum has two openings which face in different directions, probably making each tibial organ individually directional as well. The reaction of a responsive female to the calling of a nearby male is to turn quickly in his direction and then locomote directly toward him (REGEN, 1913; ALEXANDER, 1960).

If the male and female contact head-on, whether the male was calling or not his initial reaction is apparently the same as that elicited by contact with another male or with a juvenile. But an antennated female characteristically neither retreats nor displays aggressive behavior. Rather, she is most likely to become instantly immobile, and this response releases courtship rather than aggression in the male. Occasionally, an inexperienced male, or a territorial or for other reasons hyper-aggressive male, will repeatedly force the retreat of a female encountered head-on. At this point it also appears that in some species a specific chemo-tactile stimulus is received by the male from

the female (HÖRMANN-HECK, 1957), and that this is also involved in initiating courtship.

A calling male ordinarily begins courtship instantly if he is touched lightly from behind. In courtship, most field crickets lower their tegmina from the 45° angle characteristic during production of the calling song, tilt them roof-

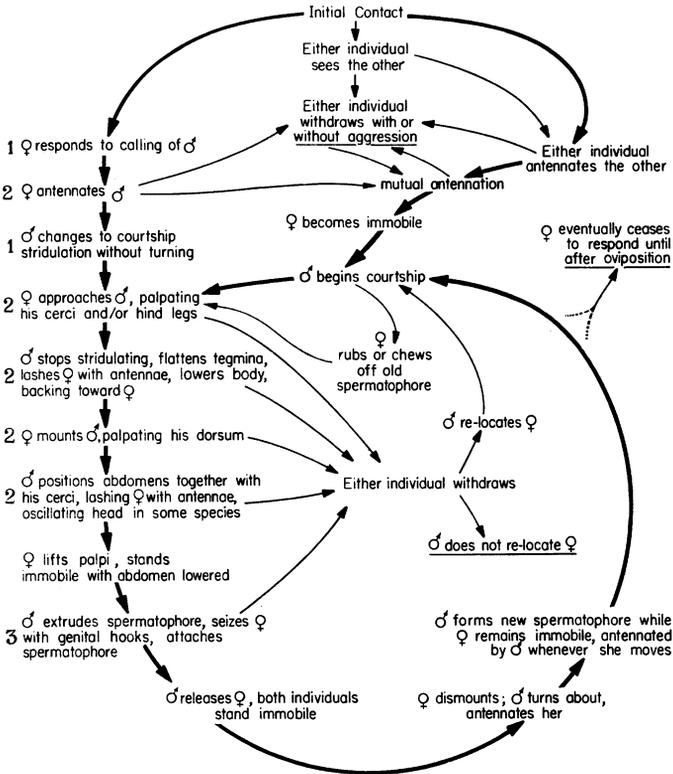
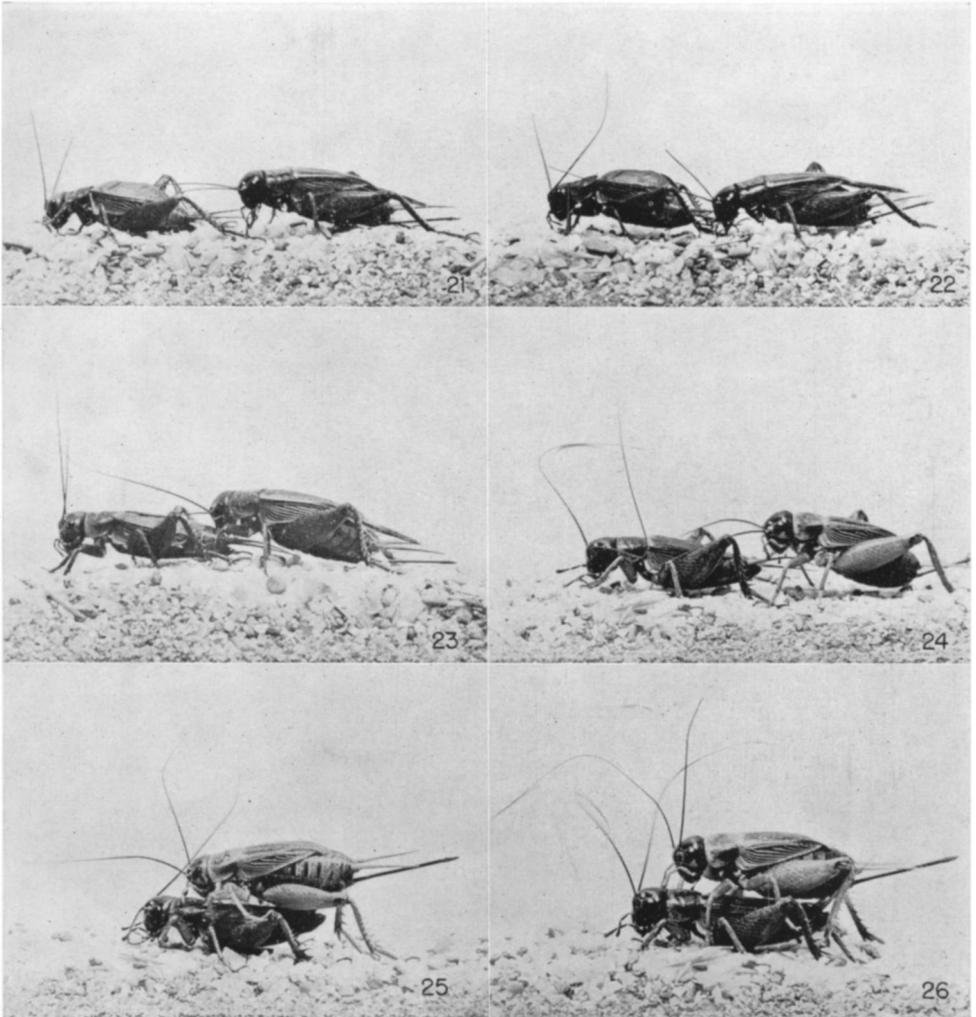
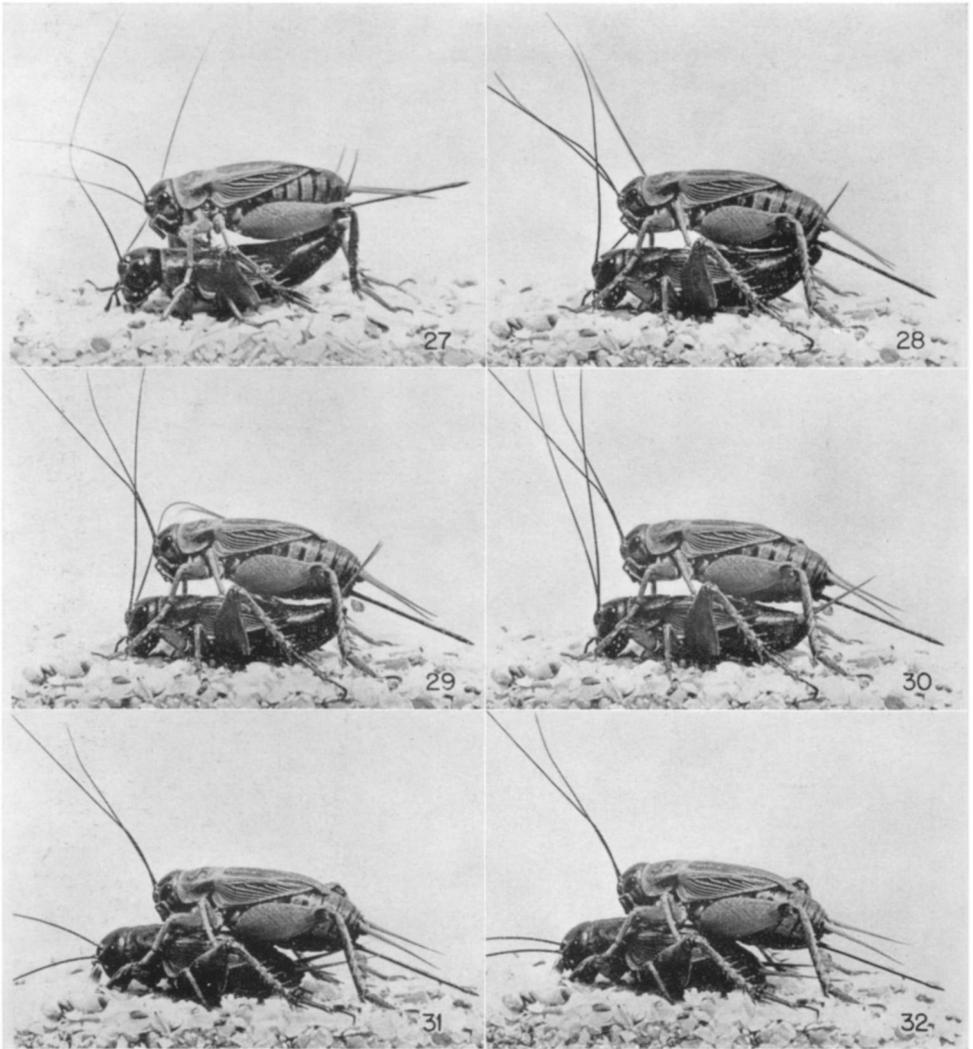


Fig. 20. A diagram of the kinds of interactions occurring between adult male and female field crickets. Heavy lines indicate sequences which usually result when sexually responsive conspecific individuals encounter in high-density populations (right) and low-density populations (left). Terminating responses are underlined. Superscripts on left indicate important areas of interspecific discordance: (1) acoustical; (2) tactile, chemical; (3) tactile, mechanical.

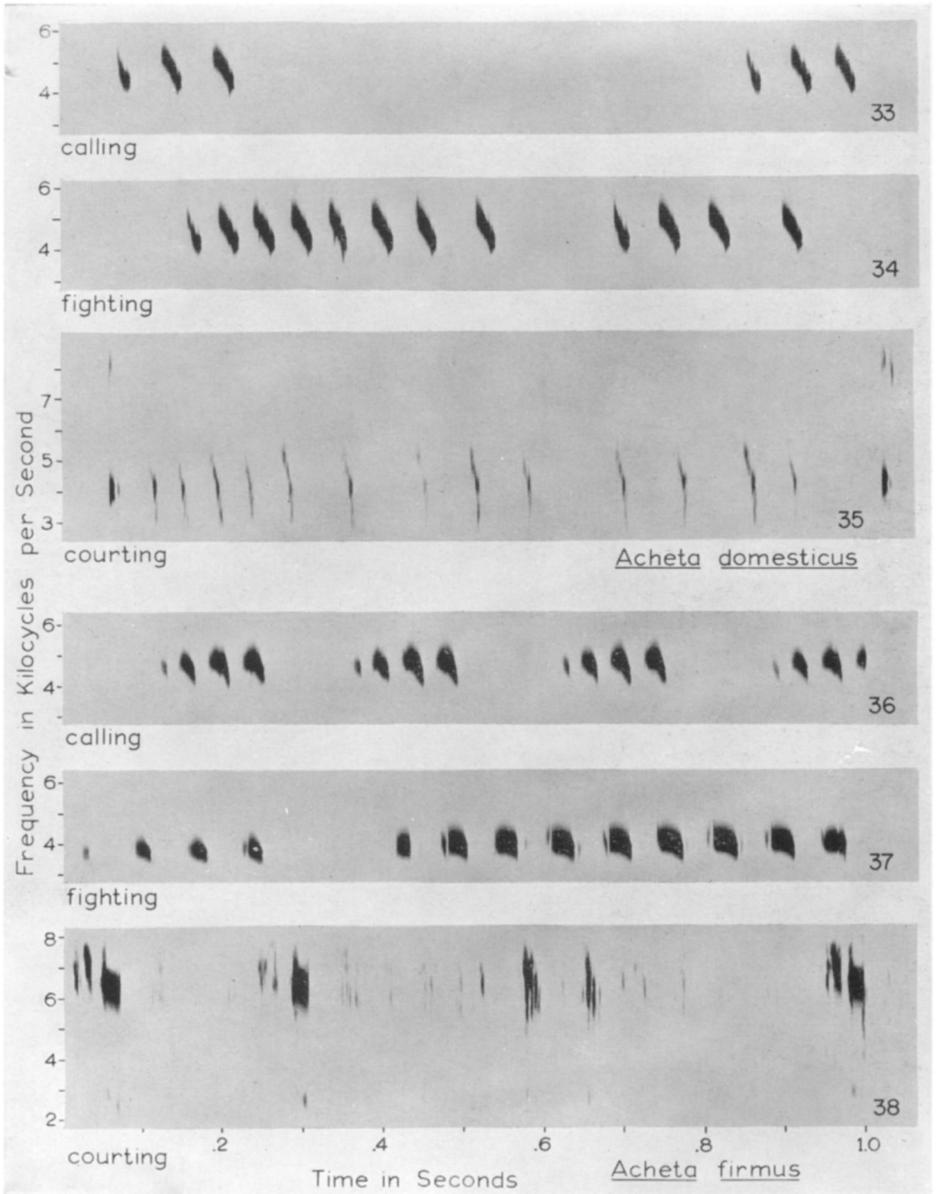
like over the abdomen (Figs 21-22), and scrape them together with much less pressure, producing sound during both the opening and the closing stroke rather than just during the closing stroke as in the calling song. Courtship in *Acheta* species is a distinctive, soft, noise-like chatter, quite unlike the other sounds of the species (Figs 35, 38, 41, 56). This sound affects the female in a distinctive manner, perhaps chiefly because it lacks the characteristics which



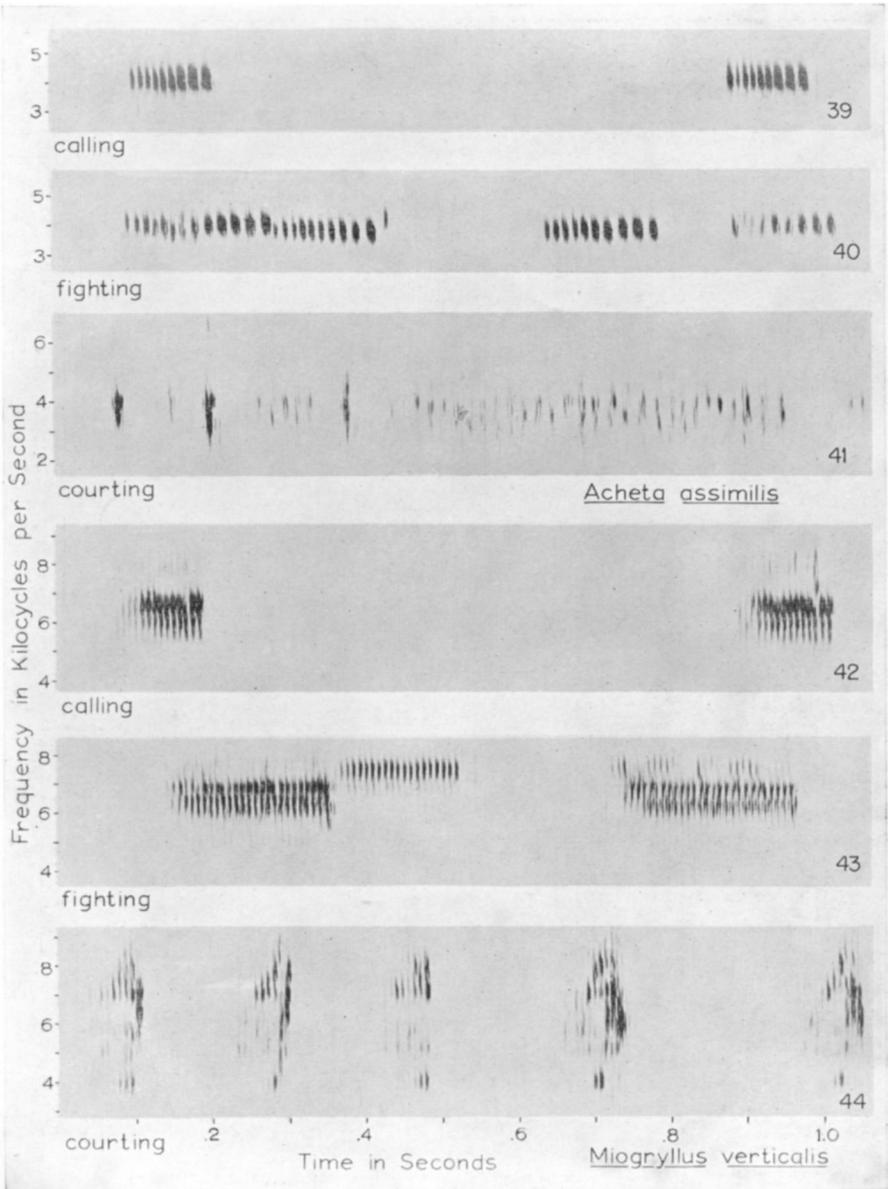
Figs 21-26. Photographs of courtship and the assumption of the copulatory position: Figs 21-22, female palpating male's appendages as he courts; Figs 23-24, female starting to mount, male flattening body and beginning to lash antennae; Figs 25-26, female mounting and palpating male's dorsum, male positioning abdomens' with cerci and lashing female with antennae.



