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MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN, NO. 141

A Comparative Study of Communicative Behavior in Grasshoppers

BY
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Ann Arbor
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN
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Francis C. Evans, Editor

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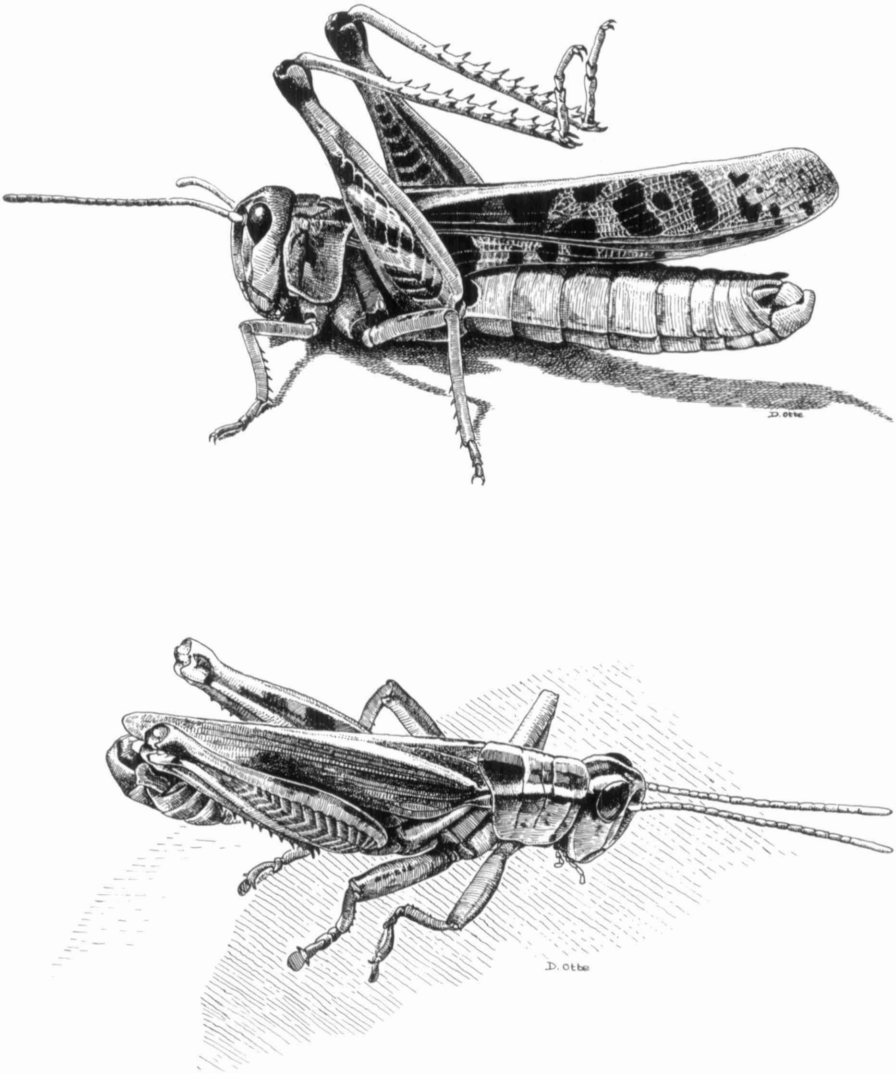

Frontispiece

Femur-tipping by a courting male of *Pardalophora haldemanii* (above). A male of *Melanoplus bivittatus* preparing to pounce onto a female (below).

INTRODUCTION

Comparative studies in behavior constitute repositories of information on animal groups which may be useful in most branches of biology; they also generate principles concerning behavior, furnish information on species relationships, and provide suitable evolutionary frameworks for more specialized investigations on behavior. The present study, a survey of communication in North American grasshoppers, attempts to answer several general questions: (1) What kinds of communicative systems are represented in the North American fauna? (2) What factors have caused the evolution of differences in communication? (3) How do communicative signals originate, and how do they become elaborated? (4) Can differences in communication aid in taxonomic work on grasshoppers? I have made this study as inclusive as possible, at the expense of more detailed investigations on the behavior of individual species, on the grounds that some of these questions are best approached through broadly comparative study.

The seven families of North American grasshoppers (Acridoidea) contain about 1100 species. Most are in the family Acrididae, comprising three main subfamilies, the Oedipodinae (ca. 200 species), the Acridinae (ca. 150 species), and the Catantopinae (ca. 500 species). In this study communication has been examined in 71 species of Oedipodinae, 31 species of Acridinae, 10 species of Catantopinae, and one species each of Cyrtacanthacridinae and Romaleinae. A few observations were made on the acoustical behavior of the Pneumoridae and Pamphagidae in South Africa in 1965. This information is compared with that of Jacobs (1953) and Faber (1953), who examined communication in 41 species of European grasshoppers.

Differences in communication seem to result from selection (1) for species distinctiveness in the context of reproductive isolation and/or (2) for effectiveness in communication under different environmental circumstances. That some diversity is owing to selection for species distinctiveness appears to be widely accepted; how different habitats or habits can produce differences in communication may be less well understood. What effects, for instance, have diurnal or nocturnal habits had on communication, and what are the consequences of living in vegetation as opposed to living on the ground? Both acoustical and visual communicative signals are employed by grasshoppers, but why is one type of signal more prevalent in certain circumstances than in others?

Distinctiveness in communication has already been used to elucidate taxonomic problems concerning groups of very similar species of grasshoppers (Faber, 1929). In North America, taxonomic work on ensiferans has come to be based heavily on song differences (Alexander, 1957a, 1957b; Walker, 1957, 1962, 1963, 1964). The present study indicates that differences in song and in behavior associated with reproduction may be valuable in distinguishing similar species in several groups of grasshoppers.

Since the publication in 1872 of Darwin's *The Expression of the Emotions in Man and Animals,* a main endeavor of ethologists has been to determine the origins and evolution of communicative signals. Detailed comparative studies, mainly on birds, have furnished most of the principles concerning the evolution of such behavior (Daanje, 1950; Armstrong, 1950; Tinbergen, 1952; Morris, 1956). Among the attempts to reconstruct the evolution of arthropod signals are those of Crane (1949, 1952) on spiders and mantids, Spieth (1952) and Manning (1965) on *Drosophila,* Jacobs (1953) on grasshoppers, Lindauer (1961) on bees, Alexander (1962) on crickets, and Lloyd (1966) on fireflies. In the present study I have further considered the evolution of grasshopper communication.

Reproductive behavior and the communication patterns associated with it tend to diverge very rapidly in a group of interacting species, whereas other kinds of behavior, such as grooming, feeding, or locomotion, usually evolve more slowly and are likely to show fewer differences among species. It is for this reason that studies on behavioral evolution deal primarily with sexual behavior. Furthermore, systematic analyses of taxa with special efforts to examine closely related species have furnished the most reliable information concerning the origins of signals and the details of their evolution. This follows from two facts: (1) In general, species that are similar are related or share an exclusive common ancestor, so that the ancestral condition of the characteristics under investigation can sometimes be inferred. (2) Evolutionary rates differ between lineages, making it possible in some cases to observe the probable stages in the evolution of a character. In this investigation six or more species were studied for each of four genera and from two to four species for each of thirteen genera.

The classification followed in this study is a combination of those proposed by Uvarov (1966) and Dirsh (1961, 1965) with that conventionally used by North American taxonomists. The subfamily Oedipodinae as used below includes genera that have traditionally been included in the Oedipodinae by American taxonomists and is also consistent with the classification of Uvarov. The name Gomphocerinae, as used by Uvarov, includes all the members of Acridinae examined in this study. For discussions of the classification of Acridinae and Oedipodinae, see Dirsh (1961), Rehn and Grant (1959, 1960), and Uvarov (1966).

ACKNOWLEDGMENTS

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METHODS OF STUDY

This study was begun in the summer of 1965 by an examination of the behavior of grasshoppers on the E. S. George Reserve, Livingston County, Michigan. A few short trips around Michigan and Ohio were taken to collect species related to those examined on the Reserve. In 1966, field trips were taken to Texas (May), to California (June), to Florida (August), and to California and central Mexico (October). In 1967, field trips were taken to New England (July), to Colorado (August), and to California (August). On these trips grasshoppers were usually collected by the roadside or within sight of the roadway.

In the laboratory, observations were made with animals confined in glass terraria of various sizes (6″ x 10″; 8″ x 16″; and 12″ x 30″). The terraria were arranged so as to resemble the habitat of the species. An incandescent lamp was placed above each terrarium, and a thermometer 3″ above the substrate. Animals were transferred to the laboratory in vials or in small gauze cages. The period between capture and observation of animals varied from a few hours to a few days. The time of day at which terrarium observations were made varied from species to species, but most species were observed at night because the days were used for collecting and field observations.

Sound recordings were made with a Uher 400 Report L tape recorder and a Uher Dynamic Microphone Model M514, supplemented in the field by a 22 inch parabolic reflector. Sounds were analyzed by means of a Vibralyzer (Kay Electric Co.). The recording of visual signals and other non-acoustical movements was done by one or more of the following methods: (a) in the case of variable movements, careful and repeated observations were made and set down in word descriptions; (b) records of rates, numbers of strokes, and durations of movements, were sometimes obtained by scraping or tapping the microphone or some nearby structure corresponding to the parameter of the actual signal and analyzing the resulting sound with the Vibralyzer; (c) photographs were made with a 35 mm camera to record postures or the amplitude of movements; (d) a motion picture camera was also employed to study a few species.

Except for certain signals involving flight, there appears to be a close correspondence between behavior occurring in the field and that occurring in the laboratory. In the case of species observed only in the laboratory, I think it is reasonable to assume that the signals I actually observed also occur in the field. However, it is possible, and in some cases probable, that some patterns were omitted. Furthermore, behavior patterns normally performed by receptive females were not observed in many species, because, unlike males, females are sexually responsive for short periods only.

The following keys were of assistance in the identification of the species examined in this study: Morse, 1895; Blatchley, 1920; Alexander, 1941; Ball et al., 1942; Tinkham, 1948; McNeill, 1901; Coppock, 1962; Bruner, 1904; Gurney, 1940b; Rehn, 1919b; Brooks, 1958. Comparisons were also made with identified specimens in the University of Michigan Museum of Zoology. I. J. Cantrall kindly assisted in the identification of Catantopinae.

PRINCIPAL BEHAVIOR PATTERNS

To clarify the descriptions given in the next section, I here provide a brief and very general statement of the principal patterns of grasshopper behavior involving communication—pair formation and courtship, aggression and repulsion—and of the basic non-communicative movements that are closely associated with signalling. Some information on sound production and hearing in grasshoppers is also included. The signals discussed below are more or less mutually exclusive. Sometimes, however, what at first appear to be two distinct signals can be shown to be extremes of a series, representing different intensities of response; in such instances the extremes and the intermediates are considered under a single heading. Unless stated otherwise, the behavior patterns listed are displayed by males.

Signals can be named according to the function that they serve, for example, "calling" and "male-spacing," or they can be named according to the patterns of movements of the display, for example, "stridulating" or "femur-jerking." At times, however, the function of a certain display is not immediately obvious, and even if it is known for one species, it may not be the same in a different species. Therefore, it is usually safer to name the display according to the pattern of movement. In a few cases in this study when the function is known, movements or displays are named according to the function that they serve.

PAIR FORMATION AND COURTSHIP

Pair formation is here defined as the initial coming together of a male and a female in connection with copulation, and courtship is defined as the interaction of male and female after the pair has been formed and before the pair copulates. The exact point at which pair formation ends and courtship begins is not always clear; in some species separation of the two phases seems quite arbitrary and is made for convenience only. But the inability to differentiate between them is not important if the entire pairing process is described (see Table 1).

ATTRACTION OF FEMALES.—In many grasshopper species solitary males produce female-attracting (or calling) signals. Some species of Oedipodinae perform specialized flights which are rendered conspicuous by either the flashing of colored wings or the production of loud flight noises or both (CF in Table 1). In many species of Acridinae solitary males stridulate, usually by rubbing the hind femora against the forewings (CS). Many other species, however, evidently do not possess female-attracting signals.

TABLE 1

TYPES OF SEXUAL BEHAVIOR IN GRASSHOPPERS

	Pair Formation			Courtship		Copulation	
Oedipodinae	CF	S	Af	Aw	Si	M	—
	—	S	Af	Aw	Si	M	—
	—	S	—	Aw	Si	M	—
Acridinae	CS	S	Af	Aw	Si	M	—
	CS	S	—	Aw	Si	M	—
	—	S	—	Aw	Si	M	—
	—	S	—	Aw_s	—	M_x	MS?
Catantopinae	—	S	—	Aw_s	—	M_x	MS

CF = calling or female-attracting flight; CS = calling or female-attracting stridulation; S = orientation on female by sight; Af = approaching by flying; Aw = approaching by walking; Aw_s = approaching by walking, but approach is stealthy; Si = signalling during the approach; M = mounting the female and female is aware of the mounting attempt; M_x = mounting in which the female is evidently not aware of the mounting attempt; MS = species-specific signalling by the male after he has mounted.

VISION IN PAIR FORMATION.—Vision is very important in pair formation and courtship of all diurnal species. Males are highly sensitive to movement and orient on and approach moving individuals by sight (S). Even in species where males attract females, the final stage of pair formation involves visual orientation and approaching; pair formation in these species can therefore also occur in the absence of female-attracting signals.

APPROACHING.—In all of the species studied, males will at least occasionally approach females by walking (Aw), but in many Oedipodinae and a few Acridinae they sometimes do so by flying (Af). In all Oedipodinae and most Acridinae the approach is accompanied by visual or acoustical signalling (Si). In a few Acridinae and all Catantopinae the approach is stealthy; instead of signalling, the male slowly and furtively moves up to the female (Aw_s).

MOUNTING.—In all species, the male mounts the female when he is sufficiently close. When on top of the female, the male lowers the end of his abdomen beneath that of his mate and grasps her genitalia with his own. In the Oedipodinae and most Acridinae the female is aware of a male's impending attempt to mount, because he signals before doing so (M); sexually receptive females either remain passive or signal their receptivity in some fashion, while those which are sexually unreceptive perform movements to inhibit mounting by males. In these species the male performs no species-specific signals after mounting.

In some Acridinae and all Catantopinae, the female appears to be mounted "by surprise" (M_x) and will indicate that she is receptive or unreceptive only after she is mounted. In these species the male begins to signal vigorously in a species-specific manner only after mounting, and will continue to signal until the genitalia are attached.

COPULATION.—After the male has attached his genitalia to those of the female, insemination occurs. This is indirect and involves the use of a spermatophore, produced by the male after mounting and attachment of genitalia. In *Gomphocerus rufus* its shape is "determined by the opening of the male's aedeagus and by the lumen of the [female's] receptaculum, into which the gel-like material is pressed" (Loher and Huber, 1965). After copulation the spermatophore breaks, and the female retains the tube while the male retains the sac. The presence of the spermatophore in the female makes her unreceptive to further copulations until the tube is resorbed by the receptaculum (Haskell, 1958; Uvarov, 1966).

AGGRESSION AND REPULSION

Grasshoppers do not fight. "Aggression" is used here to denote any behavior which seems to have the function of separating individuals. Thus, a display by one individual which causes an approaching individual to turn aside or to stop approaching is an "aggressive" display. Likewise, "repulsion" denotes any behavior performed by either males or females which causes the respondent to leave. "Aggression" and "repulsion" have been used interchangeably to some extent, although the former term has usually been applied to interactions between males in which no contact was established.

TYPICAL COMMUNICATIVE MOVEMENTS

NON-GRADED (STEREOTYPED) MOVEMENTS

FLIGHT DISPLAYS.—In many species of Oedipodinae solitary males perform specialized flights which evidently attract sexually receptive females of their own species. In such performances males fly up from the ground and snap their hindwings or flash their brightly colored hindwings or both, and settle back to the ground again. Flight noise, or *crepitation,* is usually species-specific.

APPROACHING FLIGHTS.—In many Oedipodinae, males approach females by flying. In some species, the hindwings are brightly colored or contrastingly marked, and some of these species also crepitate.

STRIDULATION.—Rubbing one part of the body against another, usually the hind femur against the forewing, is a widely-used signal device and is frequently employed as a female-attracting signal. Three distinct types of stridulation occur in the Oedipodinae. The most common, *ordinary stridulation,* consists of relatively slow, high-amplitude up and down movements of the hind femora against the forewings (Fig. 1a). *Vibratory stridulation* consists of relatively low-amplitude, rapid vibration of the femora against

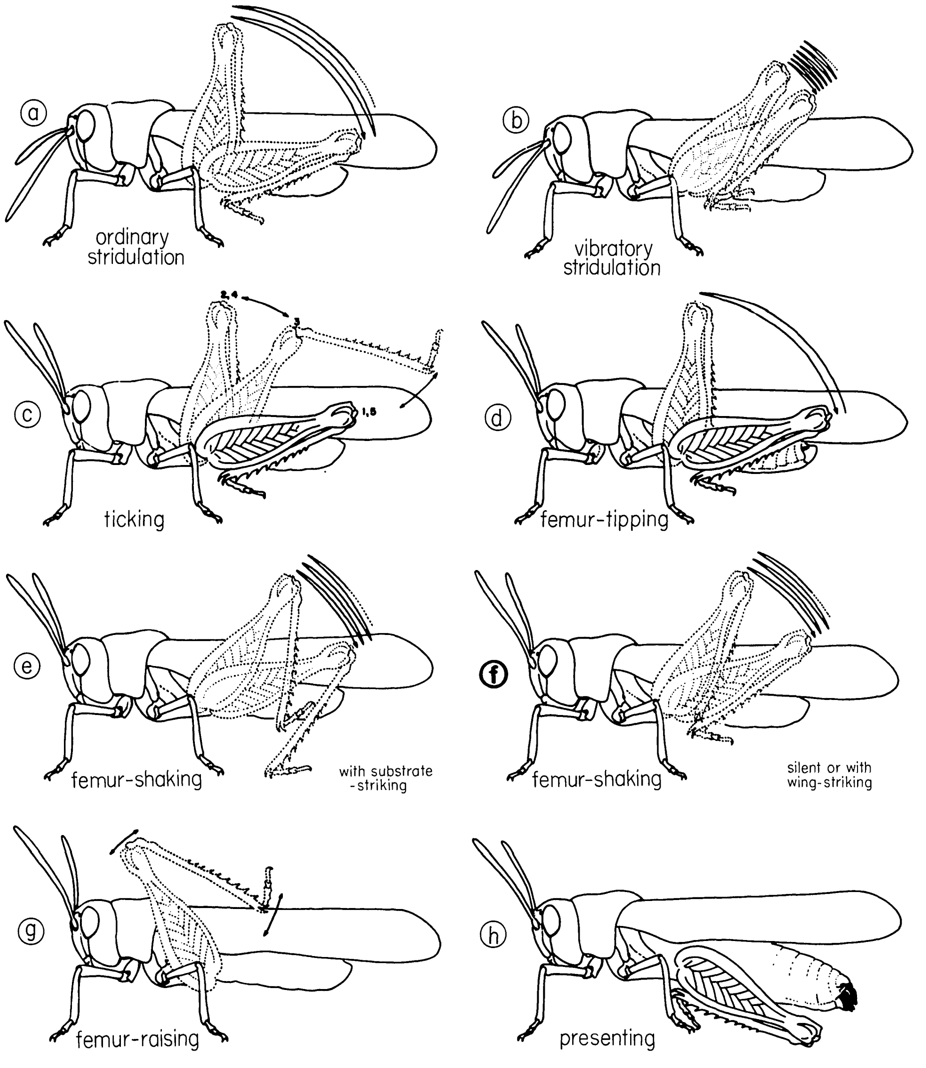

FIG. 1. Signals and postures commonly occurring in grasshoppers: (a) *ordinary stridulation*—a slow, stereotyped, repetitive or non-repetitive, high amplitude movement in which the femur rubs against the forewing; (b) *vibratory stridulation*—a fast, stereotyped, repetitive, low amplitude movement in which the femur rubs against the forewings; (c) *ticking*—a stereotyped, repetitive or non-repetitive movement in which the tibiae are kicked out and struck against the ends of the forewings; (d) *femur-tipping*—a silent, stereotyped, non-repetitive raising and lowering of the femora; (e) *femur-shaking* (with substrate-striking)—a stereotyped, repetitive shaking of the femora in which the ends of the tibiae strike the substrate to produce substrate vibration or a drumming sound; (f) *femur-shaking* (silent or with wing-striking)—similar to (e) but the movement is silent, or the femora strike the forewings; (g) *femur-raising*—a slow, graded, non-repetitive movement which may or may not be accompanied by mild upward kicking motions of the tibiae; (h) *presenting*—a variable, graded posturing of the female in response to male courtship, in which the end of the abdomen is made more accessible to the male.

the forewing (Fig. 1b). *Ticking* consists of raising the femora and then kicking out with the tibiae so as to strike the end of the forewing (Fig. 1c).

FEMUR-TIPPING.—This is the most common femoral movement in the Oedipodinae. It consists of a single quick raising and lowering of the femora (Fig. 1d), is usually silent, and normally occurs in male-male encounters. Tipping is a visual display which usually leads to the separation of males before they touch one another, but in some species it is performed by courting males. The movement is rendered conspicuous by the markings on the inside of the femur. When the femora are in the resting position these bright markings are invisible.

FEMUR-SHAKING.—This movement consists of shaking the femora, usually repetitively. There are several kinds of shaking: (a) silent, (b) shaking in which the tibiae strike the substrate, and (c) shaking in which the femora strike the forewings (Fig. 1e,f). It is performed by both males and females (mainly in the Oedipodinae) and causes the separation of individuals. In a few species shaking is a courtship signal.

GRADED (NON-STEREOTYPED) MOVEMENTS

FEMUR-JERKING.—Jerking is a disturbance movement produced only by individuals touched or mounted by other individuals. The intensity of the movement seems to depend on the degree of disturbance. All gradations occur, from a small upward jerk of the femora through a few degrees, to an extensive upward thrust to about the vertical position accompanied by a kicking-out of the tibiae.

FEMUR-RAISING.—Raising the femora and holding them in a nearly vertical position is a disturbance posture or a male-rejection posture assumed by most species (Fig. 1g). The degree of raising and forward tilting depends on the extent of the disturbance. The posture is assumed by both males and females. If mounting is attempted, the intruder is kicked away with quick upward thrusts of the tibiae. While the femora are held in the raised position, the tibiae are sometimes extended away from the femora, sometimes in a horizontal position above the back of the animal. At other times the tibiae execute small up and down movements which probably constitute a visual display.

PRESENTING.—Sexually responsive females of many species of Oedipodinae lower the hind femur nearest the approaching male and spread both femora away from the abdomen. In some species the end of the abdomen is turned toward the male (Fig. 1h). The presenting response is graded, seems to attract males and to render females more accessible to males. Presenting females always allow males to mount and to attach their genitalia. The posture varies in elaborateness both within and among species.

KICKING.—Both sexes of all species apparently kick out with their hind tibiae when disturbed by other individuals.

FEMUR-FORWARD-SWINGING.—In some species, chiefly the members of the Catantopinae, individuals swing their femora from the resting position all the way to the head and back again in a single rapid motion when touched from either the side or the front. Usually, only the leg nearest the intruder is swung forward.

SPARRING.—When individuals touch one another with their forequarters, they often strike out at one another with their forelegs and occasionally with their middle legs.

SIDEWAYS BODY-JERKING.—A few species have been observed to rock their bodies from side to side when disturbed; others do this while mounting females. I have seen copulating males and non-copulating females perform this movement when they were touched by other individuals.

REGURGITATION.—Most if not all grasshoppers regurgitate a brown fluid when handled. When a male of *Dichromorpha viridis* pounced onto a second copulating male the latter regurgitated and turned its head quickly toward the intruder for a few seconds, then withdrew the liquid.

WING-FLAPPING.—In most if not all winged species, individuals occasionally flap their wings several times in quick succession in a variety of circumstances. The movement is performed by individuals on the ground, and its function is for the most part unknown. In two species (*Arphia pseudonietana, Dissosteira carolina*) males flapped their wings when a bombyliid fly attempted to settle on them. In other species the movement has evidently assumed a courtship function.

TYPICAL NON-COMMUNICATIVE MOVEMENTS

FLYING.—Table 2 is a classification of flight in grasshoppers. Flights occurring in sexual contexts and not believed to serve a communicative function seem to be rare. Unspecialized approaching flights that appear to serve mainly a locomotive function occur in some species.

TABLE 2

CLASSIFICATION OF FLIGHT IN GRASSHOPPERS

I. DISPERSION FLIGHTS

- A. Wandering flights (short, more or less non-directional flights which seem to have a dispersive function and which are not construed to be migratory or a part of sexual behavior).
- B. Migratory flights.
  - 1. Nomadic flights (migratory flights, usually extensive, somewhat directional, by solitary individuals).
  - 2. Swarming flights (migratory flights by aggregated individuals).
- C. Unspecialized approaching flights (flights by one individual toward another which are not species-specific and have not been elaborated as communicative signals, but which seem to serve a purely locomotory function).

II. SIGNALLING FLIGHTS

- A. Ritualized approaching flights (flights toward another individual in a species-specific fashion, involving communication through brightly colored wings, flight noises or both).
- B. Calling flights (flights by males or females(?) which attract the opposite sex; usually such flights are performed by solitary males; usually colored wings or flight noises or both are present, causing flight to be acoustically and visually conspicuous).

III. DISTURBANCE FLIGHTS (FLIGHTS OF ESCAPING INDIVIDUALS)

APPROACHING.—This term refers to the orienting and advancing of one individual on another and does not include chance movements. Approaching can usually be distinguished from chance movements without difficulty by the behavior of the male just prior to advancing, by his orientation to the individual being approached, and by the position of his antennae.

ANTENNA-POINTING AND HEAD SIDE-TO-SIDE MOVEMENT.—Males of species that do not announce their approach usually move toward the female slowly and stealthily, holding their antennae straight forward as they advance. Before mounting the female, a male moves his forequarters, particularly the head, from side to side several times. This latter movement presumably allows him to gauge the distance to the individual being approached.

MOUNTING.—This term refers to the movement of a male onto a female's back in preparation for copulation, and does not include haphazard climbing of one individual over another. Mounting and chance climbing can usually be distinguished readily by the preceding movements, the antennal position, and the behavior after contact.

ATTACHING.—After mounting, the male lowers the end of his abdomen on either side of the female's abdomen and, from below, attaches his genitalia to those of his mate.

TAPPING WITH ANTENNAE.—In many species, perhaps all, the male sometimes taps the female with his antennae as he mounts. Since the movement

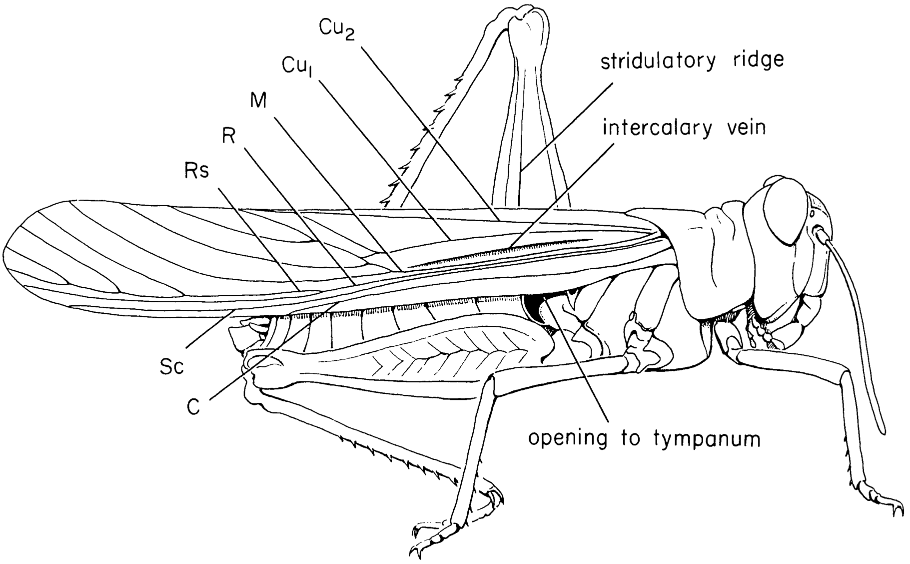

FIG. 2. Diagram illustrating the sound-producing and hearing apparatus and forewing venation in typical Oedipodinae; the stridulatory ridge is rubbed against the rough intercalary vein. In the Acridinae a row of pegs occurs in place of the stridulatory ridge and these are rubbed across the radius. (C=costa; Sc=subcosta; Rs=radial sector; R=radius; M=media; Cu=cubitus).

does not seem to differ among species, it probably merely serves to orient the male during mounting.

MECHANISMS OF SOUND PRODUCTION AND HEARING

Grasshoppers constitute one of the larger groups of sound producing animals. The pertinent literature on sound production and hearing in grasshoppers have recently been reviewed by Kevan (1954) and Uvarov (1966).

SOUND PRODUCTION.—The following list of mechanisms illustrates the considerable diversity existing among the Acridoidea in their sound-producing abilities. Usually a corrugated or serrated surface on one part of the body (the file) is rubbed against a ridge on another part (the scraper). For each stridulatory mechanism I have indicated the parts of the body that are rubbed against one another, and which part serves as the file and which as the scraper.

1. FEMUR AGAINST FOREWING: (a) a row of tubercles on the inside of the femur (file), a raised vein of the forewing (scraper) (Acridinae); (b) bumps along the intercalary vein of the forewing (file), a ridge on the inside of the femur (scraper) (most Oedipodinae); (c) a ridge on the inside of the femur is struck against a raised vein of the forewing—no file and scraper can be recognized (*Heliastus* species). (Fig. 2)
2. TIBIA AGAINST FOREWING: (a) a series of parallel veinlets on the forewing (file), tibial spurs (scraper) (Hemiacridinae and Pamphagidae); (b) inner spines of the tibiae (file), a raised vein of the forewing (scraper) (*Brachycrotaphus* species); (c) no file and scraper—the tibia is kicked out and strikes against the end of the forewing (*Encoptolophus sordidus*).
3. FEMUR AGAINST ABDOMEN: (a) pegs on the femur (file), longitudinal ridges on the abdomen (scraper) (*Phonogaster cariniventris*); (b) ridges on the abdomen (file), ridge on the femur (scraper) (Pneumoridae).
4. TIBIA AGAINST ABDOMEN: ridges on the abdomen (file), spurs on the hind tibiae (scraper) (*Charora pentagrammica*).
5. MIDDLE TIBIA AGAINST HINDWING: teeth on the tibiae (file), thickened veins on the hindwing (scraper) (*Prionotropis flexuosa*).
6. FOREWING AGAINST HINDWING: serration on the hindwing (file), raised veins on the underside of the forewing (scraper) (Romaleinae).
7. FOREWING AGAINST FOREWING AND HINDWING AGAINST HINDWING: Apparently there is no specialization of structures (*Schistocerca gregaria*), and both movements seem to occur simultaneously.
8. FLIGHT CREPITATION: Snapping sounds are made with the wings during flight—with or without specialization (thickened anal veins—Fig. 3) (Oedipodinae).
9. MANDIBULAR SOUNDS: There is no apparent specialization in the structure of the mandibles for sound production (*Calliptamus italicus*).
10. HIND TIBIAE DRUMMING THE SUBSTRATE: The tibiae do not seem to be specialized for producing sound (Oedipodinae).
11. HISSING: Sound is made by expelling air through the spiracles (*Romalea microptera*). This sound may not have a communicative function and may only be incidental to the emission of pheromones during disturbance.

MECHANISM OF CREPITATION.—It is not yet known precisely how the snapping sounds are produced during flight. Cutting off the forewing did not affect the sound produced, but crushing the thickened anal veins (Fig. 3) suppressed sound (see Isely, 1936, for summary of opinions and experiments). This wing sound-producing mechanism has been compared to a fan which produces a soft "snapping" sound if it is opened suddenly. Thus,

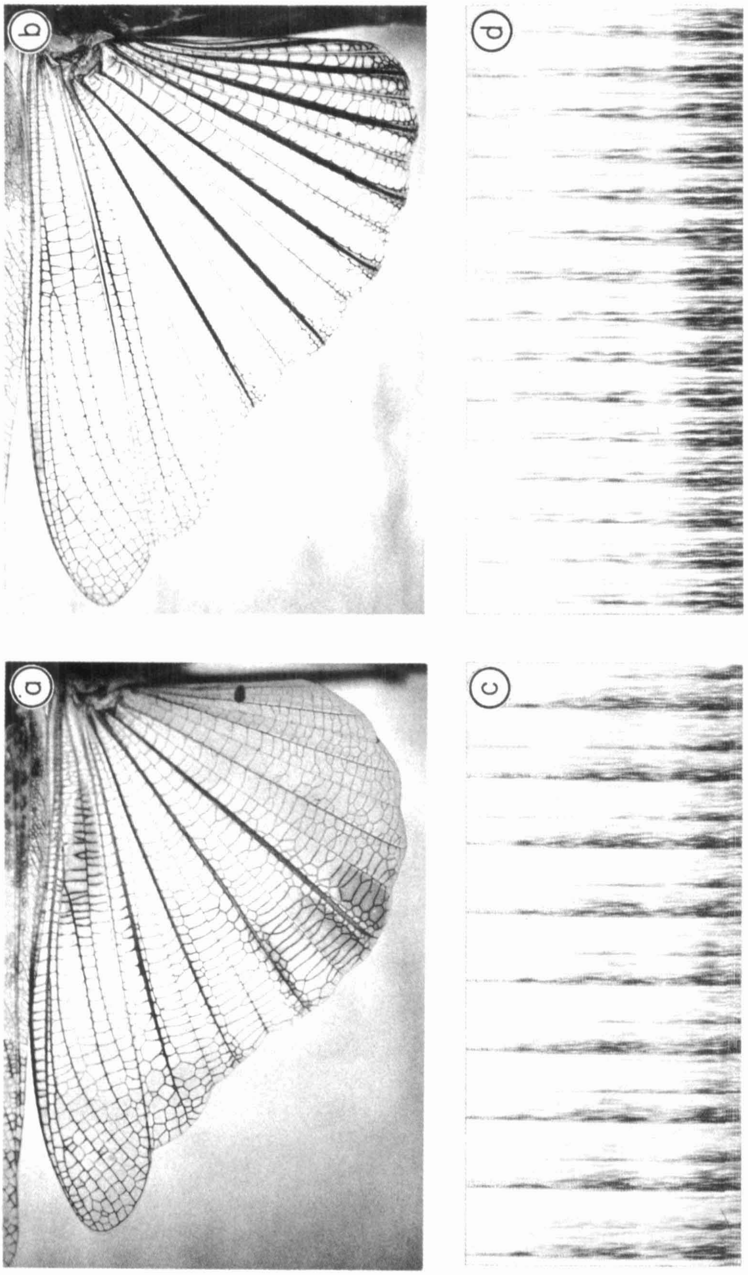

FIG. 3. (a) Hindwing of *Circotettix rabula* and (b) hindwing of *Aerochoreutes carlinianus*, showing the thickened anal veins. (c) Audiospectrographs of crepitation of *C. rabula* showing a single soft popping sound. (d) Audiospectrographs of *A. carlinianus* showing double loud and soft popping sounds.

it was suggested that the membranes between the anal veins produce a snapping sound when they suddenly become taut. When I manipulated the wings of two loud crepitators, *Circotettix rabula* and *Aerochoreutes carlinianus,* a slightly different form of the fan model of sound production was indicated. In these species, I elicited snapping or popping sounds from the wings without extending them suddenly. When I extended the wings and lowered them at the same time, the distal half of the membranes between the thickened anal veins suddenly popped out and flattened. Tension was placed on the veins, for the membrane popped back into the folded position again when the wings were released and allowed to return to the resting position. Membranes not associated with thickened veins did not pop out in this fashion. In popped-out wings there was a sudden transition from a taut, flattened distal portion of the membrane to a partly folded, unflattened proximal portion. A slow playback of sounds produced by these species and audiospectrographs of their sounds suggested that as the thickened veins and the membranes between them first pop into the taut position, they produce the louder snapping sounds, and as they pop out into the relaxed position they produce a softer popping sound (Fig. 3). The "in-popping" sound was not heard when the wings were manipulated by hand. If this is the mechanism by which sound is produced, then it is unique in grasshoppers, but in certain respects it is quite similar to the mechanism of cicadas. As in cicadas, it is the vibration of a membrane which produces the sound (see Haskell, 1961).