Figs 27-32. Photographs of late stages of copulation in field crickets (Figs 24, 25, 26, 28, 29, 30, 31, 32 form a single sequence) : Figs 27-28, attachment of the spermatophore; Figs 29-32, stages of relaxation before the female dismounts.

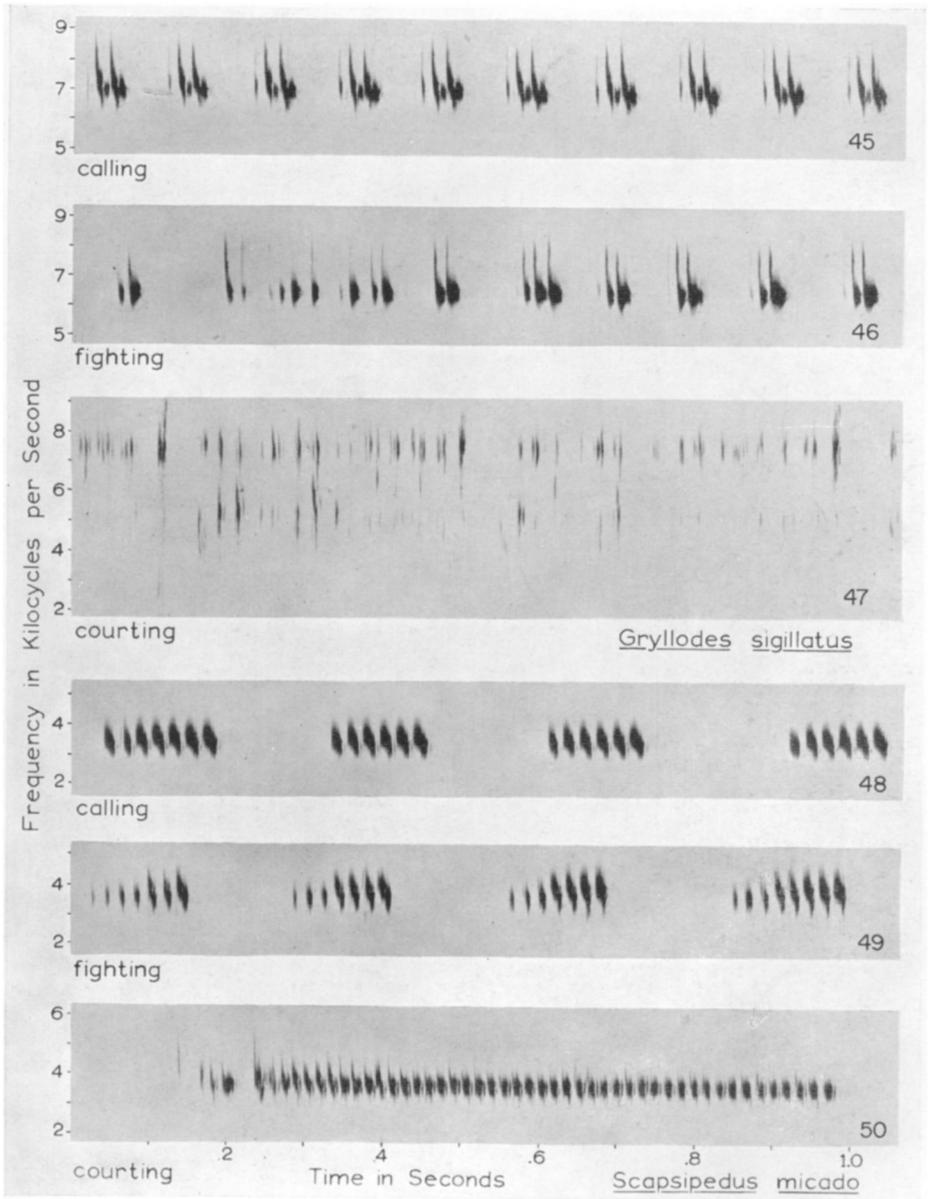


Figs 33-38. Audiospectrographs from the basic sound signals of two crickets with calling songs made up of irregularly delivered chirps (75-80° F.).

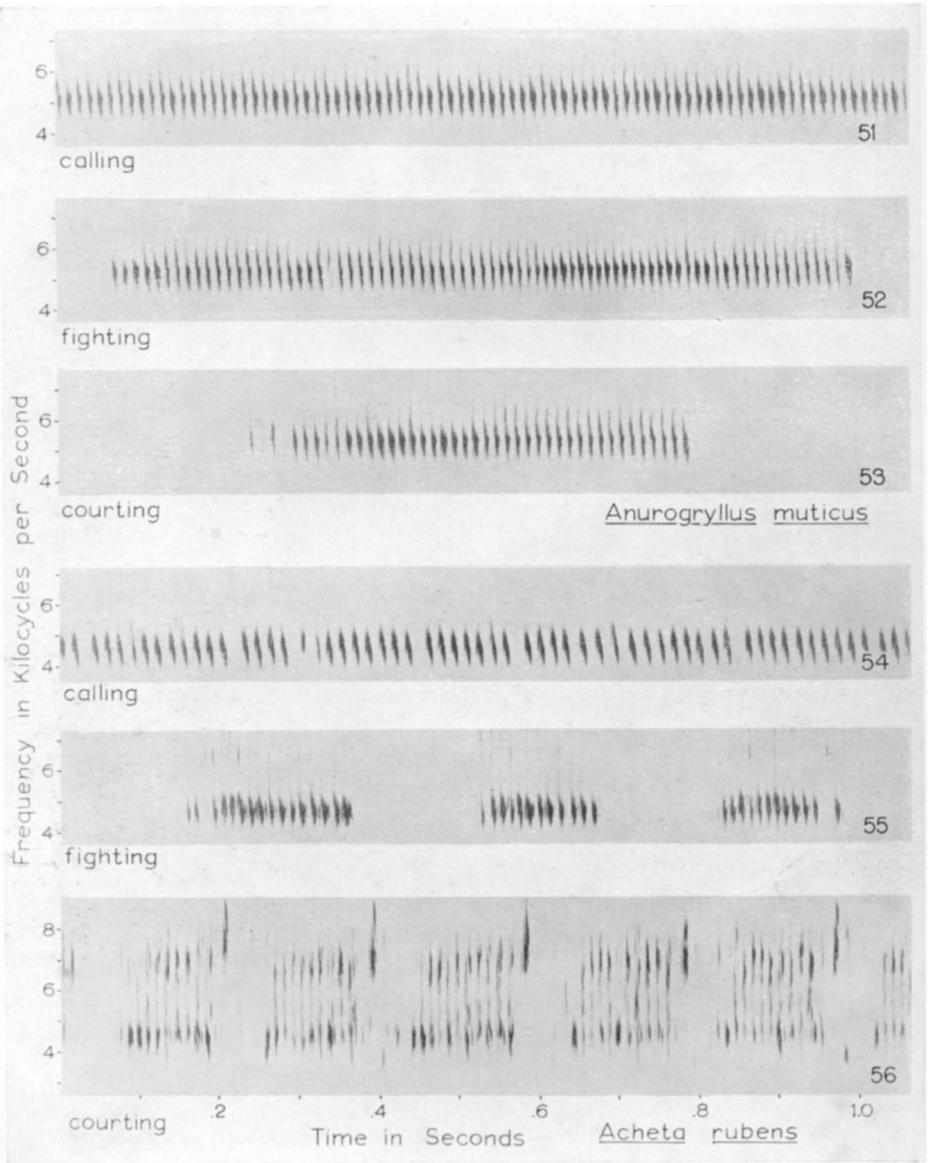


Figs 39-44. Audiospectrographs from the basic sound signals of two crickets with calling songs made up of slowly and regularly delivered chirps (75-80° F).

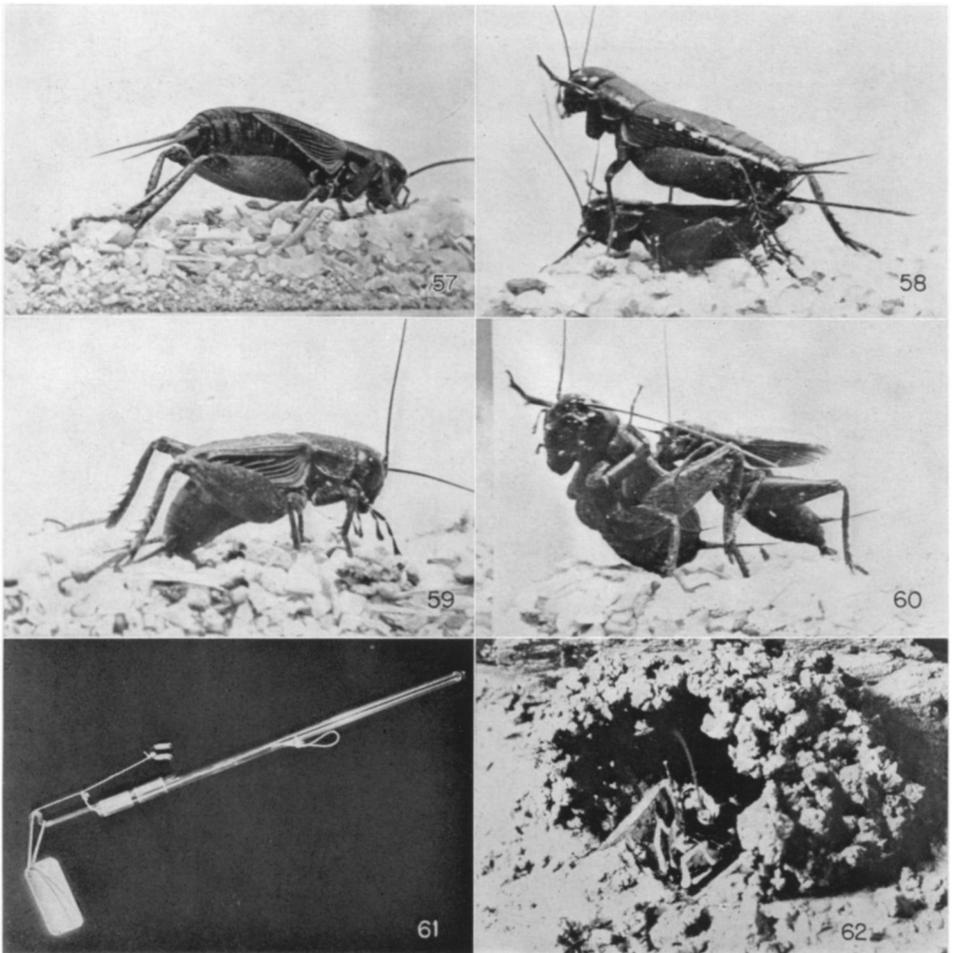
Fig. 43. Second chirp by *Nemobius fasciatus* (de Geer).



Figs 45-50. Audiospectrographs from the basic sound signals of two crickets with calling songs made up of rapidly and regularly delivered chirps (75-80° F.).



Figs 51-56. Audiospectrographs from the basic sound signals of two crickets with trilling calling songs (75-80° F.).



Figs 57-62. Photographs of cricket activities and a stimulating device: Fig. 57, female ovipositing in dry sand under stimulus of the courtship song; Fig. 58, a large female having difficulty mating with a very small male of another species; Fig. 59, a female rubbing off a spermatophore from a previous copulation while under stimulus of the courtship song; Fig. 60, the small male in Fig. 58 dominating a very large aggressive male of another species just after the smaller male had copulated; Fig. 61, a device used to stimulate crickets to fight — either alone or in conjunction with playing of aggressive stridulation — pulling the string causes the bristles to move in a manner resembling the lashing of cricket antennae; Fig. 62, adult male of *Scapsipedus micado* in typical resting position inside his hooded burrow.

allow her to locate the calling song so precisely (ALEXANDER, 1960). The female locomotes upon hearing the courtship song (at least in some species, but see HASKELL, 1953), but with little directionality. Ordinarily the courting male is directly in front of the female when he begins courtship, and her locomotion causes her to walk directly up on his back into the copulatory position. Appropriately, the male continues to be primarily the signaller during the courtship sequence, and the female is generally the more active member of the pair.

A male cricket may turn his posterior toward the female either before or after beginning to stridulate distinctively. The initial courting sounds, especially those made while the male is still facing the female, are transitory sounds containing a mixture of the soft, noise-like phrases of the courtship song and the clear, concise pulses of the calling and aggressive sounds. This sound has been termed "mixed courtship" by ALEXANDER (1957b). In *Nemobius* species, the sound made during this early stage of courtship is often quite distinctive (ALEXANDER 1957c; ALEXANDER and THOMAS, 1959).

After the male has turned away from the female, his sound quickly changes to the completely distinctive courtship song, and there is a more or less exaggerated rocking or swaying of the body from side to side, in time with the motion of the tegmina. This activity is continued by the male until the female starts to mount, whereupon he flattens the tegmina against his body, lowers his abdomen against the substrate, and moves slightly backward, facilitating the mounting of the female (Figs 23-24). If the female does not touch his cerci or other parts of the posterior body within a few seconds after courtship is begun, the courting male begins to ease backward, continuing his stridulation. If he touches the female and she does not retreat, he will continue to slide back under her, courting continually, lowering the body, and guiding his posterior under the female with his cerci. If the female continues to back away very slowly, allowing repeated contact with the male's cerci, or if she remains in contact but does not allow the male to back under her, this sort of courtship can go on for several minutes. However, if the female retreats upon contact with the male and he does not contact her within a short period of time as he eases backward, he will raise his wings and produce a few chirps reminiscent of the aggressive sounds as he turns about (ALEXANDER, 1957b, Figs 7-8; 1960, Selection 1). An exploration of the area which was immediately behind the male then follows, this often accompanied by the loud, clear, "aggressive" chirps. If during this search the male again contacts the female, the process is repeated. If the female is not responsive, but allows the male to contact her over and over again in this fashion, never moving far enough away for him to permanently lose contact with her, this alterna-

tion of activities may go on almost indefinitely. If the male is unable to relocate the female, his aggressive-like chirps may lead directly into production of the calling song, or he may cease stridulating and turn directly to other activities.

When the sexual responsive female walks up on the back of a courting male, her orientation is aided by the vibration of his upturned cerci along the sides of her abdomen (Fig. 25-28), and perhaps as well by her continual palpation of the male's dorsum (Figs 25-26). A chief point at which female crickets suddenly stop responding to the courtship of other species is just as their palpi touch the male's posterior appendages (Figs 21, 22, 24), the tip of his abdomen (Fig. 23), or the dorsal surface of his abdomen or pronotum (Figs 25-26). This palpation is of interest because of the location of chemoreceptors on the palpi of crickets and the importance of dorsal glands in the sexual behavior of many Tettigonioidea (*cf.* CHOPARD, 1938). The females of most species probably receive cues at this point which reduce the chances of interspecific copulation when the other chief deterrents — species differences in the nature of the calling and courtship songs of the males — have for some reason been by-passed. No dorsal glands are known in the Gryllinae, but in some American field crickets the depression in the dorsal surface of the pronotum representing the apodemes to which the large leg muscles are attached are often filled with a waxy substance. Whether or not this is involved in the response of the mounting females remains to be discovered (but see Fig. 25).

As the female mounts, the male lashes his antennae against her continually and positions the tips of the abdomens together with his upturned cerci (Figs 23-26). In some species the male's head or his whole forebody is rotated from side to side in a peculiar manner during this phase of the copulatory sequence. After mounting, the female lifts her palpi (Fig. 27) and stands motionless over the male with the tip of her abdomen lowered, this facilitating the seizure of her subgenital plate by the male with his epiphallal hook (Fig. 28). The male then extrudes the spermatophore and attaches it to the female (Fig. 29). The male's antennae and cerci then cease to vibrate and he releases the female. The two stand motionless for a second or two, the cerci and abdomen of the male drop slowly (Figs 30-32), and eventually the female steps off the male's back. She is inseminated as an osmotic process in the spermatophore causes the sperm to be ejected (KHALIFA, 1949).

Immediately upon separating from the female, the male turns about, antennates her dorsum briefly, and goes into a distinctive post-copulatory behavior. Such behavior seems to occur in most crickets; it has been described for various species by RICHARDS (1952), KHALIFA (1950), HUBER (1955),

and HÖRMANN-HECK (1957), and every species in our laboratory has exhibited it in one form or another. The male either stands immobile with his antennae across the female's back or else he turns about and stands facing at some angle away from her. The angle of turning is reasonably consistent, and 180° turning seems most characteristic of burrowing species. Males which turn away from the female then extend the antennae sideways at a 90° angle from the body and cause them to whirl slightly at intervals.

If the female begins to locomote or otherwise move about during the post-copulatory period, the male quickly antennates her into immobility again. If the two individuals are forcibly separated during this time, the activity of both greatly increases, and the male promotes a similar kind of interaction with any conspecific individual he meets. The increased activity of the female during such separation, and the positiveness of her reaction to the male's antennation, indicate that a specific response on her part is involved. Further, a male which has recently copulated is usually unsuccessful in promoting post-copulatory behavior in a normal, uninterrupted fashion with a female which has not copulated.

The principal function of the post-copulatory behavior has always been assumed to be that it prevents the female from removing the spermatophore while it still contains sperm. The same function has been ascribed to the feeding of female tree crickets (*Oecanthinae*) upon the male's metanotal gland following copulation and to the feeding of female ground crickets (*Nemobiinae*) upon the male's tibial or tegminal gland. Similarly, the great mass of the spermatophore in *Tettigoniidae* is presumed to function in delaying the female in eating it. HUBER (1955) found that female field crickets left with the males with which they had copulated did retain the spermatophore longer than females removed into isolation immediately after copulation, but even females placed into isolation retained the spermatophores until they probably were largely emptied (*cf.* SPANN, 1934; KHALIFA, 1949).

An additional function of the post-copulatory interaction which may equal or exceed in importance the delaying of the female's removal of the spermatophore is that of keeping the female near the burrow or singing location of a sedentary, territorial male, thereby allowing him to copulate with her repeatedly and monopolize her for a considerable period of time. The rise in aggressiveness on the part of the male following copulation re-inforces this temporary monopolization. In tests with two males and one female of *Acheta pennsylvanicus* per cage, the dominant male in every case completely monopolized the female for hours at a time, copulating with her at intervals of an hour or less before his characteristic post-copulatory behavior

and his temporary rise in aggressiveness had subsided each time. These tests were performed in cages less than a foot square in which it was impossible for the subordinate male to court the female without being interrupted by the dominant male. To test the effectiveness of the post-copulatory rise in aggressiveness in promoting monopolization of the female, the subordinate males of several pairs were allowed to copulate with a female while the other male was penned in one corner of the cage. When the separating partition was removed, the dominance order of the two males was decisively reversed. The previous dominant was repeatedly repelled from the vicinity of the female, and the post-copulatory interaction between the previously subordinate male and the female continued. Eventually, the newly dominant males were penned off, and the old dominants were allowed to copulate. This again reversed the dominance status of the two males and allowed the original dominants to monopolize the females. These results have an interesting bearing upon interspecific mating selectivity tests involving two males and a single female; the dominance relationship of the two males might actually be more important than which one was conspecific with the female.

The functional significance of the post-copulatory interaction is clear. An adult male occupying a crevice or burrow will not go far from his singing location in pursuit of a temporarily contacted female. If the female is sexually responsive and has retreated accidentally, she will ordinarily be called back by the stridulation of the male, initiated upon temporary contact with a female (or with another male); if she is not sexually responsive, pursuit by the male and the consequent chance of his losing contact with his burrow or crevice would reduce his efficiency as a signaller, since a permanently located male is more efficient in attracting females than a rover. If the female is kept immobile near the male's burrow after copulation, she is available for subsequent copulation as soon as the male has produced another spermatophore and the male has not lost contact with his burrow. This greatly increases the effectiveness of the formation of compatible pairs through the mechanism of the calling song. In *Nemobius sylvestris* the importance of this temporary monopolization of the female through post-copulatory interaction has become even more exaggerated. In this species the spermatophore attached by the male during the initial copulatory act is small and practically non-functional, and it is not until the second copulation that effective insemination takes place (GABBUTT, 1954). Temporary monopolization of the female may have actually become the only important consequence of the post-copulatory interaction in many crickets, with delay in removal of the spermatophore a minor, coincidental result of the particular responses involved. In this respect crickets cannot be directly

compared to Tettigoniidae, for the male tettigoniid is usually unable to produce another spermatophore for a very long time, and a single copulation per meeting of male and female is probably the rule.

Exactly what it is about the act of copulation that causes post-copulatory behavior and the rise of aggressiveness in the male is still unknown. Removal of the spermatophore with tweezers from courting males of *A. pennsylvanicus* did not induce post-copulatory behavior, and such males began courting again less than fifteen minutes later, before another spermatophore was available. On one occasion a female mounted such a male, and he probed at her abdomen for some time with no spermatophore apparent, until she finally dismounted. Such behavior was also reported by SPANN (1934). When copulations were interrupted after a female had mounted a male but before the spermatophore had been transferred, post-copulatory behavior did not occur. However, on one occasion a male which had failed to attach a spermatophore after a mounting more than a minute in length, showed a definite rise in aggressiveness (Table XX). In two cases males which had been courting off and on for a long time in some way got rid of the spermatophore without attaching it to the female, and then went into typical post-copulatory behavior. A male often carries a spermatophore so long that it becomes darkened and dry and apparently cannot be successfully attached to a female. If such a male is approached by a female and removes the useless spermatophore himself by chewing or rubbing it off, as usually happens, the appearance of post-copulatory behavior during the period before the appearance of the new spermatophore might keep the female near, though her response would probably be incomplete.

Under ordinary circumstances post-copulatory behavior is apparently released only when the spermatophore is removed by the male himself, either during copulation or with his mouthparts or hind legs after the spermatophore has become useless and several attempts at copulation have failed. The long sequence of tactile stimulation occurring during the act of copulation may have significance in this context, and also in connection with releasing the post-copulatory rise in aggressiveness. It has already been shown that tactile stimulation is associated with changes in the aggressive state in other situations.

A female cricket will copulate repeatedly without ovipositing, but she eventually refuses to copulate—usually after a day or two of continuous contact with males—and becomes sexually responsive again only after oviposition has been made possible by the introduction of damp sand or soil. If no damp surface is available, an inseminated female frequently probes at a dry surface, though without depositing eggs. The insertion of the ovi-

positor into the substrate is apparently elicited through contact of the palpi with a damp surface; females often stand with their palpi in the oviposition dish (damp sand) or against the wick of the waterers in our cages and repeatedly stab the ovipositor into the dry sand behind them. Their consistent failure to deposit eggs in such situations, however, suggests that the ovipositor itself bears sensory apparatus which must encounter dampness before the eggs can be released.

If a female which has lost sexual responsiveness through repeated copulation without oviposition is continually courted by a male, she is stimulated to begin oviposition movements, stabbing the ovipositor repeatedly into the substrate when there is no moisture available (Fig. 57). Likewise, when a female which is still carrying a spermatophore from a previous copulation is courted, she usually begins directly to chew and rub at the attached spermatophore (Fig. 59). Copulation is often begun before the old spermatophore is removed, and in such case the male may successfully dislodge it while attaching the new spermatophore, it may simply be pushed to the rear without becoming dislodged from the female, or the male may repeatedly fail to attach the new spermatophore until the female herself pauses between mountings to remove the old one. On one occasion, a female was observed to have three spermatophores attached near her genital opening.

SPECIES DIFFERENCES IN SEXUAL BEHAVIOR, AGGRESSIVE BEHAVIOR, AND TERRITORIALITY

INTRODUCTION

Members of the subfamily Gryllinae are morphologically so similar to one another that only in extreme cases, primarily between genera, are structural differences sufficient to prevent interspecific copulation or aggression when behavioral barriers are lacking. As a result, most cases of interspecific incompatibility are due to discordances of a behavioral nature. Fig. 58 illustrates one kind of exception to this rule, a female of a large species of *Acheta* having difficulty mating with a male of a very small species. Transfer of the spermatophore was eventually accomplished after several unsuccessful mountings by the female, but it is unlikely that these two species would interbreed significantly in the field. Another case in which at least partial morphological incompatibility exists is in matings between the house cricket, *Acheta domesticus*, and the American field cricket, *A. veletis*. Female house crickets rarely respond to the courtship of *veletis* males, but in the several cases when mounting has been observed, the male was for some reason unable to grasp the female's subgenital plate, and thus unable to get the spermatophore into position for attachment. No differences are apparent in the structure of the

subgenital plate or other external genitalia of the females of these two species, but as shown by comparing REHN and HEBARD (1915, Figs 8, 11) and SNODGRASS (1937, Figs 32, 35), males of both *Acheta domesticus* and *Grylloides sigillatus* lack the median recurved hook which is prominent dorsally on the epiphallus of American *Acheta* (and the European field cricket, *Gryllus campestris*), and which is apparently used in holding the female's abdomen while the spermatophore is attached. KHALIFA (1950) does not state exactly how the male house cricket attaches the spermatophore, and no observations in this regard have been made in the present study. Morphological differences preventing copulation may be the reason that *A. domesticus* has never been successfully crossed with either American or European field crickets, even though many interspecific crosses have been carried out between the last two groups (*cf.* COUSIN, 1954, 1955). It should be emphasized that even when significant morphological differences are present, behavioral discordances are probably the usual isolating factor in field encounters; most interspecific hybrids in Gryllinae have been obtained in stress matings, that is, situations in which males and females of different species are kept together for long periods of time, usually the entire adult life, with no chance to separate from one another and no chance to mate with conspecifics. Extrapolation from such tests to the natural situation would have to include an estimation of the frequency of similar conditions in the field.

Because of the significance of behavioral discordances in preventing interspecific copulation, comparisons of the degrees and kinds of behavioral differences between species should take into account whether or not the adults of the species are (or ever have been) reproductively active at the same time and in the same place. All sympatric species of field crickets in eastern North America have distinctive songs (ALEXANDER, 1957a), except for the closely related, seasonally isolated species, *A. pennsylvanicus* and *A. veletis* (ALEXANDER and BIGELOW, 1960). Some of these eastern species are morphologically very similar to one another. In western North America there are several field crickets which are allopatric with the eastern species and which differ morphologically from them more clearly than they do in song characters (unpubl. data). Future investigations will probably show that such situations are not uncommon.

The location of interspecific discordances in the normal sequence of sexual events — beginning with the response of the female to the calling song of the male and ending in repeated copulations (Fig. 20) — is of some interest in comparative behavioral studies. An isolating factor involving an early stage in the sequence is obviously a more efficient one from the point of view of wasted time and energy on the part of the participants than a factor which

can only operate late in the sequence, such as after the sexually responsive pair has been formed. For example, the calling song of the male cricket is a highly efficient isolating mechanism, not only preventing wasted time and energy during sexually significant interspecific encounters (except for the few that occur accidentally), but also preventing any sort of activity leading specifically toward such encounters. This fact undoubtedly accounts for the consistent presence of unusually great differences among the calling songs of otherwise similar species which live together.

Observable variations among species of Gryllinae with respect to sexual behavior and aggressive behavior can be divided into two classes: (1) differences in the nature of the specific stimuli known to be essential for the release of successive behavioral events occurring in the normal sequence of interactions between conspecifics, and (2) differences which at least at the present time and in the contexts studied seem incidental to the release of the normal sequence of interactions between conspecifics. Differences of the first kind (such as in the calling song which brings the adults together, or in chemical stimuli which release courtship in the male or mounting in the female) are the characteristic sort found among closely related species; differences of the second kind (such as in gross structure of the courtship song, in head-wobbling by the male during copulation, or in the position assumed during post-copulatory behavior) are most often found between species in different genera or between congeneric species which do not appear to be closely related. Behavior differences which appear to be incidental may have been important at some earlier time with respect to interactions between conspecifics, they may be important in fostering discordances in interactions with species not tested, or they may have evolved in connection with some situation only indirectly connected with behavioral interactions between individuals, such as the ecological situation in which mating normally takes place. These suggestions will be clarified by the examples which follow.

Differences in Acoustical Behavior.

All of the sounds of Gryllinae are composed of series of sound pulses delivered at various rates and in various rhythms. These pulses are made by rubbing a scraping edge on the inner margin of the left (lower) tegmen along a row of tiny teeth (file) on the undersurface of the right (upper) tegmen. An occasional male has the left tegmen uppermost; this appears to be genetically determined, for though the tegmina are nearly identical in crickets, normally right-winged individuals cannot be changed into left-wingers by reversing the tegmina, even if this is done immediately after molting. This has been demonstrated by HÖRMANN-HECK (1957) and also in our labora-

tory several times. Unless the tegmina are damaged the cricket always flips them back to the original position, either shortly afterward, or in the case of teneral specimens when the tegmina have hardened or when the male first starts to stridulate.

In the calling songs of Gryllinae the sound pulses are clear and concise, and strongly dominated by a frequency corresponding to the number of file teeth struck per second. Each pulse is ordinarily down-slurred (*e.g.*, Figs 33, 36), because of a wider spacing of the teeth toward the lateral edge of the tegmina, because of a slowing of the stroke while the file and scraper are in contact, or because of these two influences acting together. The stridulatory apparatus of a cricket may be compared somewhat to the mechanism of a mechanical phonograph in which the frequencies delivered depend upon the rate at which projections in the groove of the record are struck by the needle. When the record speed is slowed, the frequencies of the sounds produced drop, and when the temperature drops and a cricket slows its rate of wingstroke, so does the frequency of its sound drop.

The chief kinds of differences occurring among the calling songs of different Gryllinae are in the pulse rate (wingstroke rate) and in the length and spacing of pulse groups. Pulse rate varies between extremes of approximately 15 and 100 pulses per second in different species (*cf.* Figs 33, 42). The pulses may be delivered in groups of consistent length containing 2, 3, 4, 5, or 6 pulses (Figs 33, 36, 45, 48), in longer groups not so consistent in length (Fig. 42), or in more or less continuous trills (Figs 51, 54). When the pulses are delivered in groups (chirps), the groups may be delivered either slowly (Fig. 33) or rapidly (Fig. 45) — from extremes of about one per two seconds to about ten per second — and either regularly or irregularly. In comparisons among species, as pulse groups become longer their length becomes less consistent, and as pulse groups are delivered more rapidly their repetition rate becomes more regular.