Within a single species several methods of sound production may be employed. For example, Uvarov (1966) notes that *Sphingonotus savignyi* possesses three methods of sound production: rubbing the femur against the forewing, rubbing the forewing against the hindwing, and wing crepitation. In this study *Encoptolophus sordidus* was found to possess four different methods of producing sound: wing crepitation, striking the forewing with the tibia, rubbing the femur against the forewing, and drumming the substrate with the tibiae. Table 3 lists the families of Acridoidea and the subfamilies of Acrididae and indicates the incidence of specialized hearing organs (tympana) and of specialized stridulating apparatus among them. The types of sound-producing mechanisms that are known for each group are indicated by numbers which correspond to the list of sound-producing mechanisms given above. Many species of Oedipodinae possess three methods of sound production. Most species of Acridinae possess only one method.

THE PRESENCE OR ABSENCE OF TYMPANA.—Table 3 indicates two interesting relationships between hearing and sound-production. Some grasshoppers possess tympana but evidently do not communicate acoustically, e.g., the Catantopinae. Other grasshoppers have well-developed sound-producing mechanisms and produce acoustical signals but lack a tympanum, e.g., the Pneumoridae.

In the first group it is possible that sounds are made which are in-

TABLE 3

Occurrence of Tympanum and Sound-producing Mechanisms in the Acridoidea[1]

Group	Tympanum	Specialized Sound-prod. Mechanism	Type of Sound-producing Mechanism
Eumastacidae	–	–	
Proscopiidae	–	–	
Tanaoceridae	–	+	3b
Pneumoridae	–	+	3b
Xyronotidae	–	+	3b
Trigonopterygidae	–	–	
Charilaidae	+	+	6
Pamphagidae	+,–	+	2a, 5
Lathiceridae	–	–	
Pyrgomorphidae	+,–	–	
Ommexechidae	+,–	+	1
Pauliniidae	+	–	
Lentulidae	–	–	
Acrididae			
Dericorythinae	+,–	+,–	
Chilacridinae	+,–	–	
Romaleinae	+,–	+	6, 11
Lithidiinae	–	–	
Hemiacridinae	+,–	+,–	2a
Tropidopolinae	+,–	+,–	
Oxyinae	+,–	–	
Coptacridinae	+,–	–	
Calliptaminae	+,–	–	9
Euryphyminae	+,–	–	
Eyprepocnemidinae	+,–	–	
Catantopinae	+,–	–	9
Cyrtacanthacridinae	+,–	–	7, 9
Egnatiinae	+,–	+,–	4
Eremogryllinae	+,–	+	1a
Truxalinae	+,–	+	1a
Acridinae	+,–	+,–	1a, 2a, 2c, 3a, 8, 9
Oedipodinae	+,–	+	1b, 1c, 2b, 2c, 7, 8, 9, 10

[1] Modified from Dirsh (1961). For key to numbers and letters indicating types of sound-producing mechanisms, see text, p. 15.

audible to the human ear and produced with unspecialized sound-producing structures, or that sounds made by moving (jumping or flying) individuals are of communicative significance. A further possibility is that tympana are used to detect the approach of predators. However, tympana tend to be lacking in wingless families, and absent or reduced in brachypterous members of groups in which they are normally well-developed (Uvarov, 1966), suggesting that flight and hearing by means of tympana are in some fashion associated. Such a secondary reduction or loss has occurred independently in several groups. Of the ten species of Catantopinae examined in the present study, tympana were present in the nine species possessing wings but lacking in the wingless species (*Paraidemona mimica*).

In the Pneumoridae, sound is probably perceived through other kinds of receptors. Haskell (1956) has shown that tergal hair sensillae are capable of responding to the sounds of conspecific males in several European Acridinae.

The presence of a tympanum in the absence of a specialized sound-producing mechanism, and the presence of a specialized sound-producing mechanism in the absence of a tympanum, suggests that either character may be gained or lost independently of the other. The complexity of the tympanum and the similarity among tympana of various groups suggest that this organ was acquired but once and that it has subsequently been lost a number of times. In contrast, the variety of sound-producing mechanisms to be found among grasshoppers, even within a single species, suggests that their acquisition has been relatively easy and that it has occurred independently a number of times.

SOUND RECEPTION.—Experimental studies (see Uvarov, 1966:191) have indicated that the majority of species are most sensitive to frequencies well within the hearing range of humans, but that some are most sensitive to frequencies inaudible to the human ear. The frequencies of maximum sensitivity are 10 kc/s for *Arphia sulphurea,* 3–7 kc/s for *Locusta migratoria,* 4–10 kc/s for *Oxya japonica,* and 20 kc/s or more for species of *Chorthippus, Omocestus,* and *Stenobothrus.*

Most studies (Pumphrey and Rawdon-Smith, 1939; Haskell, 1956a, 1961; see also Uvarov, 1966, and Michelsen, 1966, for references and discussions) suggest that the ability to discriminate pitch is less important to grasshoppers than the ability to discriminate temporal modulation of sound. If this is true, then it is relatively unimportant that the analysis of sound signals (audiospectrographs) include the particular frequencies to which the animals are most sensitive, providing, of course, that some sounds of other frequencies by which the temporal modulation can be analyzed are produced.

RATE OF SOUND PRODUCTION AND AMBIENT TEMPERATURE.—Figure 4 indicates that the rate of crepitation among the Oedipodinae is relatively independent of the ambient temperature. This may be achieved by behavioral regulation of body temperature. On many occasions I observed individuals of *Arphia pseudonietana* and *Spharagemon collare* orienting at right angles to the sun and lowering their bodies to the substrate in the cooler morning hours, but facing the sun and elevating their bodies in the hot hours of the day. This was particularly noticeable in the latter species. Individuals of some western species of *Trimerotropis,* e.g., *californica* and *rebellis,* climbed onto small promontories, faced the sun, and elevated their bodies from the substrate after they had alighted on the hot sand. Other individuals walked into the shade where they did not assume the above posture. Still others were found perched on vegetation several feet above the ground. These facts suggest that in diurnal grasshoppers, females need not change their responsiveness to males as the temperature changes, as cricket females must (Walker, 1957).

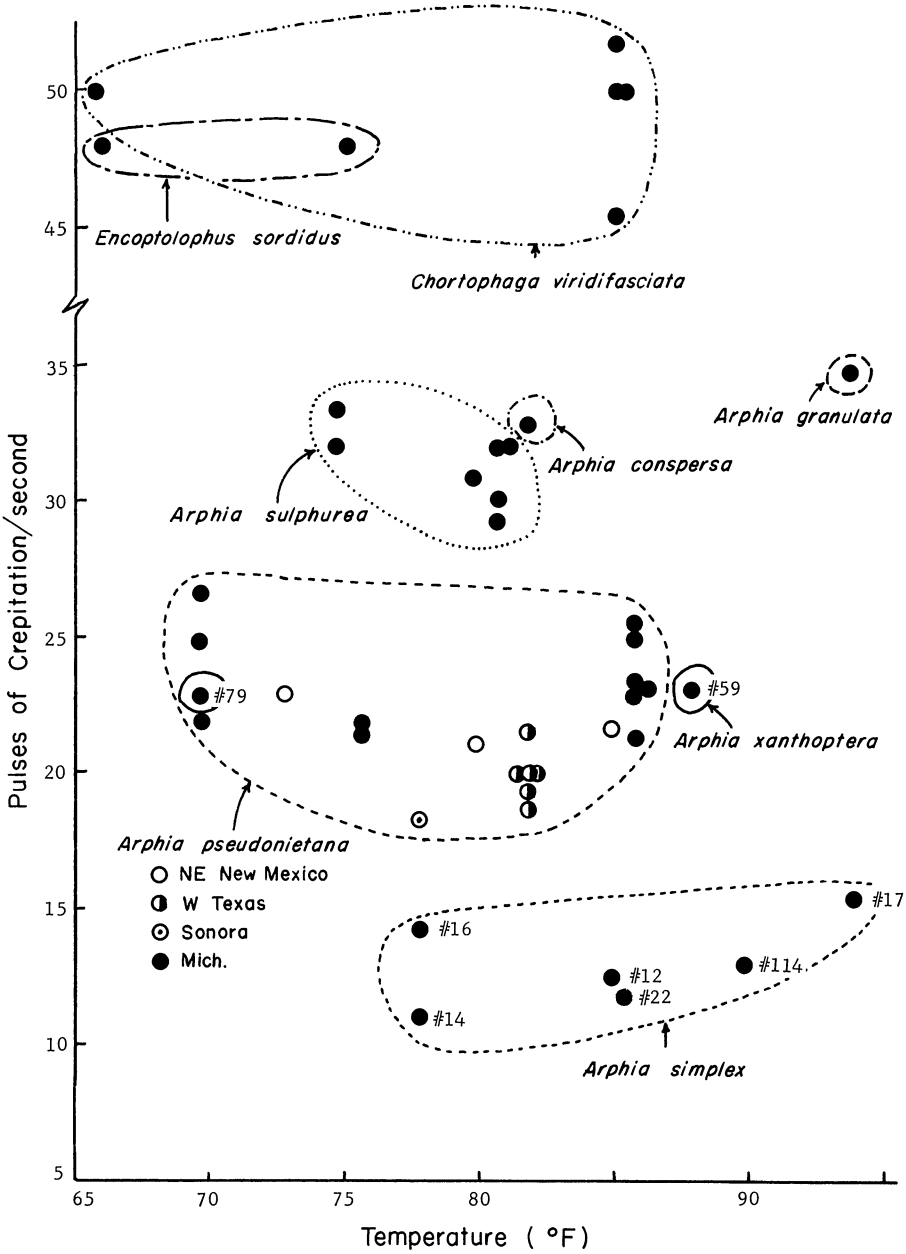

FIG. 4. Rate of crepitation plotted against ambient temperature (measured at waist level) of eight species. Crepitation rate is evidently relatively independent of the ambient temperature. *E. sordidus, C. viridifasciata,* and *A. sulphurea* were from the same localities in southeastern Michigan. Numbers indicate collecting localities: #12, Calcasieu Par., La.; #14, Adams Co., Ohio; #16, Ripley Co., Mo.; #17, Randolph Co., Ark.; #22, Burnet Co., Texas; #59, Hocking Co., Ohio; #79, Laclede Co., Mo.; #114, 25 mi. W. Cd. Valles, Mexico.

DESCRIPTION AND COMPARISON OF BEHAVIOR

SUBFAMILY OEDIPODINAE

Members of the Oedipodinae are usually ground inhabitants, occurring in regions of sparse vegetation. Most of them possess a raised intercalary vein between the medial and the cubital veins which is used in stridulation, and there are no stridulatory pegs on the inside of the hind femur. In addition, the hind wings are usually colored and often have a black band near the border.

GENUS *Arphia* Stal

This genus, consisting of perhaps 12 species, occurs in northern Mexico, throughout the United States, and in parts of Canada and Alaska. In the United States east of the Rocky Mountains there are six well-defined species, but in the western states the genus is probably in need of revision. In this study the communicative behavior of the six eastern species was examined.

Arphia sulphurea (Fabricius)

This species is widely distributed across the eastern United States from the Atlantic coast to Oklahoma, and lives in dry upland pastures and open woodlands (Blatchley, 1920; Somes, 1914; Coppock, 1962; Hubbell, 1922a).

PAIR FORMATION.—The flight display of *A. sulphurea* is in general typical for the genus. Males snap their yellow wings as they make short flights. The length, duration, and height of crepitating flights are quite variable but the two extreme conditions are: (1) Longer flights,—up to 10 feet or so in length and up to 1.5 seconds in duration,—in which males fly in a straight line and in a low arc (at most two feet) above the vegetation and in which crepitation occurs during much of each flight, but is most pronounced during the latter portion; (2) shorter flights in which males fly a few inches straight up into the air and return to their original perching area. Flights of the first type were made by solitary males and those of the second type in the presence of other individuals. The following observations illustrate the two extremes of flight display: (1) A solitary male performed six crepitating flights, all in the same direction. Each flight was straight and from four to six feet in length. Between flights the male moved very little—he took a few steps at most and produced no signals. A few seconds after the 6th flight a female *Pardalophora apiculata* alighted about three feet behind the male. The latter immediately flew, crepitating, toward the female and alighted 10 inches from her. A pile of leaves separated the two so that the male could not see the female. The male began to stridulate and to produce femur-tipping motions. For the next five minutes he walked about and repeatedly produced bursts of ordinary stridulation, all the while remaining within a few inches of where he had alighted originally. Then he made a short vertical crepitating flight six inches into the air and back again. Remaining in the same area, he continued to stridulate and tip his femora. A few minutes later he made a second vertical flight of a few inches. Then he again stridulated and tipped as he walked about. Eight minutes later he stopped stridulating but remained in the area. The *Pardalophora* female had in the meanwhile walked away. No vibratory stridulation was made. (2) Another male was observed making 5–10 foot flights, again moving in a single direction and not stridulating between flights. Then a male of *P. apiculata,* flushed by me, landed about three feet from him. The male flew in a new direction toward the *Pardalophora* male and began stridulating and tipping his femora, but the *Pardalophora* was not visible to him, and he soon stopped moving.

On sunny days solitary males engage in the flight display repeatedly, with intervals between successive performances varying from about 15 seconds upward, and walk about, stridulating occasionally, between flights. Females are not known to crepitate. These observations and other indirect evidence suggest that crepitation attracts sexually responsive females (see *Arphia simplex* and *Chortophaga viridifasciata).*

On the George Reserve I observed hundreds of flight displays by males but did not see females approaching displaying males. Observations of such an event may be highly fortuitous, however, because females are not continuously sexually responsive and because the movement of females toward males by walking through vegetation is usually quite inconspicuous.

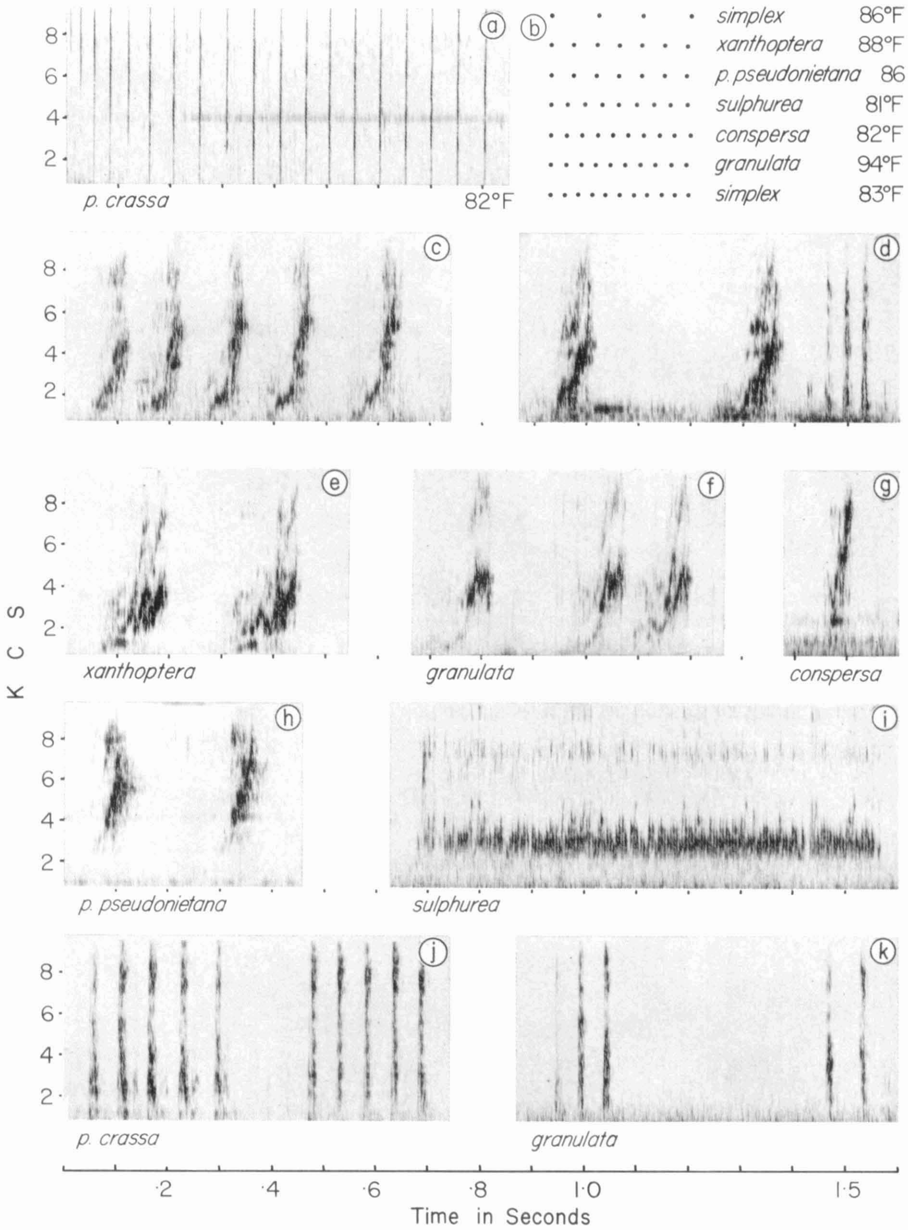

FIG. 5. Audiospectrographs of *Arphia* acoustical signals: (a) crepitation of *A. pseudonietana*; (b) comparison of typical crepitation rates of the six species studied; the last line indicates the wingbeat rate of *A. simplex* during normal flight; (c) *A. sulphurea* ordinary stridulation; (d) *A. simplex* ordinary stridulation (produced by one male) and femur-shaking with wing-striking (produced by a second male in response to the stridulation of the first male); (e) *A. xanthoptera* ordinary stridulation; (f) *A. granulata* ordinary stridulation; (g) *A. conspersa* ordinary stridulation; (h) *A. pseudonietana* ordinary stridulation; (i) *A. sulphurea*, vibratory stridulation; (j) two males of *A. pseudonietana* alternating in producing aggressive femur-shaking with wing-striking; (k) two males of *A. granulata* alternating in producing aggressive femur-shaking with wing-striking.

Pairing also occurs in the absence of the flight display. Males were frequently observed rapidly approaching moving individuals while producing courtship signals. I saw males approaching individuals of their own species, individuals of other grasshopper species, and even a caterpillar. Stridulation by solitary wandering males is perhaps also instrumental in pair formation (see, for instance, *Pardalophora apiculata*); in the laboratory, females responded to such stridulation by moving or presenting, thus attracting the attention of males.

COURTSHIP.—Courting males produced femur-tipping, ordinary stridulation, and vibratory stridulation. Femur-tipping (Fig. 1d) was the most commonly observed signal and was performed by wandering solitary males, courting males, and aggressive males. Males approaching females almost always produced ordinary stridulation (Fig. 1a). A series of leg strokes yielded a burst of variably spaced pulses of sound (Fig. 5c). Up to eight pulses were produced in rapid succession, but the usual number was two to four. The rate at which these were delivered varied, but the pulse structure was uniform, suggesting that each pulse constitutes a morpheme (smallest complete signal) and that the delivery rate is only involved in the redundancy of the signal.

Ordinary stridulation was performed only by courting males, either during or between successive advances. The most rapid series of pulses were produced by momentarily stationary males; single pulses were produced either by stationary males or advancing males. Vibratory stridulation (Figs. 1b, 5i), when present, always followed ordinary stridulation in courtship. It was always produced by stationary males, either when the individual being courted was lost or retreating, and was performed by one leg at a time; when several (1–3) bursts occurred in quick succession, the hind femora alternated in producing them. Femur-tipping occurred when males first observed an individual and also during temporary halts in their approach. This signal was rarely absent from an encounter.

In nine courtship sequences, a Michigan male displayed femur-tipping and ordinary stridulation as he approached the female, and when the latter moved away he stopped and produced 1–3 bursts of vibratory stridulation. Three similar sequences by Oklahoma males were also seen. On eight other occasions Michigan males performed vibratory stridulation after they had accidentally walked past, and out of sight of, the individual which they were courting. I saw females respond to approaching males by (1) quickly hopping away, (2) moving away more slowly, permitting courting males to follow, (3) remaining stationary and making either no movement at all or only feeble femur-tipping motions, and (4) remaining stationary and shaking or raising their femora, or both.

COPULATION.—Even though males attached their genitalia, copulation did not always ensue; males sometimes detached after a few seconds, dismounted and walked away. The reason for such terminations is not known. In the field I saw two males court and mount the same female one after the other with a minute between. Each male remained on the female with genitalia apparently attached for about 15 seconds, then dismounted and walked away without signalling. No signals by the female were seen either before or during mounting. Two copulations lasted 30 minutes each, and another about 90 minutes. During copulation females sometimes moved about and fed, carrying the males with them.

AGGRESSION.—Femur-tipping was observed in 50 or more encounters between males. The femora were tipped synchronously from a horizontal resting position up to between 60° and 90°; upstrokes and downstrokes had about the same duration, and the tibiae were generally held within a few degrees of the femora throughout the movement. Occasionally only one femur was tipped. Femur-tipping was also produced by solitary males, perhaps functioning to inhibit movement or approaches by other males. Femur-tipping of females is less precise, slower, and tends to be more graded than that of males. The effect on males seems variable; sometimes it appeared to attract males, at other times to inhibit their approach.

Femur-shaking (Fig. 1f) occurred in most encounters between males; when present, it always followed femur-tipping. Tipping alone was sometimes followed by separation of males, but males that continued to approach one another, after tipping, exchanged bursts of shaking before eventually separating. Males usually separated before touching one another. The only time I saw males of *sulphurea* establish contact was when one male courted and touched a copulating pair with his antennae.

In several other species, males shook only after contact was established. Males of *sulphurea* that came into close proximity sometimes shook in perfect alternation with one another. During femur-shaking the forewings are struck. Each burst of shaking consists of 3–8 strokes (with a sound similar to that in Fig. 5j).

Females disturbed by males or by other females raised their femora to the repelling position; small tibial kicking motions sometimes accompanied this gesture (Fig. 1g). In such displays the femora were tilted up to 135° from the resting position and the tibiae were often held parallel to the back. Females usually repelled males by raising their femora and only rarely by shaking them.

Arphia simplex Scudder

This species lives in dry grassy areas and occurs in northeastern Mexico, and in Texas, Oklahoma, eastern Kansas, eastern Nebraska, western Iowa, and southeastern South Dakota. A few (perhaps relict) populations occur in the Ozarks and southern Ohio.

PAIR FORMATION.—The flight displays of *simplex* are dramatic. The rate of crepitation is less than one half that of *sulphurea* (Fig. 5b). The sound is much louder and the duration of the flights are on the average longer; males also tend to hover in the air more than males of *sulphurea*. The durations of six crepitations by Adams Co., Ohio, males were 3.5, 1.5, 4.0, 4.0, 5.0 and 6.0 seconds. Elsewhere, crepitations seemed to be of similar length. Like *sulphurea,* crepitating flights are mostly straight. The wing color seems to be either yellow or orange. Specimens from the Louisiana population were all orange-winged, whereas specimens from the Ohio, Missouri and Arkansas populations were all yellow-winged.

Pair formation involving crepitation was observed once in Louisiana by R. D. Alexander and J. E. Lloyd (pers. comm.). A male was flushed 12 times in a 15 to 20 square foot area. These disturbance flights were very similar to unprovoked flight displays. One flight was about 20 feet in length; all others were 6–12 feet. After the 12th flight, a female flew directly toward the performing male and landed less than a foot from him within a second after he alighted. The female was captured at this time. Since females of this and other *Arphia* species have never been seen to fly when not disturbed, as males will do, and since this female flew directly towards the male and landed next to him immediately following his flight, it seems likely that she was being attracted to the crepitating male.

COURTSHIP AND AGGRESSION.—Courtship and aggressive signals are similar to those of *sulphurea* (Fig. 5); tipping, shaking, ordinary stridulation, and vibratory stridulation are all similar in form and in regard to the contexts in which they are performed. Vibratory stridulation did not occur during 30 courtship sequences by individuals from Calcasieu Parish, Louisiana, nor was it observed in the courtship of individuals from Adams County, Ohio. Either the signal is never produced by members of these populations or the conditions eliciting it were not realized during these observations. Vibratory stridulation was, however, recorded in the courtship of males from Burnet and Gillespie Counties, Texas. Aside from this difference, individuals from the various localities behaved similarly. Males from Gillespie County produced one or two bursts of vibratory stridulation on three different occasions, each time when females retreated and courting males stopped approaching. Vibratory stridulation seems, therefore, to have the same function as in *sulphurea.* Except for a distinct difference in crepitation rate, communication in *simplex* is very similar to that in *sulphurea.* The life cycle, the geographic relations, and the morphological similarity of the two species (for instance, the shape of the vertex) suggest that *simplex* and *sulphurea* share an exclusive common ancestor.

Arphia xanthoptera (Burmeister)

Arphia xanthoptera is distributed from the 100th meridan in Texas and Oklahoma to the Atlantic coast, from northern Florida to New England, from central Texas to southeastern South Dakota.

PAIR FORMATION, COURTSHIP, AND AGGRESSION.—Flight displays of *xanthoptera* are similar to those of other *Arphia* species. The rate of crepitation is approximately 50% less than that of *sulphurea* and *granulata,* and approximately 50% greater than that of *simplex* (Fig. 5b). The color of the wings varies from yellow to orange. Vibratory stridulation appears to be lacking, but ordinary stridulation and aggressive signals are similar to those of *sulphurea* and *simplex*. On the average, the pulse delivery rate of ordinary stridulation seems slower, and the pulse duration longer, than in other *Arphia* species, but more data are required to establish this.

Arphia granulata Saussure

Arphia granulata is almost confined to the state of Florida, but ranges from Key West to southern Georgia, where it overlaps with *xanthoptera*.

PAIR FORMATION, COURTSHIP, AND AGGRESSION.—The crepitation rate of *granulata* is about 50% greater than that of *xanthoptera* (Fig. 5b) and flights seemed both longer and higher as well. This latter difference may have been owing to the higher vegetation where *granulata* was collected. The wings of *granulata* are yellow. Females of *granulata* crepitated when disturbed, though not so loudly as males. It seems likely, therefore, that sexually responsive females crepitate while flying toward displaying males (see also *Chortophaga viridifasciata*). Courtship and aggressive signals are similar to those of the above *Arphia* species. Ordinary stridulation is faster on the average than in *xanthoptera,* and as in *xanthoptera* vibratory stridulation is lacking. In ordinary stridulation the pulse repetition rate is higher and the pulse length is shorter in *granulata* than in *xanthoptera*. Unfortunately no recordings from *xanthoptera* were obtained in the area of overlap. The geographic relations of *granulata* and *xanthoptera* and the greater morphological similarity (shape of vertex, height of pronotal crest) between them than between *granulata* and *sulphurea* suggest that *granulata* and *xanthoptera* may have differentiated during one of the recent inundations of northern Florida.

Arphia pseudonietana (Thomas)

Arphia pseudonietana is distributed throughout the northern part of the prairies and in the mountains of the western United States.

PAIR FORMATION.—The flight display of *pseudonietana* is very conspicuous and is similar to those of other *Arphia* species. The wings are bright red. Pair formation initiated by crepitation has not been observed but probably occurs. Females of *A. p. crassa* crepitated loudly during disturbance flights and Cantrall (1943) reports that females of *A. p. pseudonietana* sometimes crepitate faintly during disturbance flights. On the George Reserve I frequently saw pair formation occur in the absence of flight displays. Such pairing occurred when males oriented on and approached moving females by walking or hopping.

COURTSHIP AND AGGRESSION.—Courtship and aggressive signals of *pseudonietana* are similar to those of all the above species. Vibratory stridulation was heard once, but the context in which it was produced was not determined. Females repelled males effectively by raising their femora. On one occasion a female held both femora in the raised position, making small kicking motions for several minutes while three different males courted her. The males produced bursts of ordinary stridulation as they faced her but finally departed without attempting to mount her. Shaking by females has not been observed. I frequently encountered aggregations of males on bare patches of ground. Four times several males (3, 4, 4, 5) aggregated on a bare patch by approaching another male already moving there. In no case did these males produce courtship sounds; instead, they tipped their femora intermittently during the initial part of the approach and then began to shake their femora when they were a few inches from one another. Each time, the males separated from one another within 10 seconds by walking or flying, sometimes crepitating during flight. On one occasion, a male produced a single flip with his wings when a bombyliid fly attempted to settle on him. A similar movement was performed by a male of *Dissosteira carolina,* also when approached by a bombyliid.

Arphia conspersa Scudder

A. conspersa has a very extensive distribution in open grassland and on steep brushy hillsides along the Rocky Mountains from Alaska to Mexico.

PAIR FORMATION.—The only crepitations recorded in *conspersa* were produced during disturbance flights. According to Brooks (1958) both males and females crepitate, but the contexts in which they crepitated were not indicated. Wing color varies from yellow to red in this species.

COURTSHIP AND AGGRESSION.—The courtship of individuals collected near Williams, Arizona, and in Eagle County, Colorado, was similar. Tipping, shaking, ordinary stridulation, and vibratory stridulation occurred and appeared to have the same function as in the above species. A female from near Williams presented by lowering the femur closest to an approaching and stridulating male, and the male mounted.

GENUS *Arphia:* SUMMARY

The six species of *Arphia* examined in this study are inhabitants of dry grasslands. In general, one is unlikely to find adults of more than one species of *Arphia* at any given place and time, owing to the considerable geographical and seasonal separation of the species. *A. simplex* and *A. sulphurea* are the only two species that I have collected as adults at the same localities.

Communicative behavior among the six species is similar, at least qualitatively. There are some differences in stridulation, crepitation, and wing color between various overlapping species (see Table 4 and Appendix), but little can yet be said concerning their significance.

TABLE 4

SIGNALLING IN *Arphia*

Species	crepitation flights (crep. rate/sec)	color of wings	courtship signals	aggressive signals
sulphurea	32.0–33.3 75°F 29.2–32.1 81°F	yellow to orange	ord. stridulation, vib. strid. (♀ lost), tipping	shaking (ws)[1] tipping
simplex	11.1–14.4 78°F	yellow to red	"	"
conspersa	33.3 82°F (disturbed)	yellow to reddish	"	"
pseudonietana	21.2–23.5 86°F	red	ord. stridulation, vib. strid. (♀ lost?), tipping	"
xanthoptera	20.7–23.8 70°F 23.1 88°F	yellow to orange	ord. stridulation, tipping	"
granulata	33.3–35.0 94°F	yellow	"	"

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[1] ws = with wing-striking.

Since communicative signals seem to be relatively constant within the various species, it is possible that the differences in pair-forming and courtship signals are owing to selection for divergence between overlapping closely related species. The considerable seasonal and geographic overlap of *simplex* and *sulphurea* and the apparent similarity of their ecological requirements suggest that the adults of these two species have interacted extensively and directly with one another, and that the distinct difference in crepitation ate between these species arose in a context of reproductive isolation. Vibratory stridulation has been recorded in both species but appears to be lacking in *simplex* where it overlaps with *sulphurea*.

On the basis of similar morphology and geographical relations it is likely that *granulata* and *xanthoptera* share an exclusive common ancestor, and that *granulata* diverged from *xanthoptera* during one of the recent inundations of northern Florida. It is not known whether the differences in communication are associated with the development of reproductive isolation in these two species.

GENUS *Chortophaga* Saussure

Three species have been described in this genus: *C. viridifasciata* (DeGeer) and *C. australior* Rehn and Hebard from the United States and *C. cubensis* Scudder from Cuba. Only the first two species were examined behaviorally.

Chortophaga viridifasciata (DeGeer)

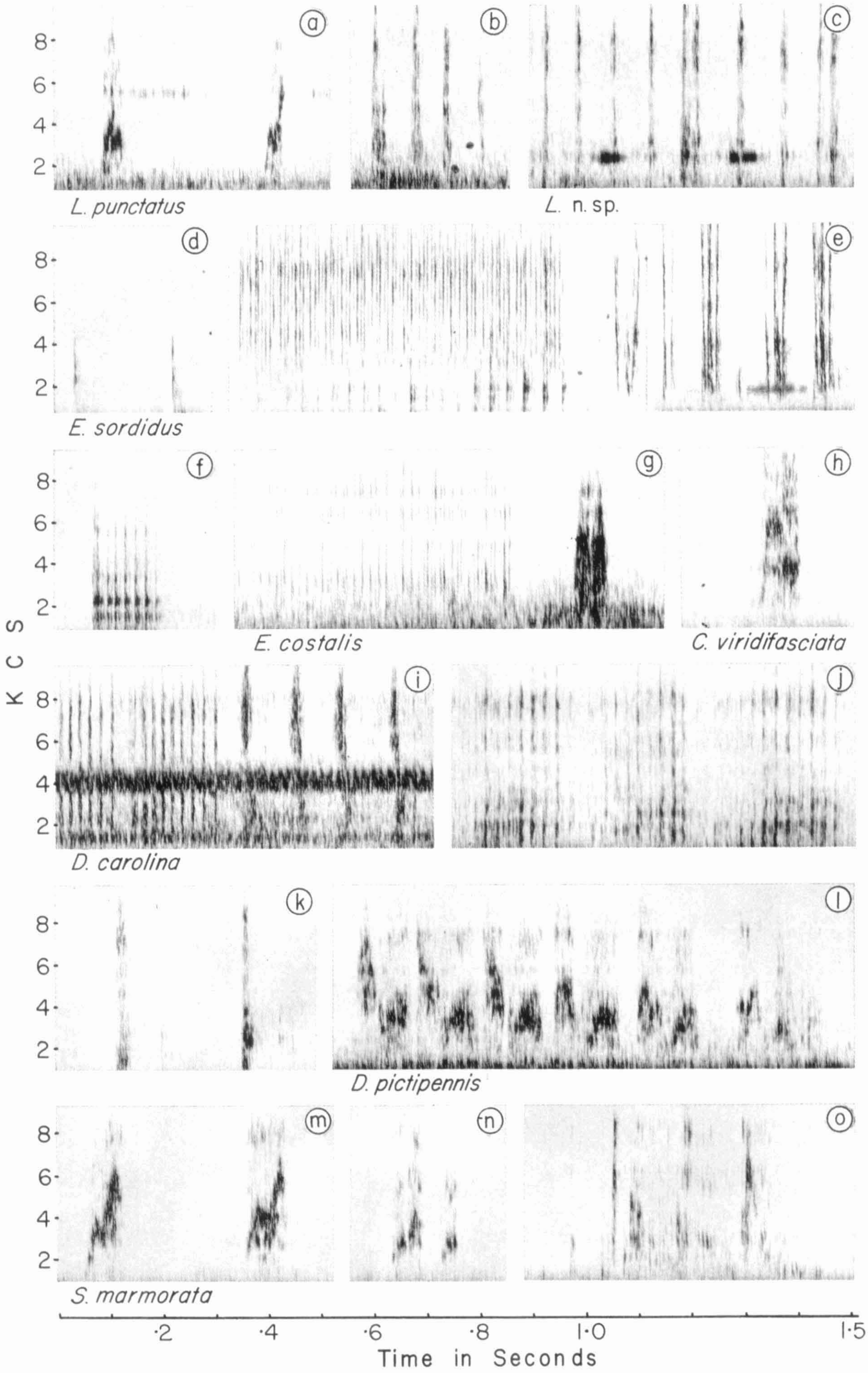
This species is found throughout the eastern half of the United States, except Florida, and occurs occasionally in the Rocky Mountains or its foothills. In the eastern states it is commonly found along roadsides, pastures, and lawns. Most of the following information is based on behavior observed in individuals from Washtenaw County, Michigan.