The pulse rate or wingstroke rate of a species is usually constant in all of its different sounds, in effect serving as the species "code." Species differences in the calling song are thus reflected in differences in aggressive and courtship sounds. In most calling and aggressive sounds, a fairly slight change in pulse rate moves the sound outside the narrow range to which the individuals of a species are sensitive (WALKER, 1957). In courtship singing, in which the file and scraper are engaged with much less force producing soft, noise-like, indistinct pulses, and in which wingstroke is often acoustically effective in both directions rather than just during its closing (against the slope of the file teeth) as in calling and aggressive sounds, pulse rate is likely much less significant.

An obvious difference has appeared among species with respect to the structural relationships between calling and aggressive sounds. In species in which the calling song is a succession of slowly and more or less irregularly delivered chirps or pulse groups (suggesting that chirp rate is a character of minor importance), the aggressive sounds are long, irregularly delivered chirps; *Acheta pennsylvanicus*, *A. veletis*, *A. domesticus*, and *A. firmus* are species in this category (cf. Figs 33-34, 36-37, and ALEXANDER, 1957b, Fig. 2). In all these species the pulse rate is slow; the calling song chirps contain 3-5 pulses, while aggressive chirps contain up to 15-20 pulses. In species such as *A. assimilis* and *A. fultoni* ALEXANDER, both the chirp rate and the length of individual chirps are very regular in the calling song (suggesting greater behavioral significance), and aggressive sounds are made not by lengthening the chirp but by increasing the chirp rate (Figs 45-46, 48-49). Pulse rate is usually very fast in these species, further suggesting that the chirp has become the important phoneme; WALKER (1957) found that the regular chirper, *Oecanthus niveus* (De Geer), responds to pulseless chirps almost as well as to pulsed chirps, but not to a continuous trill at the normal pulse rate. In species with trilling calling songs, such as *Anurogryllus muticus*, *Acheta rubens* (Scudder), and others, aggressive sounds are made by breaking the trill into short, separated units, or chirps (Figs 51-52, 54-55). Apparently the structure of the calling song, the most important signal possessed by field crickets now, largely determines the methods by which the species can evolve distinctive sounds operating in specific fashions in other situations. This dependence is further illustrated by the fact that various *Miogryllus* and *Nemobius* species which also have chirping and trilling calling songs, though with their particular structure surely evolved independently from the same kinds of songs found in *Acheta* species, produce aggressive sounds which relate to the structure of the calling song in exactly the same way as those discussed above (cf. Figs 42-44, and ALEXANDER and THOMAS, 1959).

The degree to which the aggressive sounds differ from the calling song varies from one species to another, but this does not necessarily correlate with the violence of aggressiveness exhibited by the males or with the tendency of the males to behave aggressively. Thus, *A. domesticus* is probably the least aggressive species discussed here, but its aggressive chirps are as distinct from the calling rhythm as those of *A. firmus*, a highly aggressive species (compare Figs 33-34, 36-37). In *Gryllodes sigillatus* and *Scapsipedus micado* Saussure the aggressive sounds are barely distinguishable from the calling rhythm (Figs 45-46, 48-49), but there is no correlating reduction in aggressiveness.

Both chirping and trilling *Acheta* species have courtship songs which are more or less continuous series of pulses. Although the courtship song is probably more different from the calling song in the Gryllinae than in any other group of crickets, it varies relatively little from one species to another, except in pulse rate. In most species, a short, sharp "tick", slightly louder and clearer (having fewer emphasized frequencies) than the other pulses in the song, occurs either regularly between all pulse groups or alternate pulse groups or else more or less irregularly (*cf.* Figs 35, 38, 41). However, there is a great deal of variation in how often and how regularly this tick appears, even from one individual to another within the same species, so its significance is still in doubt. It is interesting that the courtship songs of Gryllinae species which live together are less different from one another than the calling songs, this further substantiating the suggestion that the calling songs are more efficient isolating mechanisms than the courtship songs, and that there has been more selection for distinctiveness in the calling song because of its location in the interaction sequence between male and female.

In some species of field crickets, the courtship song is apparently necessary to stimulate the mounting of the female (HÖRMANN-HECK, 1957; HUBER, 1955). However, in others the female will mount almost as readily upon a silent male, or even one from which the tegmina have been completely removed. KHALIFA (1950) was unable to get females to mount courting male house crickets from which the tegmina had been removed, but GHOURI and McFARLANE (1957) and KENNETH C. SHAW (personal communication) found that the females in their cultures mounted readily upon males from which the tegmina had been removed. The courtship sound itself would thus appear to function in some species simply in shortening the period of time between initial contact of the male and female and assumption of the copulatory position, or in increasing the percentage of times that a courted female will mount, rather than operating as a necessary unit in the courtship sequence. Since there is no evidence that sound ever operates as a repellent in crickets, the isolating value of the courtship song is also limited because of the nature of its function.

Although the courtship songs of different species of *Acheta* usually differ from one another only in pulse rate or in other less obvious fashions, in other genera of Gryllinae the courtship song may be quite different. *Gryllodes sigillatus* courts in a fashion suggesting a common origin with the courtship singing of *Acheta* and *Gryllus* species (Fig. 47), but *Miogryllus verticalis* (Serville) simply increases the number of chirps and shortens the chirps when approached by a female while calling (Fig. 44); ALEXANDER

and THOMAS (1959) compare the sounds of the latter species with those of *Nemobius fasciatus* (De Geer). *Scapsipedus micado* produces distinctive, long phrases well separated from one another during courtship (Fig. 50), and *Anurogryllus muticus* is also distinctive, producing short, separated chirps during courtship rather than the continuous soft chatter characteristic of *Acheta*, *Gryllus*, and *Gryllodes* species (Fig. 53). There may be a relationship here with the fact that *Anurogryllus* trills in the calling song; also this extensively burrowing species, as with the mole crickets, appears to possess a sound signal in addition to those found in other Gryllinae. This is a short, sharp chirp produced by lone, excavating males, by males simply locomoting through the burrows, and by males upon contact with other individuals in the burrow or around its entrance. A similar sound is produced by the females in some mole crickets as well as by the males (BAUMGARTNER, 1911). This sound seems to serve as a kind of "recognition" signal which has evolved in connection with the development of more complex behavioral interactions in these rudimentarily social insects. If this interpretation is correct, it would appear to be the only intraspecific sound signal known in insects which has become isolated from a direct involvement in sexual behavior and which bears equal significance for the male and the female.

HÖRMANN-HECK (1957) describes a difference between the courtship singing of the two European field crickets, *Gryllus campestris* and *G. bimaculatus*, which in the absence of clearer descriptions and some kind of objective analysis or illustration is difficult to compare with the variations just described. Apparently, *campestris* possesses a peculiarity not found in *bimaculatus*, in that it produces short, sharp sounds during courtship and continually changes the position of the tegmina. Whether this happens only at the start of courtship or at the beginning of each phrase is not clear. Perhaps this characteristic is either the same as or very similar to the short, sharp "tick" previously described in the courtship singing of various American *Acheta*. Or it may be similar to the kind of courtship phrase produced by *Scapsipedus* and *Anurogryllus* in which there is continual shifting of the tegmina. HÖRMANN-HECK found that hybrids between *campestris* and *bimaculatus* produce this short, sharp sound less frequently than *campestris* males do, and that the response curve of offspring produced in backcrosses resembles that of the parent used in the backcross, suggesting monofactorial transmission.

The evolutionary sequence by which the different signals now possessed by the Gryllinae have appeared is of some significance in understanding the relationships between structure and function in the stridulations of the

various species. This sound communicative system apparently has a common origin with that possessed by other Gryllidae and by the Tettigoniidae; in both families the auditory organs are tympana located on the front tibiae, and the stridulatory apparatus is located on the tegmina. The functions of the signals evolved by different members of these families are similar; some species lack courtship or aggressive sounds, and a few have developed stridulatory reactions to disturbances (ALEXANDER, 1960). There seems to be little doubt that the earliest significant sounds produced by members of this group were produced during courtship; the female mounts the male in most species, with all others appearing to have been derived from ancestors in which this was the case, and in every species there is some special stimulus produced by the male which induces the female to assume the copulatory position. In Oecanthinae there is an attractive metanotal gland; Nemobiinae possess glands on the hind tibiae or on the tegmina (GURNEY, 1947); Gryllinae have specialized courtship songs; and in one species of Eneopterinae, *Hapithus agitator* Uhler, which possesses neither a courtship song nor a specialized gland, the female simply eats the tegmina as she mounts. Tettigoniidae have various chemically attractive areas on the dorsum (GURNEY, 1947; FULTON, 1930), as do the cockroaches which copulate in a female-above position (ROTH and WILLIS, 1954).

The first sounds of Tettigonioidea must have been soft, and effective only during pre-copulatory maneuvers among individuals in close proximity. As soon as actual auditory significance appeared, selection must have operated to increase the efficiency of the stridulatory apparatus and of the auditory organs so that increasingly intense sounds became operative across greater and greater distances. As distance and directionality increased, the calling function as it now exists emerged; the presence of the female is no longer required to elicit the signal, and the sound alone is sufficient to attract the female across relatively great distances. The operation of the long-range calling sound can thus be viewed as initially an extension of the courtship function, its distinctiveness appearing as the calling function became more remotely connected to the close-range maneuvers preceding copulation.

Although the primary function of the calling song is still the attractance of sexually responsive females, it seems inevitable that it should have frequently developed significance for other males. This is especially true since the evolution of the ability to produce the calling song accurately and uninterruptedly for long periods of time appears to be intricately with auditory feedback—or the effects upon a male of hearing his own sound—accounting part for the evolution of sensitivity in the male auditory organs (ALEXANDER, 1960). In some species today, the primary effect of the calling sound upon

other males is attractance, but in others it appears to operate chiefly as a mildly aggressive signal. In this study the calling song has been observed to elicit stridulation and fighting behavior in hyper-aggressive males on several occasions. Its similarity to the aggressive sounds in many species indicates that it is probably at least mildly effective in reinforcing retreat and subordination as well, as the more distinctive aggressive sounds of related species have been shown to do. Individual chirps made by fighting individuals, even in species with elaborate aggressive sounds, are often indistinguishable from chirps in the calling song.

Thus, it seems reasonable to suggest that the aggressive sounds of crickets and the aggressive situation itself have evolved as modification and intensifications of milder interactions among males in which the calling song was principal signal, just as the calling function must have evolved as an elaboration of the courtship function. The structural relationships between calling and aggressive sounds in different species reinforce this suggestion. The two sounds can be viewed as differing from one another in "emphasis." In the species which make aggressive sounds by increasing the number of pulses in the calling chirps, there is a definite correlation between the intensity of combat and the length of the chirps, indicating a quantitative relationship within the aggressive situation itself.

It has been noted that when two crickets are locked in combat and one of them stridulates, the other nearly always pauses and then chirps as soon as the first male's stridulation terminates; this is much more frequent than broadly overlapping or simultaneous stridulation. This appears to be a matter of successive inhibition and stimulation such as was described by ALEXANDER (1960) operating in the alternation of phrases in chorus by neighboring katydids. The length of the chirp produced by one cricket during a fight probably affects the length of the chirp produced immediately afterward by the other, just as the length of a phrase produced in alternation with a male katydid (with a typewriter, for example), affects the length of his phrases. In the katydid, *Pterophylla camellifolia* (Fabricius), two males in close proximity produce very long phrases in rapid alternation just as two fighting crickets do (ALEXANDER, 1960). These interactions reflect not only the stimulative effect of one male's calling upon another, but also part of the difference between the effect of the calling sound and that of the aggressive sound.

In field crickets with other kinds of aggressive sounds, similar analogies can be drawn. Thus, when a species with a very regular and important chirp rate increases the chirp rate while fighting, inhibition is probably effected because the stream of chirps has become, in effect, a single signal to the

non-chirping adversary. A similar effect must be produced when a trilling species breaks the trill into short bursts during aggression; the result in every case seems to be that a male is less likely or unable to start stridulating during aggressive sounds. The inhibitory and stimulative functions in aggressive stridulation may be closely allied to the inhibition and stimulation occurring as a result of auditory feed-back in the singing of a single male, or that occurring during specialized chorusing in some species, this suggesting an even more direct connection between the evolution of structure and function in calling stridulation and aggressive stridulation.

Differences in Chemical and Tactile Stimuli.

Aside from differences in acoustical behavior, there appears to be only a single major area of discordance in interspecific interactions among field crickets, and this is with respect to chemo-tactile stimuli emanating either from the male or from the female, or perhaps from both in some cases. When the calling song is by-passed, as in stress matings in the laboratory, the most common discordance in interspecific matings occurs when the female touches either the tip of the male's abdomen (HÖRMANN-HECK, 1957) or the dorsal surface of his abdomen or pronotum (Figs 25-26). At this point the female usually backs away and then she either completely loses interest or else she keeps returning under the influence of the courtship song, although repeatedly ceasing to respond upon contact. A similar discordance occurs sometimes when males of different species engage in combat. After interlocking mandibles, one or both males suddenly withdraw and wipe or clean the mouthparts vigorously. This is usually followed by exploratory re-approaches and a general inability of the males, even though both are very aggressive, to stand face-to-face in sustained combat. Chemo-receptors are present on the palpi and on other portions of the mouthparts (FRINGS and FRINGS, 1949; DETHIER and CHADWICK, 1948), and it seems likely that either or both of these are responsible for positive responses to chemical stimuli produced by conspecifics and repulsion or lack of attraction to chemical stimuli produced by members of other species.

HÖRMANN-HECK's (1957) note that the male of *G. bimaculatus* requires both a chemical and the usual tactile stimulus from the female to begin courting appears to be unusual; every male tested in our laboratory courted readily upon touch alone when in the proper state. It is most often the case that the female is the primary discriminator, and this is easily understood because of the generally more deleterious consequences of gamete wastage by the female as compared with gamete wastage by the male.

The situation described by HÖRMANN-HECK has further interesting aspects. Because the males of *G. campestris* court all conspecifics which do not react aggressively or flee upon contact, and because the females of the sympatric species *G. bimaculatus* require only the courtship singing of the male to initiate assumption of the copulatory position, matings between *campestris* males and *bimaculatus* females are easily obtained. On the other hand, the males of *bimaculatus*, requiring a specific chemical stimulus from the conspecific females as well as the usual tactile stimulus, rarely court *campestris* females, and the latter, requiring a specific chemical stimulus from the tip of the abdomen of conspecific males, rarely respond to the courting of *bimaculatus* males even when it occurs. The result is that *bimaculatus* males and *campestris* females practically never mate, even in stress situations.

There is little evidence that mechanical tactile responses differ sufficiently among species of Gryllinae to very often cause discordance during sexual or aggressive encounters. This is difficult to determine, for even conspecific individuals mating for the first time generally have difficulty in properly assuming the copulatory position. The female may strike the male with such force that she repeatedly causes him to retreat from her approach, or the female may fall off the male several times before the spermatophore is finally attached. When size differences are great, a small individual sometimes retreats upon contact with a large individual in the same manner as when startled by gross external disturbances. Unless the previously mentioned inability of *A. veletis* males to attach spermatophores to *A. domesticus* females is due to a mechanical tactile effect, no other persistent inter-specific differences of this kind have been observed.

Except for an anal fluid ejected by mole crickets (*cf.* BAUMGARTNER, 1910, and GRIFFITH, 1937), no broadcast chemical stimuli are evident in interactions among crickets. Visual stimuli are likewise of minor importance, and this is to be expected because most crickets are nocturnal to one degree or another. Apparently, the sound-signalling system is the sole device for long-range communication among Gryllinae, and this is undoubtedly one of the important reasons for its consistent specificity and elaborateness.

Differences in the Copulatory Position.