PAIR FORMATION.—*C. viridifasciata* males crepitate loudly during flight displays. The flight display is therefore audibly conspicuous, but since the wings are largely transparent, it is not visually prominent. More than 50 crepitating flights by solitary males lasted no longer than two seconds each, and most were about one second in duration. In an area where the vegetation was about six inches in height, males flew up to three feet above the ground. Flights were either straight or sinuous, and several times a male returned to the spot where his flight had started. The length of flights varied from two inches, by a male approaching a female, to 15 feet, by a solitary male.

Females are attracted to crepitating males and approach them by flying or walking. I collected teneral individuals and separated males and females for two weeks, then scattered both sexes around a small grassy area surrounded on three sides by a heavy growth of spruce and watched them for 2.5 hours. More than 20 crepitation flights were performed by males. Nine times, one or more females were seen flying in the direction of a crepitating male (altogether 15 females were thus attracted) from distances up to 10 feet. Previous to this, females had never been seen to fly except when disturbed. Females crepitated in flight and always flew in a straight line, sometimes making two or more short flights towards the male. On seven occasions no pairing occurred, apparently because males and females did not see one another after alighting. Usually the female flew within a second or so of the male flight, but three females flew after a delay of about 30 seconds. Twice, when several females were making short crepitating flights towards males, they seemed to be responding and following one another. On two other occasions, female flights apparently took place without being preceded by a male flight. I did not see females flying away from performing males. No males flew in the direction of other crepitating males. Two interactions which ended in copulation, and another which probably did so, were as follows: (1)A male crepitated; two females flew, crepitating, in his direction; the male walked toward one of the females a few inches away, mounted and copulated. The sequence was a few seconds in duration. (2) A male crepitated; a female flew towards him (2 ft flight), then hopped in his direction; the male walked, hopped, and made two very short (2 inches) crepitating flights toward the approaching female; he stridulated as he walked; they touched; he mounted, and they copulated. The entire sequence lasted only a few seconds. (3) A male crepitated (6 ft flight), and just as he alighted a female made two short crepitation flights directly towards him. He then made another very short flight (1 foot), and the female advanced by walking in a new direction, again directly towards the male. The latter moved into a clump of grass and was followed by the female. This sequence lasted less than 10 seconds.

Several times one male approached and courted another male without crepitating. Apparently, pair formation can occur in two ways: either (1) females are attracted to crepitating males, or (2) males see and approach moving females. On at least 20 occasions, solitary males stridulated as they walked about between flights. Whether or not females are also attracted to this sound or move in response to it, thus attracting the attention of males, is not known.

A difference, perhaps an adaptation to different habitats, exists between the flight displays of *C. viridifasciata* and *Arphia* species. Males of the former do not descend im-


a
b
c
L. punctatus
L. n. sp.
d
e
E. sordidus
f
g
h
E. costalis
C. viridifasciata
i
j
D. carolina
k
l
D. pictipennis
m
n
o
S. marmorata
K C S
8
6
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·8
1·0
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Time in Seconds

mediately from grass stalks on which they have alighted after flying, and they often remain on such perches until the next flight. Also, males of *C. viridifasciata* often climb grass stalks and fly from there. *Arphia sulphurea* and *A. pseudonietana* always drop to the ground immediately after alighting on a grass stalk and never climb onto such perches before flying.

COURTSHIP.—Ordinary stridulation was the only movement produced by approaching males and was always present (observed in each of 24 approaches). Such stridulation consists of single-pulsed sounds produced on the downstroke of both femora (Fig. 6h). Males wandering about alone in the field sometimes stridulated. Usually, however, males stridulated only when approaching other individuals.

On five occasions, I saw females present as they were approached by stridulating males. Each time the femur nearest the male was spread away from the abdomen. Sometimes both femora were lowered and spread away in this fashion, and twice they were also shaken. In the laboratory, a male made a short flight from one end of the terrarium to the other and landed about eight inches away from a female; the female, which had been motionless for a long time, immediately became very active, turned toward the male and approached him, making femur-tipping movements, like those of males. She stopped three inches from the male, who saw her and stridulated as he approached. Before he touched her, the female spread her femora and shook them slightly. The male then tapped the female rapidly with his antennae and tipped his femora as he mounted and attached. In one series of nine observations, about five males tipped their femora every time after mounting females. Femur-tipping by two mounting males was also observed in the field. Twice, males also shook their femora as they mounted.

Three copulations lasted 35, 45, and 45 minutes. When females have copulated they apparently do not do so again for some time and may resist subsequent copulation attempts (see Loher and Huber, 1965). As an example, in the laboratory a female copulated for 45 minutes and five minutes after separating was mounted by a second male; she presented, and he appeared to attach but dismounted and walked away 15 seconds later. A third male mounted, and the same thing happened. A few minutes later a fourth, stridulating male approached this female. Before he reached her, she raised her femora into the repelling position; he stopped advancing and did not attempt to mount.

AGGRESSION.—Males perform femur-tipping almost exclusively in encounters with other males and while mounting females. The movement itself differs from that of *Arphia* species in that the downstroke is much faster than the upstroke, and the duration of the movement is also faster. During tipping, the tibiae are extended to about 45° from the femora. Occasionally the latter move asynchronously. Femur-tipping of females is similar to that of males but was seldom seen. In females, as indicated above, the movement may attract the attention of males. Males also shook their femora in encounters with other males. The movement consisted of holding the

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FIG. 6. Audiospectrographs of signals of various species of Oedipodinae: (a) *Lactista punctatus* (Sinaloa), ordinary stridulation, 84°F; (b) same, aggressive femur-shaking with substrate-striking, 84°F; (c) *Lactista* (near *punctatus*) (San Luis Potosi), courtship femur-shaking with wing-striking, 94°F; the two extra pulses of sound are aggressive sounds produced in the same fashion by another male nearby; (d) *Encoptolophus sordidus* (Mich.), ticking, 76°F; (e) same, vibratory stridulation, first a long burst, then a series of short bursts (some substrate-striking with the tibiae occurred while producing the long burst); (f) same, aggressive femur-shaking with substrate-striking; (g) *Encoptolophus costalis* (New Mex.), a burst of vibratory stridulation followed by a single pulse of ordinary stridulation, 85°F; (h) *Chortophaga viridifasciata* (Mich.), ordinary stridulation, 90°F; (i) *Dissosteira carolina* (Mich.), hovering flight showing the transition from the initial fast wing-beat to the final slower wing-beat (the wide dark band is background noise), 81°F; (j) same, alternating stridulation, 85°F; (k) *Dissosteira pictipennis* (Monterey, Cal.), ticking, 85°F; (l) same, ordinary stridulation; (m) *Scirtetica marmorata* (N. Florida), ordinary stridulation, 91°F; (n) same, two-pulse stridulation; (o) same, alternating vibratory stridulation. Temperatures taken 3 inches above substrate.

femora at about the 45° position and then shaking or vibrating them very rapidly. Neither the substrate nor the forewings were struck during the movement. The movement could barely be heard as a low pitched hum. Males shook either before or after establishing contact; in all cases it was followed by their separation. When touched, males also jerked their femora upwards and sometimes raised and held them in an upright position, as did females. The aggressive signals of males from Tulsa, Oklahoma, were similar to those of Michigan males. Females repelled males by kicking and by raising their femora to vertical or tilting them forward.

Chortophaga australior Rehn and Hebard

This species is largely confined to the state of Florida, but it has been collected at several localities in Georgia, where it evidently overlaps with *viridifasciata.* I examined individuals from Gainesville, Florida.

Pair Formation.—Flight performances of *australior* males are quite similar to those of *viridifasciata* males. A comparison of crepitations by disturbed males, however, suggests that the crepitation rate of *australior* is higher than that of *viridifasciata* (see Appendix). Crepitation by *australior* females is somewhat slower than that of males, but is louder than that of *viridifasciata* females. In Florida I flushed a female of *australior;* she flew directly away and crepitated as she did so. As she alighted, about 15 feet in front of me, a male about 20 feet to my left flew up and crepitated directly towards the female, alighting within a foot of her. Both were motionless for about a minute, then the male tipped his femora about five or six times, while the female remained motionless; eventually he walked away.

Courtship.—Femur-tipping is similar to that of *viridifasciata,* and it is performed in most encounters. In *australior,* however, it seems to be the only signal made by courting males. Fourteen times I saw males approach and mount females. All approaches had the following in common: (1) males approached moving females at right angles, (2) stopped and tipped their femora, one to three times, and then (3) attempted to mount. Three times males made antennal contact with the females before tipping. Twice males tapped the tops of the females' heads as they mounted. This movement resembled that seen in *C. viridifasciata.* Twice females lowered the hind femur nearest the male as the male mounted, but no such behavior was observed in 13 other courtship interactions.

Aggression.—Aggressive behavior is similar to that of *viridifasciata.* Males several inches apart exchanged femur-shaking signals. No substrate-striking or wing-striking occurred, but shaking was audible as a low pitched hum. Females did not shake their femora. One copulating male made several upward jerks of his femora once when approached by another male, and once when there was apparently no disturbance.

Table 5 summarizes the similarities and differences in the behavior of *viridifasciata* and *australior.*

TABLE 5

Signalling in *Chortophaga* and *Encoptolophus*

Species	crepitation rate /sec		courtship signals	aggressive signals
C. viridifasciata	45.4–51.7 60.0 (disturbed)	85°F 88°F	ord. stridulation only	tipping, shaking (si)[1]
C. australior	68.4–73.3 (disturbed)	94°F	tipping only	"
E. sordidus	48.0 48.0	66°F 76°F	tipping (sometimes), vib. strid. (trills and bursts), ticking	tipping, shaking(ss)[1]
E. costalis	62.5 (disturbed)	80°F	tipping (sometimes), vib. strid. (trill only), ord. stridulation	"

[1] si = silent; ss = substrate-striking.

GENUS *Encoptolophus* Scudder

Only two of the seven species of this genus were encountered during this study: *E. sordidus* (Burmeister) and *E. costalis* (Scudder). Until 1934 *sordidus* and *costalis* had commonly been considered distinct species. At that time Hebard (1934b) designated *costalis* as a race of *sordidus,* because he found specimens intermediate between the two. He stated simply, "Recent additions to our series have convinced us that two species cannot be recognized and that *costalis* must be considered the western race of *sordidus.*" Because specimens are so easily assignable to either *sordidus* or *costalis* (except for a few cases offered by Hebard), and because the courtship behavior and the habitat preferences of the two forms are quite different (see below), I have tentatively treated them as separate species.

Encoptolophus sordidus (Burmeister)

This species is distributed across the northeastern section of the United States from eastern Nebraska to New England. In this region it occurs in dry, densely grassed fields. In South Dakota (Hebard, 1925a) it "appears late in the season and, unlike *E. costalis,* prefers waste weedy areas rather than prairie or plains conditions."

PAIR FORMATION.—Crepitation flights are frequent and are performed by solitary males. I saw two kinds of flights in this species: crepitating flights and short, low, soundless flights. One or several silent flights sometimes occurred between crepitation flights. Like *C. viridifasciata,* males of *E. sordidus* often did not drop to the ground after alighting on vegetation, but remained perched there until the next flight. Between flights males walked about. Femur-tipping was the first signal made while approaching. Tipping, however, was also produced by solitary males wandering through the vegetation.

COURTSHIP.—Three acoustical signals are performed by courting males. Ticking, the first acoustical signal produced in a courtship sequence, is executed as follows: The femur is raised nearly vertically, and the tibiae are kicked out one at a time. As each tibia is kicked out, it strikes the end of the forewing, producing a ticking sound (Figs. 1c, 6d). From two to four such ticking sounds were produced in each series; left and right legs alternated in making the ticks. This signal was only given by stationary males. Trilling, the second sound signal, is made by holding one or both femora against the forewing and vibrating it (them) (Figs. 1b, 6e—first part). Trills also were produced only by stationary males. Stuttering, the third sound signal in a courtship sequence, is similar to the trilling sound, but with few leg movements. Instead of a continuous series of short sharp pulses, the pulses are produced in bursts of two and three pulses each (Fig. 6e—last part). This signal was always made by courting males that were rapidly approaching other individuals, and it appeared just before mounting was attempted.

The following relationships were observed among the three sound signals: (1) If only one signal appeared before mounting, it was the stuttering signal. Mounting was not preceded directly by either ticking or trilling. For instance, in 12 mountings 10 were preceded by stuttering and two were not preceded by any signal. (2) If two signals appeared before mounting, the first in the sequence was trilling, and the second was stuttering. Stuttering was never preceded directly by ticking. (Example: trill–trill–stutter–mount.) (3) If all three signals appeared before mounting, the order of appearance was always ticking, then trilling, then stuttering. (Example: tick–trill–stutter–trill–stutter–stutter–mount.) Alternation between trilling and stuttering was observed on several occasions when males were pursuing females. (4) Several bursts of ticking, trilling, or stuttering may be given in succession (see above examples). (5) Ticking and trilling were always given by stationary males and stuttering always by advancing males. (6) Males sometimes advanced between ticking and trilling and between trilling and stuttering.

Four kinds of female responses to male courtship signals occurred: (1) When a male approached a female (while stridulating), the female remained more or less motionless and the male mounted. (2) A female produced a slow tipping to about 60° following ticking and trilling by a male four inches away. The male saw and approached her. When he touched her, she first lifted both femora slightly, then lowered the femur closest to the male and exposed her abdomen; the male mounted. (This sequence occurred twice.) (3) A female moved; a male facing her ticked, trilled, then stuttered as he approached her. She exposed her abdomen by lowering the femur closest to him, and he mounted. (4) A male approached a female, producing courtship signals. The female tipped the near femur, very much as males tip theirs. The male turned away before touching her.

Aggression.—Femur-tipping occurred in most encounters, and the movements varied according to the proximity of individuals. When males were far apart, the movements were like those of *Arphia* species, where the tibiae were held close to the femora; when males were close to one another the tibiae were flung out so that they were at right angles when the femur reached the vertical position. Two variations were also seen in females. In the first, females lifted and lowered the femur very slowly in response to the signals of males and appeared to indicate receptivity. The second was very much like the femur-tipping signals of males and appeared to have a rejecting function (see above). Females also raised their femora to repel males (Fig. 1g). Femur-shaking is very rapid, and the tibiae strike the substrate. Males that were either near contact or that had established contact produced this signal. Females did not shake their femora.

The following observation illustrates the contexts in which femur-tipping and femur-shaking are produced. Male A saw male B move about three inches away. A ticked and advanced towards B. A stopped momentarily, then ticked and trilled. B answered with femur-tipping; A returned the femur-tipping, then stuttered as he advanced toward B once more. B tipped and shook his femur; A stopped advancing before contact was established, produced femur-tipping and walked away. Two sequences of this sort were watched. In the field I twice saw the following sequence: Male A approached moving male B. A tipped his femora, and B answered with the same signal. They established antennal contact, still giving femur-tipping signals. Then both males shook their femora several times, and one of the males flew away, crepitating.

Encoptolophus costalis (Scudder)

E. costalis occurs on the Great Plains from Texas to Canada. I studied it on the highlands east of Raton, New Mexico.

Pair Formation.—Crepitation by solitary males occurs as it does in *E. sordidus,* and both males and females crepitate when disturbed, but the crepitation rate in males is higher than in *sordidus* (see Table 5).

Courtship.—In each of four courtship sequences males produced two kinds of stridulation, a trill of vibratory stridulation similar to the trill produced by *sordidus,* and single pulses of ordinary stridulation usually lacking in *sordidus* (Fig. 6g). Courtship was as follows: When an individual moved nearby, males produced a single burst of vibratory stridulation (a trill) while standing motionless and then produced a single pulse of ordinary stridulation while moving toward the moving indivdual (observed twice) or while motionless and facing the moving individual (observed twice). Immediately after producing the latter sound, they attempted to mount. Twice stridulation was preceded by femur-tipping. Once, a courting male jumped onto another male and was repelled with femur-tipping and femur-shaking. One of the females lowered the femur closest to the courting male, spread it away from her abdomen, and turned the end of the abdomen toward the courting male as he mounted.

Aggression.—Femur-tipping and femur-shaking appeared to be identical in all respects to those of *sordidus.* Both movements were also produced by females.

Table 5 summarizes some aspects of communication in *Chortophaga* and *Encoptolophus* species. Flight displays in these two genera are similar in that (1) the hindwings are more or less colorless and not contrastingly marked and (2) single bursts of crepitation with a rapid pulse rate are performed both by disturbed and undisturbed males. Females of both genera crepitated when disturbed and possibly also when approaching performing males. During femur-tipping the femora are lowered faster than they are raised. Femur-shaking is very rapid and of short duration in both groups, but the substrate is struck by the two *Encoptolophus* species. Both genera also tend to inhabit areas of thicker vegetation (see also Table 14).

GENERA *Lactista* AND *Platylactista*

Morphologically and behaviorally these two genera appear to be most closely related to the genus *Arphia.*

Lactista gibbosus Saussure

This species occurs in southern California and Baja California (Hebard, 1931c). I collected it with *Trimerotropis pallidipennis* and *Psoloessa thamnogaea* at Alpine, California.

PAIR FORMATION.—Two males crepitated during disturbance flights. One other crepitation was heard, but the situation evoking it was not determined. The hindwings of *L. gibbosus* are bright yellow and are bordered by a black band.

COURTSHIP.—Ordinary stridulation was performed during each of four approaches by males (sound similar to that in Fig. 6a). Sound was apparently produced only on the downstroke, and both femora were employed.

AGGRESSION.—Femur-tipping and femur-shaking movements are like those produced by *Arphia* species. During femur-tipping, upstrokes and downstrokes have about the same duration, and during femur-shaking the femora strike the tegmina. Each burst of shaking consisted of 1–6 strokes.

Lactista punctatus (Stal)

Hebard (1932b) recorded this species from Sonora to Vera Cruz and Oaxaca, Mexico. He reported that all the specimens from Vera Cruz (including Tampico) examined by him were dark in color, with red wing discs and blue tibiae, in contrast to the yellow-winged individuals with brown or black tabiae from western Mexico. A comparison of the courtship of yellow and red-winged individuals and the absence of clear intermediates between them suggest strongly that the red-winged individuals from Vera Cruz belong to a separate, as yet undescribed, species (see *Lactista* near *punctatus).* I collected *L. punctatus* in Sonora, Sinaloa, Jalisco, and Tamaulipas, Mexico.

PAIR FORMATION.—Aside from a single crepitation by a female during a disturbance flight, I heard no crepitations by this species, even though several of the populations encountered were very dense. Near Mazatlan more than 50 individuals were flushed from open ground, but none crepitated. Pair formation was observed once in the field. A female flew about four feet after being flushed. Immediately after she alighted, a male about 2.5 feet from her began to walk and hop towards her over open ground; he stopped momentarily several times and tipped his femora during these stops. As he advanced he made three bursts of ordinary stridulation: four pulses when he was 1.5 feet from the female, two pulses when he was nine inches away and two pulses when he was two inches away. When he reached the female he mounted her.

COURTSHIP AND AGGRESSION.—Courtship and aggressive signals are similar to those of *L. gibbosus* and *Arphia* species. Approaching males produced ordinary stridulation (Fig. 6a) and femur-tipping. From one to three strokes were produced per burst of shaking (Fig. 6b). Femur-tipping was produced in all encounters between males. During femur-tipping the femora often moved asynchronously.

Lactista (near *punctatus)*

In this study I collected specimens of this apparently undescribed species along the roadside 25 miles west of Cd. Valles and on the beach at Tampico.

PAIR FORMATION.—No crepitations or flight performance occurred. However, I only observed this species for a short period at both localities. Since the species possesses red hindwings, it seems likely that flight is sometimes involved in pair formation.

COURTSHIP.—This species has evidently lost ordinary stridulation. Femur-shaking with wing-striking has been incorporated into courtship behavior, but it is also produced in aggressive encounters. I observed three courtship sequences in which males shook their femora as they approached and attempted to mount females. Each burst of shaking consisted of 2–8 strokes (Fig. 6c).

AGGRESSION.—Femur-shaking, performed in aggressive encounters between males, consisted of one or two strokes, the single ones being more common (Fig. 6c). Femur-tipping signals were also given.

Platylactista azteca (Saussure)

According to Tinkham (1948), *P. azteca* has a wide distribution in the desert regions of the Southwest. I collected it in Sutton County, Texas, near Imuris, Sonora, near Elota, Sinaloa, near Cd. Valles, San Luis Potosi, and near Cd. Victoria, Tamaulipas.

PAIR FORMATION.—At each locality males seemed to crepitate only during disturbance flights. It is possible that pair formation is initiated by the females' movements which males see, and towards which they either walk or fly, and that males announce their approach by crepitating.

COURTSHIP.—Courtship resembles that of *Arphia* and *Lactista* species closely. All of the ten observed approaches by males towards other individuals were accompanied by ordinary stridulation; both femora were employed in producing sound. The intervals between pulses in a burst of stridulation seemed to vary less than in *Arphia* species, and each burst of stridulation consisted of 2–4 leg strokes. A female presented to a male that stridulated as he approached her; closely following his stridulation and before he reached her, the female spread both femora away from her body and lowered them to the substrate. The male mounted.

AGGRESSION.—Femur-tipping is also similar to that of *Arphia* species. In male–male encounters, males also jerked their femora upwards and against the forewings to produce a sharp ticking sound. Usually only one jerk was produced, but several double strokes were observed. The signal was given in all close interactions between males, but no contact was established.

GENERA *Lactista* AND *Platylactista*: SUMMARY

Table 6 summarizes the information on *Lactista* and *Platylactista* species. Flight displays by solitary males are either rare or lacking in these species. The colored wings and crepitation may be important signalling devices of approaching males, but I did not see approaching by flying as it occurs in *Trimerotropis* and *Heliastus* species. Individuals of *L. humilis* Hebard (from Mexico) and *L. australis* Bruner (from Colombia) possess almost clear hindwings and an indistinct dark outer band. The hindwings of *Platylactista micrus* Hebard (from Mexico) are similarly indistinct. Since these species all inhabit open ground, it is possible that the loss or reduction of the flight display is owing to a change in habitat. For a comparison of the habitats of *Lactista, Platylactista, Arphia, Chortophaga,* and *Encoptolophus* species, see Table 14.

TABLE 6

SIGNALLING IN *Lactista* AND *Platylactista*

Species	flight signals	color or wings	courtship signals	aggressive signals
L. gibbosus	occasional crepitation	yellow	ord. stridulation	tipping, shaking (ws)[1]
L. punctatus	no crepitation	yellow	ord. stridulation, tipping	"
L. (near *punctatus*)	"	red	shaking (ws) (2–8 strokes)	tipping, shaking (ws) (1 & 2 strokes)
P. azteca	"	pale yellow	ord. stridulation	tipping, shaking (ws)

[1] ws = with wing-striking.

GENUS *Pardalophora* Saussure

Pardalophora apiculata (Harris)

This species is distributed in grasslands in the northern and eastern United States and in the prairie provinces of Canada. I collected it in Michigan, Ohio, Kentucky, and Missouri. At some localities it was sympatric with *P. phoenicoptera* and *P. haldemanii.*

PAIR FORMATION.—Males of *apiculata* possess flight displays which are visually conspicuous owing to brightly colored hindwings, but crepitation is lacking. During three summers of field work I observed about 20 flights by apparently undisturbed males. A solitary male flew twice in a 30-second period; he flew once, then walked about and stridulated several times and flew again. Another solitary male made four short (8–10 ft.), low (2 ft.), straight flights and produced two kinds of courtship stridulation between flights.

A third male made three similar flights, but did not stridulate between flights. The relative rarity of flights and the occurrence of pair formation in the field in the absence of flights leads me to believe that such flights are relatively less important in pairing than in *Arphia* and *Chortophaga* spp.

The following field observations illustrate how pair formation was achieved in the absence of flight. (1) A female walked past a silent, stationary male, who rapidly approached her and mounted (observed three times). (2) A male wandered about in the field stridulating. Nearby, a female that had been motionless began to make femur-tipping movements, apparently in response to the male's stridulation. The male approached her and mounted. (3) A female that had been silent and motionless presented when a male stridulated close by. The latter turned towards her and mounted. (4) During a 25 minute period a male walked about 60 feet and made 51 stops, some of them several minutes in length. The distances he travelled between stops varied from a few inches to about two feet. He stridulated four times—each time with no other individuals nearby.

COURTSHIP.—Ordinary stridulation and vibratory stridulation were produced by courting males. Two varieties of ordinary stridulation were discernible. Type I stridulation (Fig. 7a) consisted of 1–4 strokes of *both* femora. I saw it produced by males approaching stationary females, by males following retreating females, by isolated males that had recently had encounters with females, and by solitary males that had not recently had an encounter with a female, but were actively moving about through the grass. Type II stridulation (Fig. 7b,c) consisted of a rapid series of strokes with one femur, producing bursts of stridulation varying in length from 4 to 18 pulses. Sound was sometimes produced on both upstrokes and downstrokes. When several bursts of stridulation were produced in quick succession, left and right femora sometimes alternated in the production. This signal was usually given by stationary males just before they approached females.

Vibratory stridulation (Fig. 7d) is quite similar to that of *Arphia* spp. It was only made by courting males that had just lost females and by solitary males wandering about in the field. Six out of eight times that males produced vibratory stridulation in the laboratory, it was produced just after females were lost. On one of these occasions a burst of ordinary stridulation and a burst of vibratory stridulation were followed closely by femur-tipping signals from the female. Her movement seemed to attract the male; he approached and mounted, and copulation ensued.

The following series of field observations illustrate the context in which ordinary and vibratory stridulation are produced: I heard a male giving several bursts of ordinary stridulation and found him pursuing a female and making several attempts to mount. She disappeared in some leaves. First, the male remained motionless for a while; then he began to walk about and stridulate actively. In the next ten minutes he alternated between walking about and stridulating, and stopping and remaining motionless for several minutes. Eleven periods of walking about occurred, but the male did not wander more than a foot from where he had lost the female. Both kinds of stridulation accompanied the walking periods. Just before he began to walk about, and also during momentary stops, he gave bursts of ordinary stridulation. Immediately after he stopped walking he always produced a burst of vibratory stridulation, followed by a prolonged period of immobility. Nine single bursts and two double bursts of vibratory stridulation were given. I could detect no response on the part of the female a few inches away. When the female walked past the male he turned towards her, made a long burst of ordinary stridulation, then approached, giving several shorter bursts. The female moved to one side, and he went past her, stopped, produced a burst of vibratory stridulation and then remained motionless. With a second female the same sequence occurred twice. The male did not tip his femora during these sequences.

When approached by courting males, females (presumably sexually responsive) behave (display?) in a characteristic fashion. This behavior consists of (a) spreading the femora away from the abdomen and lowering them against the substrate, (b) vibrating the femora, and (c) turning the end of the abdomen in the direction of the courting male. Sometimes the movement was made in immediate response to the stridulation of a courting male, and on other occasions in response to the approach of non-stridulating males or even females. On several occasions when a male began to lower his abdomen on the side other than that to which the female's abdomen was bent, she bent her abdomen to the other side. In eleven such presenting sequences, vibration of the femora was sometimes omitted, but lowering of the femur nearest the approaching male and

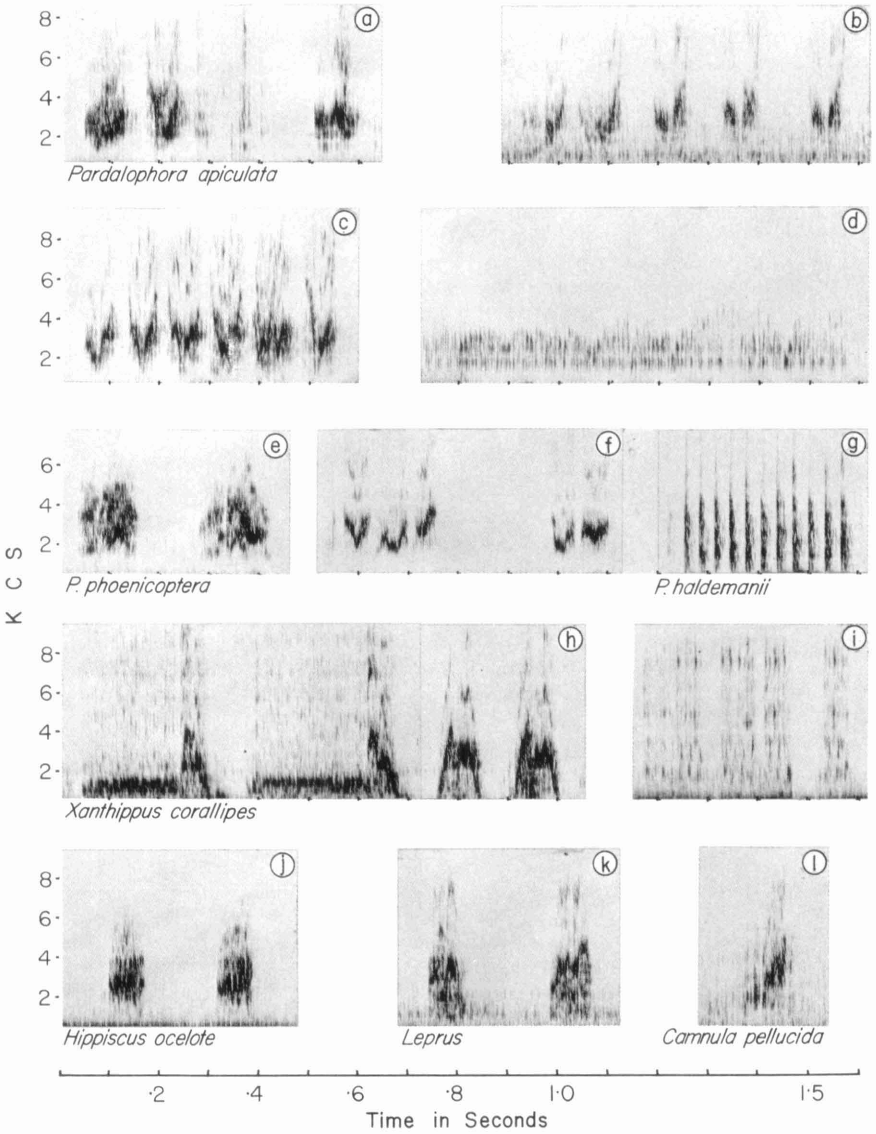

FIG. 7. Audiospectrographs of signals of various Hippisci: (a–c) *Pardalophora apiculata* (Mich.), ordinary stridulation, at 88°F, 98°F, and 88°F resp.; (d) same, vibratory stridulation, 88°F; (e–f) *P. phoenicoptera* (S. Ohio), ordinary stridulation, 94°F; (g) *P. haldemanii* (Mich.), courtship femur-shaking with substrate-striking, 94°F; (h) *Xanthippus corallipes* (Texas), two bursts of vibratory stridulation each appended with a pulse of ordinary stridulation, followed by two pulses of ordinary stridulation without vibratory stridulation, 88°F; (i) same, vibratory stridulation without ordinary stridulation; (j) *Hippiscus ocelote* (S. Ohio), ordinary stridulation, 95°F; (k) *Leprus robustus* (Sonora), ordinary stridulation, 105°F; (l) *Camnula pellucida* (Mich.) ordinary stridulation, 86°F. Temperatures taken 3 inches above substrate.

turning of the abdomen in his direction always occurred. Presenting females always allowed males to mount and the movement seemed to render the females more accessible for copulation.

In Ozark County, Missouri, a female responding to the stridulation of a male stridulated audibly by pressing her femora to her forewing and vibrating them; she continued to stridulate for the first minute of copulation. Several Michigan females stridulated briefly while presenting, but such stridulation was not the usual occurrence.

Four copulations observed in entirety lasted 2 hours, 2 hours, 1.5 hours, and 1 hour respectively. At the end of copulation, males and females walked away from one another, and no further interactions occurred.

AGGRESSION.—Tipping was performed in almost all encounters between males, but shaking was usually performed only after contact between males had been established. Males in copula always shook their femora when they were touched by other males. Both tipping and shaking movements were silent.

Female disturbance signals are of several kinds: femur-tipping, femur-jerking, and femur-shaking. Tipping was considerably less precise than in males, and sometimes it seemed to attract males. All gradations of movements from a simple tipping motion to an extensive forward tilting of the femora together with tibial kicking motions were produced. Jerking occurred when females were touched; they often jerked one or both femora sharply upwards, striking the intruder and causing him to depart. Jerking the femora upwards and kicking out with the tibiae may be combined into a single movement. Shaking varied from a series of jerks to a fast, almost vibratory movement.

Pardalophora phoenicoptera (Burmeister)

This species is confined to the southcentral and southeastern United States. I found it in grassy fields and in small open woodland meadows in southern Ohio, Kentucky, and Missouri.

PAIR FORMATION.—At five localities I saw no flight displays, but perhaps they occur occasionally as they do in *apiculata*.

COURTSHIP.—Males produced ordinary stridulation (Fig. 7e) and when pursuing females just before mounting. Ordinary stridulation of a faster variety (Fig. 7f), somewhat resembling Type II ordinary stridulation of *apiculata,* was also produced, just prior to mounting. Ordinary stridulation was not recorded often, but it seems to resemble that of *apiculata* rather closely in structure and in the context in which it is produced. Vibratory stridulation was not heard.

Presenting by females was similar to that in *apiculata.* On one occasion a stridulating male approached a female. The latter lowered the femur nearest the male and simultaneously lowered her abdomen, turning it towards him. He mounted and copulation ensued. On another occasion, in response to the approach of a stridulating male, the female lowered both femora, spread them 45° from her abdomen and vibrated them; the male mounted. On other occasions females were entirely passive when they were approached and mounted.

AGGRESSION.—Aggressive signals are like those of *apiculata.* Tipping by females was slower and less precise than that of males. Shaking was only produced by males touched by other individuals.

Pardalophora haldemanii (Scudder)

P. haldemanii is widely distributed over the central portion of the prairies, from central North Dakota southward to northern Texas, and extends eastward through the Prairie Peninsula through Iowa, northern Illinois, Indiana and into southern Michigan.