All field crickets mate with the female mounting the male, and there are few if any variations within the genera *Gryllus* and *Acheta*. However, in *Scapsipedus micado*, and possibly also in *Anurogryllus muticus* (the latter based on a single, incomplete observation), there is an interesting variation

which may have evolved in association with the position taken up by the male and female during post-copulatory behavior. In *Scapsipedus* the male rotates out from under the female after attaching the spermatophore and the two stand end-to-end with the genitalia attached for a few seconds before separating. This is similar to the method of copulation of some Blattidae and Tettigoniidae. Rarely, the pair dismounts without rotating, as in other crickets. When the rotation occurs, the two insects then simply remain in the position taken up, with the male facing away from the female during the post-copulatory period. In such cases there is no preliminary antennation of the female by the male following copulation. A peculiar variation in the behavior of the male during the act of copulation occurs within both of the field cricket genera, *Acheta* and *Gryllus*. In every species, when the female starts to mount, the male lowers the rear portion of his body, rears up his forebody slightly, and begins to lash at the female with his antennae. This antennal lashing continues all through the act of copulation until the spermatophore is finally attached; the nature of it can be clearly discerned by comparing Figs 22-27 with Figs 28-32. In the American species *A. rubens*, the male exaggerates this action by moving the head from side to side and rotating it back and forth while he continually whips the antennae across the female's body. According to HÖRMANN-HECK (1957) and HUBER (1955), *G. campestris* exaggerates the head-wobbling even more, so that the whole fore-part of the body has become involved in the oscillating motion. As with most American *Acheta* species and *A. domesticus*, *G. bimaculatus* lacks this behavior. HÖRMANN-HECK found the character to be inherited to different degrees in hybrids between *bimaculatus* and *campestris*, and she obtained complicated ratios in backcrossing and in subsequent generations of hybrids, leaving the mode of inheritance somewhat unclear. No function has been found for this behavior, and it does not appear to affect the readiness of females to mount the male, in either conspecific or heterospecific matings.

Differences in Post-Copulatory Behavior.

There are consistent variations in post-copulatory behavior among Gryllinae, chiefly with respect to the position assumed by the male in relation to the female when post-copulatory behavior begins. In *A. domesticus*, the male simply turns and lays his antennae across the female's dorsum, remaining in this position until a new spermatophore is ready for transfer, at which time he turns about and begins courtship again (KHALIFA, 1950). In *A. veletis*, *A. pennsylvanicus*, and apparently both *G. campestris* and *G. bimaculatus*, the male antennates the female immediately following their

separation, then he turns away from the female at an angle of about 90° and extends his antennae laterally. This is the position maintained until the male again begins to court. It is resumed following antennation of the female after interruptions caused by outside disturbances or by the female starting to move away or chew off the spermatophore. While in this position the male occasionally whirs the antennae in a distinctive fashion, and HÖRMANN-HECK found this behavior much more frequent in *campestris* than in *bimaculatus*. Hybrids were much like *campestris*, suggesting complete dominance and monofactorial transmission.

The degree of turning away by the male is even more pronounced in *Scapsipedus*. This species, as with *Anurogryllus*, and to a lesser extent the American and European field crickets, is an extensive burrower. It appears that the turning-away of the male in post-copulatory behavior and the side-ways extension of the antennae have become elaborated in species which normally copulate in or at the entrance of a burrow. The female is thus prevented from leaving the male's presence even though he is facing away from her and out of contact with her. In our cages, crevices are not always available, and unless copulation takes place in a corner of the cage, this kind of post-copulatory behavior is often interrupted by the female walking away from the male. Eventually the male turns about in such cases, and failing to contact the female he begins rapid exploratory locomotion, resuming the post-copulatory position when the female is again contacted.

Differences in Aggressiveness.

Variations in the amount of aggressiveness exhibited by males in particular situations undoubtedly occur among different species of Gryllinae. For example, males of *A. domesticus* are much less aggressive than those of most native American field crickets. The males fight less often, and their fights are less severe. Variations in this characteristic occur as well among North American species, but because of the many complicating factors discussed in this paper, such as territoriality, isolation, copulation, and the effects of previous wins and losses, a precise evaluation of such variations must await more detailed investigation. HÖRMANN-HECK (1957) discusses a difference in aggressiveness between the male juveniles of *G. campestris* and *G. bimaculatus* and cites evidence that the difference is determined by a single pair of genes, with incomplete dominance exhibited in F_1 hybrids. Neither HÖRMANN-HECK nor HUBER (1955) seems to have noted the strong effects of particular behavioral events—or the possibility of long-term effects—upon the aggressive state of crickets. Possibly this effect is largely absent in European species, but HUBER's note that males

of *G. campestris* which have just copulated frequently fight when they meet suggests that it is present to some degree.

As would be expected, interspecific discordances in sexual encounters are generally more frequent and more complete than discordances in aggressive encounters. Males of species which never interbreed often fight together with no apparent distinction from fights between conspecifics. This emphasizes the specificity of male-female interactions and its important role in reproductive efficiency and isolation.

Differences in Burrowing and Territoriality.

A comparison of the aggressiveness of the males of different species of Gryllinae leaves little doubt that there are correlations—probably both ontogenetically and phylogenetically—between the degree of aggressiveness in individuals and the degree of expression of such characteristics as burrowing and territoriality. Species which rarely burrow (*e.g.*, *Acheta domesticus*) are much less aggressive than species which are regularly found living in burrows (*e.g.*, *Acheta veletis*, *Gryllus campestris*), and which additionally show elaborate forms of territoriality. Interestingly, severe fights appear rarely to occur in confined groups of *Anurogryllus* males, although this species is the most extensive burrower and in some ways the most territorial species of Gryllinae in North America. For example, five males were confined in a narrow cage one inch wide and 30 inches long. Each excavated a burrow several inches deep, with horizontal chambers near the ground surface. Between the time that all individuals had finished burrows and the death of the first individual nearly two months later, no shifting of burrows occurred and no male was ever seen in another male's burrow. No daytime contact was seen between males, and only twice did a male emerge from his burrow during the day. Each individual obtained food and water from pieces of apple and raisin dropped near the entrance of the burrow; the cricket mined up under the apple until it was partly sunk and protruded into the ceiling of a chamber. Raisins and lettuce were cut and carried into the burrows. Both *Anurogryllus* and *Scapsipèdus* have elaborated the body-reversing, shaking, kicking behavior (Fig. 1), and this is the type of aggressive activity most frequently seen, even in head-on encounters. Sustained combat has been observed in the field, but the circumstances regarding burrow-occupancy were not known. It appears that territoriality in these crickets has advanced into a stage characterized by pronounced reduction of stress in aggressive behavior, an essentially non-combative, "threat" activity sufficing in most situations.

Several unsuccessful attempts were made to induce permanent occupancy

of different niches in the same compartment by two closely matched *Acheta* males. In the most elaborate of these, one male was provided with a round pillbox surrounded by mounds of sand, the other with a square pillbox located within a simple maze of wooden walls. Each pillbox was left partly filled with sand so that the male could hollow it out himself. Each male was allowed to occupy his niche in solitary for two weeks, with food and water near its entrance, then a glass partition between the niches, which were 30 inches apart, was removed. During the first night the males switched niches, and they reversed positions several times during the next week when the test was finally terminated. Permanent occupancy of particular burrows by field cricket males in nature must be a combined result of territoriality, wide spacing of individuals, and peculiarities of terrain which reduce the chances of a male leaving his own burrow and approaching another.

Several kinds of burrowing behavior are evident in Gryllinae. MCGREGOR (1929) describes a "scratching" or "pawing" by females of a California *Acheta* species which is much like the digging of a dog or a ground-nesting wasp. The same behavior has been observed in our laboratory in Texas crickets which may be the same species. "Scratching" is performed in excavating a shallow hole into which the abdomen is inserted during oviposition, causing the eggs to be deposited much deeper than in other species. In loose sand, *Acheta* and *Anurogryllus* males sometimes form shallow depressions by using the forebody, head, and forelegs in a "bulldozing" fashion, repeatedly pushing forward, backing up, and pushing forward again. Male #2's tunnel under the water vial was developed in this manner. *Acheta* males excavate in solid soil by seizing a chunk of soil or a pebble in the mouthparts, backing away, depositing the chunk to one side, re-entering and repeating. *Anurogryllus* and *Scapsipedus* males excavate in the same fashion when starting their burrows, but when the burrow has become a little longer than the insect (about maximum length for *Acheta* burrows), *Anurogryllus* males then seize the chunk at the deep end of the burrow, turn about, walk forward out of the burrow, deposit the chunk alongside the entrance, turn about, walk forward into the burrow and repeat. The mouth of the burrow usually becomes closed during this deep excavation, and then the cricket simply carries the soil from the deep end of the burrow and plasters it against the ceiling of an upper part of the burrow. The result is that a mound of small chunks of soil slowly pushes out where the old mouth of the burrow was located. By thus "mining" under a source of food, the male develops a "self-feeder" by partly burying the object so that it protrudes into his chamber from above. New openings are developed to the burrow in other locations.

The method of deep excavation in *Scapsipedus* has not been observed, but Fig. 62 shows the elaborate hood that this species constructs over the entrance to its burrow. This "awning" is very delicate and is composed of approximately one thickness of clay chunks removed individually from the burrow.

GHOSH (1912) describes the burrowing of *Brachytrupes achatinus* Stoll. The cricket bites and pellets the earth, then draws it under the body and throws it out behind with the legs. As the burrow deepens, the cricket turns at intervals and pushes the loose soil out of the burrow with its broad, flat head.

Additional elaborations of nest construction in subterranean species include the building of enlarged horizontal chambers (*Anurogryllus*) in which food materials are accumulated, eggs are deposited, and in which the cricket sits immobile for long periods. A cricket entering or sitting in such a chamber often rises high on his legs and presses his entire dorsum against the ceiling briefly in a characteristic fashion. Mole crickets (*Gryllotalpinae*) also excavate numerous short blind alleys about the length of the body which they utilize in reversing direction in the burrow. Either the cricket's head or its posterior is inserted into the blind alley to make the turn, and the entire reversal is so quick that it seems to be a single motion.

In addition to partly burying large particles of food (and probably mining up under roots in a similar fashion), *Anurogryllus* cuts up bits of vegetable matter, such as leaves, grass, seeds, and small plant stems, and carries them into the burrow, accumulating them in the enlarged chambers. This individuation of responses to different materials is poorly known, but elucidated to some degree by the following observations. An excavating male was watched in a glass-walled cage as he removed soil from the deep end of his burrow and plastered it against the ceiling of an upper chamber. After several identical excavating runs, the male accidentally knocked a bit of lettuce down his burrow as he returned with a chunk of soil. On his next descent he returned carrying the lettuce, but did not even approach the "plastering" end of the chamber, rather dropping the lettuce to one side about an inch from the mouth of the vertical burrow, where it had been lying previously. Returning into the burrow he brought up a chunk of soil and plastered it as before, and continued normal excavation. In another instance, an excavating male seized what appeared to be a large chunk of clay and moved directly toward his plastering site with it. After a few steps he stopped, dropped the chunk, and manipulated his mouthparts a moment. Then he picked up the chunk and started off again, stopped and repeated his previous action. During the third repetition the observer saw

that the now partly cleaned object was really a clay-covered bit of raisin. Eventually the male consumed the entire particle. Apparently he began to treat it each time as a piece of soil, but was interrupted in his action by the taste. On a third occasion, a female *Anurogryllus* was watched carrying bits of leaves into a burrow. After picking up two tiny pieces and carrying them directly into the burrow, she picked up a weed stem about two inches long and carried it cross-wise in her mandibles to the burrow entrance, dropped it there (apparently upon antennal contact with the burrow entrance), went into the burrow, returned immediately facing outward, picked up the long stem, and backed into the burrow. In about a minute she returned, picked up another bit of leaf and walked directly into the burrow. The material she was transporting was being picked up about 20 cm. from the burrow entrance.

These observations are incomplete and anecdotal, but they leave no doubt as to the complexity of this species' reactions to the various objects which it carries in and out of its burrows. A still different response must be shown to eggs and young nymphs, for the eggs are deposited in chambers in the burrows, and the female remains in the burrow until after they hatch and the young nymphs go on their separate ways at about the second or third instar.

The largely subterranean existence of *Anurogryllus* and *Gryllotalpa* is also associated with a change in food habits. Most Gryllinae approach omnivory and can be reared continuously in the laboratory on dry dog food or chick's tarter and a separate supply of water; *Anurogryllus* and *Gryllotalpa* die unless moist animal or vegetable material is available.

In the genus *Scapsipedus*, the males exhibit a modification of the mouth-parts which is apparently associated with burrowing; the mandibles and palpi are exceedingly long and the face is somewhat dished or concave. Females of *Scapsipedus* have heads resembling those of other Gryllinae. In *Loxoblemmus*, the head of the females resembles the head of males of *Scapsipedus*, while the head of the male is even more drastically modified (SAUSSURE, 1877). In both *Anurogryllus* and Gryllotalpinae, the female lacks a long external ovipositor.

AGGRESSIVENESS, TERRITORIALITY, AND POPULATION DENSITY

In times of low population density, adult male field crickets are rarely seen moving about and are almost never found in close proximity. But in certain species there are either occasional or regular build-ups of population in which the adults become so numerous that they literally cover the ground

and pile up under lights at night. Two major changes are apparent when such build-ups occur: (1) there is a much higher percentage of macropterous individuals in species which produce both micropterous and macropterous individuals, and (2) the adults seem to tolerate one another to a much higher degree, and even to actively aggregate under certain conditions. These "phase" differences are reminiscent of the migratory and non-migratory phases in locusts; their appearance can be largely accounted for on the basis of the behavioral phenomena described in this study. They differ from the kinds of phase changes occurring in locusts in that, except for the single morphological change in wing length, the sequence can apparently be completely reversed at any point, and there is no evidence of any transfer of characteristics from generation to generation.

Fig. 63 is a diagram illustrating the effects of initial isolation (such as might occur in a period of low population density) and initial crowding (such as might appear in a period of high population density) upon the behavior of individual crickets, especially males. Initial isolation results in a sequence leading to hyper-aggressiveness, territoriality, sedentariness, and increased production of the calling song by males. Initial crowding prevents the appearance of such characteristics and promotes compatibility among individuals crowded together in groups. The two different sequences may be described as being re-inforcingly effective in promoting a maximum of successful copulation in low-density and in high-density populations, respectively. Territorial calling males present an acoustical field of maximum size and continuity, both in time and in space, to the females of the species during times of low density populations, while non-aggressive, active males increase the likelihood that a maximum of females will copulate successfully a maximum number of times in periods of high density populations. In addition, low percentages of macropterous individuals in times of low population density prevent detrimental dispersal of the species, while high percentages of macropterous individuals in times of high population density take advantage of such times to disperse the species into new localities.

Some of the above variations can be shown to exist between species which have different modes of life. Thus, *Acheta domesticus* and *A. desertus* Pallas (*cf.* SELLIER, 1954, for the latter) are gregarious species which rarely burrow; under certain circumstances both produce high percentages of macropterous individuals. These species can be contrasted with *Gryllus campestris*, *Acheta veletis*, and *A. pennsylvanicus*, species which burrow, probably exhibit more aggressiveness than individuals of *A. domesticus* regardless of differences in individual history, and rarely produce macropterous individuals in nature. However, much of the range of variation exhibited between the

two divergent sequences in Fig. 63 can also appear among the individuals of a single species. Especially susceptible, it seems, are species with two generations per season, such as *A. rubens*. This species overwinters as late nymphs and the first generation matures in May and June. This generation is never very abundant, the males burrow extensively, and adults are rarely found in numbers around lights. Of 50 pre-August specimens of *rubens* in the

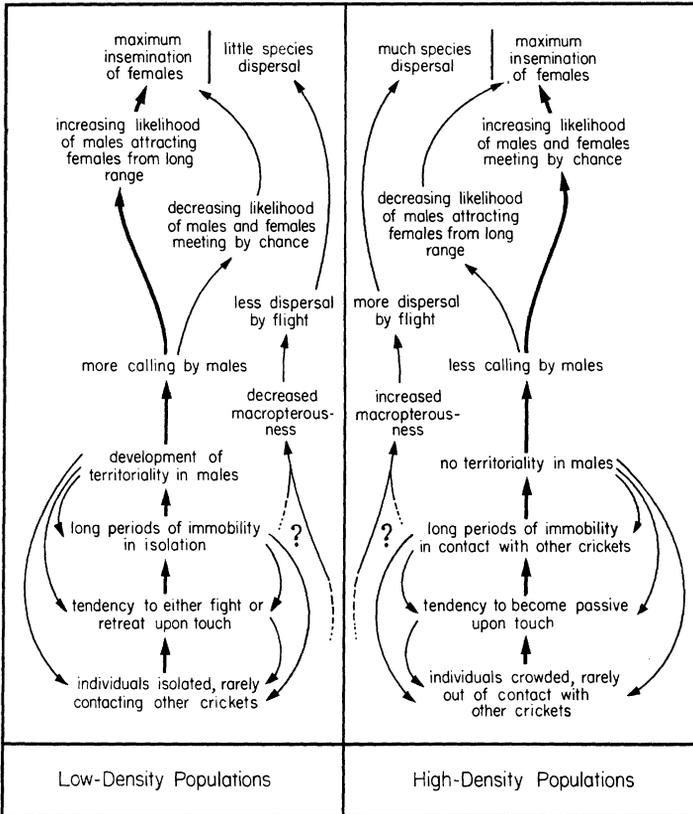


Fig. 63. A diagram suggesting some of the effects of population density upon the behavior of crickets.

University of Michigan Museum of Zoology, only four (8%) were macropterous. By contrast, the second generation of this species, maturing in late summer and fall, is often extremely abundant, appearing in such numbers on lighted city streets that one imagines that he is driving his automobile across popcorn. Of 150 post-July specimens of *rubens* in the UMMZ, 112 (75%) were macropterous.

The exact basis for macropterousness and micropterousness in crickets is still unknown. SELLIER (1954) has investigated several aspects of the problem using various European species of Gryllinae and Nemobiinae. In the burrowing, normally micropterous species, *G. campestris*, he found that neither adjustments of temperature, light, and humidity, nor castration produced macropterous individuals. But acceleration of development by preventing the onset of diapause in the ninth nymphal instar did produce macropterousness. This was done by massive injections of brain tissue from younger nymphs of *G. campestris* or from nymphs of *G. bimaculatus*. SELLIER concludes that the brain produces a non-specific "morphogenic" substance which prevents diapause and induces wing growth, that the threshold for wing growth upon stimulation from the brain is higher in some species than in others, and that the sporadic appearance of macropterous individuals in *G. campestris* can be attributed to an abnormal functioning of the brain. These results compare favorably with the above findings in *A. rubens*; they suggest, in fact, that the same mechanism operates in *rubens*, diapausing nymphs of the overwintering generation becoming largely micropterous and non-diapausing nymphs of the summer generation becoming largely macropterous. But several questions remain, and there seems to be little doubt that the mechanisms determining the extent of macropterousness vary among species. Thus, SELLIER found that *A. burdigalensis* Latrielle produces a higher percentage of macropterous individuals under high, even temperatures than under low, fluctuating temperatures; in other species he found genetic determination of wing length, obscured to one degree or another by environmental factors. SELLIER did not investigate the effects of nutrition, but Dr PHILLIP STONE of the University of Missouri has obtained evidence (personal communication) that this factor is of some importance in producing macropterous individuals in *A. domesticus*.

The American species which is probably most comparable to *G. campestris* in life history and behavior is *A. veletis*. As with *campestris*, this species overwinters as a late juvenile, burrows, is reasonably aggressive, and produces macropterous individuals only sporadically. *A. veletis* has a very close relative, *A. pennsylvanicus*, which is known to differ only in overwintering in the egg stage, in ovipositor length, and in being physiologically incompatible with *veletis* (ALEXANDER and BIGELOW, 1960). Examination of the specimens of these two species in the UMMZ collection shows that 12 of 314 *veletis* and 37 of 1000 *pennsylvanicus* are macropterous — 3.9% in each case. If the same mechanism operates here as in *campestris*, one might wonder why there is not a higher percentage of macropterousness in *pennsylvanicus*, which diapauses only in the egg stage.

An additional question involves the close correlation between species habitat and percentage of macropterousness. Among the Gryllinae and Nemobiinae studied in Europe and America, *Acheta vernalis* (Blatchley), *A. fultoni* Alexander, *Nemobius tinnulus* Fulton, and *N. sylvestris* (Bosc.) are all invariably micropterous. The last two are egg-overwinterers, the first two are nymph-overwinterers. But all occur in woodlands or more or less stable, climax vegetative associations. Further, the species of Gryllinae and Nemobiinae which produce high percentages of macropterous individuals, whether nymph-diapausers or egg-diapausers, are mostly located in "pioneer" vegetative associations, or areas which change rapidly and must be continually re-invaded if the species is to survive. *Acheta rubens* (Scudder), *Nemobius fasciatus* (De Geer), and *N. allardi* Alexander and Thomas are good examples. The last two species are most closely related to *N. tinnulus*, one of the micropterous species listed above.

A problem of relevance to the present approach is whether or not behavioral events in the life of a cricket nymph may in some species affect wing length in the adult. As noted earlier, ELLIS (1959) has shown that continual touching of isolated migratory locusts — even with mechanically driven wires — brings about changes tending toward the migratory phase. Several authors have reported that isolated individuals in various Orthoptera mature more slowly than non-isolates (FAURE, 1932; PETTIT, 1940; CHAUVIN, 1946, 1958; NORRIS, 1959). CHAUVIN (1958) found that isolated nymphs of *Acheta domesticus* require more time to mature than non-isolates, and significantly, he was able to eliminate this effect by removing the antennae and cerci of the crickets. In our laboratory delayed maturation has been evident in isolated nymphs of several cricket species. Adult isolates of both Gryllidae and Tettigoniidae frequently live up to ten or twelve times as long as non-isolates.

If accelerated development is the crucial item so far as determination of wing length is concerned, then increased macropterousness due to highly nutritious diets, high, even temperatures, breaking of diapause (either by manipulations of temperature or by brain injections), and tactile stimulation resulting from crowding may have essentially the same basis. If this is the case, then behavioral events are capable of initiating all of the behavioral and morphological changes which combine to produce rudimentary phase differences among the individuals of various cricket species (Fig. 63). In field populations the production of macropterous individuals as a direct result of overcrowding has obvious selective advantages.

The exact manner in which tactile stimulation brings about various changes in behavior — and possibly morphology as well — is unknown. Intensive

study of the bases for rudimentary phase differences in crickets and their analogues (or homologues) in cockroaches might greatly accelerate understanding of phase changes in locusts and their evolution. This should be an area of considerable interest to neurophysiologists and students of behavioral development as well. An important question is when and how the various kinds of changes become irreversible. There are also problems relating to the intensity of the various effects. CHAUVIN's experiments were performed in very small chambers so that the effects of contact between two individuals could best be contrasted with the effects of isolation. As a result, little difference was observed among groups of two, three, and five crickets. However, in field populations, or in crickets caged in larger chambers it is possible that there would be a gradient effect depending upon the number of crickets in the chamber. These results would have great significance for studies on the basis of developmental rate and on interspecific differences in developmental rate.

Although the sequences indicated in Fig. 63 can apparently be reversed in the laboratory by placing crowded individuals into isolation and *vice versa*, and apparently by doing this at any time in the life of a given individual, nevertheless it can be seen that these sequences are essentially irreversible under natural conditions because the individual units in each sequence reinforce one another. Once a male becomes hyper-aggressive and territorial as a result of isolation, he is increasingly unlikely to become involved in a crowded situation in the field which could reverse the process. On the other hand, a macropterous male emigrating into a locality unpopulated or sparsely populated by members of his own species would undoubtedly adjust in the direction of increasing aggressiveness and territoriality. This would surely enhance the effectiveness of emigrants in establishing new populations. The signalling role of the male and the correlation between habitat and extent of macropterousness may be the primary reasons that phase differences in crickets have retained their rudimentary and flexible nature.

TERRITORIALITY AND THE EVOLUTION OF SOCIAL BEHAVIOR IN INSECTS

The several steps in the evolution of territoriality which are evident in comparisons of different species and genera of Gryllinae bear an interesting relationship to the evolution of social behavior. Social behavior in insects has apparently evolved from two kinds of beginnings: (1) the aggregation of individuals of the same generation and of about the same age or stage of development, such as overwintering or nesting queens in Hymenoptera (compare MICHENER, 1958, and PARDI, 1948a), and (2) the attenuation of

parent-offspring relations. Each of these beginnings is eventually followed by the other if social interactions continue to be elaborated, and the primary difference between them is in the order of appearance of specific behavioral interactions rather than in the kind that appear.

In the first case above, PARDI has shown how dominance-subordination relations can play an important role. The dominant queen in a group nesting together is the one with the largest ovary; the act of subordination is to release to the dominant a drop of fluid which has nutritional value in connection with further enlargement of the ovary. The result is a re-inforcement of dominance which is directly associated with ability to lay eggs. This effects a division of labor and results in the dominant becoming the functional queen and the subordinates becoming functional workers (see also, FREE, 1955).

In the second case above, there is usually an initial isolation of the breeding pairs, and this is the kind of potential "beginning" illustrated by the *Gryllinae*. The steps in this process may be enumerated as follows:

1. unusual restriction of movement (cyclic or permanent)
2. attachment to a particular spot
 - a. special reactions to the spot, such as unusually long periods of time spent in it, repeated examination and exploration, consistent returns.
 - b. modification of the spot, such as odor deposition, hollowing out, construction of webs, modification of the entrance.
3. transportation of materials out of and into the nest
 - a. removal of material during excavation.
 - b. removal of fecal pellets and other waste products (or their deposition only in special locations or only when outside).
 - c. introduction of materials later eaten.
 - d. introduction of materials later incorporated in modification (construction).
 - e. translocation within the nest of materials later eaten.
 - f. translocation of eggs within the nest.
4. attenuation of parent-offspring relations.
5. increase in complexity of sibling relations.
6. division of labor.
7. development of sterile castes.

Whether this process is ontogenetic or phylogenetic, it begins with a pair of individuals and culminates in the development of a colony. Among the orthopteroid insects, the highest order of complexity in this sequence is

reached in the Isoptera, and the sequence is traced out ontogenetically—doubtless with some variations from the above order—each time a new colony of termites is founded by a pair of reproductives. Elsewhere among the orthopteroids, the first four steps are probably completed in the Embioptera and the Dermaptera (MELANDER, 1902; WHEELER, 1923). Among the Gryllinae, *Anurogryllus muticus* completes the first three steps, at least to 3e; other species exhibit none of the behavioral characteristics listed, and still others—as demonstrated by the various experiments reported here—exhibit different stages of intermediacy between the extremes. There is an interesting difference in this regard between the behavior of the Isoptera, Embioptera, and Dermaptera, and that of the Gryllinae. In the former groups it is the female which initiates the sequence, while in the last one it is the male which initially becomes sedentary. In *Anurogryllus* the female becomes attached to the burrow originally begun by the male after being attracted there by his song. Probably the vegetable materials accumulated by the adults in chambers of the burrow are later eaten not only by the female but also by the young nymphs which spend one or two instars with the female in the burrow. Special behavioral interactions may occur between the adult female and the young nymphs. HAYSLIP (1943) found that *Scapteriscus acletus* Rehn and Hebard and *S. vicinus* Scudder seal their eggs in cells, but the female of *Gryllotalpa hexadactyla* Perty places her eggs in the end of her burrow and “guards” both the eggs and the young nymphs. GHOSH (1912) reports that the females of *Brachytrupes achatinus* inject their eggs shallowly into the soil at the ends of their burrows, and the young nymphs remain in the adults’ burrows only two or three days after hatching.

Apparently, no one has noted any special activity of crickets inhabiting burrows with respect to the disposition of fecal pellets. Only a single instance of defecation was noted in a territorial cricket during this study. An *Acheta* male, after a long period of immobility inside an inverted pillbox, backed slowly out in a straight line, stopped a few inches away, dropped a fecal pellet, and walked immediately straight back into the pillbox and became motionless as before. No other cricket was ever seen to locomote backward in this distinctive fashion.

The brief survey given above of variations in the behavior of closely related species of crickets, especially with regard to aggressiveness, territoriality, burrowing, and various aspects of the life history, shows how the different steps in the development of social behavior such as that exhibited by termites and web-spinners can occur through related stages in the step-by-step superimposition of simple changes in behavior patterns

upon the existing mode of life in solitary species. Several phenomena become elaborated along with the complexity of interactions among individuals. Thus, the development of more and more extensive burrows, the elaboration of territoriality, and the transportation into the burrow of materials which can later be utilized as food begin the process of independence from inclement seasons and place the species well upon the way toward continuous breeding. Increased attachment to the burrow and long periods of time spent in close proximity by groups of individuals inside the burrow increase the chance that selection will act to favor genetically-based changes in behavioral interactions leading toward social existence. In the proper situation the process becomes an accelerating and re-inforcing one, each modification which is successfully super-imposed upon another tending to increase the likelihood of further modification in that direction. In assessing the chances that the burrowing crickets will continue to elaborate social behavior, two facts seem significant: (1) the increased length of adult life as a result of isolation and the *Anurogryllus* female's isolation in the burrow with her eggs, and (2) the appearance of stridulatory apparatus in female mole crickets after an interchangeable sound signal had become a part of the species' repertoire.

SUMMARY

Most contacts between adult male field crickets involve aggressive behavior by one or both individuals and terminate with the obvious retreat of one individual. Aggressive behavior consists of one or more of several actions: in mild encounters there is either rearing of the forebody, lashing of the antennae, and shaking of the body, or else rearing of the hind body, kicking with the hind legs, and shaking of the body; in intense encounters, antennal lashing and rearing of the forebody are followed by spreading the mandibles, stridulating distinctively, rushing forward, sparring with the forelegs, butting with the head, and grappling, wrestling, or biting with the mandibles. A male is often flipped back or thrown sideways, but mutilation as a result of fighting is rare, and only in the most intense encounters is the winner determined by what seems to be superior strength or fighting ability. The outcomes of most encounters are determined by the relative tenacity of the two males, and the intensity of aggression exhibited is correlated with the length of the fight, continued aggressive activity developing into increasingly severe combat until one male finally retreats.

Groups of adult male field crickets caged in small arenas form essentially linear dominance hierarchies which are stable for short periods of time and which can be described in terms of several characteristics: (1) each male dominates all or nearly all of his encounters with males below him in the hierarchy, (2) the total number of encounters by individual males decreases gradually toward the bottom of the hierarchy, (3) the intensity of aggression exhibited during encounters decreases more or less gradually toward the bottom of the hierarchy and the numbers of no-decision and no-aggression encounters and actively homosexual contacts increase, and (4) encounters between males which rank next to each other are usually more intense than encounters between males which are far apart in the hierarchy.

With certain specific exceptions cricket hierarchies are consistent with the initial encounters between individuals. A male's position can be adjusted upward temporarily by (1) copulation, (2) isolation, (3) occupation of a crevice or burrow, or (4) domination in very aggressive encounters. It can be adjusted downward temporarily by severe losses. A male attains the highest position he can hold in a non-territorial, all-male hierarchy about 12 days after molting to adulthood and retains it until he begins to be noticeably feeble before death as a result of "old age". When other factors are not involved, larger males usually, but not always, dominate smaller males. Blinding, removal of all but the basal three-eighths inch of the antennae, or the attachment of a cardboard "crest" to a male's pronotum did not change status. Complete removal of the antennae caused peculiar behavior and lowered a male partway in the hierarchy.

The aggressive stridulation of the males of Gryllinae is distinct from the sounds made in other situations. Stridulation by one male during combat usually causes the other male to stridulate, and in most species, both males stridulate during intense aggression. Dominant males stridulate during aggression more frequently than subordinate males, and the dominating male in an intensively aggressive encounter nearly always stridulates after antennal contact has been lost through the retreat of the subordinate. The subordinate male rarely chirps after an encounter, and if he does it signals an impending rise in his status.