PAIR FORMATION.—No flight performances were observed in Michigan or Kansas, but individuals were scarce at the study localities in these states. The hindwings of *haldemanii* are either yellow or red.

COURTSHIP.—Femur-tipping and femur-shaking were the only signals produced by courting males. In more than 30 courtship sequences shaking was always present, tipping was usually present, and stridulation was never present. Unlike other *Pardalophora* species the ends of the tibiae were vigorously struck against the substrate during shaking, producing a drumming sound audible several feet away (Fig. 7g).

Aggression.—Tipping in *haldemanii* seemed somewhat more intense than in other *Pardalophora* species. The femora were often raised to more than 90° and the tibiae were often extended at right angles to the femora. Tipping was sometimes produced by solitary males but was especially prevalent in male–male encounters. Shaking occurred infrequently in aggressive contexts. Unlike other *Pardalophora* species, *haldemanii* males shook without having established contact with one another. Shaking in courtship was similar to that in aggression.

Pardalophora saussurei (Scudder)

This species ranges from northeastern Mexico, through central Texas and Oklahoma and extends into southern Kansas.

Pair Formation.—During two hours of collecting in eastern Texas, I saw only disturbance flights, even though numerous individuals were present and other species were performing flight displays.

Courtship.—Ordinary stridulation was recorded only once—in a male approaching, and attempting to mount, a female. On another occasion, when a male approached and mounted a female, he produced several femur movements which resembled stridulatory movements, but no sound was produced. Twice a male only tipped his femora before attempting to mount a female. Presenting occurred twice; one female responded to the approach of a male by spreading her femora away from her abdomen and by lowering and shaking them.

Aggression.—Both males and females tipped their femora in encounters. Males also shook their femora silently when touched by other males.

Table 7 compares the behavior of *Pardalophora* species and other species of Hippisci. There is considerable sympatry among the four species. The distribution of *haldemanii* is almost completely contained within the range of *apiculata*. However, *apiculata* and *saussurei* evidently have only a relatively narrow zone of overlap in Oklahoma.

TABLE 7

Signalling in the Hippisci

Species	solitary flight signals	wing color	courtship signals	aggressive signals
P. apiculata	infrequent and without crepitation	red	ord. stridulation, vib. strid. (♀ lost)	tipping, shaking (si)[1]
P. phoenicoptera	”?	red	ord. stridulation	”
P. saussurei	”?	yellow	ord. stridulation, tipping	”
P. haldemanii	”?	yellow or red	shaking (ss), tipping	tipping, shaking (ss)[1]
H. ocelote	”?	yellow or red	ord. stridulation	tipping, shaking (si)
X. corallipes	”?	yellow	vib. stridulation and ord. strid. in several combinations	”
L. robustus	”?	yellow	ord. stridulation, tipping	tipping, shaking (ss)
C. pellucida	none	transparent	”	tipping, shaking (si)

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[1] si = silent; ss = with substrate-striking.

GENUS *Hippiscus* Saussure

Hippiscus ocelote Saussure

H. ocelote is the only member of this genus. It appears to reach its greatest abundance in South Dakota, Nebraska, Kansas, Oklahoma, and eastern Texas, but it also extends throughout most of the eastern states. I collected it at eight localities in the following states: Ohio, Tennessee, Georgia, Missouri, Oklahoma, and Nayarit, Mexico.

PAIR FORMATION.—Flight displays by solitary males appear to be lacking in this species. This fact was also noted by Blatchley (1920). Pair formation may be similar to that in *Pardalophora* species. The color of the hindwings is yellow or red, and both colors can be found at a given locality.

COURTSHIP.—Four times approaching males produced ordinary stridulation (Fig. 7j) before attempting to mount; twice they did not signal at all. On the four occasions when I observed males mounting, they rapidly tapped the heads of the females; twice this tapping was accompanied by a pronounced lateral rocking of the male's head. Similar behavior was observed in *Pardalophora phoenicoptera* and *Xanthippus corallipes*. Twice, while a male was mounting, the female lowered the femur on the side from which he was mounting and spread it away to about 40° from her abdomen. When two males mounted the same female and attempted to attach, one from either side, the female lowered and spread both femora away from her abdomen.

AGGRESSION.—Femur-tipping and silent femur-shaking were produced in encounters between males.

GENUS *Xanthippus* Saussure

There are perhaps 10 or more species in this genus and seven subspecies of *X. corallipes* have been described. In this investigation only *X. c. pantherinus* (Scudder) was studied.

Xanthippus corallipes (Haldeman)

The distribution of *X. corallipes* as given by Newton and Gurney (1957:479) extends from Canada to Mexico and from Arizona, Nevada, and Oregon east to the Dakotas, Kansas, and Texas. Five subspecies have been reported from Arizona alone (Ball et al., 1942). I collected *Xanthippus corallipes* at three localities in eastern and central Texas, in Shackelford, Anderson, and Burnet counties.

PAIR FORMATION.—I saw no flight displays by members of this species. However, the hindwings are banded and have a yellow wing disk.

COURTSHIP.—In three courtship sequences both ordinary stridulation and vibratory stridulation were recorded; both types were produced with one femur. In one sequence, a male produced bursts of vibratory stridulation while remaining stationary (Fig. 7i), but the situation eliciting stridulation was not determined. These bursts were made with one femur held at approximately 45°, and following each burst the femora rapidly dropped to the horizontal position without making any sound. The sound produced in another sequence differed from the one just described in that the femora were brought to bear against the forewing when the femur was dropped after each burst of vibratory stridulation, thus producing a sound which was a combination of vibratory stridulation and ordinary stridulation (Fig. 7h). The third courtship sequence was completely recorded, and the sounds produced are shown in Figure 7h. The first section of this latter sequence consisted of three bursts of vibratory stridulation, each appended with a single pulse of ordinary stridulation; the second portion consisted of four pulses of ordinary stridulation. Both the length of the bursts and the interval separating them were quite constant. Only one femur was employed throughout.

AGGRESSION.—Both tipping and silent shaking were employed in male–male interactions. I saw shaking only twice, both times when a male was being walked upon by another male. Isolated males also made small upward jerks of their femora from the horizontal position through five to ten degrees. The function of these movements is not yet known.

GENUS *Leprus* Saussure

Seven species have been described in this genus. All of them occur in the southwestern United States or Mexico. Only one species was examined in the present study.

Leprus robustus is reported in the United States only from Arizona, New Mexico, Colorado, and western Texas (Newton and Gurney, 1956:1004). I collected it near Imuris, Sonora, Mexico.

Pair Formation.—The population near Imuris was dense, but I neither heard nor saw any flight displays during an hour of observation.

Courtship.—In courtship, males produced tipping and ordinary stridulation. Femur-tipping was slower than in *Pardalophora* spp., lasting approximately 1.5 seconds. The femora were tipped to the vertical position, and the tibiae were extended to about 90° from the femora but were tucked against the femora on the downstroke. Stridulation was made with one or both femora, and sound appeared to be produced on both upstrokes and downstrokes. Stridulation (Fig. 7k) was only performed by males that approached and attempted to mount females.

Aggression.—Both tipping and shaking with substrate-striking occurred in male–male encounters, but contact between males was not necessary to elicit shaking.

GENUS *Camnula* Stal

Camnula pellucida (Scudder)

C. pellucida is the only member of this genus. It is found at higher elevations throughout the western states, occurs abundantly in the northern parts of the prairies, and ranges eastward through the northern states and southern Canada to the Atlantic states.

Pair Formation.—Four populations, three in Michigan and one in Kane County, Utah, were exceptionally dense in comparison to populations of other oedipodine species that I encountered. Most of my field observations of *C. pellucida* were made in a grassy area near the shore of Lake Superior in Michigan. I saw no flights other than disturbance flights and found aggregations of individuals in small open areas, less than 12 inches in diameter, in the grass. In a large open area a few feet in diameter I found several aggregations. On four occasions I saw the formation of aggregations involving 2–10 individuals apiece; each time, an isolated male, walking across a bare piece of ground, attracted several other males, and within a few seconds an aggregation had been formed. Males attempted to mount one another, aggressive signals were exchanged, and in less than 15 seconds the aggregations had dissolved. Although no aggregations were initiated by females, those containing females lasted for several minutes. Males dispersed by walking and not by flying, as males of *Arphia* species often do. Elsewhere in Michigan, males made short flights up to 2 feet towards other moving males. Throughout its range *C. pellucida's* hindwings are colorless, unlike other Hippisci.

Courtship.—One or both femora were used to produce ordinary stridulation (Fig. 7l). Femur-tipping is sometimes produced by courting males.

Aggression.—Tipping and shaking occurred in encounters between males, but both signals were decidedly less frequent than those of the other Hippisci studied. I saw silent shaking only once, even though numerous situations which would have elicited it in other species occurred. Femur-tipping was also less frequently produced and less precise than that observed in other members of Hippisci. Often only one femur was tipped, and when both were tipped they seldom moved synchronously.

GENUS *Spharagemon* Scudder

In his revision of this genus Morse (1895) recognized nine species belonging to three species groups: *crepitans, bolli, robustum,* and *inornatum* in the *bolli* group; *saxatile, equale,* and *humile* in the *equale* group; *cristatum* and *collare* in the *collare* group. Later (1904) Morse described *planum* as a subspecies of *saxatile.* Blatchley (1920) and Hebard (1937) considered *planum* to be a distinct species, but both authors cited little evidence for their belief. Behavioral information and the presence of what appear to be morphological intermediates between *planum* and *saxatile* in the UMMZ collection are, I believe, consistent with Morse's designation. There has been doubt as to the status of *humile* because the median carina of the pronotum is cut by two sulci in some specimens, causing them to resemble members of the genus *Trimerotropis* in this respect. Because of this, Hebard (1929, 1937b) placed *humile* in *Trimerotropis.* Since this species appears to be very similar behaviorally and morphologically to *equale,* and since the median carina of *equale* and *saxatile* is also cut by two sulci in some individuals (as noted by Hebard), *humile* is here tentatively treated as a member of the genus *Spharagemon. S. inornatum* was synonymized by Hebard (1937b) as a race of *bolli.* Behaviorally specimens from near Raton, New Mexico, answering to the description of *inornatum* seem inseparable from *bolli. S. cristatum* was also synonymized by Hebard (1937b) as a race of *collare,* but their pair-forming and courtship patterns are very distinct, indicating that two species are probably involved. *Spharagemon robustum* Morse (from Mexico) and *S. superbum* Hebard (from Texas) were not encountered in this study.

On the basis of behavioral studies, what appear to be seven different species are thus far distinguishable. These are: *collare, cristatum, bolli, crepitans, saxatile, equale,* and *humile.*

Spharagemon collare (Scudder)

S. collare appears to extend at least from southcentral Colorado (near Alamosa) north to Alberta and east through the Great Lakes region to New England. It is primarily an inhabitant of dry, open sandy area with scanty vegetation (Fox, 1914a; Brooks, 1958; Cantrall, 1943).

PAIR FORMATION.—I spent many days observing grasshoppers in sandy areas of the George Reserve during the summers of 1965, 1966, and 1967. Only about 10 crepitations by *collare* were heard during this time, even though the species was very abundant in the area and was observed throughout the adult season. Of these crepitations five were made during disturbance flights. One flight with crepitation was seemingly performed spontaneously; the cause of the remaining flights was not determined. By comparison, *Spharagemon bolli,* which is less abundant, often crepitated more frequently in an hour than *collare* did in three seasons. It seems unlikely, therefore, that crepitations play a significant role in pair formation. In Michigan individuals pair formation is achieved, it appears, mainly by males orienting on and approaching moving females. Males stand inconspicuously on open ground for long periods, and rapidly approach a variety of moving individuals: males and females of their own species and individuals belonging to other species. Many approaches were made toward grasshoppers several feet away. Courtship signals are seemingly not given at any particular time during the approach. In one instance a male approached a *Melanoplus confusus* female from a distance of five feet and produced several one- and two-pulse stridulations within the first two feet of the approach; she disappeared into the grass before he reached her, and he did not follow. In the same area a moving *Ageneotettix deorum* male was twice pursued, but the pursuits were broken off before contact was established. Another male *collare* pursued an *Arphia pseudonietana* female; he stridulated several times as he approached, but stopped following when she disappeared into the grass. One male approached a male and female of *Ageneotettix deorum,* touched them, then walked away. On ten occasions one male approached a conspecific male; aggressive signals were exchanged, and the males separated without establishing contact.

COURTSHIP.—All stridulations were made by males approaching other individuals. The femora were usually pressed against the wings on both upstrokes and downstrokes (Fig. 8d). Sometimes, however, sound was produced only on the upstroke (Fig. 8c). Males did not tip their femora during courtship. Three courtship sequences involving individuals from near Alamosa, Colorado, resemble those of Michigan individuals.

AGGRESSION.—Femur-tipping seems to have a purely aggressive function. The femora are raised 45°—80° from horizontal, and the upstroke is a little faster than the downstroke. Males tipped the femora highest when in close encounters with other males. Femur-shaking also has an aggressive function. The ends of the tibiae are vigorously struck against the substrate, producing a drumming sound that is audible several feet away. Contact need not be established for shaking to be elicited. Three times, the following sequence occurred: A male stridulated as he approached a female. Another male several inches away shook his femora immediately following stridulation, and the courting male stopped courting, failing even to establish contact with the female. The female had not made repelling motions. I did not see such an interruption when only a male and a passive female were involved. Femur-raising by females is very much like that of other species and was effectively employed in repelling courting males. Females also repelled males by shaking their femora and striking the substrate and occasionally by tipping their femora.

Spharagemon cristatum Scudder

S. cristatum was described by Scudder and later considered merely a subspecies of *collare* by Hebard (1937b), because all transitions in pronotal crest height—the basis for the original separation—could be found. Behavioral observations clearly suggest that

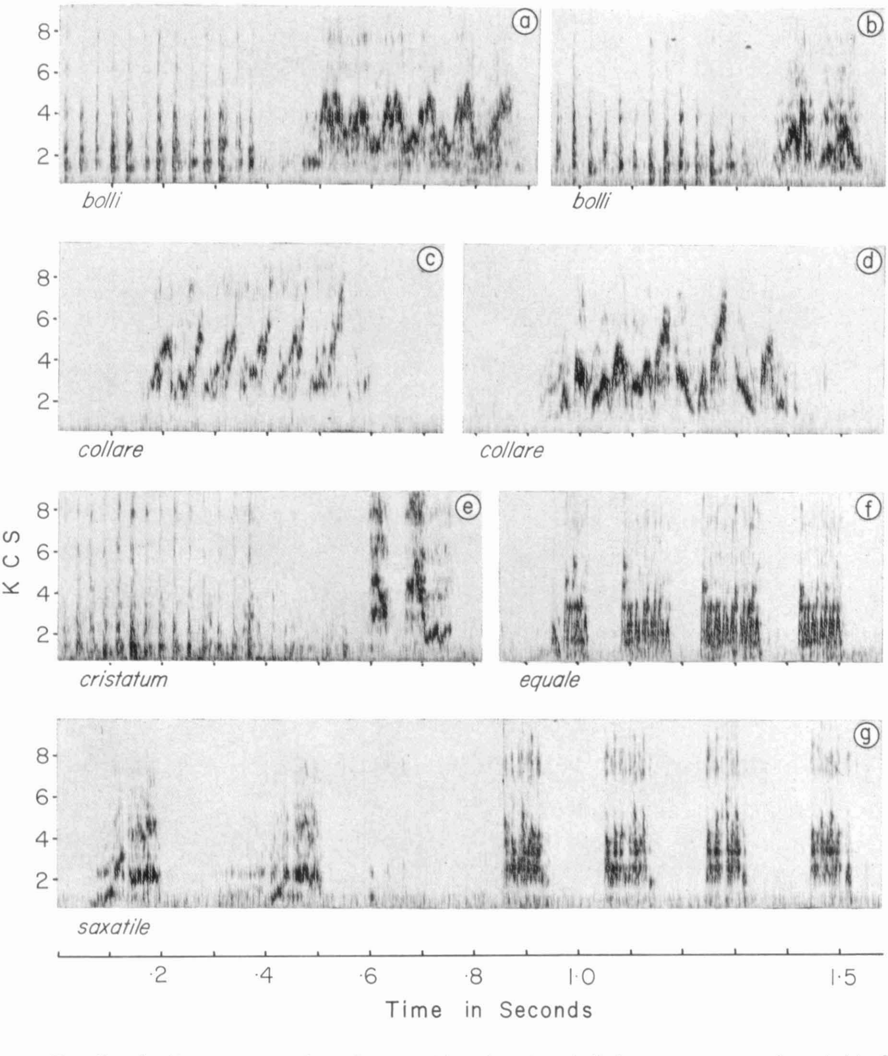


FIG. 8. Audiospectrographs of courtship signals of *Spharagemon* species; (a,b) *S. bolli* (Mich.), femur-shaking with substrate-striking followed by ordinary stridulation—usually only two pulses followed shaking, 98°F; (c,d) *S. collare* (Mich.), ordinary stridulation, 94°F and 100°F, resp.; in (d) sound was produced on both the upstroke and the downstroke, in (c) only on the downstroke; (e) *S. cristatum* (Texas), femur-shaking with substrate-striking followed by ordinary stridulation, 80°F; (f) *S. equale* (W. Kansas), bursts of vibratory stridulation, 87°F; (g) *S. saxatile* (Pennsylvania), two pulses of ordinary stridulation followed by bursts of vibratory stridulation. *S. humile,* not shown, produced femur-shaking with substrate-striking, as in (a), followed by bursts of vibratory stridulation as in (f). *S. crepitans* produced only bursts of femur-shaking with substrate-striking. Temperatures taken 3 inches above substrate.

two species, morphologically very similar, are involved. Additional behavioral information in the probable zone of contact would be desirable. However, I have tentatively treated them as different species. The probable zone of contact or overlap between *cristatum* and *collare* is in Oklahoma or Kansas. *S. cristatum* is found southward from the contact zone into eastern Mexico and perhaps east to Florida; it may also extend northeastward to Virginia.

PAIR FORMATION.—Unlike *collare, cristatum* frequently makes flight displays. I heard numerous crepitating flights by males both in eastern Texas and near Cd. Valles in San Luis Potosi, Mexico. Along an east Texas roadside more crepitations were produced by a single *cristatum* male in an hour than by a population of *collare* in many more hours of observation on the George Reserve in Michigan. This Texas male performed in an area with several bare patches of ground, each several feet in diameter. In Mexico, I heard 20 or more crepitations in about 40 minutes.

COURTSHIP.—In *cristatum* femur-tipping and femur-shaking occur in courtship as well as in aggressive situations. I observed males turn toward and approach females 26 times. In 25 of these approaches stridulation followed shaking (Fig. 8e); only once was shaking observed without stridulation. Stridulation was always brief, consisting of one or two strokes. The rates of shaking and stridulation were consistent, but the length of the shaking burst and the interval between shaking and stridulation were quite variable (see Appendix). Shaking was usually preceded by tipping.

AGGRESSION.—In encounters between males, both tipping and shaking (with substrate-striking) occurred. Aggressive shaking and courtship shaking are essentially identical. The behavior of *cristatum* females was similar to that of *collare* females: femur-raising, femur-shaking, and femur-tipping signals were performed: the first two were used to repel males. Once when a male observed and approached a copulating pair, both male and female tipped and shook their femora, and the approaching male stopped courting.

Spharagemon bolli Scudder

This species occurs across the greater part of the eastern United States but is absent from the Florida peninsula where *S. crepitans,* its presumed closest relative, occurs. It normally inhabits dry grassy woodlands.

PAIR FORMATION.—Males made frequent solitary crepitation flights in the field, and they seemed to walk about much more than males of *collare,* both in the field and in the laboratory.

COURTSHIP.—Like *cristatum, bolli* has incorporated shaking into courtship behavior but has retained ordinary stridulation. Shaking with substrate-striking was part of each courtship sequence, and stridulation, when present, always followed shaking and never occurred alone. In 25 courtship sequences both shaking and stridulation occurred 18 times (Fig. 8a, b), courtship with only shaking occurred 6 times, and approaching and mounting with no signal occurred once. Bursts of stridulation were short as in *cristatum,* usually with only one or two leg strokes (Fig. 8b); occasionally longer bursts of stridulation were produced (Fig. 8a). Femur-tipping almost always preceded femur-shaking during courtship. The similarity in the courtship of *cristatum* and *bolli* is striking, especially in view of the fact that morphologically *bolli* is much more like *S. saxatile* and *S. equale.*

AGGRESSION.—Both tipping and shaking occur in encounters between males. In one of 18 encounters both individuals merely tipped their femora, in four one male tipped while the other both tipped and shook, and in ten one male shook and stridulated as he approached another male (causing the latter to shake), but as he turned away he stopped stridulating. In all encounters males separated within 10 seconds and did not attempt to mount one another. During shaking the tibiae struck the substrate, producing a drumming sound that was audible several feet away. Females shake and tip their femora much as males do, and the movements appear to have a repelling function. One female shook and tipped her femora when she was approached by a courting male, and the male stopped approaching.

Spharagemon crepitans (Saussure)

In general appearance and behavior *S. crepitans* is most like *S. bolli.* It is almost restricted to Florida but has been reported on the Georgia coast. In the panhandle region of Florida it is sympatric with *S. bolli,* but it is not known whether the two species ever occur together at the same localities.

PAIR FORMATION.—I did not observe the behavior of this species in the field. Two males found in the Ocala National Forest in Florida were put into a terrarium along with several females of *S. saxatile.* No cross-specific mountings occurred, but the approaches observed were probably normal.

COURTSHIP.—Courtship of *crepitans* closely resembles that of *bolli.* The only difference seems to be that *crepitans* never stridulates. Males turning towards and approaching moving individuals made only femur-tipping and femur-shaking movements. No stridulation occurred in 18 approaches.

AGGRESSION.—The following observations attest to the fact that in contrast to *bolli,* femur-shaking is not an aggressive signal in *S. crepitans*: (1) Male A followed male B; when they established contact only femur-tipping movements occurred. (2) Male A mounted male B; the males separated after making femur-tipping movements. (3) Male A attempted to mount male B; he was unable to do so; the males separated without producing femur-shaking signals. (4) Two males came into contact three times; femur-tipping but no femur-shaking was produced. (5) A male of *S. saxatile* and a male of *S. crepitans* touched one another; the *crepitans* male only tipped his femora, while the *saxatile* male produced both femur-tipping and femur-shaking signals. *(S. saxatile* shakes only in aggressive situations.)

Spharagemon saxatile planum Morse

As noted above, Blatchley (1920) considered *planum* and *saxatile* to be distinct species. The apparently slight morphological differences and the close similarity in courtship behavior between the populations from New England *(saxatile)* and those from the Appalachian Mountains *(planum)* suggest that these taxa are conspecific.

PAIR FORMATION.—I heard numerous crepitations in one hour in the field, at least some of them from solitary males, suggesting that pair formation is sometimes effected by crepitation.

COURTSHIP.—A single courtship sequence in the field was as follows: A male made a one-second crepitating flight covering a few feet. Shortly after alighting, a male *Dissosteira carolina* settled about 12 inches from him. The *planum* male rapidly approached the latter and made six irregularly spaced pulses of stridulation as he advanced. The *carolina* male then tipped his femora, and the *planum* male stopped advancing before contact was established. In the laboratory, males made seven attempts to mount females. In four cases, the male approached the female and faced her at right angles before attempting to mount. In one sequence a male maintained this orientation as the female he was facing turned around. Stridulation was observed in only one sequence: a male, observing a female moving close by, approached the latter while producing both ordinary stridulation and a series of short bursts of vibratory stridulation (Fig. 8g). The sequence of stridulations was as follows: After he had turned towards the female and while he was still stationary, the male produced two pulses of ordinary stridulation. Then, as he moved toward the female and circled about her, he produced eight regularly spaced bursts of vibratory stridulation, all of similar length. When he had stopped advancing again, he produced two more bursts of ordinary stridulation. In response to this the female raised her femora, and a male an inch or so on the other side of the female shook his femora. The courting male did not attempt to mount.

AGGRESSION.—I observed femur-shaking with substrate-striking about 50 times. It was made only by males that were being approached or touched by other individuals. Males also tipped their femora when they encountered one another.

Spharagemon saxatile saxatile (Morse)

I collected juveniles and teneral adults of this species on some rock outcroppings at the crest of a hill near New Haven, Connecticut.

PAIR FORMATION.—Both Morse (1920) and Blatchley (1920) report hearing crepitations by *saxatile,* but I did not record any myself.

COURTSHIP.—Three males provided a total of five courtship sequences. In four of these, the male attempting to mount made several pulses of ordinary stridulation, but one sequence consisted of a single pulse of ordinary stridulation, then two bursts of vibratory stridulation and finally two more pulses of ordinary stridulation. Ordinary stridulation was made with both femora and vibratory stridulation with one. Femur-tipping was not made by courting males.

AGGRESSION.—Aggressive behavior is similar to that in *planum*. Males often jerked their femora sharply upwards when they were touched. No regular shaking by females occurred, but several jerks made in quick succession somewhat resembled a crude form of shaking.

Spharagemon equale (Say)

This species occurs in the Great Plains from central Texas to southern Alberta.

PAIR FORMATION.—I made no behavioral observations of this species in the field. Crepitation has not been recorded and is not mentioned in the literature.

COURTSHIP.—The only individual of this species which I found was a male taken 20 miles west of Colby, Kansas. When he was placed in a terrarium with two male and two female *Hadrotettix trifasciatus*, a species somewhat similar in appearance to *S. equale*, six courtship sequences were observed. Although no mountings occurred, the approaches and the signals produced were probably normal. Bursts of vibratory stridulation somewhat resembling those of *S. saxatile* were produced during each of six approaches (Fig. 8f). Bursts of varying lengths (0.05—0.15 seconds) were produced in quick succession, separated by intervals of fairly constant length. Each series of bursts was produced with one femur, and in every case the femur was held 40°—60° above horizontal as it vibrated against the forewing. The male stridulated as he walked about, facing the individual being courted.

AGGRESSION.—Tipping and shaking with substrate-striking were produced in aggressive encounters with *H. trifasciatus* in the terrarium.

Spharagemon humile (Morse)

According to Hebard (1929), *humile* lives only in the mountainous portions of southern Colorado and does not extend eastward beyond the foothills into the Great Plains. Along the foothills *equale* and *humile* are apparently sympatric. I studied individuals from near Denver and Raton, New Mexico.

PAIR FORMATION.—Crepitation was performed by solitary males over open ground. It consisted of a single burst, up to five seconds in duration. Males flew up and circled over one spot, then returned to the places from which the flights originated.

COURTSHIP.—Courtship in *humile* differs from that of *equale* in that bursts of shaking are produced before bursts of vibratory stridulation (see Fig. 18). I saw more than 20 courtship sequences by several males from near Denver. Each time males approached females or other males, they first shook their femora. In about half the approaches, males made bursts of vibratory stridulation following shaking. Vibratory stridulation was absent only when contact was established immediately after shaking. In less than half the courtship sequences, tipping preceded shaking. A male from near Raton courted once. He shook his femora, then made three bursts of vibratory stridulation.

AGGRESSION.—Tipping was always present in more than 30 male–male encounters, but shaking was produced only once by a male that was touched from the side. Females repelled males by raising and tipping their femora.

GENUS *Spharagemon*: SUMMARY

This genus is more diverse than the comparable eastern genus *Arphia* in two regards. First, a greater variety of ecological situations is inhabited, from open sand *(S. collare)* and open rocky surfaces *(S. saxatile)* to grassy, wooded situations *(S. bolli)*. Second, courtship behavior is more varied among the species (Table 8). This latter difference may be due to the greater amount of seasonal and habitat overlap between the adults of the various species (see Reproductive Isolation).

In *S. collare* crepitation is rare and pair formation is brought about when males see and approach females on open, bare patches of ground. But in *S. saxatile, S. bolli, S. cristatum* and *S. humile* crepitation is common and is presumably a female-attracting signal. Crepitation has not been heard in *equale* or *crepitans,* but these two species have not been adequately studied in the field.

TABLE 8

SIGNALLING IN *Spharagemon, Dissosteira,* AND *Scirtetica*

Species	solitary flight signals (crepitation rate)	courtship signals	aggressive signals
S. collare	very rare	ord. stridulation	tipping, shaking (ss)[1]
S. cristatum	common (37.7/sec 90°F)	shaking (ss), ord. stridulation, tipping	"
S. bolli	common (40.0/sec 76°F)	"	"
S. crepitans	unknown	shaking (ss), tipping	tipping
S. saxatile	common (43.3/sec 78°F)	ord. stridulation, vibr. stridulation	tipping, shaking (ss)
S. equale	unknown	vibr. stridulation (in bursts)	"
S. humile	common (38.4/sec 80°F)	shaking (ss), vibr. stridulation (in bursts)	tipping, shaking (ss) (rare)
D. carolina	common, two speeds while hovering	tipping (ws) (two kinds), alt. stridulation	tipping (si and ws),[1] shaking (ss)
D. pictipennis	common, in short bursts	ticking, ord. stridulation	tipping, shaking (ss)
S. marmorata	common, (50.0/sec 90°F)	alt. vibr. strid., ord. strid. (2 kinds), tipping	"

[1] ws = with wing-striking; ss = with substrate-striking; si = silent.

In each of the three species groups of this genus, femur-shaking has been incorporated (apparently independently) into courtship behavior. It has combined with ordinary stridulation twice: once in the *bolli* group (in the ancestor of *bolli* and *crepitans),* and once in the *collare* group (in *cristatum).* It has combined with vibratory stridulation in *humile* of the *equale* group. In each case it precedes stridulation in the courtship sequence. Concomitant with the incorporation of femur-shaking into courtship, there seems to have been a complete loss of stridulation in *crepitans* and a reduction in *bolli* and *humile.* A similar phenomenon was found in one or more species of *Lactista, Pardalophora, Trimerotropis,* and *Conozoa.* In *crepitans* shaking is no longer present in aggressive contexts, and in *humile* its occurrence seems reduced. This reduction, also observed in other genera, seems to be associated with the incorporation of shaking into courtship (see Origin and Evolution of Signals).

GENUS *Dissosteira* Scudder

Four species are currently included in this genus, *Dissosteira carolina (*Linnaeus), *D. longipennis* (Thomas), *D. spurcata* Saussure, and *D. pictipennis* Bruner. The first two species appear to be closely related; the last two are morphologically similar to one another, but not strikingly so. In general appearance this genus seems to be most closely related to the genus *Spharagemon;* these two genera comprise the Group Spharagemones. Only *D. carolina* and *D. pictipennis* were available for this investigation. Signalling in these species is summarized in Table 8.

Dissosteira carolina (Linnaeus)

This well-known grasshopper is widely distributed in the United States and Canada. Apparently the only areas in which it does not occur are the hot deserts of southwestern United States. Its close association with open patches of ground is well documented in the literature.

PAIR FORMATION AND COURTSHIP.—*D. carolina* is perhaps most noted for its habit of hovering in flight over bare patches of ground. Males rise almost vertically to a particular height where they hover. During approximately the first half of each flight the wing beat frequency is about four times that of the second half of the flight (Fig. 6i). The sound produced is not a loud crackling sound like that of *Arphia* species but has a sibilant or lisping quality. Flights commonly last more than 15 seconds, and at the end of each flight males drop to the spot from which they flew. Flights are also relatively uncommon when compared to *Arphia* species; one may wait for half a day to see a single hovering flight, even though many individuals are present and otherwise quite active. Hovering flights apparently vary little over the range of the species. Similar flights have been described in New England (Morse, 1920) and in British Columbia (Buckell, 1920). A single flight by a male in northeastern New Mexico appeared to be identical to those of Michigan males.

The following observations on hovering flights were made in Michigan: (1) A male flew up and hovered, while another male and a female, about two feet away, did not move. When the hovering male dropped to the ground, the other male immediately flew up and alighted next to him. Aggressive signals were exchanged, and the males separated a few seconds later. The female continued to remain motionless. (2) A male hovered and descended, and as he alighted a male nearby made a short flight and landed close to him. A minute thereafter, the performing male made a second flight, in which he first hovered six feet above the ground, then gradually rose to a height of about 15 feet. About 30 seconds later he descended and landed within six inches of his original perch. A female, 12 inches from the performing male, was observed throughout, but remained motionless. A few minutes after the second flight both males flew away. (3) A male hovered five feet above the ground. During the flight five males flew toward him, all of them from distances of 10 feet or more. All settled within two feet of where he was to alight. They were not bunched initially, having come from various directions; but they soon began to walk toward one another and exchange aggressive signals. The performing male descended and flew to where the others had aggregated. All six males milled about, giving both shaking and tipping signals. One male assumed the courtship posture, dropping his abdomen. In the next 30 seconds they dispersed by flying and walking. (4) A male hovered five feet above the ground, but no males were seen responding to him. He made a second hovering flight several minutes later; this time one male flew towards him as he alighted but did not land so close that they exchanged aggressive signals. After several more minutes the same male made a third hovering flight, and this time three males flew towards him, one of them landing right next to him. The two closest males exchanged aggressive signals, and then one of them flew away. (5) Five hovering flights were observed by the roadside near Mio, Michigan. During or just after each flight, several—in one case, 12—males flew towards the performer. All aggregations formed in this manner were short-lived, and the males dispersed after a few seconds.

Although females did not fly to hovering males, this display probably has the function of attracting sexually receptive females. Pair formation is often initiated by movement of females. One afternoon a female flew up, apparently without being disturbed, and landed about 10 feet away, suggesting that sexually responsive females might sometimes attract males by flying. No hovering flights by males occurred during this time.

Sometimes solitary males of *D. carolina* sit in one spot for many minutes and stridulate, presumably to attract sexually responsive females. Stridulation consists of alternately raising and lowering the femora and pressing them against the forewings on the downstroke. As each femur descends it seems to vibrate against the wing. I have termed this behavior alternate stridulation (Fig. 6j). The following observations suggest that the signal is a female-attracting signal: (1) A male flew up from a small patch of bare ground surrounded by dense grass, hovered for approximately 10 seconds, then dropped back to the same spot. He remained motionless for a few minutes, walked about for a minute or so, produced one song of alternate stridulation, then walked about on the bare patch and flew away. There were no other individuals about. (2) In the laboratory a male produced alternate stridulation. He sang five times before he was touched by another male and stopped stridulating. The male stridulated again and continued for the next five minutes. A female walked past him twice but I could not determine whether she responded to him or not. He appeared unresponsive to her, for he continued stridulating. Twice more, during stridulation, a female walked up to him and touched him, but he did not move except to turn away and stop stridulating. In each case, the female walked away. It looked as though the female had walked to the male in response to these stridulations. In the next two hours this male did not stridulate again, nor did he court any females. (3) A male courted a female. Periodically he attempted to mount, but the female rejected him by raising her femora. She then walked away and climbed a grass stalk; the male followed and climbed an adjacent grass stalk. While facing the female, the male produced alternate stridulation and continued song after song for about five minutes. Another female then walked directly toward the stridulating male. He turned toward her, approached and mounted. This second female had twice walked toward the stridulating male in (2). (4) A female was approached by a male. As he faced her, he moved forward three or four times and touched her with his antennae; his abdomen was lowered in the typical courtship stance. Every time he touched her she raised her femora, and he backed up slightly. The male then produced alternate stridulation while about two inches from her. The female showed no response to this stridulation. The male gradually approached the female while still stridulating. When he touched her she hopped away. (5) The female of (4) moved in the direction of another male that had been stridulating during the course of her previous encounter. First she turned toward the source of the sound (she had been facing at right angles to the source). Other individuals were motionless. She moved directly toward the stridulating male, stopped momentarily between two songs and then moved forward again during the next song. As she advanced another male touched her and caused her to move in a different direction. The stridulating male also stopped stridulating at about this time. (6) A male produced many songs between five or six attempts to mount a female.