A relatively specific set of artificial stimuli, such as simultaneous playback of aggressive sounds and simulated antennal lashing, is required to elicit the full display of aggressive behavior in a male unless he has just stopped behaving aggressively after winning a fight, is behaving territorially, or has just copulated. In such cases, a male can be stimulated into aggressive activity with either tactile or auditory stimuli alone, indicating a temporary "conditioning" or "priming" effect. Similarly, the courtship sequence can be initiated in a male which is calling, or one which has just stopped courting, by crude tactile stimuli much less specific than those required to elicit courting in any other situation. There is no apparent connection between "priming" for courtship and "priming" for aggression.

Recent losses decrease a male's inclination to fight, and the dominance status of two males can be reversed over and over again by "defeating" the dominant repeatedly between encounters by means of artificial stimuli. Fighting or retreat is induced more quickly when aggressive sounds are played as the male is lashed with bristles simulating cricket antennae, and conditioning is stronger.

Courtship of one male by another occurs with increasing frequency in groups of males isolated from females and is most likely to occur in encounters in which (1) one male approaches another from behind, especially if the approached male is calling at the time, or (2) one or both males display little or no aggressive behavior upon contact and fail to retreat. A courted male may react aggressively, move placidly away, or actively mount the courting male and become temporarily immobile much as a responsive female does. Contacts between males can result in repeated performance of the entire courtship and copulation sequence except for the actual attachment of the spermatophore. Lone males sometimes begin courtship upon cercal contact with inanimate objects (especially while calling) or upon cercal contact with their own vibrating underwings during pre-flight motions, and they may deposit spermatophores upon screened cage surfaces.

If crevices are available, males will enter them, and strongly subordinate males will be routed. When crevices are not available, niches or burrows are hollowed out in suitable substrates. Crevice or burrow occupation by an adult male cricket is characterized by: (1) restriction of the total area traversed by the occupying male, (2) long periods of time spent in the crevice, (3) repeated movement in and out of the crevice and detailed palpal and antennal examination of it, (4) distinctive "sallies" or "patrols" outside the crevice at intervals, during which encountered food and water is consumed and encountered males and females are fought and courted, respectively, (5) unusually

direct returns to the crevice after being outside, (6) unusually aggressive reactions to contact with other males, and (7) a decrease in the number of encounters with other males. Occupation of crevices or burrows by males in a confined group affects the activity of the entire group by: (1) decreasing the number of encounters taking place, (2) causing a higher percentage of intense encounters, and (3) changing the location of encounters. A "sallying" male is primed for aggression and locomotes distinctively, carrying his palpi drawn up and back, and walking in a reared-up fashion.

When a male enters a crevice he is immediately able to dominate individuals to which he was slightly subordinate while both were in the open, and this "invulnerability" dominance is further enhanced later by a "familiarity" dominance and an "isolation" dominance, the last a result of the territorial male's restricted movements and fewer encounters. All of these effects probably combine to produce the stability of natural colonies of field crickets in many species, in which males occupy spaced burrows and rarely encounter one another, and in which individual males remain in the same locations for all or nearly of their adult lives. Permanent location of males at sites spaced so far apart as to be only within range of hearing maximizes the temporal and spatial size and continuity of the acoustical field available to the females of the species, and enhances the effectiveness of the calling songs of individual males as guides for sexually responsive females. Burrow-occupying males do not pursue either males or females far from the burrow, but temporary contact with other crickets usually results in long-continued production of the calling song by causing temporary production of aggressive or courtship sounds through which the male is stimulated, either by external auditory feedback, by some kind of internal feedback, or by both, to keep stridulating and gradually adjust into the calling rhythm. This has the desirable effects of calling back a departing female if she is sexually responsive and reinforcing the repulsion of a subordinated male. A lone territorial male within hearing of other males sings more continually at the appropriate times than a male repeatedly interrupted by contacts with other males, or a male completely isolated from the stimulative effects of the singing of other males.

The peculiar post-copulatory behavior of crickets keeps the male and female together and promotes repeated copulation and temporary monopolization of the female by the particular male involved. This monopolization is further enhanced by the post-copulatory rise in aggressiveness in males; when two males are placed with one female, the dominant monopolizes the female as long as she remains sexually responsive, but if the subordinate is allowed to copulate with her first, then he becomes the monopolizer. It is suggested that delay in removal of the spermatophore by the female has become a minor, coincidental function of post-copulatory behavior in field crickets.

Aside from differences in acoustical behavior, chiefly with respect to the calling song, there are few obvious interspecific differences in sexual and aggressive behavior among North American field crickets. Most discordances in interspecific interactions at close range appear to derive from chemo-tactile stimuli. The result is delay or failure of females to mount males of other species and allow them to attach the spermatophore, and, less frequently, inability of males of different species to engage in sustained combat with one another. Comparisons of structure and function in cricket sounds suggest that the first significant sounds operated in courtship; the calling function probably evolved as an outgrowth of the courtship situation, and the aggressive function later as an outgrowth of the calling function.

The behavioral peculiarities associated with isolation on the one hand (aggressiveness, territoriality) and with crowding on the other hand (gregariousness, high mobility) are associated in divergent sequences of an ontogenetic nature which produce an effect somewhat analogous to that produced by phase differences in migratory locusts. These sequences are re-inforcingly effective in promoting a maximum utilization of reproductive capacity in times of low population density and high population density, re-

spectively; the latter utilizes high population density in dispersing the species into new localities.

Comparison of the behavior of different species of field crickets and related Gryllinae suggests some of the probable intermediate stages in the evolution of social behavior in insects through an initial isolation of breeding pairs and their attachment to and modification of particular localities.

LITERATURE

- ALEXANDER, R. D. (1957a). The taxonomy of the field crickets of the eastern United States (Orthoptera: Gryllidae: *Acheta*). — Ann. Ent. Soc. Amer. 50, p. 584-602.
- (1957b). Sound production and associated behavior in insects. — Ohio Jour. Sci. 57, p. 101-113.
- (1957c). The song relationships of four species of ground crickets (Orthoptera: Gryllidae: *Nemobius*). — Ohio Jour. Sci. 57, p. 153-163.
- (1960). Sound communication in Orthoptera and Cicadidae. — Animal Sounds and Communication (LANYON and TAVOLKA, ed.). Symposium of The American Institute of Biological Sciences 7, p. 38-92.
- and BIGELOW, R. S. (1960). Allochronic speciation in field crickets, and a new species, *Acheta veletis*. — Evolution 14, p. 334-346.
- and THOMAS, E. S. (1959). Systematic and behavioral studies on the crickets of the *Nemobius fasciatus* group (Orthoptera: Gryllidae: Nemobiinae). — Ann. Ent. Soc. Amer. 52, p. 591-605.
- ALLEE, W. C. (1952). Dominance and hierarchy in societies of vertebrates. — Structure et Physiologie des Sociétés Animales (P. P. GRASSÉ, ed.). Colloques Internationaux du Centre National de la Recherche Scientifique 34, p. 157-181.
- BAERENDS, G. P. (1941). Fortpflanzungsverhalten und Orientierung der Grabwespe *Ammophila campestris* Jur. — Tijdschr. Ent. 84, p. 68-275.
- BAUMGARTNER, W. J. (1910). Observations on the Gryllidae. III. Notes on the classification and on some habits of certain crickets. — Kans. Univ. Sci. Bull. 5, p. 309-319.
- BIGELOW, R. S. (1958). Evolution in the field cricket, *Acheta assimilis* Fab. — Canadian Jour. Zool. 36, p. 139-151.
- (1960). Interspecific hybrids and speciation in the genus *Acheta* (Orthoptera, Gryllidae). — Canadian Jour. Zool. 38, p. 509-524.
- BOVBJERG, R. V. (1953). Dominance order in the crayfish *Orconectes virilis* (Hagen). — Physiol. Zool. 26, p. 173-178.
- (1956). Some factors affecting aggressive behavior in crayfish. — Physiol. Zool. 29, p. 127-136.
- CARPENTER, C. R. (1958). Territoriality: a review of concepts and problems. Behavior and Evolution (ROE, and SIMPSON, ed.). — Yale Univ. Press, p. 224-250.
- CHAPMAN, R. F. (1959). Observations on the flight activity of the red locust, *Nomadacris septemfasciata* (Serville). — Behaviour 14, p. 300-334.
- CHAUVIN, R. (1946). Notes sur la physiologie comparée des Orthoptères. V. L'effet de groupe et la croissance larvaire des Blattes, des Grillons et du Phanéroptère. — Bull. Soc. Zool. Fr. 71, p. 39-48.
- (1958). L'action du groupement sur la croissance des grillons (*Gryllulus domesticus*). — Jour. Insect Physiol. 2, p. 235-248.
- CHOPARD, L. (1938). La Biologie des Orthoptères. — Encyclopédie Entomologique 20 (Serie A), p. 1-541. Paris, Lechevalier.
- COLLIAS, N. E. (1944). Aggressive behavior among vertebrate animals. — Physiol. Zool. 17, p. 83-123.
- COUSIN, G. (1954). Hybridation interspécifique. Hérité quantitative. Transmission des types structuraux spécifiques dans le croisement *Gryllus peruviansis* Sauss. X *Gryllus campestris* L. — Caryologia, Suppl. 6, p. 871-882.

- (1955). Sur la fertilité et le schéma des assemblages génétiques des combinaisons hybrides obtenues des croisements entre deux espèces du genre *Gryllus*: *G. campestris* L. X *G. bimaculatus* De Geer. — *Compte Rendu des Séances de L'Académie des Sciences, Paris.* 241, p. 1178-1180.
- CRANE, J. (1958). Aspects of social behavior in fiddler crabs, with special reference to *Uca maracoani* (Latreille). — *Zoologica* 43, p. 113-120.
- DETHIER, V. G. and L. E. CHADWICK (1948). Chemoreception in insects. — *Physiol. Rev.* 28, p. 220-254.
- ELLIS, P. (1959). Learning and social aggregation in locust hoppers. — *Animal Behaviour* 7, p. 91-105.
- FAURE, J. C. (1932). The phases of locusts in South Africa. — *Bull. Ent. Res.* 23, p. 293-405.
- FREE, J. B. (1955). The behaviour of egg-laying workers of bumblebee colonies. — *Brit. Jour. Animal Behaviour* 3, p. 147-153.
- FRINGS, H. and M. FRINGS (1949). Loci of contact chemoreceptors in insects. — *Amer. Midl. Nat.* 41, p. 602-658.
- FRISCH, K. VON (1950). *Bees: Their Vision, Chemical Senses, and Language.* — Cornell Univ. Press, Ithaca, N. Y., p. 1-119.
- FULTON, B. B. (1930). Notes on Oregon Orthoptera, with descriptions of new species and races. — *Ann. Ent. Soc. Amer.* 23, p. 611-641.
- (1937). Experimental crossing of subspecies in *Nemobius* (Orthoptera: Gryllidae). — *Ann. Ent. Soc. Amer.* 30, p. 201-207.
- (1952). Speciation in the field cricket. — *Evolution* 6, p. 283-295.
- GABBUTT, P. D. (1954). Notes on the mating behaviour of *Nemobius sylvestris* (Bosc.) (Orth., Gryllidae). — *Brit. Jour. Animal Behaviour* 2, p. 84-88.
- (1959). The bionomics of the wood cricket, *Nemobius sylvestris* (Orthoptera: Gryllidae). — *Jour. Animal Ecology* 28, p. 15-42.
- GRIFFITH, M. E. (1937). A mole-cricket at bay. — *Jour. Kans. Ent. Soc.* 10, p. 27-28.
- GHOSH, C. C. (1912). The big brown cricket (*Brachytrypes achatinus*, Stoll). — *Mem. Dept. Agric. India* 4, p. 161-182.
- GHOURI, A. S. K. and J. E. McFARLANE (1957). Reproductive isolation in the house cricket (Orthoptera: Gryllidae). — *Psyche* 64, p. 30-36.
- and — (1958a). Observations on the development of crickets. — *Canad. Ent.* 90, p. 158-165.
- and — (1958b). Occurrence of a macropterous form of *Gryllodes sigillatus* (Walker) (Orthoptera: Gryllidae) in laboratory culture. — *Canad. Jour. Zool.* 36, p. 837-838.
- GURNEY, A. B. (1947). A new species of *Pristoceuthophilus* from Oregon, and remarks on certain special glands of Orthoptera (Gryllacrididae: Rhaphidophorinae). — *Jour. Wash. Acad. Sci.* 37, p. 430-435.
- HASKELL, P. T. (1953). The stridulation behaviour of the domestic cricket. — *Brit. Jour. Animal Behaviour* 1, p. 120-121.
- HAYSLIP, N. C. (1943). Notes on biological studies of mole crickets at Plant City, Florida. — *Fla. Ent.* 36, p. 33-46.
- HÖRMANN-HECK, S. von (1957). Untersuchungen über den Erbgang einiger Verhaltensweisen bei Grillenbastarden (*Gryllus campestris* L. X *Gryllus bimaculatus* De Geer). — *Zeitschr. für Tierpsychologie* 14, p. 137-183.
- HUBER, F. (1955). Sitz und Bedeutung nervöser Zentren für Instinkthandlungen beim Männchen von *Gryllus campestris* L. — *Zeitschr. für Tierpsychologie* 12, p. 12-48.
- JACOBS, M. E. (1955). Studies on territorialism and sexual selection in dragonflies. — *Ecology* 36, p. 566-586.
- KATO, M. and K. HAYASAKA (1958). Notes on the dominance order in experimental populations of crickets. — *Ecol. Rev.* 14, 311-315.

- KHALIFA, A. (1949). The mechanism of insemination and the mode of action of the spermatophore in *Gryllus domesticus*. — Quart. Jour. Microscop. Sci. 90, 281-292.
- (1950). Sexual behaviour in *Gryllus domesticus* L. — Behaviour 2, p. 264-274.
- KORMONDY, E. J. (1959). The systematics of *Tetragoneuria*, based on ecological, life history, and morphological evidence (Odonata, Corduliidae). — Univ. Mich. Mus. Zool. Misc. Publ. 107, p. 1-79.
- LAUFER, B. (1927). Insect-musicians and cricket champions of China. — Field Mus. Nat. Hist., Anthropology Leaflet 22, p. 1-27.
- LOHER, W. (1959). Contributions to the study of the sexual behavior of *Schistocerca gregaria* Forskal (Orthoptera: Acrididae). — Proc. Roy. Ent. Soc. London (A) 34, p. 49-56.
- LOWE, M. E. (1956). Dominance-subordinance relationships in the crawfish *Cambarellus shuffeldtii*. — Tulane Studies in Zool. 4, p. 141-170.
- MACGREGOR, E. A. (1948). Odour as a basis for orientated movement in ants. — Behaviour 1, p. 267-296.
- (1929). The true cricket — a serious pest in California. — U.S. Dept. Agric. Circ. 75.
- MELANDER, A. L. (1902). Two new Embiidae. — Biol. Bull. 3, p. 16-26.
- MICHENER, C. D. (1953). Problems in the development of social behavior and communication among insects. — Trans. Kans. Acad. Sci. 56, p. 1-15.
- (1958). The evolution of social behavior in bees. — Proc. Tenth Intern. Congress Ent. (1956) 2, p. 441-447.
- MOORE, N. W. (1952). On the so-called "territories" of dragonflies (Odonata-Anisoptera). — Behaviour 4, p. 85-100.
- NOBLE, G. K. (1939). The experimental animal from the naturalist's point of view. — Amer. Nat. 73, p. 113-126.
- NORRIS, M. J. (1959). Reproduction in the red locust (*Nomadacris septemfasciata* Serville) in the laboratory. — Anti-Locust Research Bull. 36, p. 1-46.
- PARDI, L. (1948a). Dominance order in *Polistes* wasps. — Physiol. Zool. 21, p. 1-13.
- (1948b). Beobachtungen über das interindividuelle Verhalten bei *Polistes gallicus* (Untersuchungen über die Polistini, No. 10). — Behaviour 1, p. 138-172.
- PETTIT, L. C. (1940). The effect of isolation on growth in the cockroach *Blattella germanica* (L.) (Orthoptera Blattidae). — Ent. News 51, p. 293.
- PUKOWSKI, E. (1933). Ökologische Untersuchungen an *Necrophorus* F. — Zeitschr. Morph. Ökol. Tiere 27, p. 518-586.
- REGEN, J. (1913). Über die Anlockung des Weibchens von *Gryllus campestris* L. durch telephonisch übertragene Stridulationslaute des Männchens. Ein Beitrag zur Frage der Orientierung bei den Insekten. — Pflügers Arch. ges. Physiol. 155, p. 193-200.
- REHN, J. A. G. and M. HEBARD (1915). The genus *Gryllus* (Orthoptera) as found in America. — Proc. Acad. Nat. Sci. Phila. 67, p. 292-322.
- RICHARDS, T. J. (1952). *Nemobius sylvestris* in S. E. Devon. — Entomologist 85, p. 83-87, 108-111, 136-141, 161-166.
- ROTH, L. M. and E. R. WILLIS (1954). The reproduction of cockroaches. — Smiths. Misc. Coll. 122, p. 1-49.
- SAUSSURE, H. DE (1877). Mélanges orthoptérologiques, 5th fascicule. — Mém. Soc. de Physique et d'Hist. Nat. Genève 25, p. 1-352.
- SELLIER, R. (1954). Recherches sur la morphogénèse et le polymorphisme alaires chez les Orthoptères Gryllides. — Ann. Sci. Nat. 11th Ser. 16, p. 595-740.
- SNODGRASS, R. E. (1937). The male genitalia of orthopteroid insects. — Smiths. Misc. Coll. 96, p. 1-107.
- SPANN, L. (1934). Studies on the reproductive system of *Gryllus assimilis* Fabr. — Trans. Kans. Acad. Sci. 37, p. 299-340.