The behavior I observed most frequently in this species was walking and flying by males toward other moving individuals. Courtship did not begin until a male was approximately six inches away. Males always tipped their femora while approaching. There are two kinds of tipping: in one of them movement is silent, in the other the tegmina are struck on the upstroke (Fig. 6k). Both movements consist of a fast upward jerk to about 50° and a slower lowering of the femora. Both males and females tipped their femora silently while interacting with other individuals or while walking about alone. Frequently males switched from silent tipping to tipping with wing-striking while following females and before attempting to mount. During the latter movement the tegmina were struck repetitively, and the repetition rate was faster than in silent tipping. Sometimes males attempted to mount after making only silent tipping movements. More than 10 mounting attempts occurred where silent tipping and abdomen-lowering were performed, but in which tipping with wing-striking was absent.

AGGRESSION.—Both silent tipping and tipping with wing-striking were commonly performed by interacting males. The latter movement was much more common, however, and was never performed by solitary males or females. The repetition rate of the two types of tipping was about the same. Femur-shaking resembles that of *Spharagemon* species. In *D. carolina,* however, males shook only when they had actually established contact with one another. I saw only one female shake her femora; she shook when approached by a courting male, who did not attempt to mount. Males did not attempt to mount any of ten or more females that had their femora raised in the repelling position. In the literature it is repeatedly mentioned that males aggregate. This they do, but the aggregations are of short duration and they seem to develop only because of the habit of approaching any moving individual. Because some moving individuals turn out to be females, the advantage of approaching is clear.

Dissosteira pictipennis Bruner

This species occurs only in California. I collected it in a small ravine in rolling country with grass and live oaks near Monterey, and also near Yosemite and Mariposa.

Pair Formation.—Crepitation was produced in bursts (three pulses per burst and about four bursts per second). Males did not hover in flight like *D. carolina*. Each of the two longest crepitating flights contained 10–15 bursts of crepitation. One male flew a distance of approximately 15 feet and three feet above the ground. After alighting he walked about on the ground and made many stops, tipping his femora whenever he did so. I observed one male walk to a female that had alighted three feet from him. As he advanced he made three kinds of signals: tipping, ticking, and ordinary stridulation. The female remained motionless at first, then raised and lowered her femora slowly as the male neared her. From four inches away the male rushed towards her and attempted to mount without further signalling. The female repelled him with movements of her hind femora.

Courtship.—Males possess two main courtship signals (see above): ticking (Fig. 6e) and ordinary stridulation (Fig. 6l). Monterey males always ticked before producing ordinary stridulation (n = 8). Each ticking movement is similar to ticking in *Encoptolophus sordidus*. From three to five ticks, produced alternately with left and right legs, were performed in each series. The interval between the tick-series and ordinary stridulation was fairly constant. Bursts of ordinary stridulation were made with three to six synchronous up and down movements of the femora (Fig. 6l). The stroke period became progressively slower and the sound less intense during each burst. A male at Yosemite produced only ordinary stridulation as he approached a female.

Aggression.—Males tipped and shook their femora in encounters with other males. The substrate was struck during shaking.

GENUS *Scirtetica* Saussure

Two species, widely separated geographically, belong to this genus. *S. marmorata* (Harris) occurs in the eastern United States, and *S. ritensis* Rehn is known only from the Santa Rita Mountains, Arizona.

Scirtetica marmorata (Harris)

Scirtetica marmorata is found along the Gulf and Atlantic coasts from Gulfport, Mississippi, to New England and has been collected at several localities in Ontario and Michigan. Two subspecies are generally recognized: *S. m. marmorata* from New England, Ontario, and Michigan, and *S. m. picta* from the Southeast. Only specimens from the latter area were examined in this study. At four localities in Florida this species occurred in sandy, open wooded areas. In overall appearance and in its patterns of crepitation, ordinary stridulation, femur-tipping, and femur-shaking. *S. marmorata* appears most similar to species of *Spharagemon*. The similarity is most striking between *S. marmorata* from the northern states and *Spharagemon saxatile*. Signalling in *S. marmorata* is summarized in Table 8.

Pair Formation.—Males performed loud and comparatively long crepitating flights in the open, sandy, pine and oak woods of northern and central Florida. Although I found no distinct aggregations of males, I had the impression that there were cycles in the crepitating activity of males in a given area of the woods. Blatchley (1920) made the following observations: "He [*S. marmorata*] has the most prolonged stridulation [= crepitation] of any locust known to me. He zig-zags in his flight almost at right angles, sometimes staying in the air for half a minute, flying all about an acre or more, and finally alighting on the sand within a yard of where he arose."

Courtship.—In addition to femur-tipping and ordinary stridulation, *S. marmorata* performs a unique and complicated movement in courtship. This movement was made repeatedly by a single courting male. First, both femora were lifted to vertical; at this position the angle between the femora was approximately 60°. From this position both femora were jerked forward twice through about 20°; they moved together or alternately. No sound was produced during this initial phase. Then the femora were lowered, one preceding the other, to about the 45° position. Then one femur vibrated against the forewing as it was lowered through 30° or so. It was raised again to the 45° position, with no stridulation occurring on the upstroke. As it was being raised, the other femur vibrated against its forewing as it was lowered; on its upstroke the first femur was lowered once more. These movements resulted in the production of three or four bursts of vibratory stridulation (Fig. 6o), which were always preceded by a two-pulse burst of ordinary stridulation (Fig. 6n). The ordinary and vibratory stridulations were separated by a fairly constant interval varying from 0.62 to 1.0 seconds. This male also produced ordinary stridulation while facing the female (Fig. 6m).

The only extended courtship interaction I saw was as follows: The male turned towards a moving female, tipped his femora once, and then, as he faced the female at right angles, produced a pulse of ordinary stridulation, paused for three seconds and produced the two-pulse stridulation, and following closely upon this, the complicated vibratory stridulation. The last two movements always occurred together. In the next four minutes he produced two-pulse stridulations and vibratory stridulations 13 times; interspersed between these signals he produced one, two, three, or four pulses of ordinary stridulation. Pulses of ordinary stridulation were produced singly or in pairs. While the courting male was thus facing the female, a non-courting male moved nearby; the courting male turned to him and produced several pulses of ordinary stridulation, in response to which the non-courting male tipped and shook his femora. The female raised her femora and held them in the vertical position whenever the courting male stridulated. Throughout the interactions he did not attempt to mount and only touched her with his antennae.

AGGRESSION.—In males, tipping and shaking (with substrate-striking) are the main aggressive signals. Females rejected males by raising and jerking their hind femora, and by kicking.

GENUS *Tropidolophus* Thomas

Tropidolophus formosus (Say)

This strikingly distinctive species, the only member of the genus, occurs from Mexico through eastern New Mexico and Colorado and through western Texas, Oklahoma, and Kansas to southeastern Wyoming (Newton and Gurney, 1957:479). Westwards, it extends into southern Arizona. In Arizona, *T. formosus* is found in desert grasslands, where it feeds on low shrubs such as *Malvastrum* and *Sphaeralcea* in areas of thick grass (Ball et al., 1942). At two localities in western Texas I found it walking about on vegetation, and at one locality I saw a male crossing bare ground as he walked from one shrub to another. I also found a female feeding on top of a low (12 inches) bush. No other species of Oedipodinae walk about on vegetation in this manner.

PAIR FORMATION.—In the field a male flew and landed on a low shrub on open ground. He fed on the shrub for 2.5 minutes, then climbed off and walked across the bare ground and climbed onto another low shrub, on which he produced several bursts of ordinary stridulation. He flew again, crepitating, and landed on a third low shrub, on which he produced two bursts of stridulation, then moved down to the ground and onto a rock. From this he flew, crepitating, and alighted on a fourth low shrub. These observations indicate that although *T. formosus* is adapted to climbing about on vegetation its pair-forming and courtship behavior is essentially similar to that of many other Oedipodinae.

COURTSHIP.—Males approaching females produced ordinary stridulation (Fig. 10k). The sound was considerably less intense than in most Oedipodinae and had a more sibilant quality. Only one femur produced each burst of stridulation and the sound was made on both upstroke and downstroke. Courtship of *T. formosus* is unique in several respects. First, the approach of males toward other individuals is not steady; forward motion is in a series of jerks, and the repetition rate of these jerks is approximately that of stridulation. Also, immediately following stridulation the male jerks his femora upwards through 5°–10° as he proceeds towards the female. The rate of these jerks, too, is the same as that of stridulation. Body-jerking and femur-jerking, or both, continue to be produced during mounting. On one occasion femur-jerking was continued while a male was attaching his genitalia. This jerking of the body may be advantageous on vegetation where body jerking motions could more easily be felt through the substrate.

AGGRESSION.—Femur-tipping in *T. formosus* was not precise; the tibiae were extended to various angles from the femora and were not flexed when the femur was lowered. Often only one femur was tipped, but when both were tipped they usually moved asynchronously. The duration of tipping was about one second. Femur-shaking was a rapid motion which could be heard as a low-pitched hum. During shaking the femora were held at about 45° and the tibiae were held at angles of a few degrees to more than 90° away from the femur. Occasionally the tibiae were held at about 45°

from the femora and struck the substrate. Femur-jerking is also an aggressive signal; males both shake and jerk their femora when touched. A female shook once; she produced several bursts of shaking while a mounted male attempted to attach his genitalia.

T. formosus is the only species of Oedipodinae known that has evolved the habit of living on top of vegetation. In so doing it has come to resemble a species of Acridinae, *Acrolophitus hirtipes,* in a number of morphological features: (1) Individuals are green; (2) they have long slender legs, particularly the hind femora; and (3) the hind tibiae possess many more spines than is usual for the Oedipodinae. Females of *T. formosus* have short wings (hence are flightless) and some of them are brown instead of green. In spite of this change in habitat *T. formosus* has retained the communicative behavior which is typical of the Oedipodinae, but because of its distinctive appearance the nature of its relationships to other Oedipodinae is difficult to determine.

GROUP PSINIDIAE

This group includes the genera *Derotmema* Scudder, *Trachyrhachys* Scudder, *Psinidia* Stal, *Mestobregma* Scudder, *Metator* McNeill, *Trepidulus* McNeill, and *Rehnita* Hebard. The members of these genera possess large heads, globose and protruding eyes, and slender legs and forewings. Signalling in this group is summarized in Table 9.

TABLE 9

SIGNALLING IN THE PSINIDIAE

Species	solitary flight display	wing color	courtship signals	aggressive signals
Psinidia fenestralis	none?	pink	ord. strid., tipping	tipping, shaking (ss)[1]
Derotmema haydenii	none?	yellow, red	ord. strid., tipping	"
Mestobregma p. plattei	none?	yellow	tipping (rapid)	tipping (slow), shaking (ss)
Mestobregma p. corrugata	none?	yellow, red	ord. strid., tipping?	tipping, shaking (ss)
Trachyrhachys kiowa kiowa	?	transparent	shaking? vib. strid.? tipping?	tipping, shaking (ss)
T. k.fuscifrons	silent flights	yellow	ord. strid., tipping (fast)	tipping (slow), shaking (ss)

[1] ss = with substrate-striking.

GENUS *Psinidia* Stal

Two species are traditionally included in this genus, *P. fenestralis* (Serville) and *P. amplicornis* (Caudell) (Rehn, 1919a). *Amplicornis* (from Victoria, Texas) was described as a variety of *Psinidia* (= *Trachyrhachys*) *sulcifrons* by Caudell (1903). Two subspecies of *Psinidia fenestralis* have been described, *P. f. fenestralis* (Serville) from the eastern Gulf and Atlantic coasts, and *P. f. frater,* restricted, according to Rehn, to the coastal regions of Texas. The antennae of both *P. amplicornis* and *P. f. frater* are flattened proximally. Individuals collected by me in Anderson Co., Texas, had flattened antennae but were not identified with certainty because *P. amplicornis* and *P. f. frater* were not compared in detail; I have tentatively considered them as *P. fenestralis* because they were behaviorally quite similar to *P. fenestralis* from Florida.

Psinidia fenestralis (Serville)

P. fenestralis, a sand-inhabiting species widespread along the eastern coastal regions, is found occasionally in isolated colonies in sandy regions in the interior (Vestal, 1913;

Froeschner, 1954; Rehn and Hebard, 1916). I collected *P. fenestralis* in Anderson County, Texas, in Alachua, Marion, and Gulf counties, Florida, in Horry County, South Carolina, and in Berrien County, Michigan. While individuals were always on sand, the amount of cover in which they occurred and in which they were abundant varied considerably. At any given locality individuals seemed to inhabit areas with the least amount of cover. This species is commonly found with *Scirtetica marmorata* and *Trimerotropis maritima,* but it seems to inhabit a wider variety of situations than either of these two species.

PAIR FORMATION.—A population in east Texas, one in western Michigan and four populations along the Gulf and Atlantic coasts all appeared to lack a flight display. Crepitation also appeared to be lacking in the flight of disturbed individuals. Somes (1914) and Morse (1920), however, reported a faint flight crepitation by males. These sounds may have been incidental flight noises and not a specialized sound production.

COURTSHIP.—Florida and Texas males stridulated when they approached females and attempted to mount. I did not see Michigan males court. Stridulation consists of single strokes of the femora. The intervals between 24 such stridulations, 16 by Texas males and eight by Florida males, were not consistent, varying from 0.2 seconds upwards. When two stridulations occurred within a fraction of a second of one another, they were always produced by different femora. The repeated production of single strokes of stridulation by courting males suggests that the pertinent information is contained within a single pulse of sound. Males walked about the terrarium and tipped their femora frequently. The signal appears to have the same function that it does in other Oedipodinae. The tipping movement is not very precise; the femora are rarely tipped together, the speed of the movement varied from 0.6 seconds to 1.0 seconds, and the height to which the femora were raised varied considerably.

AGGRESSION.—Both tipping and shaking commonly occurred in encounters between males, although each signal sometimes occurred alone. The femora struck the substrate males, although each signal sometimes occurred alone. The femora struck the substeate during shaking. The rate of shaking in Florida and Michigan males was considerably slower than that in Texas males. Some morphological difference, chiefly in the antennae, also exist between these two groups. Females tipped their femora, raised them, and kicked out with their tibiae to repel males, but no femur-shaking occurred.

GENUS *Derotmema* Scudder

Derotmema haydenii (Thomas)

Derotmema haydenii is widely distributed over the western United States. It occurs from Alberta to Mexico and from southern California and Nevada, east to the Dakotas, Oklahoma, and Texas (Newton and Gurney, 1956:938). It lives on dry, bare soil with sparse vegetation (Ball et al., 1942; Brooks, 1958).

Four subspecies have been described in this species: *haydenii,* which occurs in the Great Plains from Montana to New Mexico, *rileyanum* from the Great Basin, *mesembrimum* from northern Mexico and Western Texas, and *laticinctum* from western Texas to southern California (see Rehn, 1919a; Ball et al., 1942). I collected specimens on open ground in desert grasslands near Douglas, Arizona (*h. laticinctum*), near Bicknell, Utah (*h. rileyanum*), Pueblo, Colorado (*h. haydenii*), at Big Pine, California (*h. rileyanum*?) and near San Luis Potosi, Mexico (unidentified subspecies).

PAIR FORMATION.—I neither saw nor heard any flights by solitary individuals. Near Douglas, Arizona, two males of *D. haydenii* twice hopped toward a much larger moving female of *Trimerotropis latifasciata.* Flights by disturbed males were low, direct, and without crepitation. At all localities males walked about on the open ground, occasionally producing femur-tipping movements.

COURTSHIP.—Utah Population: Males stridulated during each of three approaches; a single stroke of ordinary stridulation was produced during one approach and three pulses of sound during two other approaches. Both femora were used in producing the soft, barely audible pulses of sound.

Colorado Population: I saw six courtship sequences: twice males only tipped their femora before attempting to mount, twice males tipped and then stridulated before mounting, and twice males only stridulated before attempting to mount. In femur-tipping the downstroke was faster than the upstroke. Sometimes the femora were tipped several times in quick succession (about two per second).

California Population: A male courted a female seven times, always first tipping his femora and then stridulating. The stroke rate and the number of strokes of stridulation were variable. During femur-tipping the femora were sometimes raised to about the 135° position. Tipping sometimes occurred several times in quick succession (about 4 per second).

AGGRESSION.—Two aggressive signals were common in all populations. Femur-tipping was produced in most encounters; the movement was rapid, and the upstroke was faster than the downstroke. The femora were tipped to vertical, and the tibiae were extended to 45° from the femora at the highest portion of the movement. Femur-shaking was performed by males touched by other males. During shaking the tibiae struck against the substrate. I saw another form of shaking once in Utah individuals. This was slower and interspersed between bursts of the other form of shaking; in it, the femora did not strike the substrate but instead struck the tegmina lightly. Femur-shaking by Colorado females was observed once. A female touched by another female raised her femora and shook them in the raised position. Females also jerked their femora when touched, sometimes repetitively, so that the movement was almost like femur-shaking.

GENUS *Mestobregma* Scudder

Mestobregma plattei (Thomas)

M. plattei occurs from northern Mexico to western Canada and from Utah and Arizona east to South Dakota and Kansas (Newton and Gurney, 1957:109). Three subspecies have been described: *p. plattei* (Thomas) on the Great Plains to southern Colorado, *p. corrugata* (Scudder) from northern New Mexico southwards and *p. rubripenne* (Bruner), from central and southern Arizona (Rehn, 1919a). I found *p. corrugata* on open ground in the desert grassland near Bicknell, Utah, and *p. plattei* on open ground and open sand at two localities in the San Luis Valley of Colorado.

PAIR FORMATION.—I did not hear or see any flights by solitary individuals. Presumably pair formation occurs primarily as a result of males approaching moving females.

COURTSHIP.—Utah Population (probably *p. corrugata*): Males approached and attempted to mount females seven times. They stridulated during four of the approaches (producing a single stroke of stridulation two times and three strokes of stridulation two times), but failed to stridulate during three other approaches. Sometimes sound was produced on both up- and downstrokes, yielding two closely spaced pulses of sound per stroke, but usually sound was produced only on the downstroke. I did not record the presence or absence of femur-tipping during these approaches. Colorado Population (probably *p. plattei*): Seven approaches and mountings were observed: two in the field and five in the laboratory. Tipping was present and stridulation was lacking in all approaches. Tipping by courting males differed markedly from that performed by aggressive males; each tipping movement was rapid and several were performed in quick succession. In the field two males rapidly approached a third moving male and made rapid, courtship-type tipping movements as they advanced. When the three were within several inches of one another they began to produce slow tipping motions (about one second in duration).

AGGRESSION.—Femur-tipping and femur-shaking (with substrate-striking) were performed in encounters between males. In some encounters both signals were performed. For instance, when a male approached and touched a copulating pair, the copulating male tipped, then shook his femora; the approaching male then also shook, tipped, and departed. In Colorado males, aggressive tipping was about one-fifth as rapid as courtship tipping.

GENUS *Trachyrhachys* Scudder

Trachyrhachys kiowa fuscifrons (Stal)

There are behavioral indications that the two subspecies *T. k. kiowa* and *T. k. fuscifrons* may be separate species. But neither subspecies has been studied intensively and intervening populations have not yet been examined. Hebard (1931a, 1934a), and other orthopterists believe that *T. kiowa* is a single species, varying in wing color from yellow to transparent and in banding pattern from banded to unbanded from the eastern and southeastern portion of the range to the western and northern portions of the range. This species lives in areas of bare ground and short grass (Blatchley, 1920; Hebard, 1937; Coppock, 1962). I collected it in Livingston Co., Michigan, Washington Co., Maryland, Anderson Co., Texas, and in open vegetation with short grass in Harmon Co., Oklahoma. Only the behavior of individuals from Maryland, Michigan and Kansas was studied.

Pair Formation.—Males observed in an old stone quarry in Livingston County, Michigan, made no crepitation flights. Instead, they ran about on open ground and at times stood motionless for many minutes. Unlike *Spharagemon collare,* which otherwise behaves similarly, *fuscifrons* males occasionally made short, low flights for which the stimulus is unknown. As males walked about, two kinds of femur-tipping were produced: fast and slow (see below). Males approached other moving individuals by walking and hopping. Approaching by flying was not observed but may occur in view of the fact that the hindwings are colored.

Courtship.—Courtship of Michigan and Maryland individuals was similar. In the laboratory I observed four sequences in each group. During each approach, males produced single strokes of stridulation, using both femora. As a Maryland male mounted a female he tapped her head with his antennae. The movement was similar to that observed in *Pardalophora phoenicoptera, Chortophaga viridifasciata* and *Hippiscus ocelote.* In the field, Michigan males twice approached other moving males, producing the fast type of femur-tipping (0.2 seconds), but without stridulating. The males being approached produced much slower (duration: more than one second) tipping motions; these were followed by equally slow tipping motions by the approaching males and the separation of the males.

Aggression.—Aggressive femur-tipping was much slower than the tipping motions performed by approaching males. It varied from 1.5 to 2 seconds in duration and usually led to the separation of males. But when males established contact with one another, they shook their femora, striking the substrate with the tibiae.

Trachyrhachys kiowa kiowa (Thomas)

I collected two males and a female on open ground in Sherman County, Kansas, and saw no pair formation in the field.

Courtship.—Observations made on the courtship of this species were confusing. Four times males shook their femora as they approached other individuals. Twice males mounted, but no copulation ensued. Each male approached and mounted a female more than five times without producing any acoustical signals. Although males did not stridulate while approaching, one of them produced three bursts of vibratory stridulation as he walked about the chamber.

Aggression.—The duration of femur-tipping varied: walking males produced rapid tipping motions lasting about 0.2 seconds; stationary males produced tipping lasting about 0.5 seconds. I saw no very slow tipping such as occurs in *fuscifrons,* even in encounters between males. In male–male encounters males shook their femora, striking the substrate with the tibiae.

GENUS *Trimerotropis* Stal

This genus includes 50 or more species. Most occur in the western United States or Mexico. A few extend into Canada, or eastward to the Atlantic coast or into Central and South America. Although this genus seems for the most part quite distinctive, there are species which seem intermediate between it and the genera *Conozoa* (e.g., *Trimerotropis bilobata*), *Spharagemon* (e.g., *Spharagemon humile*), and *Circotettix* (e.g., *T. verruculata*). *Hadrotettix* is another closely related genus (see Gurney, 1940a). The major revision of the genus is that of McNeill (1901), which has been the main source for the identification of the species encountered in this study, particularly the western species. Since only 18 of the species in this genus were examined, little can be said about the overall relationships among the various members. Several inconsistencies between behavioral information and the current taxonomy of this group have been encountered and are discussed in the following descriptions. The most notable of these involve the species *T. maritima, T. verruculata,* and *T. californica.*

Trimerotropis pallidipennis (Burmeister)

Trimerotropis pallidipennis is widespread and very common in the western United States, particularly in the Southwest (Newton and Gurney, 1957:432). It is not abundant east of the shortgrass prairies, limited perhaps by an excess of vegetational cover. It ranges from western Canada into South America and appears to be most abundant in desert and semi-desert regions. Two subspecies are currently recognized: *T. p. pallidipennis* in the southern portions of the range and *T. p. salina* McNeill in the northern portions of the range. I watched only members of the former subspecies, which was collected and observed at the following localities: (1) near Albany, Texas; (2) Sutton County, Texas; (3) Lubbock, Texas; (4) Pecos River, Texas; (5) Big Bend National Park, Texas; (6) near Van Horn, Texas; (7) near Lordsburg, New Mexico; (8) near Douglas, Arizona; (9) Alpine, California; (10) near Warner Springs, California; (11) near San Luis Potosi, Mexico; (12) near Presidio, Texas; (13) at Crow Junction, Colorado; (14) near Trinidad, Colorado; (15) near Alamosa, Colorado; (16) San Gabriel Mountains—near Glendora, California; (17) Yosemite National Park, California, and (18) Mariposa, California.

PAIR FORMATION.—I heard or recorded crepitation at all localities except Albany and Yosemite; recordings were made at (3), (6), (7), (10), (11), (14), (15), and (16). Courtship stridulation was recorded at (1), (2), (7), (9), (10), (13), (16), and (18), but only heard at (4), (5), (6), and (8). I saw courtship of individuals from (14), (15), and (17). Some observations suggest that crepitation initiates pair formation but this has not yet been proven. For instance, at Big Bend National Park many individuals were present around a parking lot and adjacent bare areas, and crepitation flights were frequent. One male flew, landed, then walked in a straight line, stopping periodically; during these stops he tipped his femora, and sometimes produced several bursts of stridulation as he advanced. After several minutes of wandering he flew up, crepitated, landed ten feet away, and began to walk about again. The same alternation of crepitation and walking by lone individuals was observed near Lubbock, Texas, near San Luis Potosi, Mexico, and near Trinidad, Colorado. Near Van Horn, Texas, however, where there were large numbers of *T. pallidipennis,* crepitations were very few compared to those by *Arphia pseudonietana,* which was abundant in an adjacent area of open vegetation and semi-open ground. Near Presidio, many individuals occurred on a rocky hillside, and again crepitations were decidedly rare. The apparent rarity of crepitation flights in some populations cannot yet be explained. Crepitation consists of a series of bursts, and each burst consists of 3–6 wing snaps (Fig. 17). The number of bursts produced during a flight depends on the length of the flight. Females do not crepitate.

COURTSHIP.—Ordinary stridulation, the only acoustical signal made by courting males, consisted of a rapid up and down movement of a single femur producing a trilling sound (Figs. 9a, b, c). Each trill consisted of 2–14 leg strokes. One to eight trills were produced in quick succession by males advancing toward females. Successive trills were spaced at constant intervals. A single trill was heard and seen once, and two or more trills were heard and seen more than ten times. In the field I made the following observations: (1) Pecos River: When a flushed female flew and landed on open ground, a male began to approach her from four feet away. When he was about a foot from her, he produced several series of trills in quick succession; she remained stationary and passive as he approached and mounted. I saw a similar sequence involving a different male and female at the same locality. (2) Near Douglas, Arizona: A female of *Trimerotropis latifasciata,* a similar appearing species, flew and landed on open ground. Four *pallidipennis* males and two *Derotmema haydenii* males ran and hopped towards her from various directions, all from more than three feet away. One *pallidipennis* male flew toward the female producing three bursts of crepitation. The other *pallidipennis* males stridulated as they approached. The female raised her femora and tilted them forward to the repelling position; the males milled about her, stridulating and exchanging aggressive signals. A few seconds later she flew again, alighting 10–15 feet away; both *pallidipennis* and *Derotmema* males hopped towards her once again, and one of the former attempted to mount, but was prevented from doing so when she raised her femora. (3) Alpine, California: A male flew toward a female that had just alighted. He landed about four feet from her; as he approached her he shook first one femur then the other, alternating about three times. The movement appeared similar to that made during stridulation, but I detected no sound. When he was a foot from the female he produced an audible *pallidipennis* type of stridulation. He finally mounted her. The soundless movements preceding stridulation were not seen in courtship observed in the laboratory.

The stridulation rate of individuals collected at Crow Junction, Colorado, was considerably slower than that of other populations recorded (Fig. 9c). This marked difference may be owing to geographic variation in this character. Unfortunately no crepitation flights were recorded at this locality.

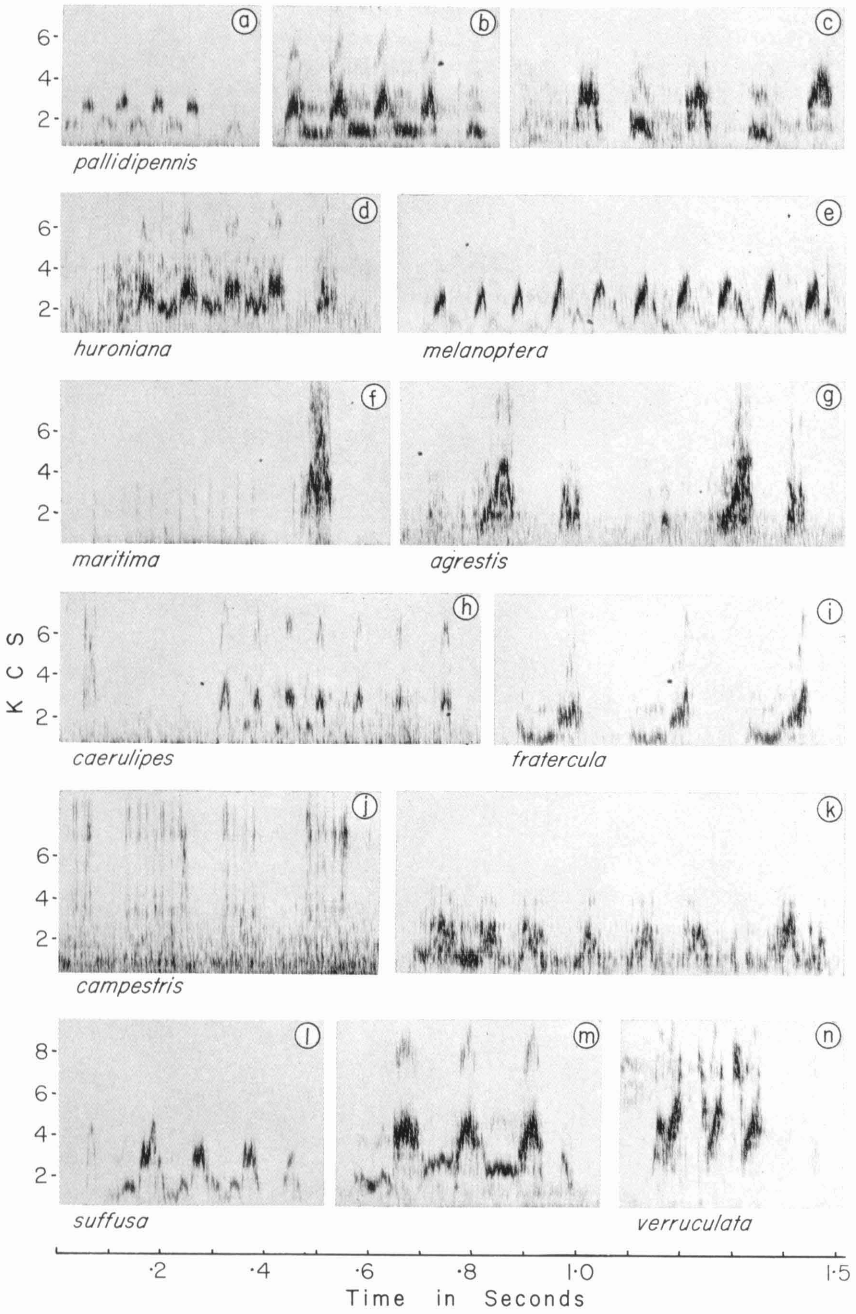
Aggression.—Femur-tipping in *T. pallidipennis* is characterized by a rapid, jerk-like upstroke and a relatively slow downstroke. The femora move synchronously and are tipped up to about 80° from horizontal. The height of the upstroke seems to depend on the intensity of the aggressive interaction. Solitary males frequently tipped their femora, usually to about 45°, but typically males tipped most often in encounters with other males. Solitary males, however, did not shake their femora. During shaking the ends of the tibiae always struck the substrate, and occasionally the tegmina. Males sometimes produced one to several bursts of ordinary stridulation during the flight of another individual in the same terrarium. The rate of the leg movement was more rapid than in courtship, stridulations ended when flight ended, and stridulating males remained stationary throughout. The function of this behavior is not known.

Trimerotropis huroniana E. M. Walker

T. huroniana is known from the northern shores of Lake Michigan and Lake Huron, from one locality on Lake Superior and from several islands in Lake Michigan. On the basis of both the morphology and the behavior, this species seems to have been derived from *T. pallidipennis.* While this species is found in the same habitats as *T. maritima,* the two species are geographically separated. Only *maritima* occurs along the southern beaches of Lake Michigan and Lake Huron, and only *huroniana* occurs along the northern beaches (Hubbell, 1929). These two species have not been found together at one locality. This may be due to the presence of some sort of competition between them, since no natural boundaries to their northward or southward distributions seem to exist. The boundaries between them appear to have shifted considerably in the last 30 years. In 1941, according to Cantrall's collections, the transition from *maritima* to *huroniana* on the western Michigan shore was somewhere between Pierport and Platte River Point. According to my collections made in 1965 and 1966, the transition seems now to be about 50 miles farther south between Pentwater and Muskegon. On the eastern Michigan shore, Hubbell (1929) recorded *huroniana* from two localities in Huron County and *maritima* from one locality in St. Clair County. In 1966 I collected *maritima* in St. Clair, Huron, and Bay counties and *huroniana* only as far south as Iosco County. In Ontario the transition point was in the vicinity of Southampton (Walker, 1902b). Since I did not make the 1965 and 1966 collections at precisely the same localities as the earlier collections, it is not certain that any shifts have occurred, but a gain for *huroniana* along the west coast and a gain for *maritima* on the east coast is suggested. These two species may be competing on four different fronts, the north-south shores of Lake Michigan and Lake Huron. A more detailed tracing of the distributions of the two species along each shore would be desirable.

Pair Formation.—At five localities *huroniana* occurred only on open sand with scattered grasses. At two dense populations in Grand Traverse and Cheboygan counties, Michigan, I heard only two or three crepitating flights other than those made during disturbance, but I did not determine the contexts of these crepitations. Usually, two or three bursts of crepitation were produced during each flight. In general, crepitation is similar to that of *pallidipennis.* The wings are only faintly yellow and the wing band is less conspicuous than in *pallidipennis.*

Fig. 9. Audiospectrographs of courtship signals of *Trimerotropis* species: (a) *T. pallidipennis* (Texas), ordinary stridulation, 85°F; (b) same, (Alpine, Calif.), ordinary stridulation, 93°F; (c) same (SE Colorado), ordinary stridulation 85°F; (d) *T. huroniana* (Mich.), ordinary stridulation, 86°F; (e) *T. melanoptera* (NE New Mex.), ordinary stridulation, 86°F; (f) *T. maritima* (W Mich.), femur-shaking with substrate-striking followed by one pulse of ordinary stridulation, 90°F; (g) *T. agrestis* (Colo.) ordinary stridulation, 95°F; (h) *T. caerulipes* (Mariposa, Calif.), ticking type of ordinary stridulation followed by a trill of ordinary stridulation, 82°F; (i) *T. fratercula* (Colo.), ordinary stridulation, 87°F; (j) *T. campestris* (NE New Mex.), vibratory stridulation, 90°F; (k) same, ordinary stridulation; (l) *T. verruculata* (Yosemite), ordinary stridulation, 85°F; (m) same (Utah), 95°F; (n) same (Mich.), 80°F. Temperatures measured 3 inches above the substrate.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Time in Seconds

COURTSHIP.—Ordinary stridulation is very similar to that of *pallidipennis;* it was given in bursts, which contained 2–8 pulses (Fig. 9d). Approaching males often produced a series of trills; the number of trills appeared to depend on the distance between male and female after stridulation had commenced. Males stridulated only while advancing. Each series of trills was produced with one femur, and intervals separating successive trills in a series were quite constant. Nine of twelve mounting attempts were preceded by stridulation. The remaining attempts may have been preceded by femur-tipping.

AGGRESSION.—Tipping and shaking signals are also similar to those of *pallidipennis.* I did not see females either tip or shake their femora.

Trimerotropis (near *pallidipennis*)

A species of *Trimerotropis,* which I have been unable to identify and which is very similar to *T. pallidipennis* but slightly smaller, was observed and recorded by R. D. Alexander near Bakersfield, California, in May, 1967 (pers. comm.). This species was found in light vegetation characteristic of habitats of *pallidipennis.* Crepitation was very similar to that of *pallidipennis,* consisting of regular bursts (Fig. 10a).

COURTSHIP.—A single lengthy approach of a male was observed. A disturbed female flew past a male and settled on bare ground. The male flew a short distance toward her and then began to approach by walking. As he approached he produced four kinds of signals: (1) a silent "flipping" movement with the hind femora (probably femur-tipping); (2) single pulses of ordinary stridulation (Fig. 10b); (3) bursts of femur-shaking with wing-striking (Fig. 10c); (4) trills of ordinary stridulation as in *pallidipennis* (Fig. 10d). Usually the single pulses of ordinary stridulation were preceded by "flipping" movements of the femora. First, series (2–8) of single, irregularly spaced stridulations, interspersed with single bursts of shaking, were produced as the male advanced. Then, just before the male attempted to mount, he produced two trills (of three and five strokes) of ordinary stridulation. The whole sequence, using the numbers given above to designate the movements, was as follows: 2–2–2–2–2–2–2–3–2–2–2–2–2–2–3–2–2–2–2–2–2–2–2–3–2–2–2–3–2–2–3, male stops 18 inches from female; female moves; male advances, producing 2–2–2–2–2–2–3–2–3–2–2–3–2–2–2–4–4, and mounts female.

Aggressive behavior was not observed in this species.

Trimerotropis melanoptera McNeill

This species occurs on shortgrass plains from eastern Colorado, through New Mexico to western Texas, southeastern Arizona, and Sonora (Newton and Gurney, 1957:432; Ball et al., 1942; Tinkham, 1948). It is broadly sympatric with *pallidipennis.* I studied it near Raton, New Mexico.

PAIR FORMATION.—I frequently heard and saw crepitation flights by solitary males. These were similar to those produced by *pallidipennis,* but the crepitation rate was about one-half that of *pallidipennis,* and the burst rate was also considerably slower (Fig. 17). I did not see males approach other individuals by flying as in *pallidipennis.* Morphologically, *melanoptera* is somewhat similar to *pallidipennis;* it differs in being darker, in possessing a very broad dark band on the hindwings, and in being slightly larger. Because of the difference in wing coloration, flying males of these two species can easily be distinguished.

COURTSHIP.—I saw three courtship sequences in the field. As males approached females they first produced a series of femur-tipping motions; then, when they were about a foot away, they produced trills of ordinary stridulation (Fig. 9e) sounding very much like trills produced by *pallidipennis.* Unfortunately I did not record courtship stridulations by *pallidipennis* at the same localities.

AGGRESSION.—Femur-tipping and femur-shaking are very much as in *pallidipennis* except that tipping is somewhat slower.

Trimerotropis californica Bruner (includes *Trimerotropis strenua* McNeill?)

Individuals of *Trimerotropis* collected near Benson and near Gila Bend, Arizona, in the San Gabriel Mountains, California, and in the Mojave Desert, near Lancaster, California, can be construed on behavioral grounds to belong to the same species. In the keys of McNeill (1901) and Ball et al. (1942), the Arizona specimens key out as *T. strenua.* The San Gabriel specimens key out as *californica* and the Mojave specimens appear somewhat intermediate but perhaps closer to *californica.* McNeill described *T. strenua* from a single male from Boise City, Idaho, and stated that this species was very closely related to *T. californica*. California and Arizona populations share similar pair-forming signals and courtship patterns. Rehn and Hebard (1905, 1910a) thought it probable on the basis of morphology that *strenua* does not constitute a separate species from

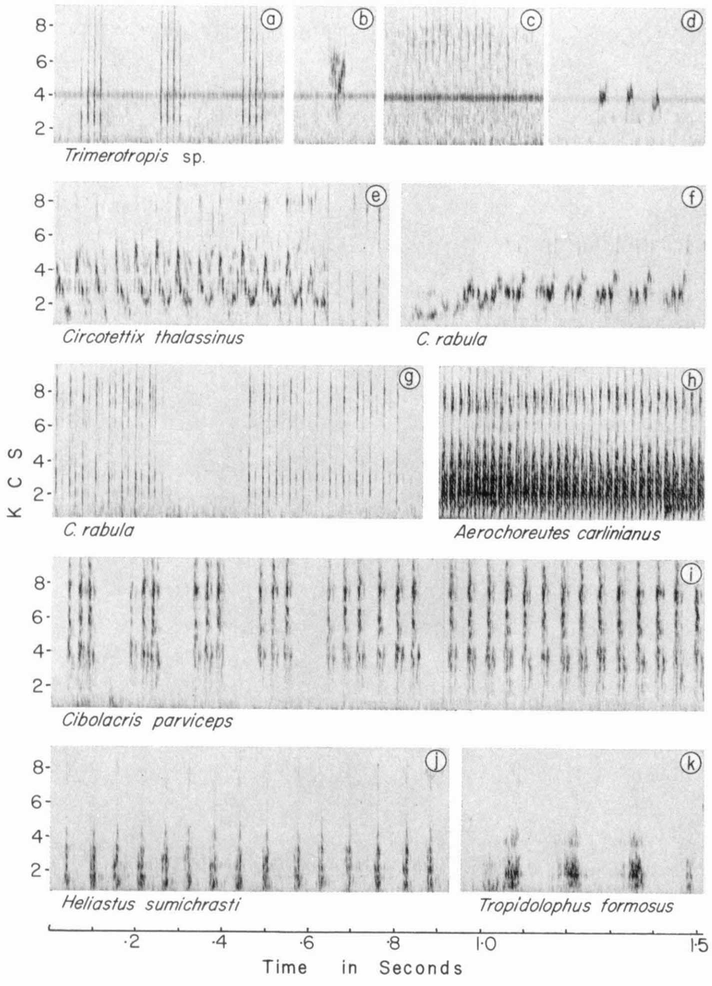

FIG. 10. Audiospectrographs of signals by various species of Oedipodinae: (a) *Trimerotropis* (near *pallidipennis*) (Bakersfield, Calif.), flight crepitation, 75°F; (b) same, single-pulse ordinary stridulation; (c) same, courtship femur-shaking with wing-striking; (d) same, trill of ordinary stridulation; (e) *Circotettix thalassinus* (White Mtns., Calif.), trill of ordinary stridulation by one male (first portion) and aggressive femur-shaking with wing-striking by a second male in response to the signal of the first male, 93°F; (f) *Circotettix rabula* (Eagle Co., Colo.), trill of ordinary stridulation, 92°F; (g) same, flight crepitation, 90°F; (h) *Aerochoreutes carlinianus* (Las Animas Co., Colo.), flight crepitation, 86°F; (i) *Cibolacris parviceps* (Indio, Calif.), courtship femur-shaking with wing-striking, 104°F; (j) *Heliastus sumichrasti* (Tampico, Mexico), courtship femur-shaking with wing-striking, 96°F; (k) *Tropidolophus formosus* (Brewster Co., Texas), ordinary stridulation, 91°F. Temperatures in (g) and (h) taken at waist level; remaining temperatures taken 3 inches from substrate.

californica. I shall tentatively consider the various individuals as belonging to the same species. Bruner's designation, *T. californica,* takes priority. According to Newton and Gurney (1957: 456) *T. strenua* is found in desert regions of the southwest and extends from northern and western Mexico to Oregon and Idaho, and from southern California east to Texas, New Mexico, and western Colorado.

PAIR FORMATION.—I collected after sundown near Benson and heard no crepitations. Near Gila Bend I tape-recorded a single crepitation. In the San Gabriel Mountains and on the Mojave Desert in California I heard numerous crepitations, some by solitary males. All crepitations consisted of a single burst. In the Mojave desert most individuals were found either on low vegetation or on shaded ground, apparently because of the high surface temperature.

COURTSHIP.—Benson and Gila Bend Populations: Shaking with substrate-striking was the only courtship signal produced. Nine times males shook their femora as they turned toward other individuals or while approaching and trying to mount females. Twice, a male shook as he turned toward another male. San Gabriel Population: During two approaches males tipped and shook their femora. During five approaches males only shook their femora. One mounting attempt was not preceded by femoral movements. The substrate was struck during shaking. Mojave Population: Nine approaches and attempts to mount were all accompanied by one or more bursts of femur-shaking. A male wandered about a female, facing her continuously, and produced three bursts of shaking before attempting to mount. In no case did tipping precede shaking.

AGGRESSION.—Benson and Gila Bend Populations: Tipping was the only aggressive signal produced in 25 male – male encounters, even though contact was established in several of these encounters. Shaking may have lost its aggressive function entirely in this part of the species range. San Gabriel and Mojave Populations: Males of these two populations shook their femora *only* when touched. Females tipped, shook and raised their femora when repelling males.

In general appearance *californica* is most similar to *pallidipennis.* These two species overlap broadly geographically and seasonally in the western United States and sometimes occur at the same localities. There may be some ecological separation of these species. At a locality in the San Gabriel Mountains, California, numerous individuals of *pallidipennis* but no *californica* occurred olong the open roadway. But along an adjacent stony and sandy river bed with scattered shrubs and bushes *californica* was abundant and *pallidipennis* was absent.

Trimerotropis maritima (Harris)

Currently, three eastern *maritima*-like species are generally recognized: *T. maritima, T. citrina,* and *T. acta.* On the basis of morphology, sexual behavior, and hybridization experiments it can be argued that a single species is in fact involved. Tibial color, the width of the black band on the hind wings, the degree of fasciation of the tegmina and the color of the inner face of the hind femora have been used to distinguish these three forms. These characters do not vary concordantly, and all intermediate conditions can be found at some localities. In general, the animals on the beaches have lighter color. Those along the north Atlantic coast (New Jersey to Massachusetts) usually have yellow tibiae, while those farther south usually have red tibiae. Carothers (unpublished) crossed specimens of *maritima* and *citrina* (specimens in UMMZ collection). She got fertile F_1s and backcrosses. Sexual behavior also suggests that a single species is involved. I studied the behavior of specimens of all three types from the following localities: (1) Ipperwash Provincial Park (Lake Huron), Ontario; (2) Berrien County, Michigan; (3) Ottawa County, Michigan; (4) Huron County, Michigan; (5) St. Clair County, Michigan; (6) Jackson County, Florida; (7) Franklin County, Florida; (8) Pinellas County, Florida; (9) Volusia County, Florida (6 miles inland from Ormond Beach); (10) Ormond Beach, Florida; (11) Nassau County, Florida; (12) Horry County, South Carolina; (13) Long Island, New York; and (14) Comanche County, Oklahoma. At all locations except (6), (9) and (14) individuals occurred on sandy dunes either near lakes or the ocean. At the remaining localities they occurred in open sandy areas.

PAIR FORMATION.—I observed pair formation in the field at localities (5), (6) and (9). At (5) a disturbed male flew a distance of 15 feet and landed on open sand. Immediately after landing another male flew towards him from six feet away, producing a single burst of crepitation during the last portion of the flight. The approaching male landed nine inches from the other male. Both remained perfectly motionless for about 30 seconds; when the first male moved slightly, the second immediately turned toward and approached him. The approaching male produced about five pulses of ordinary stridulation when the two were six inches apart, then shook his femora and produced two pulses of ordinary stridulation in quick succession when three inches apart. The stationary male tipped his femora several times as he was approached. The approaching male then also tipped his femora. When the two males touched they continued to tip their femora, and one of them produced a burst of shaking. No mounting was attempted and the males separated.

At locality (6) a disturbed female flew and alighted 30–40 feet from me. Immediately after her flight, or perhaps even during the end of it, a male from somewhere to my right flew directly toward the female, landing about two feet from her. About a second later a second male flew 20 feet directly towards them and landed close to the male. The second male crepitated during the last few feet of flight. All three individuals then remained motionless.

At locality (9) a male ran toward a female that had just landed 15 feet away. When he was a few inches from her he shook and stridulated twice in quick succession. The female raised her femora, then flew away.

At all three of the above localities I found many individuals, but the only crepitations heard were those produced during approaching and disturbance flights. Perhaps crepitation does not initiate pair formation but merely announces a male's approach.

COURTSHIP.—Shaking with substrate-striking precedes stridulation in courtship (Fig. 9f). Shaking, however, is sometimes the only signal given. In four of 24 courtship sequences by Long Island males, stridulation preceded femur-shaking, but in each case, stridulation also followed shaking. Stridulation was never the only signal performed by approaching males. Table 10 indicates the number of courtship sequences in which both shaking and stridulation were produced, the number in which only shaking was produced, and the number in which no signals were performed before mounting was attempted. In three out of 24 courtship sequences, Long Island males tipped their femora before performing the other two signals. Stridulation usually consisted of a single stroke of both femora.

AGGRESSION.—Tipping is similar to that of *pallidipennis*. In male—male encounters the femora were usually tipped to the vertical position. Shaking in aggressive situations appears to be identical to that in courtship situations. In the laboratory, males from localities (2), (4), and (7) stridulated during the flight of other individuals; males from

TABLE 10

NUMBERS OF COURTING SEQUENCES IN *Trimerotropis maritima*

Collecting locality	Involving shaking, then stridulating	Involving shaking only	Involving no signals
Berrien Co., Michigan	7	8	0
Ipperwash, Ontario	11	17	0
Ottawa Co., Michigan	1	1	0
Huron Co., Michigan	0	3	2
St. Clair Co., Michigan	3	1	0
Jackson Co., Florida	4	5	0
Franklin Co., Florida	0	1	0
Pinellas Co., Florida	2	2	0
Volusia Co., Florida	2	0	0
Ormond Beach, Florida	0	13	0
Nassau Co., Florida	0	1	1
Horry Co., South Carolina	0	2	1
Comanche Co., Oklahoma	0	2	0
Long Island, New York	23	1	0

(2) and (7) produced two and three pulses of ordinary stridulation, and a male from (4) produced a longer burst of stridulation. This behavior is quite similar to that observed in *pallidipennis,* but its function is not known.

Females tipped, raised, and shook their femora when rejecting males. A female from Long Island often jerked her femora when touched by other individuals, sometimes repetitively up to about four jerks per second; the movement appeared to be intermediate between the graded femur-jerking movements and non-graded, stereotyped femur-shaking. The substrate was not struck during jerking.

Trimerotropis agrestis McNeill

According to Newton and Gurney (1957: 316) *T. agrestis* occurs from northern New Mexico and western Utah to western Nebraska and eastern Montana. I found a dense population of this species a few miles east of the Great Sand Dune National Monument in the San Luis Valley of Colorado. Individuals were crepitating and walking about on bare sand among the vegetation, mostly sunflowers and scattered, thick bunches of grass. *Mestobregma plattei* and *Spharagemon collare* occurred in the same area.

PAIR FORMATION.—I heard many crepitations by solitary males, each consisting of a single burst. A male flew, crepitating, towards a female that had just landed. As he walked toward her he tipped his femora several times. When he was about six inches from her, he produced four strokes of ordinary stridulation and then mounted her.

COURTSHIP.—Four courtship sequences in the laboratory were like the one observed in the field. Males produced ordinary stridulation (Fig. 18g) as they approached and attempted to mount females, but femur-tipping did not precede stridulation every time.

AGGRESSION.—Femur-shaking (with substrate-striking) and femur-tipping were performed in aggressive encounters even when no contact between males was established. Femur-tipping is similar to that of *pallidipennis.*

Trimerotropis gracilis (Thomas)

T. gracilis is apparently found mainly in areas covered with sage brush from northern Arizona and New Mexico, north to Washington and Montana and from northwestern California, east to Colorado and western South Dakota (Newton and Gudney, 1957: 409). In the San Luis Valley of Colorado I found individuals on bare ground in sage brush areas at three localities.

PAIR FORMATION.—Crepitation flights by solitary undisturbed males were frequent, and males ran about on the bare ground between crepitations. Males and females crepitated during disturbance flights. During crepitation flights the wings of males and females do not snap with each wing beat; instead, a snapping sound is produced every third or fourth beat of the wings. Consequently, the crepitation rate is comparatively slow. The near-silent wingbeats can be heard and seen not to correspond to the crepitation rate.

COURTSHIP.—Two courtship sequences involving different pairs occurred in the field: (1) A female flew and crepitated when she was disturbed. When she alighted a male five feet away walked towards her, producing single pulses of ordinary stridulation and femur-tipping signals. The number of stridulations increased when he was near the female. The female spread both femora away from her abdomen as the the male mounted. (2) A male approached a female that had just alighted. He produced irregularly spaced single pulses of stridulation during the entire approach (3–4 feet), but no femur-tipping movements were made. The female also spread her femora away from her abdomen as the male mounted. Femur-tipping in these two courtship sequences consisted of both upstrokes and downstrokes of about equal length.

In the laboratory I saw nine courtship sequences. Three times males mounted females without first signalling. Three times males tipped femora and stridulated before mounting. Three times males only stridulated before mounting.

AGGRESSION.—Tipping and shaking are aggressive signals. During shaking the tibiae usually strike only the substrate, but on one occasion both the substrate and the forewings were hit. In the field two males tipped their femora as one approached the other. When they were within a few inches of one another, both switched to shaking. They separated without touching one another. In this encounter the upstroke of femur-tipping was faster than the downstroke.

Trimerotropis campestris McNeill

The limits of distribution of this species are, approximately, northern Arizona and New Mexico to western Minnesota and to Alberta (Newton and Gurney, 1957: 368). At four localities in the foothills of the Rocky Mountains of Colorado and New Mexico I found *T. campestris* in grassland with scattered openings of bare ground. Some individuals were on a hillside at an elevation of about 10,000 feet. Near Denver the species is sympatric with *T. pallidipennis* and *Spharagemon humile*. Near Raton, N.M., it lives with *T. fratercula, Circotettix rabula, Spharagemon bolli* and *Arphia pseudonietana*.

Pair Formation.—I tape-recorded crepitation by solitary males near Raton; elsewhere I collected under conditions in which crepitation is not likely to occur. A single burst of crepitation was produced during flight. Both males and females crepitated during disturbance flights.

Courtship.—Courting males performed three types of movements: (1) Bursts of vibratory stridulation (Fig. 9j) were made with one femur during all 38 approaches observed. (2) Femur-tipping sometimes preceded vibratory stridulation. (3) Trills of ordinary stridulation (Fig. 9k) were performed 11 times after males had stopped approaching. Vibratory stridulation was produced while actually advancing; it consisted of bursts of slightly irregular length and the number of bursts varied with the distance to the individual being approached. Ordinary stridulation was only produced when males stopped approaching, for example, when females escaped or made repelling motions. But at times the reason for stopping was not evident. From two to ten strokes made up each trill.

Aggression.—Shaking and tipping are aggressive signals—both were similar to those of *pallidipennis.*

Trimerotropis verruculata (Kirby)

This species is morphologically and behaviorally similar to the next species, *T. suffusa* Scudder. A careful investigation has not yet been conducted, but such a study may indicate that a single, widely distributed and geographically variable species is involved. The ranges of the two species supposedly meet near the boundary between British Columbia and Alberta. According to Hebard (1929), *suffusa* was sometimes mistaken for *verruculata.* The distribution of *verruculata* follows closely the southern edge of the boreal forest region from western Canada to Nova Scotia. The species occurs mainly on exposed rocky or gravelly surfaces (Morse, 1919; Brooks, 1958).

Pair Formation.—Flight displays were very dramatic. Four flights by a male along a stony beach of Lake Superior lasted 30–60 seconds, and the male hovered 1–15 feet above the ground. Several times he remained over one spot, then flew about 40 feet and hovered again; crepitation was present throughout the flights. Snapping sounds were produced in pairs. The interval between the two snaps of a pair was fairly constant, but that between pairs varied somewhat. When the male was rising to a higher elevation burst intervals were comparatively short; when he was dropping to a lower elevation burst intervals were longer. Burst intervals of males remaining at one elevation were intermediate in length. This male's display took place in the vicinity of a single female, but I did not observe her behavior at the time. Walker (1898: 263) ocasionally heard females crepitate; the sound was similar to that of the male though less intense, but the context in which they crepitated was not indicated.

Courtship.—Courtship is similar to that of *verruculata* (Fig. 9l, m). Utah males made sequences (Fig. 9n). Males produced single-stroke ($n=151$), double-stroke ($n=127$) and triple-stroke stridulations ($n=11$) with one femur while approaching. The stroke rate varied between 10.0 and 14.4 per second.

Aggression.—Aggressive behavior is similar to that of *pallidipennis.* The substrate was always struck with the tibiae during shaking, but several times the male also struck his forewings at the same time. One male raised his femora and tilted them forward when touched by a female.

Trimerotropis suffusa Scudder

T. suffusa is found from British Columbia and Alberta, south along the Rocky Mountains to Colorado, Utah, and Arizona, and along the Sierra Cascade Mountains to California. In Canada it "inhabits bare, rocky areas and is often rather common on areas of coal or dark shale outcrops." (Brooks, 1958). In Kane County, Utah, I found individuals on a pile of exposed dark clay along the road near a river. At two localities near a mountain stream in Eagle County, Colorado, they were on dark exposed rocks which in one case were surrounded by a heavy growth of grass. At Yosemite National Park this species was on open ground by the roadside and at the margin of a natural meadow.

Pair Formation.—The flight display of *suffusa* from Kane County, Utah, was virtually identical to that of *verruculata* (see Appendix). I heard several long crepitating flights (30 – 40 seconds), in which males hovered over several spots. A series of three short flights, each lasting 2 – 3 seconds, was performed by one male as follows: The male flew up from a bare patch of ground and landed on another several feet away; 10 – 15 seconds later, he flew again and this time dropped back to the same place; after another 10 – 15 seconds he repeated the latter performance. No other individuals were near him. In Yosemite National Park I recorded only the crepitation of disturbed males. This was similar to the crepitation of a disturbed male of *suffusa* from Vail, Colorado.

Courtship.—Courtship is similar to that of *verruculata* (Fig. 91, m). Utah males made stridulations of 1 – 4 strokes while approaching. The average stroke rate was slower than that of *verruculata* (8–10 per second at 95°F). Yosemite males produced longer bursts of stridulation (see Appendix for comparison). Each burst of stridulation was produced with one femur and the femora sometimes alternated in producing successive bursts of a series. No tipping occurred.

Aggression.—Tipping and shaking were only produced in aggressive situations. In Utah males the femora always struck the substrate but occasionally they struck the forewings at the same time. In males from Yosemite, however, the femora always struck the forewing and the tibiae failed to strike the substrate. Females repelled courting males by raising their femora to near vertical.

Trimerotropis fratercula McNeill

This species is known from the Rocky Mountains and its foothills in Colorado and New Mexico. I recorded and collected it near Beulah, Colorado, and near Raton, N.M., collected it 20 miles northeast of Alamosa, and heard it in the foothills just west of Denver. At each locality it occurred on sparsely covered ground.

Pair Formation.—Crepitation by solitary males occurred at each locality. Near Beulah a male flew and crepitated repeatedly, and between two flights he walked over a rocky, sparsely vegetated hillside tipping his femora and producing ordinary stridulation. Crepitation was produced in bursts and was similar to that of *T. suffusa* (Fig. 17). During disturbance flights females crepitated very much as males do.

Courtship.—Ordinary stridulation was the only signal performed in nine courtship sequences by several males. Each burst or group of stridulations was produced with one femur; the femora sometimes alternated in producing successive bursts (Fig. 9i).

Aggression.—Males tipped and shook their femora when approached or touched by other individuals. The substrate was struck with the tibiae during shaking, but twice the tegmina were also struck at the same time. A female shook her femora after she had raised them to the vertical position, but did not strike the substrate.

Trimerotropis cincta (Thomas)

T. cincta has been collected from northern Arizona and New Mexico to Oregon and western South Dakota (Newton and Gurney, 1957: 388). In Colorado I collected individuals on the lower slopes of the Rocky Mountains in areas covered with pine trees and containing much exposed gravel.

Pair Formation.—Crepitation by solitary males consisted of one to several bursts of irregular length (Fig. 17). A few males flew up and circled above one general area. One male flew for about 50 feet before alighting. Disturbed females did not crepitate.

Courtship.—Both silent shaking and ordinary stridulation are produced by courting males. Shaking was present in each of 18 approaches observed, but ordinary stridulation followed femur-shaking in only 10 courtship sequences. One of the males from the San Luis Valley was yellow, in contrast to the dark colors of all other individuals, and matched the color of short yellow plants that blanketed the ground where he was collected. This male courted a dark female, and courtship was like that of dark males.

Ordinary stridulation usually consisted of a single pulse of sound. Tipping, similar in form to that in other *Trimerotropis* species, sometimes preceded shaking.

AGGRESSION.—Although males sometimes shook when touched by other males, this signal seemed reduced in aggressive contexts. Tipping, however, was usually present in aggressive encounters.

Trimerotropis koebelei (Bruner)

This species is known only from California. I collected it in the western foothills of the White Mountains, Inyo County, California, where it occurred on a stony hillside with scattered pinõn pine but with little other vegetation.

PAIR FORMATION.—I heard only one disturbance crepitation; it consisted of a single burst which lasted for almost the entire duration of a short flight.

COURTSHIP.—Five times, males made ordinary stridulation before attempting to mount females. Once a male made a single stroke of stridulation as he turned toward a female. He did not approach her. Twice a male attempted to mount without producing any signals. Once a male made only femur-tipping motions before attempting to mount. Stridulation was produced with one femur, and each femoral stroke resulted in two closely spaced pulses of sound.

AGGRESSION.—Both tipping and shaking were performed in encounters between males. Tipping was similar to that of *pallidipennis,* and during shaking, the ends of the tibiae struck the substrate. Males first tipped and then shook their femora in encounters, and contact between males was not necessary to elicit shaking.

Trimerotropis calignosa McNeill

This species was described from Los Angeles County, California. I collected individuals answering to the description of *T. calignosa* on bare ground near Yosemite. It was found along with *suffusa* and *pallidipennis.*

PAIR FORMATION.—I collected individuals under overcast skies, and the only crepitations recorded were those produced during disturbance flights. Crepitation consisted of a single burst produced toward the end of each flight.

COURTSHIP.—Nine mounting attempts by males were as follows: Five times no signals were apparent during approaching, twice males only tipped their femora, once a male tipped his femora and then shook them, and once a male produced two pulses of stridulation.

AGGRESSION.—Tipping and shaking with substrate-striking were produced in aggressive contexts.

Trimerotropis caerulipes Scudder

McNeill (1901) reports specimens from Marble Valley, Eldorado County, and Sissons, California, and from Portland, Oregon. I collected what appears to be *T. caerulipes* on open ground near Mariposa, California. *T. pallidipennis* and *Dissosteira pictipennis* also occurred at this locality.

PAIR FORMATION.—I heard no crepitations, even during disturbance flights. The sky was overcast, however, and *D. pictipennis,* also present, was not heard either.

COURTSHIP.—Eleven times males produced faint ticking sounds as they turned toward other individuals. In six of these approaches males also produced a trill of ordinary stridulation which somewhat resembled the trills of *pallidipennis.* Sometimes both femora moved together to produce the ticking sound on the downstroke; other times the femora moved independently and alternated in the production of successive ticking sounds. One to four ticks were produced during each courtship sequence. Trills of ordinary stridulation varied in length up to 8 strokes and followed ticking sounds (Fig. 9h).

AGGRESSION.—Femur-shaking and femur-tipping movements were performed by aggressive males. Both movements were similar to those of *pallidipennis.*

Trimerotropis thalassica Bruner

The distribution of *T. thalassica* is poorly known. I found about ten individuals in an oak grove near Live Oak Springs, San Diego County, California; all individuals were in the brown oak leaves lying on the ground in and about this grove. In the San

Gabriel Mountains, near Crystal Lake, I found two males near a live oak tree under ponderosa pines. These individuals did not crepitate.

COURTSHIP.—Four times males touched females and then mounted them without signalling. However, a one-legged male approached a female from several inches away and stridulated as he advanced. Three pulses of stridulation were given, and sound was produced only on the downstroke. Females made upward jerks of their femora, thus repelling males who attempted to mount. Female femur-tipping was similar to that of males, but it was not made as frequently and the movement was not as rapid.

AGGRESSION.—Shaking was observed more than 30 times; it was always made by males in close proximity to one another and never by males turning towards or approaching other individuals. Femur-tipping is like that of *pallidipennis* and is also an aggressive signal.

Trimerotropis fontana (Thomas)

I collected this species on open and semi-open ground in a clearing in oak woodlands in Cuyamaca State Park, San Diego County, California. *T. pallidipennis* also occurred here. The only crepitations heard were those produced during disturbance flights. The species was not numerous, however, and I spent little time in the area.

COURTSHIP.—Femur-shaking was the only signal made by males in five approaches and mounting attempts; it could barely be heard as a low-pitched hum, neither the substrate nor the forewings being struck.

AGGRESSION.—Only femur-tipping was produced by males in aggressive contexts, even where males were touched by other individuals. As in *T. californica* there appears to have been a complete change in the function of shaking from aggression to courtship.

Trimerotropis (near *fontana*)

I collected a unique male *Trimerotropis* near Crystal Lake in the San Gabriel Mountains of southern California, in an area strewn with boulders and grown to scattered live oaks and ponderosa pines. *Circotettix shastanus* and *T. thalassica* also occurred in this area. In appearance this individual was most similar to specimens in the University of Michigan collection identified as *T. fontana,* but it differed behaviorally from the *fontana* discussed above.

COURTSHIP.—This male approached individuals of *T. thalassica* and *T. calignosa* about 50 times. On one occasion he produced five pulses of ordinary stridulation, followed by a burst of femur-shaking. In all other approaches he produced one or more bursts of femur-shaking. Femur-shaking, unlike that of *fontana,* was very rapid, and the substrate was struck with the tibiae. Femur-tipping sometimes preceded femur-shaking during approaches.

AGGRESSION.—As in *fontana* this male regularly produced femur-tipping but no shaking when he was touched by other individuals.

Trimerotropis albescens McNeill

I discovered a dense population of *T. albescens* on open and semi-open ground in low, gravelly hills near Warner Springs, California. *T. pallidipennis* was also abundant at this locality. I heard a considerable number of crepitations, several by apparently solitary males.

COURTSHIP.—During each of three approaches males produced only ordinary stridulation. Only one femur was used to produce a series of stridulations; for instance, a male made three pulses of stridulation with one femur and then made two pulses with the other femur as he approached the female.

AGGRESSION.—Males tipped and shook their femora in encounters with other males; both movements were similar to those of *T. pallidipennis.*

Trimerotropis rebellis Saussure

This species was described from California. In the UMMZ collection individuals identified as *T. rebellis* were collected at San Bernardino, San Diego, Claremont, Lone Pine, Isabella, Mint Canyon, and Felton, California. I collected the species about 10 miles north of Lancaster in the Mojave Desert.

Pair Formation.—Most individuals were on or at the base of vegetation, presumably because of the ground heat (108°F at one-half inch from the surface). I heard no crepitations.

Courtship.—Stridulation is quite different from that of any other species studied. Males first produced a series of almost silent up and down movements of the femora, from a few to 50 or more strokes. During such a series both femora were gradually brought to bear against the forewings, causing a gradual increase in the sound produced. Then, suddenly towards the end, the femora moved more rapidly, and the intensity of sound increased dramatically. The last loud phase of the song consisted of 5–10 femoral strokes. During parts of the initial, almost silent phase the femora sometimes moved in alternation with one another, but in the final phase they always moved synchronously. Eleven courtship sequences were observed; in one of these, a male made 50 almost silent strokes of his femora but failed to produce the final loud phase of the song; and did not approach the female. Definite alternation of the femora during the initial phase occurred about five times. The entire signal was performed by males that were almost stationary. Femur-tipping did not precede stridulation.

Aggression.—Femur-tipping and femur-shaking were as in *T. pallidipennis.* Males also raised their femora, jerked their femora upwards and kicked out with their tibiae when they were touched by other individuals.

Trimerotropis bilobata Rehn and Hebard

I collected *T. bilobata* on open ground at two localities in Kane and Wayne Counties, Utah. In Arizona *T. bilobata* is found in sandy areas on the desert of the Upper Sonoran Zone (Ball et al., 1942).

Pair Formation.—I did not hear any crepitations other than those made during five disturbance flights. Crepitation in this species is very slow and may be similar to that of *T. gracilis* where the wings are not snapped with each wing-stroke.

Courtship.—A stationary male in a chamber with several individuals of *Mestobregma plattei* made two pulses of ordinary stridulation. In the field one male approached another and produced ordinary stridulation but did not tip or shake his femora.

Aggression.—Tipping and shaking are both aggressive signals; in the latter, the tibiae strike the substrate.

GENUS *Trimerotropis:* SUMMARY

Table 11 summarizes signalling in *Trimerotropis* species. Shaking is part of the courtship sequence in six of the species and may have been acquired independently five times. In several species courtship sequences are similar to those possessed by members of other genera. For instance, the courtship of *T. maritima* is similar to that of *Spharagemon cristatum* and *S. bolli,* and the courtship of *T. californica* is similar to that of *S. crepitans* and *Pardalophora haldemanii.* Vibratory stridulation is performed during courtship of at least one species *(T. campestris)* and resembles that produced by *S. equale* and *S. humile.* Femur-shaking and femur-tipping signals are most similar to those produced by *Spharagemon, Dissosteira, Conozoa,* and *Circotettix* species. All of the *Trimerotropis* species studied seem to possess the ability to crepitate, and in most of them crepitations are performed by solitary males. Flight displays seem to be performed less frequently than in species of *Arphia* and *Spharagemon.* In the laboratory, males of several *Trimerotropis* species stridulated unexplainably during flights of other individuals. This behavior, not known in other genera, is even performed by males of species that do not stridulate in other contexts.

GENUS *Conozoa* Saussure

Four species, all of them occurring in western and southwestern United States, have been described in this genus. Only two were encountered in this investigation; their signalling is summarized in Table 12.