- TINBERGEN, N. (1953). Social behaviour in animals with special reference to vertebrates. — New York: John Wiley and Sons, Inc., p. 1-150.
- WALKER, T. J. — (1958). Specificity in the response of female tree crickets (Orthoptera, Gryllidae, Oecanthinae) to calling songs of the males. — *Ann. Ent. Soc. Amer.* 50, p. 626-636.
- WHEELER, W. M. (1923). Social Life Among the Insects. — New York: Harcourt, Brace, and Company, p. 1-375.

ZUSAMMENFASSUNG

Die meisten Begegnungen zwischen erwachsenen Feldgrillen-Männchen lösen bei einem oder bei beiden Tieren Kampfverhalten aus und enden mit dem Rückzug eines der Partner. Dieses Verhalten besteht aus einer oder aus mehreren Teilen. Bei geringer Kampfindensität stellen die Tiere entweder den Vorderkörper auf, peitschen mit den Antennen und schütteln den Körper, oder sie stellen den Hinterkörper auf, schleudern die Hinterbeine aus und schütteln. Bei großer Kampfindensität beginnen die Männchen mit dem Antennenpeitschen, stellen den Vorderkörper auf, spreizen die Mandibeln, stridulieren, springen sich gegenseitig an, boxen mit den Vorderbeinen, stoßen mit dem Kopf, greifen mit den Mandibeln zu oder beißen. Ein Männchen wird dabei oft zurück oder zur Seite geworfen; Verstümmelungen nach heftigen Kämpfen sind jedoch selten. Es scheint, daß der Sieger nur bei sehr heftigen Angriffen durch die überlegene Körperstärke und die größere Kampffähigkeit bestimmt wird. Der Ausgang der meisten Kämpfe hängt von der Zähigkeit der Partner ab; die Heftigkeit der Auseinandersetzung steht in Beziehung zur Länge des Kampfes. Fortgesetzte Aggressivität erhöht die Intensität der Rivalenhandlungen, bis schließlich eines der Männchen zurückweicht.

Gruppen erwachsener Feldgrillen-Männchen bilden in kleinen Käfigen Rangordnungen aus, die kurze Zeit stabil sind und durch folgende Merkmale gekennzeichnet werden können. 1) Ranghohe Männchen dominieren in allen oder fast allen Begegnungen über Rangniedere. 2) Die Gesamtzahl der Begegnungen in einer Gruppe nimmt in Richtung zu den Rangniedereren ab. 3) In der gleichen Richtung verringert sich die Kampfindensität, so daß die Zahl unentschieden ausgehender Kämpfe oder nicht aggressiver Begegnungen ansteigt und homosexuelles Verhalten vermehrt auftritt. 4) Rangnahe Männchen bekämpfen sich in der Regel heftiger als Tiere, die in der Hierarchie weit voneinander entfernt sind.

Von gewissen Ausnahmen abgesehen, wird die Rangordnung nach den ersten Begegnungen der Tiere festgelegt. Die Stellung des Männchens in der Hierarchie kann zeitweise durch folgende Vorgänge oder Zustände nach oben verschoben werden:

1) Kopulation, 2) Isolation, 3) Besitz einer Spalte oder Höhle und 4) Sieg bei heftigen Kämpfen. Bei Niederlagen kann das Tier in der Rangordnung vorübergehend absinken. Ein Männchen erreicht die höchste ihm mögliche Stellung in einer nicht territorialen Gruppe ungefähr 12 Tage nach der Imaginalhäutung und behält sie bis zum Tode bei, oder bis zu einem Zeitpunkt, wo sich die "Altersschwäche" bemerkbar macht. Sofern nicht andere Faktoren hereinspielen, dominieren in der Regel größere über kleinere Männchen. Die Blendung, die teilweise Amputation der Fühler bis auf proximale Stümpfe von ca 1 cm Länge und das Aufkleben eines Stückchens Pappe auf das Pronotum (= Veränderung der Körpergestalt) ändern die Rangstellung nicht. Erst die totale Amputation der Fühler verursacht ein besonderes Verhalten und führt zu einer Erniedrigung in der Rangordnung.

Der Kampfgesang der Gryllinae unterscheidet sich deutlich von den Gesängen in anderen Verhaltenssituationen. Während eines Kampfes löst der Gesang des einen

normalerweise auch die Antwort des anderen Partners aus. Bei den meisten Arten zirpen beide Tiere während einer heftigen Auseinandersetzung. Ranghöhere singen häufiger als Rangniedere, dominierende Männchen zirpen meist auch nach einem heftigen Kampf, wenn der Besiegte geflüchtet und der gegenseitige Antennenkontakt verloren gegangen ist. Rangniedere Männchen singen seltener nach dem Kampf; tun sie das, so deutet dies auf einen bevorstehenden Anstieg in der Rangordnung hin.

Relativ spezifische künstliche Reize, wie das Rückspielen von aufgenommenen Kampfesängen während Antennenpeitschen nachgeahmt wird, lösen das vollständige Rivalenverhalten aus. In den Fällen, wo das Männchen eben einen Kampf siegreich beendet hat, territorial geworden oder zur Begattung gekommen ist, reicht ein Reiz — der Hörreiz oder der taktile Reiz — allein aus. Dies deutet auf einen „Conditionierungseffekt“ hin. In ähnlicher Weise kann das Werbeverhalten bei einem Männchen, das den Lockgesang erzeugt oder eben die Balz beendet hat, durch einfache taktile Reize angeregt werden, die weniger spezifisch sind als jene es sein müssen, um in anderen Situationen die Werbung auszulösen. Es besteht offenbar keine Beziehung in der conditionierenden Wirkung zwischen Balz und Kampf.

Eben erst erlittene Niederlagen vermindern die Kampflust des Männchens. Die dominierende Stellung des einen von zwei Männchen kann immer wieder geändert werden, wenn man es zwischen zwei aufeinanderfolgenden Begegnungen durch „Attrappen“ besiegt. Hierbei treten Kampf oder Rückzug nach kürzerer Latenz auf, wenn beide Reize — Rückspielen des Kampfesanges und künstliches Bepetschen mit Borsten — gleichzeitig wirken; der conditionierende Effekt ist dann stärker.

In rein männlichen Gruppen balzen sich die Tiere gegenseitig an und zwar um so mehr, je länger die Männchen von den Weibchen isoliert sind. Die Balz wird ausgelöst, wenn 1) ein Männchen sich einem zweiten von hinten nähert und dieses den Lockgesang erzeugt oder 2) einer oder beide Partner nicht oder nur wenig kampfgestimmt sind und bei Begegnung nicht zurückweichen. Ein angebalztes Männchen kann kämpfen, sich unverrichteter Dinge entfernen, oder das werbende Tier besteigen. Es bleibt nach dem Aufstieg bewegungslos wie ein Weibchen in der gleichen Situation. Solche Begegnungen können wiederholt die gesamte Balz- und Kopulationsfolge auslösen, wobei jedoch keine Spermatophore übertragen wird. Abgesonderte Männchen beginnen mit der Balz manchmal nach einer Reizung der Analcerci mit leblosen Gegenständen, besonders häufig in der Phase des Lockesanges. Aber auch die eigenen vibrierenden Hinterflügel können in der Phase der Flugvorbereitung die Cerci reizen, die Werbung anregen und dazu führen, daß das Männchen die Spermatophore am Käfiggitter abstreift.

Sind Spalten vorhanden, so werden sie von den Männchen in Besitz genommen; rangniedere Tiere ziehen dabei den Kürzeren und werden in die Flucht geschlagen. Ohne Spalten heben die Männchen Nischen oder Erdhöhlen in geeigneten Substraten aus. Der Besitz einer Spalte oder Höhle verändert das Verhalten in folgender Weise. 1) Das Männchen schränkt das von ihm sonst durchlaufene Gebiet ein. 2) Es hält sich lange Zeit in der Höhle auf. 3) Es bewegt sich innerhalb und außerhalb seiner Höhle und prüft sie mit den Palpen und den Antennen. 4) Es macht in gewissen Zeitabständen Patrouillen außerhalb der Höhle, nimmt dabei aufgefundene Nahrung und Wasser auf, bekämpft Männchen und umwirbt Weibchen. 5) Es kehrt auf direktem Wege zur Höhle zurück. 6) Es zeigt bei Begegnungen mit anderen Männchen sehr heftige Kämpfe. 7) Der Höhlenbesitz vermindert die Zahl der Begegnungen. Der Besitz von Höhlen durch einzelne Männchen einer Gruppe verändert das ganze Gruppenverhalten, indem 1) die Zahl der Begegnungen sinkt, 2) der Prozentsatz heftiger Kämpfe ansteigt und 3) der Ort der Begegnung sich verschiebt. Ein patrouillierendes

Männchen ist kampfgestimmt und bewegt sich in charakteristischer Weise; es stellt die Palpen hoch und zurück, und läuft mit aufgerichtetem Körper.

Sobald ein Männchen in eine Höhle eindringt, dominiert es über andere, denen es im Freien leicht unterlegen war. Diese Dominanz wird durch die Sicherheit in der Höhle, durch die allmähliche Vertrautheit mit der Umgebung und durch Isolation gefestigt. Letztere ist das Ergebnis der eingeschränkten Bewegungsfreiheit des ortstreuen Männchens und der geringeren Zahl der Begegnungen. Alle diese Faktoren wirken wahrscheinlich zusammen und sichern die Stabilität der natürlichen Kolonien der Feldgrillen bei vielen Arten, wo die Männchen weit auseinander liegende Höhlen bewohnen, sich nur selten begegnen und während der ganzen oder nahezu ganzen Adultphase am gleichen Orte bleiben. Der ständige Aufenthalt an denselben Orten, die in Hörweite auseinanderliegen, vergrößert zeitlich und räumlich die Größe und den Fortbestand des akustischen „Feldes“ für die Weibchen der gleichen Art. Die Ortstreue steigert die Wirksamkeit der Lockgesänge einzelner Individuen, die Wegweiser für paarungsgestimmte Weibchen sind. Höhlenbesitzer verfolgen Männchen und Weibchen nur in unmittelbarer Nähe des Loches; der vorübergehende Kontakt mit anderen Grillen führt aber gewöhnlich zu langanhaltenden Lockesängen. Sie werden angeregt durch eine zeitweilige Stridulation von Kampf- und Werbelauten, für die als auslösende Faktoren entweder externe akustische Rückmeldungen (Fremdgesang und Eigengesang) oder andere interne Rückmeldungen, oder beide in Frage kommen. Diese Faktoren halten die Zirptätigkeit aufrecht und geben eine Möglichkeit zur Anpassung der Laute an den Rhythmus der Lockesänge. Die Folge davon ist, daß paarungsbereite und sich entfernende Weibchen zurückgerufen und untergeordnete Männchen gemieden werden. Ein territoriales Männchen singt innerhalb des Hörbereiches anderer häufiger und kontinuierlicher als eines, das vollständig isoliert ist oder durch Begegnungen mit anderen Männchen in seinem Tun gestört wird.

Das besonders ausgebildete Nachbalz-Verhalten der Grillen hält Männchen und Weibchen zusammen, fördert wiederholte Begattungen und sichert eine vorübergehende Monopolstellung des Männchens gegenüber dem Weibchen. Dieses Monopol wird weiter gefestigt durch die besondere Kampfkraft des Männchens in der Nachbalz-Phase. Hält man nämlich zwei Männchen zusammen mit einem Weibchen, so gehört das paarungsbereite Weibchen dem Ranghöheren. Darf der rangniedere Partner zuerst kopulieren, so nimmt er gegenüber dem Weibchen Monopolstellung ein. Es wird angedeutet, daß demgegenüber das verzögerte Entfernen der angehefteten Spermatophore durch das Weibchen zu einer weniger bedeutsamen und zufällig zugeordneten Funktion der Nachbalz der Grillen geworden ist.

Abgesehen von den Unterschieden im akustischen Verhalten, vor allem im Lockesang, gibt es wenige deutliche interspezifische Unterschiede im Balz- und Kampfverhalten nordamerikanischer Feldgrillen. Die meisten scheinen sich auf die Reaktionen zu beziehen, die bei chemisch-taktiler Reizung in der Nähe wirksam sind. Dies führt dazu, daß Weibchen die Männchen anderer Arten nur zögernd oder gar nicht besteigen und damit eine Begattung erschweren. Außerdem sind die Männchen verschiedener Arten häufig unfähig, miteinander über lange Zeit zu kämpfen. Ein Vergleich des Aufbaues und der Funktion der Grillengesänge deutet an, daß die ersten (= stammesgeschichtlich ältesten) Laute bei der Werbung wirksam waren; aus ihnen entwickelte sich vermutlich der Lockesang und aus ihm der Kampfgesang.

Die Besonderheiten im Verhalten, welche einerseits mit der Isolation (Aggressivität, Territorialität) und andererseits mit dem geselligen Zusammenleben (soziale Phase, größere Beweglichkeit) einhergehen, hängen in ontogenetisch divergierenden Linien zusammen. Sie führen zu einem analogen Effekt, wie er für die Phasenunterschiede

bei Wanderheuschrecken kennzeichnend ist. Isolation und Geselligkeit und die mit ihnen verbundenen Verhaltensänderungen werden immer stärker wirksam, indem sie zu einer maximalen Ausnutzung der Fortpflanzungspotenz in Zeiten schwacher bzw. starker Bevölkerungsdichte führen. Bei hoher Individuendichte ist dann die Verbreitung der Art auf neue Standorte gewährleistet.

Ein Vergleich des Verhaltens verschiedener Feldgrillen-Arten und verwandter Gryllinae weist auf wahrscheinlich intermediäre Stadien in der Evolution des Sozialverhaltens der Insekten hin. Sie scheinen durch eine anfängliche Isolation der sich fortpflanzenden Paare und ihre Gewöhnung und Anpassung an bestimmte Plätze hervorgerufen worden zu sein.