Conozoa carinata Rehn

The distribution of *Conozoa carinata* is little known; it is common in the southern half of Arizona (Ball et al., 1942), where it occurs in sandy washes and in desert grasslands; it is also known from Sonora, Mexico. I observed individuals from

TABLE 11

SIGNALLING IN *Trimerotropis*

Species	flight crepitation	courtship signals	aggressive signals
pallidipennis	regular short bursts	ord. stridulation (bursts), tipping (sometimes)	tipping, shaking (ss)[1]
near *pallidipennis*	"	ord. strid. (single pulses and bursts), shaking (ws), tipping	?
huroniana	"	ord. strid. (bursts), tipping (sometimes)	tipping, shaking (ss)
californica	single burst	shaking (ss), tipping (sometimes)	tipping, shaking (ss) (in some populations only)
maritima	"	ord. stridulation, shaking (ss), tipping (sometimes)	tipping, shaking (ss
verruculata	2-pulse bursts	ord. strid. (bursts)	tipping, shaking (ss)
suffusa	"	"	tipping, shaking (ss) or shaking (ws) Yosemite
agrestis	single burst	ord. stridulation, tipping (sometimes)	tipping, shaking (ss)
gracilis	single burst	ord. stridulation, tipping (sometimes)	tipping, shaking (ss, sometimes also ws)
campestris	single burst	ord. stridulation, vib. strid. (bursts), tipping (sometimes)	tipping, shaking (ss)
fratercula	2-pulse bursts	ord. stridulation	tipping, shaking (ss, sometimes also ws)
cincta	irregular bursts	ord. stridulation, shaking (si), tipping (sometimes)	tipping, shaking (si)[1]
koebelei	single burst	ord. stridulation, tipping (sometimes)	tipping, shaking (ss)
calignosa	single burst	ord. stridulation, tipping (sometimes)	"
melanoptera	regular short bursts	ord. stridulation	"
caerulipes	?	ord. stridulation (single pulses and trills)	"
thalassica	prob. none	ord. stridulation	"
fontana	single burst	shaking (si)	tipping only
near *fontana*	?	ord. strid. (sometimes), shaking (ws)	"
albescens	regular short bursts	ord. stridulation	tipping, shaking (ss)
rebellis	none?	ord. stridulation, silent femoral movements	"
bilobata	single burst	ord. stridulation	"

[1] si = silent; ss = with substrate-striking; ws = with wing-striking. See Appendix for rates.

three populations, one near Douglas, Arizona, a second near Bumblebee, Arizona, and a third near Imuris, Sonora. At each locality individuals occurred on open ground.

PAIR FORMATION.—I heard crepitation by disturbed males at all three localities, and one crepitation by a disturbed female near Imuris. Crepitation was produced in bursts of irregular length. Near Imuris and Bumblebee there were large numbers of individuals, but I heard only a few crepitations other than those caused by my disturbance. Pair formation, therefore, is probably not usually initiated by crepitation. At Bumblebee two males ran up to a female that had just alighted, and near Imuris a male flew and crepitated toward a moving female. In eight instances, pair formation was initiated when an individual moved and attracted one or more males.

COURTSHIP.—The following observations on courtship behavior indicate that femur-shaking is a part of the courtship sequence: (1) Douglas Population (laboratory): A male approached a moving female, shook his femora, then stopped advancing before reaching her. (2) Douglas Population (laboratory): A male approached a moving female. He produced three bursts of shaking, and when he reached her she hopped away. Each burst of shaking lasted 0.5–0.75 seconds. (3) Bumblebee Population (field): A male approached a female that had alighted two to three feet away. He tipped his femora as he advanced, and when he was almost in contact with the female he shook his femora and attempted to mount. (4) Bumblebee Population (field): Two males approached a female walking about two feet away; both tipped their femora as they approached. One male arrived at the female, shook once and mounted. This male and female tipped their femora as the second male approached. The second male continued to tip but walked away without touching the pair. (5) Imuris Population (field): A disturbed female flew away, crepitating, and when she alighted a male three feet distant flew crepitating towards her, landing about nine inches away. He walked towards her and at a distance of six inches shook his femora and produced a single pulse of ordinary stridulaton. Before reaching her he shook and stridulated twice more. The female remained passive and the male mounted. During shaking the tibiae always seemed to strike the substrate.

AGGRESSION.—Femur-tipping was the only aggressive signal seen. One of the Douglas males tipped but did not shake when he was touched by a female and by an individual of another species. (It is possible that femur-shaking is sometimes produced in male–male encounters, but I saw only very few of these.) Femur-tipping was similar to that of *Trimerotropis* species. Unlike *pallidipennis,* however, the tibiae were extended up to 45° from the femora during tipping and were never held against the femora.

Conozoa wallula (Scudder)

C. wallula is widely distributed in California, Nevada, Oregon, Utah, and Idaho, and occurs in Washington and Wyoming (Newton and Gurney, 1956: 883). *C. wallula* and *C. carinata* appear to be completely allopatric. At Bigpine, California, *C. wallula* occurred on open and semi-open ground.

PAIR FORMATION.—Crepitation is very similar to that of *C. carinata.*

COURTSHIP.—I saw males approach other individuals four times in the field. Two males made only tipping movements before they mounted females. Two other males made tipping movements and then a burst of shaking just before mounting. The substrate was struck during shaking.

AGGRESSION.—Tipping was the only signal performed in a single aggressive encounter. Shaking may have lost its aggressive function as it seems to have done in other species in which it has assumed a courtship function.

GENUS *Hadrotettix*

Hadrotettix trifasciatus (Say)

This species is the only member in the genus and it occurs throughout the Great Plains, from Canada to Texas, and extends westward into New Mexico and Arizona. In the east it extends as far as Iowa and Missouri. It inhabits rocky and gravelly areas which are sparsely covered with vegetation (Isely, 1905, 1937; Ball et al., 1942). At Laclede County, Missouri, I found individuals in an open gravelly wash and not in the surrounding thicker vegetation.

Pair Formation.—At Sherman County, Kansas, and at Laclede County, Missouri, this species was abundant, but no flights by undisturbed individuals occurred. Both sexes, however, have contrastingly banded hindwings.

Courtship.—Ordinary stridulation was performed in five of six courtship approaches (Table 12). Tipping sometimes preceded stridulation.

TABLE 12

Signalling in *Conozoa, Hadrotettix, Circotettix,* and *Bryodema*

Species	flight crepitation	courtship signals	aggressive signals
C. carinata	irregular bursts	ord. stridulation (sometimes), shaking (ss),[1] tipping	tipping
C. wallula	irregular bursts	shaking (ss), tipping	tipping, shaking?
H. trifasciatus	none	ord. stridulation, tipping	tipping, shaking (ss)
C. rabula	irregular bursts, long flights	ord. stridulation, tipping (sometimes)	"
C. thalassinus	only disturbance crepitation heard	ord. stridulation	shaking (ws,[1] sometimes also ss) tipping,
C. shastanus	probably crepitates loudly	?	tipping, shaking (ss, sometimes also ws)
B. tuberculata	long, loud crepitation flights	ticking, wing-flapping, tipping	tipping, shaking (ss)

[1] ws = with wing-striking; ss = with substrate-striking.

Aggression.—Tipping and shaking (with substrate-striking) were performed in male–male interactions. Females rejected courting males by (1) hopping away, (2) raising the hind femora and holding the tibiae horizontally over the back while making slight upward kicking motions, (3) tipping the femora, and (4) kicking out with the hind tibiae.

GROUP BRYODEMAE

This group includes the genera *Bryodema* Fieber, *Angaracris* Bei-Bienko, *Aerochoreutes* Rehn, and *Circotettix* Scudder. The members of these genera are apparently all very loud crepitators, since they all possess hindwings with enlarged anal veins. *Bryodema* includes 13 species distributed across the steppes and cold deserts of Asia (Bei-Bienko and Mishchenko, 1951). *Angaracris* includes two species also occurring in Asia. *Circotettix* includes perhaps seven species which occur in the United States. *Aerochoreutes* is a monotypic genus very similar to *Circotettix*.

The communicative behavior of *Bryodema tuberculata* Fieber was studied by Jacobs (1953). In this study *Circotettix rabula, C. thalassinus, C. shastanus,* and *Aerochoreutes carlinianus* were examined.

GENUS *Circotettix* Scudder

Circotettix rabula Rehn and Hebard

This species is widespread in the western United States and Canada and inhabits mainly eroded hillsides. I encountered *C. rabula* at four localities on the lower slopes of the Rocky Mountains of Colorado and on flat terrain near Trinidad, Colorado. It usually occurred along steep hillsides and roadcuts, even though flat but otherwise similar adjacent areas appeared to be available. Near Trinidad a few individuals did occur on open flat ground.

PAIR FORMATION.—*C. rabula* produces the loudest crepitation of any species obeserved in this study. Crepitating flights were also longer in duration and higher than those of any other species. Many crepitation flights were in excess of 30 seconds in duration, and one lasted approximately a minute. Crepitation was not continuous but was broken up into bursts of varying length (Fig. 10g). For instance, the number of wingbeats in 16 bursts of crepitation produced during one flight was as follows: 14, 19, 9, 22, 31, 24, 31, 17, 30, 45, 25, 31, 6, 28, 34. During flights males hovered and circled through the air, and flew from a few feet to approximately 30 feet above the ground. Although generally hovering over one area, they occasionally flew up to 50 yards during a single flight. Females crepitated during disturbance flights.

COURTSHIP.—Males stridulated during three approaches. Sound consisted of trills of varying length produced with one femur (Fig. 10f). Males tipped their femora frequently in a variety of situations, but tipping did not appear to be associated with courtship in particular.

AGGRESSION.—Males tipped their femora in isolation and in encounters with other individuals. The movement closely resembles tipping in *Trimerotropis* species. One male jerked his femora upwards several times in quick succession when touched; the movement seemed somewhat intermediate between jerking and shaking. Shaking (with substrate-striking) was only performed in aggressive contexts. Sexually unreceptive females raised both femora to vertical and made mild backward kicks with their tibiae, tilted their femora far forward and also tipped their femora much as males do.

Circotettix thalassinus Saussure

C. thalassinus was collected on bare gravelly ground in the White Mountains near Bishop, California.

PAIR FORMATION.—Individuals were collected late in the afternoon. Although no crepitation by undisturbed individuals was heard, both males and females crepitated loudly during disturbance flights. As in *C. rabula,* two snapping sounds, one louder than the other, seemed to be produced with each wingstroke. The hindwings of this species are blue, in contrast to the blackish hindwings of *C. maculata* and the yellow hindwings of *C. shastanus,* two species which appear to be sympatric with *thalassinus* in the Sierra Nevada.

COURTSHIP.—In two courtship sequences males produced several trills of ordinary stridulation while approaching females (Fig. 10e). Only one femur was used to produce each trill, and the femora alternated in producing successive trills.

AGGRESSION.—Aggressive males tip and shake their femora. Tipping resembles that of *C. rabula.* In contrast to *C. rabula* and *C. shastanus,* the femora always struck the forewings during shaking, but occasionally the substrate was also struck at the same time.

Circotettix shastanus Bruner

C. shastanus is known from the Sierra Nevada and from the mountains of southern California. I collected three males and two females in the San Gabriel Mountains, but heard no crepitations in the field.

PAIR FORMATION AND COURTSHIP.—Two observations having a bearing on pair formation and courtship were made in an outdoor insectary. Males and females faced at right angles to the sun for many minutes after being placed in the insectary. When a male began to walk about, another male twice flew towards him, crepitating. These flights were 12 and 24 inches in length. After one flight the approaching male ran up to the moving male and jumped onto him. The latter shook and tipped his femora.

AGGRESSION.—Tipping and shaking movements are similar to those of *C. rabula.* A male walking about the insectary made tipping motions periodically in the absence of movement by other individuals. The tibiae struck the substrate during shaking, but occasionally the femora struck the forewings at the same time. Unreceptive females usually shook their femora when touched.

GENUS *Aerochoreutes* Rehn
Aerochoreutes carlinianus (Thomas)

I did not observe courtship and aggression in this species. However, I tape-recorded the flight displays by three males near Trinidad, Colorado (Fig. 10h). Males hovered over one spot as they crepitated. Crepitation was produced in bursts of two lengths: long bursts (0.75–1.25 seconds); interspersed with one to three very short bursts (about 0.07 seconds). One entire flight consisted of eight long bursts and lasted 15 seconds. The interval between successive long bursts was about 0.25 seconds. During each long burst males ascended, and during intervals they descended a few feet. At the end of flight males alighted on the ground within a few feet of their starting points. The flights differed from those of *Circotettix rabula* in that males only moved up and down during flight, whereas males of *C. rabula* moved considerable distances in a horizontal direction while hovering. In this regard this species resembles *Dissosteira carolina.*

GROUP BRYODEMAE: SUMMARY

The flight display of *Bryodema tuberculata* (Jacobs, 1953) is apparently quite similar to that of *C. rabula* and *A. carlinianus.* Females of *C. rabula, C. thalassinus* and *B. tuberculata* crepitate when disturbed and they probably also do so when approaching performing males. Both *C. rabula* and *C. thalassinus* produce stridulation during approaches. Males of *Bryodema tuberculata* tip their femora, kick the ends of their forewings with the tibiae (ticking), and flap their wings as they approach females. Tipping in *Circotettix* species is similar to that of *Trimerotropis* species. Shaking differs from species to species: *C. rabula, C. shastanus,* and *B. tuberculata* strike the substrate, but *C. thalassinus* strikes the forewings.

GROUP HELIASTI

Two genera, *Heliastus* Saussure and *Cibolacris* Hebard, are included in this group. *Cibolacris parviceps* is the only species in the latter genus. About nine species of *Heliastus* are known, but in this study I encountered only the species *H. benjamini, H. azteca,* and *H. sumichrasti.*

GENUS *Cibolacris* Hebard
Cibolacris parviceps (F. Walker)

This species is distributed across southwestern United States and northern Mexico. Tinkham (1948) stated, "This species, common everywhere on the desert, is decidedly saxicolous in the choice of habitat." I encountered two populations, one on a creosote covered plain near Lordsburg, New Mexico, and another in desert grassland near Bicknell, Utah.

PAIR FORMATION.—This species evidently does not crepitate. Unlike most other Oedipodinae, males possess stridulation which may have a female-attracting function (see Courtship).

COURTSHIP.—Tipping and shaking with wing-striking were performed by New Mexico and Utah individuals. Tipping was very rapid (duration, about 0.2 seconds, up- and downstrokes equal in duration), and was performed in all encounters with other individuals. Shaking consisted of striking the femora against the forewings and was produced either in bursts or continuously (Fig. 10i). Males approaching and attempting to mount females produced bursts of 3-pulse stridulations. Four times, however, males produced a series of stridulations, beginning with 8–10 bursts of 3-pulse stridulations, then switching gradually into a continuous train of pulses, when other individuals moved nearby. The following four observations (the first three on New Mexico individuals and the last on Utah individuals) indicate the contexts in which these stridulations occurred: (1) A male began to stridulate, first producing 3-pulse bursts and then switching to a continuous train of pulses when a female moved about 3 inches away. No response from the female was detected, and he remained motionless following stridulation. (2) A male stridulated as above, apparently in response to the movement of a female nearby. Immediately following stridulation the female walked directly toward the male, stopped near him and remained motionless; he remained motionless as she approached and did not stridulate again. (3) A stationary male stridulated, again beginning with bursts and ending with a continuous train. Except for grooming movements by another male nearby there was no movement by other individuals in the chamber. The stridulating male remained motionless throughout. (4) A male and female were present in the terrarium. For more than five minutes the male walked about while the female remained motionless. Then the male produced a fairly long burst of stridulation, the first section consisting of 18 3-pulse bursts of shaking and the remaining section a continuous train of 37 pulses. A female, two inches away, began to move immediately following stridulation. The male saw her, approached her, and mounted; however she swung her femora upward and forward and dislodged him. The male walked away and in a few minutes produced a similar train of stridulation. This time the female made no detectable response.

It remains a possibility that pair formation is initiated by these long trains of stridulations and that the sound causes females either to approach males or simply to move. An isolated male, collected near Joshua Tree National Monument by R. D. Alexander, produced several songs like those of New Mexico and Utah males.

AGGRESSION.—New Mexico females produced silent shaking four times when a male courted and attempted to mount; the movement was accompanied by femur-jerking and femur-raising. In another kind of shaking movement the forewing was struck producing a signal much like the continuous train of pulses produced by males. Shaking with wing-striking was produced twice, once by a female touched by another female, and once by a female touched by a courting male. The courting male did not mount. Three times males produced a short series of 3-pulse bursts when they were touched by other individuals. These males neither turned towards nor approached the individuals touching them.

GENUS *Heliastus* Saussure

Heliastus benjamini Caudell

The distribution of *H. benjamini* is poorly known, but it seems to extend mainly along the western and northwestern parts of Mexico and into Arizona and New Mexico. I collected the species on open gravelly or stony ground at five localities, from near Nogales, Arizona to near Tequila, in Jalisco. *H. benjamini* is common in gravelly river beds (Tinkham, 1948; Ball et al., 1942).

PAIR FORMATION.—I saw no flights and did not hear any crepitation in this species. Since the hindwings are brightly colored it is possible that males occasionally approach females by flying as they do in *H. azteca*.

COURTSHIP.—I saw males attempt to mount 16 times. Four times a male tipped then shook his femora as he approached a female, and before attempting to mount. In one of the sequences a male approached a female, stopped, shook his femora, approached, shook his femora again and then mounted. Twelve times males only tipped their femora before attempting to mount. Three females presented by spreading their femora away from their abdomens and lowering them against the substrate as a male touched and mounted them. Presenting occurred both when males shook during approaching and when they only tipped. During shaking the substrate was struck with the ends of the tibiae.

AGGRESSION.—Tipping was practically the only aggressive signal observed. In twelve encounters between males, five of which involved contact between males, males only tipped their femora. Only one male produced a burst of shaking when he was touched by another male. Males held their hind femora at about 45° from both horizontal and vertical axes as they walked about. Tipping was from this position and was very rapid, lasting about 0.1–0.2 seconds. Tipping by females closely resembles that of males. One of the females observed repelled a courting male by shaking the hind femur nearest him.

Heliastus azteca Saussure

This species is known from Nuevo Leon, Tamaulipas, and Durango (Bruner, 1904). Numerous individuals occurred on the rocky river bed with little or no vegetation near Ciudad Victoria.

PAIR FORMATION.—I did not see any flights by solitary, undisturbed males and neither sex crepitated during approaching or disturbance flights. Males were highly sensitive to the movements of other individuals in the field, and they frequently approached moving individuals by flying or walking.

COURTSHIP.—To observe courtship in this species, I approached females in the field causing them to fly. From one to three males usually flew toward the females soon after they alighted. Before walking the remaining distance to the females, males often remained perfectly motionless for up to a minute. Presumably they advanced only when the female moved, but on several occasions I could detect no movement by the female. Femur-tipping was the only signal produced by six different males as they walked toward the female. Tipping resembled that of *H. benjamini.* Males mounted after each approach. One female tipped her femora as she was approached—she was mounted also.

AGGRESSION.—Tipping was the only signal performed by males in close contact with one another.

Heliastus sumichrasti Saussure

According to Hebard (1925b) this species is widely distributed in Central America. It occurred on open ground near Tequila, Jalisco, together with *H. benjamini,* and along the beach in Tampico.

PAIR FORMATION.—I saw or heard no flights other than disturbance flights. Pair formation is probably like that in *H. azteca.*

COURTSHIP.—In each of three courtship sequences a male turned toward a moving female, approached her, and shook his femora before mounting. As in *Cibolacris parviceps,* only the forewings were struck during shaking (Fig. 10j).

AGGRESSION.—Both sexes frequently tipped their femora in aggressive contexts. Femur-tipping, which was rapid (duration, 0.1–0.2 seconds) and from approximately the horizontal position, was present in all male–male encounters, several times along with femur-shaking. In five encounters between males aggressive shaking resembled courtship shaking closely; however, the sound produced was less intense. One male produced no sound during shaking. A female also shook silently when a male attempted to mount her.

GROUP HELIASTI: SUMMARY

Table 13 summarizes signalling in the Heliasti. These species live on bare, rocky or sandy soil, and associated with this habit is an apparent lack of solitary flight displays and of crepitation. However, males of *H. azteca* sometimes approach females by flying, probably signalling their approach by flashing their hindwings. It is likely that the other *Heliastus* species behave similarly.

TABLE 13

SIGNALLING IN *Cibolacris* AND *Heliastus*

Species	flight displays	wing color	courtship signals	aggressive signals
C. parviceps	none	drab yellow	shaking (ws),[1] tipping (sometimes)	tipping, shaking (ws)
H. benjamini	?	bright orange-red	shaking (ss),[1] tipping	tipping shaking (ss) (rare)
H. azteca	approaching flights	bright red	tipping	tipping,
H. sumichrasti	?	bright yellow to red	shaking (ws)	tipping, shaking (ws)

[1] ws = with wing-striking; ss = with substrate-striking.

This is the only group of Oedipodinae in which all of the examined members lack ordinary stridulation. They also lack the intercalary vein on the forewing which is normally involved in the production of ordinary stridulation. Tipping and shaking appear to be the only signal movements performed by courting males. Tipping is very rapid and quite distinct from that in other Oedipodinae.

Subfamily Oedipodinae: Summary

PAIR FORMATION

Solitary Flight Displays.—Solitary flight displays occur in 38 of the 79 species examined (Tables 14, 15). Such displays seem to be rare in three species and absent from 23 others, but their status in the remaining species is uncertain. In several groups of genera—the Hippisci, Lactisti, Psinidiae, and Heliasti—solitary flight displays are for the most part lacking. A loss of the flight display, or at least a considerable reduction in the frequency of its performance, has very likely occurred in *Spharagemon collare;* its relatives still possess the display. Flight displays are usually accompanied by crepitation, but in *Dissosteira carolina* a sibilant sound is produced which is quite different from the crepitation of other species.

Approaching Flights.—Males of a number of species frequently fly toward moving females. This was particularly noticeable in *Dissosteira carolina, Trimerotropis pallidipennis, T. maritima, Derotmema haydenii,* and *Heliastus azteca.* In the last two species and their close relatives, solitary flight displays are very likely absent. All of these species possess colored or contrastingly marked hindwings.

Crepitation.—Males of 46 species crepitate. Most do so during solitary flight displays and during disturbance flights, but some, e.g., *Trimerotropis maritima* and *Conozoa carinata,* seem to crepitate only during approaching flights. Females of *Chortophaga viridifasciata* crepitate while approaching performing males, and sometimes during disturbance flights. Females of 10 other species crepitate at least during disturbance flights, and it is probable that sexually responsive females in these species crepitate when flying toward displaying males.

Display Patterns.—The various character combinations of solitary flight display, crepitation, and colored hindwing are distributed among the species of Oedipodinae for which they are known as follows: (a) solitary flight display, crepitation, colored hindwing—31 species; (b) solitary flight display, crepitation, no colored hindwing—5 species; (c) solitary flight display, no crepitation, colored hindwing—2 species; (d) solitary flight display, no crepitation, no colored hindwing—0 species; (e) no solitary flight display, crepitation, colored hindwing—3 species; (f) no solitary flight display, crepitation, no colored hindwing—0 species; (g) no solitary flight display; no crepitation, colored hindwing—13 species; (h) no solitary flight display, no crepitation, no colored hindwing—4 species.

With further observations it may be shown that crepitation and solitary flight displays are not lacking in some of the species but are simply rare.

Calling or Female-attracting Stridulation.—Stridulation by solitary males of Oedipodinae that have not recently had an encounter with females is rare when compared to the Acridinae. Stridulation by solitary, wandering males occurs in a few species, e.g., in *Arphia sulphurea, Chortophaga viridifasciata, Pardalophora apiculata, Trimerotropis pallidipennis,* and *T. fratercula.* But in only two species (*Dissosteira carolina* and *Cibolacris parviceps*) does there seem to be a specialized stridulation characteristic of solitary stationary males. In these two species such stridulation is also produced by stationary males in the presence of females, and this may be the context in which it is usually produced. The general lack of such behavior among the Oedipodinae as a whole may be owing to the fact that in the open habitats where these species generally occur visual signals operate over longer distances than acoustical signals.

Initial Approach.—It is probable that, in all species performing solitary displays, females sometimes approach the displaying males. So far this behavior has been observed in only two species. In species lacking solitary flight displays, males seem to make the initial approach. In all species, however, the initial approach is probably sometimes undertaken by males in response to movements by females. In the field I have observed males of 38 species making the initial approach.

COURTSHIP

Ordinary Stridulation.—This varies in structure from species to species; it is part of the courtship sequence in 59 species and occurs in all groups except the Heliasti.

Vibratory Stridulation.—This is part of the courtship sequence in 15 species. It occurs in nine distantly related genera and is poorly correlated with other characters,

TABLE 14

Habitat Preference, Pair Formation, Courtship and Aggression in the Oedipodinae[1]

SPECIES	HABITAT PREFERENCE						PAIR FORMATION (field data)					COURTSHIP						AGGRESSION				
	no. localities at which species was found in:					species usually lives in/on:				initial approach												
	G0	G1	G2	G3	G4		conspicuously patterned wings	solitary males with flight display	males crepitate	♀ to ♂	♂ to ♀	ordinary stridulation	vibratory stridulation	shaking with wing-striking	shaking with substrate-striking	silent shaking	femur-tipping	ticking	shaking with wing-striking	shaking with substrate-striking	silent shaking	femur-tipping
Arphia sulphurea	2	8	7	3	1	dry grasslands	+	+	+	(+)	+	+	+				+		+			+
A. simplex	1	6	7	4	2	dry grasslands	+	+	+	+	(+)	+	+				?		+			+
A. xanthoptera	2	5	5	3	1	dry grasslands	+	+	+	(+)	(+)	+					?		+			+
A. granulata		4	4			dry grasslands	+	+	+	(+)	(+)	+					?		+			+
A. pseudonietana	1	5	9	6	3	dry grasslands	+	+	+	(+)	+	+	+				+		+			+
A. conspersa			2	2		dry grasslands	+	+	+	(+)	(+)	+	+				?		+			+
Chortophaga virid.	11	10	2	1		moist grasslands		+	+	+	+	+									+	+
C. australior	1	3	1			moist grasslands		+	+	(+)	+						+				+	+
Encoptolophus sord.	3	5	2			dry grasslands		+	+	(+)	(+)		+*				+S	+		+		+
E. costalis		1	1	1		dry grasslands		+	+	(+)	(+)	+	+				+S			+		+
Lactista gibbosus				1	1	bare ground	+	?	+	?	(+)	+					?		+			+
L. punctatus			1	1	4	bare ground	+				+	+					+		+			+
L. (near *punctatus*)				1	2	bare ground	+				(+)			+			?		+			+
Platylactista azteca			2	3	5	bare ground	+		+		(+)	+					?		+			+
Scirtetica marmorata			2	6	3	sandy areas	+	+	+	(+)	(+)	+					+			+		+
Spharagemon collare			2	6	9	sandy areas	+		+		+	+								+		+
S. cristatum			1	2		sand, grasslands	+	+	+	(+)	(+)	+			+		+			+		+
S. equale			1	1		short grasslands	+	?	?		(+)		+				?			+		+
S. humile			1	2	1	short grasslands	+	+	+	(+)	(+)		+		+		+S			+R		+
S. saxatile		1	1	2	1	rock outcroppings	+	+	+	(+)	+	+	+							+		+
S. bolli		4	3	1		open woods, woods margins	+	+	+	(+)	+	+			+		+			+		+
S. crepitans		1				open woods, woods margins	+	(+)	(+)	(+)	(+)				+		+					+
Dissosteira carolina		1	2	4	11	bare patches	+	+		(+)	+						+*			+		+
D. pictipennis			1	1		bare patches	+	+	+	(+)	+	+						+		+		+
Pardalophora apiculata	3	9	5	2		dry grasslands	+	+ R		?	+	+	+								+	+
P. phoenicoptera		2	5	4	1	dry grasslands	+	?			+	+					?				+	+
P. haldemanii		2	1	1		dry grasslands	+	?			(+)				+		+			+R		+
P. saussurei		1	2	2		tall grasslands	+				(+)	+					+				+	+
Hippiscus ocelote	3	8	4			dry grasslands	+				(+)	+									+	+
Xanthippus corallipes		1	1	2		dry grasslands	+				(+)	+	+				+				+	+
Camnula pellucida	4	3	2			dry grasslands					+	+					+				+	+
Leprus robustus		1	1	1		dry grasslands	+	?			(+)	+					+			+		+
Tropidolophus formosus		1	2			low shrubs	+	+	+	(+)	(+)	+									+	+
Psinidia fenestralis			2	4	4	sandy areas	+				(+)	+					+			+		+
Derotmema haydenii					7	bare ground	+				+	+					+			+		+

Trachyrhachys kiowa fuscifrons			2	4	short grasslands	+				+	+					+			+		+
T. kiowa kiowa				1	short grasslands					+		+				+			+		+
Trimerotropis pallidip.		1	7	21	bare ground	+	+	+	(+)	+	+					+S			+		+
T. (near *pallidipennis*)				1	bare ground	+	(+)	+	(+)	+	+*		+			+			?		?
T. californica				5	bare ground	+	+	+	(+)	+				+		+S			+R		+
T. huroniana			1	5	dunes	+	+ R	+	(+)	+	+					+S			+		+
T. maritima			2	15	sandy areas, dunes	+		+	?	+	+			+		+S			+		+
T. verruculata			1	6	rocky areas	+	+	+	(+)	(+)	+							+S	+S		+
T. thalassica	1	1	1		open woods		?			(+)	+					?			+		+
T. albescens			1	2	sparse grasslands	+	+	+	(+)	(+)	+					?			+		+
T. fontana				1	bare patches		+	+	(+)	(+)					+	?					+
T. (near *fontana*)			1	1	bare patches		?	+	?	(+)	+R			+		+S					+
T. bilobata				2	desert grasslands	+	+	+	(+)	+	+					?			+		+
T. agrestis			1	1	sandy areas	+	+	+	(+)	+	+					+S			+		+
T. fratercula			4	4	rocks and hillsides	+	+	+	(+)	(+)	+							+S	+		+
T. melanoptera			3	3	short grasslands	+	+	+	(+)	+	+					?			+		+
T. koebelei				1	stony areas	+	(+)	+	(+)	(+)	+					+S			+		+
T. calignosa				2	bare patches		(+)	+	(+)	(+)	+					+S			+		+
T. caerulipes			1	1	bare patches		?	?	?	(+)	+*								+		+
T. rebellis				1	open desert	+	?	?	?	(+)	+								+		+
T. campestris		4	4		short grasslands	+	+	+	(+)	+	+	+				+S			+		+
T. gracilis				4	bare ground (sage)	+	+	+	(+)	+	+					+S		+S	+		+
T. cincta			2	3	hillsides	+	+	+	(+)	(+)	+				+	+S				+	+
Conozoa wallula			1		desert grasslands	+	+	+	(+)	+				+		+			?		+
C. carinata				4	desert grasslands	+	+ R	+	?	+	+			+		+					+
Circotettix rabula		1	3	7	steep slopes	+	+	+	(+)	(+)	+					+S			+		+
C. thalassinus				1	stony hillsides	+	(+)	+	(+)	(+)	+							+	+S		+
C. shastanus				1	stony hillsides	+	+	+	(+)	+	?					?		+S	+		+
Hadrotettix trifasc.		1	1	6	bare ground	+				(+)	+					+			+		+
Cibolacris parviceps				6	open desert					+			+			+S		+			+
Heliastus benjamini				5	dry washes	+				(+)				+		+					+
H. azteca				1	dry washes	+				+						+					+
H. sumichrasti				2	bare ground	+				(+)			+			?		+			+
Parapleurus alliaceus					moist pastures					+		+								+	+
Aiolopus thalassinus					grasslands					+	+						+			+	+
Sphingonotus coerulans					bare ground	+	?	?		+	+								+S	+S	+
Bryodema tuberculata					?	+	+	+	(+)	+						+	+		+		+
Oedipoda coerulescens					bare ground		(+)	+	?	+	+								+		+
O. germanica					?		?	?	?	+	+								+		+
Locusta migratoria					?		?	?		(+)	?							+			+
Psophus stridulus					steep slopes	+	+	+	(+)	(+)	+		+				+	+			
Celes variabilis					?	+	?	?		(+)	+									+	+

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[1] The last nine species in this table were studied by Jacobs (1953). Key to symbols: + = condition present; (+) = probably present; +S = sometimes produced in this context; +R = present but reduced in expression or rarely produced in this context; ? = presence or absence uncertain; blank = not observed and probably absent.

The indices G0 G1, etc., indicate the degree of vegetational cover where each species was found, measured roughly by the distance over which grasshoppers were judged able to see one another. G0 indicates a maximum visibility of 3 inches; G1 a maximum of 6 inches; G2 a maximum of 12 inches; G3 a maximum of 24 inches; G4 a maximum in excess of 24 inches.

* Two kinds.

TABLE 15

FEMALE BEHAVIOR PATTERNS IN PAIR FORMATION, COURTSHIP, AND AGGRESSION IN THE OEDIPODINAE[1]

SPECIES	PAIR FORMATION		COURTSHIP						AGGRESSION				
				presenting behavior									
	females crepitate	females approach displaying males	femoral movements	lower near or both femora	spread femora from abdomen	vibrate femora	turn abdomen toward male	remain passive	femur-shaking	femur-tipping	femur-jerking	femur-raising	escape
Arphia sulphurea			+		+	+		+		+?		+	+
A. simplex		+									+	+	+
A. xanthoptera													+
A. granulata	+											+	+
A. pseudonietana	+							+				+	+
A. conspersa	+			+									+
Chortophaga virid.	+	+	+		+	+		+		+	+	+	+
C. australior	+			+				+				+	+
Encoptolophus costalis	+							+	+	+	+	+	+
E. sordidus			+	+	+			+		+		+	
Platylactista azteca					+								+
Scirtetica marmorata												+	+
Spharagemon collare			+						+		+	+	+
S. cristatum			+						+	+		+	+
S. bolli									+	+		+	+
S. saxatile												+	+
Dissosteira carolina								+	+	+		+	+
Pardalophora apiculata			+	+	+	+	+	+	+	+	+	+	+
P. phoenicoptera			+	+	+	+	+	+		+		+	+
P. saussurei				+	+	+				+		+	+
Hippiscus ocelote				+	+							+	+
Tropidolophus formosus									+				+
Psinidia fenestralis								+		+		+	+
Trachyrhachys kiowa								+			+		+
Trimerotropis pallid.								+		+			+
T. verruculata											+	+	+
T. fratercula	+												+
T. huroniana								+			+		+
T. campestris	+											+	
T. thalassica										+	+		
T. gracilis	+												
T. maritima								+	+	+	+	+	+
Conozoa carinata										+			+
Hadrotettix trifasc.								+		+		+	+
Circotettix rabula	+									+		+	+
C. thalassinus	+												
Cibolacris parviceps										+		+	+
Heliastus benjamini					+				+	+			+
H. azteca								+		+			
H. sumichrasti									+	+			

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[1] Key to symbols: + = behavior observed; blank = behavior not observed.

suggesting that it may have arisen independently at least nine times in this subfamily. It appears to have arisen only once in each of the genera *Arphia, Encoptolophus,* and *Spharagemon.*

FEMUR-SHAKING.—Shaking is part of the courtship sequence in 18 species. Its occurrence in courtship in relatively few and distantly related species suggests that it has been incorporated into courtship from aggressive contexts independently a number of times.

In eight species femur-shaking is combined with ordinary stridulation during courtship and in seven of these species it precedes stridulation. In nine species femur-shaking is the main courtship signal and stridulation is apparently completely lacking.

FEMUR-TIPPING.—Tipping is performed in aggressive contexts in all 70 North American species. It occurs in the courtship sequences of 34 species, in 13 of which it is only occasionally performed. In 15 species it does not take place during courtship, and whether or not it occurs in this context is uncertain for 21 species. In most species tipping probably has an aggressive function even when present in courtship contexts, because it seems to elicit aggressive responses by males that have been approached accidentally and thus serves to shorten the interaction between males. However, in *Chortophaga australior,* where femur-tipping is the only signal performed by approaching males, and in *Mestobregma plattei, Trachyrhachys kiowa,* and *Dissosteira carolina,* where males produce two kinds of tipping, one in aggressive contexts and the other in courtship contexts, tipping probably serves a courtship function.

TICKING.—Ticking is performed by males of five distantly related species and was probably acquired independently in each species. In four species ticking is part of the courtship sequence, but in one species, *Psophus stridulus,* it is an aggressive display (Jacobs, 1953).

OTHER MOVEMENTS.—Other unique signal movements have evolved in various species: wing flapping in *Bryodema tuberculata* (Jacobs, 1953), alternate stridulation in *Dissosteira carolina,* and a unique type of vibratory stridulation in *Scirtetica marmorata.*

MORE THAN ONE COURTSHIP SIGNAL.—Twenty-seven species possess two or more courtship signals (other than tipping, which may or may not serve a courtship function). In some species one kind of signal is produced while advancing on the female and a second type when a female retreats or is lost, e.g., *Arphia sulphurea* and *Pardalophora apiculata.* In other species, e.g., *Encoptolophus sordidus, Scirtetica marmorata,* two or more signals are produced during the approach.

FEMALE RESPONSE TO MALE COURTSHIP.—Responses of sexually receptive females to courting males are poorly known in most species, but in species studied in more detail there appear to be two kinds of reaction: remaining passive, or moving the femora or abdomen. Females of some species simply lower the femur nearest the approaching male, e.g., *Encoptolophus sordidus* and others, while those of other species lower and vibrate their femora, spread them away from the abdomen, and turn the end of the abdomen in the direction of the male, e.g., *Pardalophora apiculata.* The most complete data concerning such movements have been collected for three weeks, *Chortophaga viridifasciata, Pardalophora apiculata,* and *P. phoenicoptera.* Remaining passive when approached by courting males is a very common response of females and may be universal among grasshoppers.

COURTSHIP INTERRUPTION.—In several species, e.g., *Arphia sulphurea, A. simplex* and *Pardalophora apiculata,* males stridulate when courtship is interrupted; for instance, when a female retreats from an approaching male, or when a male loses sight of a female he is approaching. In some species the stridulation produced is unique to that situation. Males of *Trimerotropis campestris* produce bursts of vibratory stridulation while approaching and switch to a single burst of ordinary stridulation when they stop advancing after a female has retreated. *Oedipoda coerulescens* males produce short bursts of vibratory stridulation as they wander about after losing a female (Jacobs, 1953). Jacobs termed these sounds *Suchlauten.* These sounds may cause some response in females which reunites male and female, but why they should differ from ordinary courtship sounds in some species and be the same in other species is not known. Similar "searching" sounds have been recorded among some species of Acridinae and in species of crickets (Alexander, 1962a).

AGGRESSION

FEMUR-TIPPING.—This signal is an aggressive movement in 77 of 78 species; Jacobs (1953) reports that it is absent in *Psophus stridulus*. Because it is so often the first signal to be produced by males in any interaction and is either absent or different in females, it is probably the main sex-identifying signal among the Oedipodinae. That is, by tipping, males elicit aggressive responses by other males and thus prevent any protracted interactions between males. In three species tipping performed in aggressive contexts is different from that performed in courtship contexts (see under "Courtship" above). Two kinds of femur-tipping are perhaps only found when the signal has assumed both courtship and an aggressive function.

FEMUR-SHAKING.—Shaking is a frequent aggressive signal in 69 species. It is apparently absent from the aggressive behavior of six species and greatly reduced in that of two species. Its absence or reduction in aggressive contexts is correlated with its presence in courtship contexts. That is, when it assumes a courtship function it tends to lose its aggressive function.

FEMUR-JERKING.—Jacobs (1953) reported that this movement was found in all species of all subfamilies he examined. It appears to be universal among the North American species as well. The movement is apparently only produced by individuals being touched and grades into femur-raising.

REPELLING MOVEMENTS BY FEMALES.—With the exception of escape, raising the hind femora is the method of repulsion or rejection most often employed by females, and it is likely to be almost universal among the species of this subfamily. Tipping, shaking, and jerking are also employed by females of many species.

SUBFAMILY ACRIDINAE

Males (and sometimes females) of Acridinae possess a row of stridulatory pegs on the inside of the hind femur. In general, the members of this subfamily live on vegetation, but some species have acquired a ground-dwelling habit. The latter resemble Oedipodinae so closely that they were classified as such until detailed observations of their morphology were made.

GENUS *Chorthippus* Fieber

According to Bei-Bienko and Mischchenko (1951) there are about 80 species of *Chorthippus*. Most occur in Europe and Asia, but one species, *C. curtipennis,* occurs in North America. The behavior of ten species was studied by European workers (see Jacobs, 1953).

Chorthippus curtipennis (Harris)

This species is widespread in the northern United States and southern Canada. In the western states it extends southwards along the Rocky Mountains and the Sierra Nevada (Hebard, 1935; Ball et al., 1942; Newton and Gurney, 1956). It is usually found in marshes and moist depressions with dense grassy vegetation.

PAIR FORMATION.—Males frequently stridulated while sitting alone on a blade of grass. Although I did not see females being attracted to solitary singing males, the calling function of similar songs has been demonstrated for some of the European species of *Chorthippus* (Jacobs, 1953), suggesting that *C. curtipennis* females are also attracted to calling males. I saw one female making stridulatory movements with her hind femora following the stridulation of males nearby, but I was unable to hear her. Her movements were similar to those of stridulating males but were less precise.

Slower songs were produced by solitary males (Fig. 11i) and faster songs were produced by males in close encounters with other males (Figs. 11j, k). However, all intermediate conditions of songs can occur, depending on the presence or absence of other males and on the closeness of the interactions. Calling songs have slower pulse rates, more pulses per song, and longer pulses than aggressive songs and are produced in the following manner: Both femora are raised to approximately 70° from horizontal, are pressed against the forewings and then lowered to produce each pulse of sound (Fig. 11i). During the first portion of each downstroke, the femora seem to move smoothly across the forewing, but at the end of the stroke they begin to vibrate or

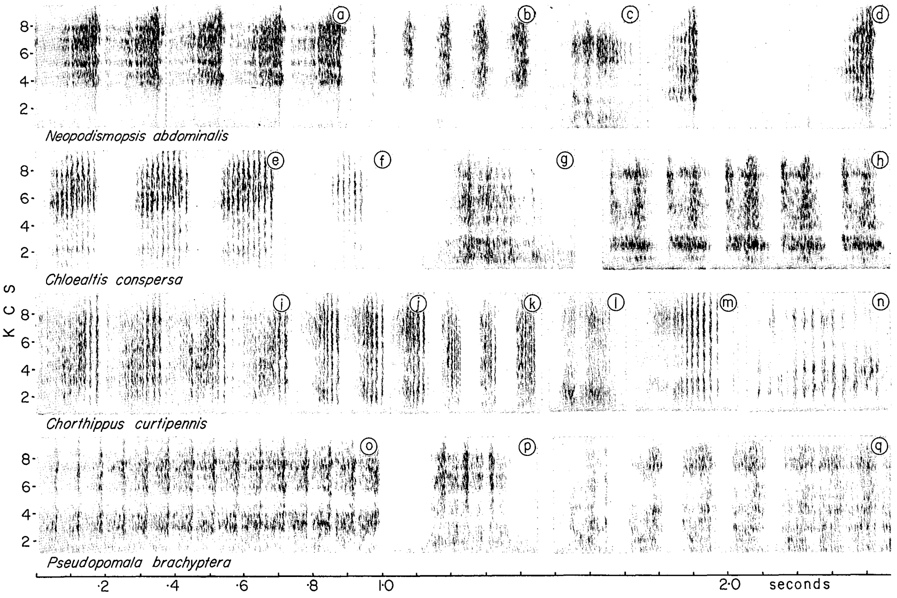

FIG. 11. Audiospectrographs of signals by various species of Acridinae; (a) *Neopodismopsis abdominalis* (Chippewa Co., Mich.), stridulation by an isolated male, 78°F; (b) same, stridulation by male touched by another male, 80°F; (c) same, initial courtship stridulation, 80°F; (d) same, advancing courtship stridulation, 80°F; (e) *Chloealtis conspersa* (Livingston Co., Mich.), stridulation by an isolated male, 98°F; (f) same, aggressive stridulation, 95°F; (g) same, initial courtship stridulation, 98°F; (h) same, advancing courtship stridulation, 98°F; (i) *Chorthippus curtipennis* (Livingston Co., Mich.), stridulation by an isolated male, 80°F; (j) same, stridulation by a male in response to stridulation of another male, 78°F; (k) same, stridulation by a male touched by another male, 78°F; (l) same, initial courtship stridulation, 80°F; (m) same, advancing courtship stridulation, 78°F; (n) same, mounting stridulation, 78°F; (o) *Pseudopomala brachyptera* (Livingston Co., Mich.), stridulation by an isolated male, 82°F; (p) same, stridulation of a male in response to the stridulation of another male, 82°F; (q) same, advancing courtship stridulation.

bounce against the forewing, producing the distinct temporal modulation observed at the end of each pulse. The modulation does not seem to be the result of tooth strikes, since these are sometimes barely distinguishable at the beginning of the downstroke. Both femora move simultaneously and synchronously throughout the song.

COURTSHIP.—I saw courtship more than 30 times and recorded three kinds of courtship sounds. The first sound, initial courtship stridulation (Fig. 11 l), was produced by stationary males in the presence of a female or other moving individuals and was made either in response to movement, or after males made antennal contact with females. Sound was produced by rubbing the femora against the forewings on the downstroke, and each signal consisted of a single stroke. One to three such signals were produced in succession, and the interval between signals was quite variable. The sound was sometimes made by males slowly approaching or following other individuals, but only after the approaching males had stopped. The length and intensity of the pulses varied. The second sound, advancing stridulation (Fig. 11m), was always produced by males rapidly advancing toward other individuals and always preceded attempts to mount. Each signal consisted of a single stroke of the femora, and 1–3 strokes were made by advancing males. A third sound, mounting stridulation (Fig. 11n), was always produced by males as they mounted and attached their genitalia. The femur farthest from the female was vibrated against the forewing to produce a whirring sound; during vibration the tibia was held fully extended. Within a second or so after attachment stridulation ended.

Except for stridulation of the answering type (see above), all female signals seemed to be graded. Occasionally females slowly raised their femora to the vertical position in response to touch or the stridulation of males. When this occurred the femora did not move synchronously, and the tibiae were extended to various angles from the femora. Femur-raising did not always repel males, for copulation occurred several times after it had been performed. When females jumped away before mounting could occur, males either produced a faster version of the calling song and then courtship stridulation or they continued producing courtship stridulation.

One sequence of courtship and copulation was as follows: A male approached a moving female 12 inches away. During momentary stops he produced initial courtship stridulation. When he was an inch from her, he began to rush toward her and to produce advancing stridulation. As he mounted and attached his genitalia, he produced mounting stridulation. After 30 minutes of copulation he dismounted and walked away. Two minutes after separating he began to sing again, and approximately 8 minutes later he courted and mounted a second female. He remained attached to her for 35 minutes. About 7 minutes after separating from the second female, he began to call again. In the meanwhile a second male courted and mounted the first female; he appeared to attach but dismounted and walked away a few seconds later. Perhaps the first male had rendered the female inaccessible to the second male by inserting a spermatophore into her spermathecal duct (see Loher and Huber, 1965).

AGGRESSION.—Aggressive songs contain fewer and shorter pulses than do calling songs (Fig. 11k). The two shortest songs that I recorded (4 and 7 pulses) were produced by a male that was being courted and touched by another male. However, on at least four occasions shorter songs with higher pulse rates were produced by males soon after they had tried unsuccessfully to mount females. Three kinds of aggressive interactions occurred: (1) The call of one male was followed closely by aggressive stridulation of another male. Males sometimes separated after such an exchange. (2) Two males moved near one another, neither stridulating initially. Then one of them produced aggressive stridulation, and the other answered immediately with the same signal. In these interactions the number of pulses produced by the two males was roughly similar, and after them separation sometimes took place. (3) One male courted and attempted to mount another. The latter produced short bursts of stridulation, and the courting male dismounted and walked away—sometimes with stridulation, sometimes without.

In all aggressive interactions between males the stridulation of one male always followed that of another.

GROUP CHRYSOCHRAOTINI

This group has been revised by Rehn (1928) and Bei-Bienko (1932). It presently includes the genera *Chrysochraon* Fisher, *Podismopsis* Zubovsky, *Euthystira* Fieber, *Mongolotettix* Rehn, *Chloealtis* Harris, *Neopodismopsis* Bei-Bienko, *Napaia* McNeill, and *Barracris* Gurney et al. The first four genera occur in the Palearctic region, the last four in the Nearctic region (see also Gurney et al., 1964). The behavior of *Chrysochraon dispar* and *Euthystira brachyptera* was studied by Jacobs (1953) and that of *Chloealtis conspersa* and *Neopodismopsis abdominalis* by me.

GENUS *Chloealtis* Harris

Chloealtis conspersa Harris

In the United States, according to Newton and Gurney (1956: 839), *C. conspersa* occurs in the northern and northeastern states but does not get into the Rocky Mountains. However, I found it in the eastern foothills of the Rocky Mountains. In Canada it is abundant in Alberta, Saskatchewan, and Manitoba and extends from British Columbia at least as far east as Ontario. Across its range *C. conspersa* is always found in the immediate vicinity of wooded areas (Walker, 1909; Blatchley, 1920; Morse, 1920; Hubbell, 1922b; Buckell, 1922b; Cantrall, 1943; Brooks, 1958). I collected *C. conspersa* in grassy and weedy margins of woods at six localities in Michigan. Near Brimley, on Lake Superior, it occurred side by side with *Chorthippus curtipennis* and its apparently closest relative *Neopodismopsis abdominalis.* Walker (1909: 140) found these three species inhabiting the same localities in Ontario. In the foothills of the Rocky Mountains near Raton, New Mexico, I heard, but did not see, both *C. conspersa* and *N. abdominalis* in the same groves of oak scrub.

Pair Formation.—I did not see pair formation in the field. Very likely, however, females are attracted to the calls of males. Calls were produced frequently by isolated males on warm sunny days. One to eight songs were sung at one spot, and males walked about among the vegetation between series of songs. I found males perched on grass, on low green oak leaves, and on dry oak leaves on the ground. Each song consisted of 8–21 strokes of the femora, and sound appeared to be made exclusively on the downstroke (Fig. 11e). On four occasions in the laboratory a female began to move during the call of the male. Twice he became aware of her movement, turned towards her and approached her. On many more occasions, however, females remained motionless during and after the call and males evidently remained unaware of their presence. In a terrarium containing three males confined to wire gauze cages and three females, a female was found sititng on top of a cage near a calling male. After a song by the latter, she made about 6 soundless strokes with her femora which resembled the stridulatory hopped away from the cage soon after I arrived. Another female produced similar soundless motions several times following the calls of males, but no pairing occurred. Similar answering behavior has been described for several European species, for instance, *Euthystira brachyptera, Chorthippus parallelus,* and a fairly close relative of *Chloealtis, Chrysochraon dispar.* Pair formation, then, seems to involve an exchange of signals by males and females.

Courtship.—Two courtship signals were present in all of more than 30 courtship sequences. The first, initial courtship stridulation (Fig. 11g), was produced by males when they became aware of the female; it was a soft sibilant sound produced by alternate or synchronous strokes of the two femora. Several strokes (up to 8) were produced in each burst, and the amplitude of the strokes became progressively smaller during each burst. This signal was also produced when males were pursuing females, and when they were unsuccessful in mounting. In each case it was made by stationary males. Sometimes several bursts of initial stridulation were produced in succession. When this occurred, the first burst was always the longest. Sometimes almost no sound could be detected during this movement. The second signal, advancing stridulation (Fig. 11h), was produced by males rapidly advancing toward stationary females, just before attempting to mount. From 4–14 regularly spaced pulses were produced, the femora moved together, and sound was emitted on the downstroke. When males were unable to mount, they switched from producing advancing stridulation to initial courtship stridulation. There appeared to be no intermediates between these two types of stridulation.

Aggression.—The stridulation occurring in aggressive contexts, i.e., in encounters between males and in encounters with other species, was somewhat different from calling stridulation (see Fig. 11f). The sound produced during each stroke was similar, but the number of strokes and the stroke rate were greatly reduced. One to seven strokes of stridulation were produced in such encounters, but in close interaction between males only single strokes were produced. Transitions between calling and aggression, such as occur in *Chorthippus curtipennis,* apparently are not found in this species. In an encounter between two males, one of the males raised his femora to vertical several times and extended his tibiae to 90°. The movement was slow, variable in duration, and the femora moved asynchronously. Several other males also raised their femora to more than 90°, in small steps, and the tibiae moved up and down as they were extended to approximately right angles with the femora. Males that were mounted by other males did not shake their femora, but produced single strokes of aggressive stridulation.

GENUS *Neopodismopsis* Bei-Bienko

Neopodismopsis abdominalis (Thomas)

N. abdominalis is widespread throughout the forest and parklands and the wetter grasslands of Canada, from Ontario to British Columbia (Brooks, 1958). In the United States the species occurs in North Dakota, Minnesota, and Michigan, and extends southward along the Rocky Mountains to New Mexico and Arizona (Newton and Gurney, 1957: 110). Buckell (1922b) states that in British Columbia *N. abdominalis* occurs in the same areas as *Chloealtis conspersa* and that females oviposit in stumps as females of *C. conspersa* do.

Pair Formation.—In the field individual males sing one to three songs at one place and then wander about through the grass before singing again. The songs of solitary males were composed of about 17 strokes of both femora (Fig. 11a). The songs of males near other males were both faster and shorter than those of isolated males, but all intermediates are apparently possible. It is also possible that regardless of the pulse rate songs of males not only attract females but also cause the spacing of males: songs of relatively fast pulse rate (8.57 per sec) were produced by a male between two courtship sequences, while he was following the individual being courted, and others of a similar pulse rate (8.33 per sec) were produced in encounters between males.

Courtship.—Unfortunately, no females were collected, and all courtship sequences observed involved males courting individuals of other species *(Chorthippus curtipennis, Trimerotropis huroniana,* and *T. verruculata).* There is no reason to believe, however, that the 15 courtship sequences observed were abnormal. Two kinds of stridulation were produced. These are perhaps homologous to the kinds of stridulation observed in the above two species. Initial courtship stridulation in this species is quite similar to that of *Chloealtis conspersa* (Fig. 11c); the sound was sometimes produced with alternate strokes of the femora, each series of femoral strokes producing three or four poorly defined pulses. The signal was produced by males before they advanced toward individuals moving nearby. The second type of stridulation, advancing stridulation (Fig. 11d), was produced only by rapidly advancing males. On several occasions courting males produced one to three bursts of the initial stridulation when an individual first moved and then produced advancing stridulation as they rapidly approached and attempted to mount. When courtship was interrupted, males nearly always switched back to producing initial courtship stridulation. Advancing stridulation consisted of 2–6 regularly spaced pulses of sound, each produced on the downstroke. As in *C. conspersa,* it was only produced during approaches and just before attempts to mount.

Aggression.—The songs of interacting males contained fewer pulses (2–11) and a slightly faster pulse rate than those of solitary males (Fig. 11b). The shortest songs were sung by the males nearest one another.

GROUP CHRYSOCHRAOTINI: SUMMARY

The behavior of the European species, *Euthystira brachyptera* and *Chrysochraon dispar* (Jacobs, 1953), appears to be quite similar to that of the two American species studied. The two European species possess initial courtship stridulation and advancing stridulation, both similar to that of the American species. Unlike the American species, however, males stridulate while mounting females. As in *C. conspersa,* females of both European species answer the stridulations of males with silent leg movements. In *E. brachyptera,* females answered and approached singing males (Jacobs, 1953). Since the behavior of a number of Acridinae is also similar to that of the Chrysochraontes, little can be said yet about relationships of these species on the basis of sexual behavior.

GENUS *Pseudopomala* Morse

Only one species is known in this genus. The genus is sometimes grouped with *Mermeria* in the group Mermeriae, even though the two genera are quite distinct in appearance.

Pseudopomala brachyptera (Scudder)

This species occurs in the prairie states from Alberta to Oklahoma and extends eastward through Iowa, Wisconsin, and Michigan to New England (Newton and Gurney, 1957). In the George Reserve, *P. brachyptera* occurs in both marshy and drier upland situations.

Pair Formation.—The calling song of *P. brachyptera* is faster than those of the three species discussed above (Fig. 11o). The femora move across the forewings without vibrating on the downstroke, and there is a steady increase in sound intensity during each song. All sound is apparently produced on the downstroke. There was a considerable difference between the pulse rate recorded in the field at 86°F and that recorded in the laboratory at 82°F; the increased rate in the latter may have been due not only to the temperature difference, but also to the presence of another male, as was the case with *Chorthippus curtipennis* and *Neopodismopsis abdominalis*. In the laboratory I had two male *P. brachyptera* confined together in a terrarium; one produced only aggressive signals, while the other produced both calling and aggressive songs.

COURTSHIP.—I saw one male court a female three times. After singing for some time he saw her moving nine inches away. He approached her slowly, stopping frequently, and singing one or more songs each time he stopped. Then from several inches away, and after singing 12 sons, he rushed forward producing stridulation with longer and slower pulses (Fig. 11g). This stridulation probably corresponds to the advancing stridulation of the species discussed above, since it is given in similar contexts. What appeared to be initial stridulation was heard once when a male became aware of the female and had not yet begun to advance toward her. No stridulation was produced as the male mounted the female.

AGGRESSION.—Two males were kept in one chamber; one sang numerous calling songs (27–36 pulses), while the other produced only short bursts of stridulation (2–5 pulses), which immediately followed the songs of the first male (Fig. 11p). One brief exchange of short stridulatory bursts by the two males was also heard, but no regular alternation of signals.

GENUS *Mermeria* Stal

In his revision of this genus Rehn (1919b) recognized six species, three of which I encountered in this study. The species of *Mermeria* are all large and slender and occur only on medium to tall grasses over much of eastern and southern United States. In all species, adults are most abundant in the summer and late summer months.

Mermeria intertexta Scudder

According to Rehn (1919b) *M. intertexta* occurs along the Atlantic coast from New Jersey to southern Florida and on the Gulf coast. It is found in both fresh and salt marsh situations but occasionally strays into adjacent dune vegetation. At the margin of a salt marsh near Port St. Joe, Florida, I found numerous individuals in medium to tall grasses. In the east and southeast, *M. intertexta* overlaps at least geographically, if not ecologically, with *M. bivittata* and *M. picta*. The latter species occurs mainly in grasses of wooded areas.

PAIR FORMATION.—I saw solitary males stridulating in the field and in the laboratory. Each burst of stridulation consisted of two to four strokes of the femora, and one or two pulses of sound were produced with each stroke (Fig. 12a). Six to 13 bursts were produced in five calls, and the burst interval for these calls varied from 0.42 to 0.60 seconds. The similarity in the calling stridulation of *M. maculipennis* and *M. intertexta* may be owing to the fact that the two species are allopatric.

COURTSHIP.—Courting males produced two kinds of stridulation. The first type was somewhat similar to the call; it was performed by males turning towards other individuals and twice by males following females (Fig. 12b). Several bursts were produced by following males. The burst intervals were similar to that of isolated stridulating males. This signal preceded the second type of courtship stridulation, in which the femur (femora?) was rubbed across the forewing, producing pulses of sound that were longer in duration and softer in intensity than those of the first type (Fig. 12c). As one male approached a female, he first produced the first type of stridulation and then two groups of the two pulses of the second type. After the second pair of pulses he mounted the female. No signals were produced by the female.

AGGRESSION.—Females jerked their femora on several occasions. Sometimes the femora were jerked silently, and at other times the wings were struck with each stroke. One female produced three bursts of silent jerking when two males began to exchange aggressive stridulation three inches from her. She jerked her femora from the horizontal position to about vertical; each burst consisted of two or three jerks, and the rate of jerking was about five per second. Another female produced a similar motion in which about eight jerks were produced in quick succession, and the forewings were struck as the femora were jerked up. The context in which this stridulation was produced was not determined, but since it resembled male aggressive stridulation it probably serves an aggressive or repelling function. Males touched by other individuals or approached by

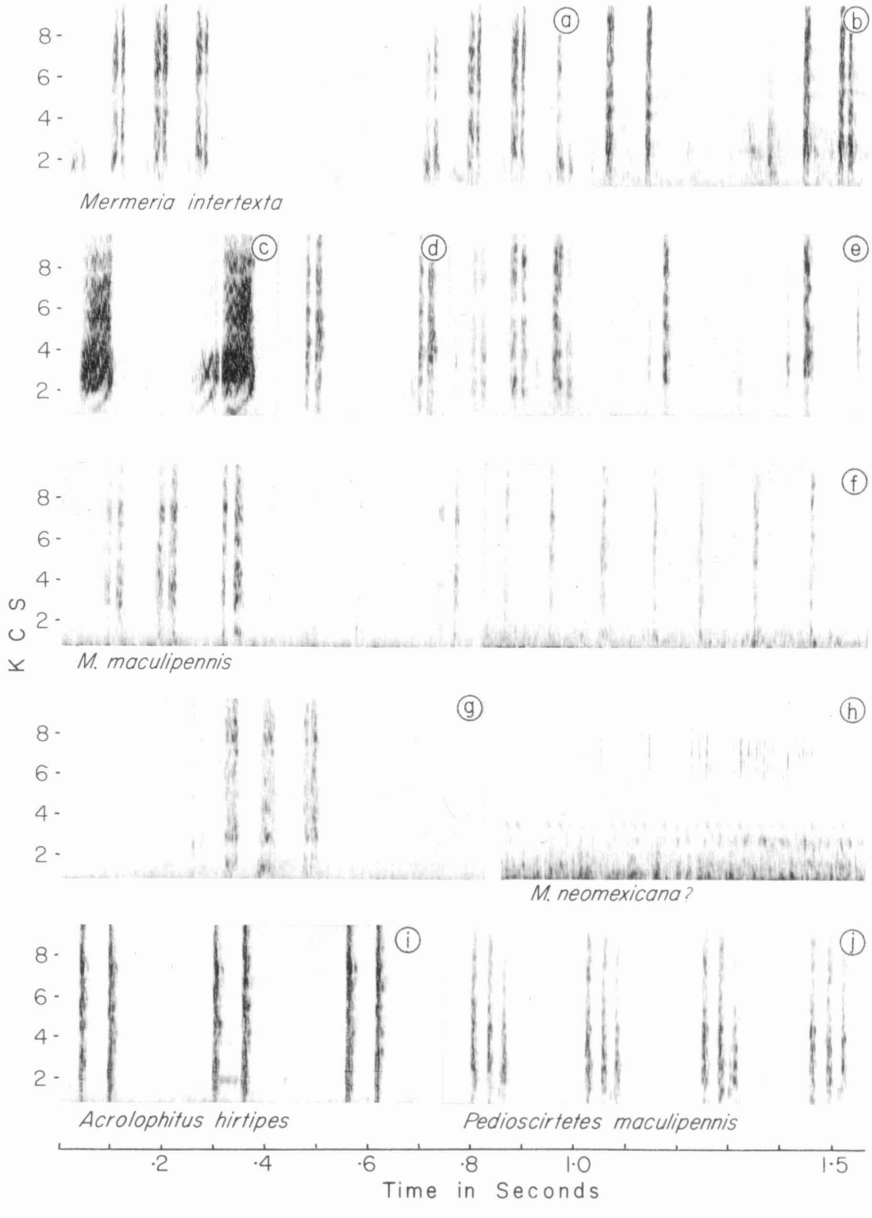

FIG. 12. Audiospectrographs of signals by various species of Acridinae: (a) *Mermeria intertexta* (Gulf Co., Fla.), stridulation by a solitary male, 85°F; (b) same, stridulation by a male following a female, 85°F; (c) same, courtship stridulation, 85°F; (d) same, aggressive stridulation by a male following a short flight of another male, 90°F; (e) same, three strokes of calling stridulation by one male, followed by aggressive stridulation by a second male nearby, 90°F; (f) *Mermeria maculipennis* (Crockett Co., Texas), calling type of stridulation by one male approaching a second male, followed by aggressive stridulation by the second male, 86°F; (g) same, stridulation by a male following a female, 86°F; (h) *Mermeria neomexicana* (Hockley Co., Texas), stridulation by an isolated male?, 73°F; (i) *Acrolophitus hirtipes* (Sutton Co., Texas), stridulation by a stationary, more or less isolated male, 92°F; (j) *Pedioscirtetes maculipennis* (Jeff Davis Co., Texas), stridulation by an isolated male, 89°F.

courting males produced a more or less regular series of femoral strokes that were not grouped as in courtship stridulation (Fig. 12e). The pulses produced with each stroke were either single or double.

Mermeria maculipennis Bruner

This species is distributed mainly in the Great Plains; it extends from Mexico to Canada, and from Arizona and Utah in the west to Iowa and Illinois in the east (Newton and Gurney, 1957: 90). It overlaps broadly, both geographically and seasonally, with *M. bivittata, M. picta, M. neomexicana,* and *M. texana,* but apparently not at all with *M. intertexta.*

COURTSHIP.—Eight courtship sequences were observed. One or more bursts of stridulation were emitted by males approaching and attempting to mount females. Males stridulated during each approach, producing a burst of 2–5 strokes of the femora (Fig. 12f). During each stroke, single or double pulses were produced. The first pulse may have been made on the upstroke and the second on the downstroke, but since the stroke amplitude was small, it was difficult to determine the exact nature of the movement. I did not hear females stridulating.

AGGRESSION.—Males produced three different aggressive or repelling movements. The first, aggressive stridulation, consisted of a series of regularly-spaced pulses of short duration produced by one femur striking against the forewing (Fig. 12f). A male produced aggressive stridulation twice when he was touched by other individuals, and twice immediately after the courtship stridulation of another nearby. One aggressive interaction between males occurred as follows: One male produced a burst of courtship stridulation while less than an inch from another, which answered immediately with three strokes of aggressive stridulation. The former then produced another burst of courtship stridulation, and the latter again answered with aggressive stridulation (Fig. 12f). Then each produced a burst of aggressive stridulation simultaneously. A second aggressive movement was a mild shaking of the femora held at the horizontal position. On one occasion a male shook when he was approached by another male. At another time a male first shook his femora slightly and then switched to aggressive stridulation when he was touched by another male. A third signal, raising the femora to the vertical position, occurred three times when a male was touched by another male. Twice one femur was held forward to about 160°. Each time the femora were raised they remained in the raised position for several seconds.

Mermeria neomexicana (Thomas)

A single song of stridulation presumed to have been made by this species was recorded near Lubbock, Texas (Fig. 12h). This species is sympatric with *M. bivittata* and *M. maculipennis* over much of its range, which is from northwestern Mexico to southern South Dakota and western Iowa (Newton and Gurney, 1957:90). Near Lubbock and in the Witchita Mountains of Oklahoma it was the only *Mermeria* species present.

GROUP ACROLOPHITI

The peculiar shape of the head and the pronotum make the members of the genera *Acrolophitus* and *Pedioscirtetes* very distinctive among the Acridinae. Presently this group is composed of only three species: *Acrolophitus hirtipes* Thomas, *Pedioscirtetes maculipennis* (Scudder), and *P. nevadensis* Thomas, the first two of which were encountered in this study.

GENUS *Acrolophitus* Thomas

Acrolophitus hirtipes (Say)

A. hirtipes is a large green grasshopper which somewhat resembles *Tropidolophus formosus* of the Oedipodinae. It is distributed mainly east of the Rocky Mountains from western Texas to Montana (Newton and Gurney, 1956: 599). In the northern states the forewings are not spotted as they are in the south. The transition area appears to be in Kansas (Hebard, 1931a).

PAIR FORMATION.—I made no observations on the sexual behavior of this species in the field. *A. hirtipes* is unusual in possessing conspicuously banded yellow and black hindwings. This character suggests that some sort of flight signal is involved in pair formation. Laboratory observations indicate that pair formation may be achieved by stridulation, which was produced by relatively isolated males, by an approaching male, and by a male in contact with a motionless female. Stridulation consisted of a series of paired, short, sharp pulses (Fig. 12i). The number of pairs of pulses produced by seven stationary and isolated males varied from 12 to 18 (mean = 16.6); there were 17 pairs in a song by the male in antennal contact with a female, and 7 pairs in the stridulation of the approaching male.

COURTSHIP.—I saw males approach and mount females on two occasions. Once, when a female approached and touched a male, he backed up, stridulated, and then approached and mounted the female. In the other case, a male approached a moving female and mounted without stridulating.

GENUS *Pedioscirtetes* Thomas

Pedioscirtetes maculipennis (Scudder)

According to Tinkham (1948), *P. maculipennis* is widely but discontinuously distributed over the Chihuahuan Desert, where it occurs in low, rocky hills (Ball et al., 1942). Little is yet known about the behavior of this species. The hindwings are uniformly black, unlike the banded pattern in *Acrolophitus hirtipes* and *P. nevadensis* and suggesting that wing color may be important in pair formation or courtship. Stridulations by solitary males were recorded in the laboratory. Four songs consisted of 14, 20, 23, and 24 bursts of three-pulse stridulations (Fig. 12j). Both femora were raised to about the 45° position and then struck against the forewings. Presumably the song attracts females.

GROUP BOOPEDONTES

The members of the genera *Boopedon* Thomas and *Morsiella* Hebard are very similar in appearance. Formerly (Bruner, 1904), all the members of the two genera were included in the genus *Boopedon*. Presently this genus includes the species *auriventris* McNeill, *nubilum* Say, and *gracile* Rehn, occurring mainly in the United States. The genus *Morsiella* (Hebard, 1925b) includes the species *flaviventris* (Bruner), *diabolica* (Bruner), *dampfi* Hebard, and *rufipes* Hebard. These species are distributed mainly in Mexico. I studied only *M. flaviventris* and *M. diabolica*. Both species occurred at the same locality.

GENUS *Morsiella* Hebard

Morsiella flaviventris (Bruner)

This species is known from Sinaloa and Nayarit in Mexico. I collected individuals in clumps of lush green grass on a well-grazed slope south of Tepic in Nayarit. The grass was not more than a foot in height, most of it much lower. *M. flaviventris* and *M. diabolica* were intermingled in the same grass clumps.

PAIR FORMATION.—I heard no stridulations in the field, possibly because the sky was heavily overcast. In the laboratory, males produced four kinds of stridulation. One appeared to be a calling type of signal, two were courtship signals, and the fourth was an aggressive signal. The calling signal (Fig. 13d) was produced eight times by more or less isolated males—on five occasions by a male in antennal contact with a female (courtship did not follow in these cases), twice by males who turned away from the female after producing it, and once by a male responding to the movement of a nearby male. The signal does not seem to have an aggressive function because another distinct signal was produced in aggressive encounters.

COURTSHIP.—Courting males produced two kinds of stridulation. The movements of the femora producing the two sounds were similar except for their rates. A slow sound was produced by stationary males that had turned toward moving females (first part of Fig. 13e), and a fast sound was produced by males advancing and attempting to mount (second part of Fig. 13e). The duration of the slow sound varied from 0.28 to 1.00 seconds, that of the fast sound from 0.09 to 1.00 seconds. In each of the four courtship sequences observed, a combination of the two sounds was produced. Males did not stridulate as they mounted females.

AGGRESSION.—Aggressive stridulation by males was produced five times in alternation

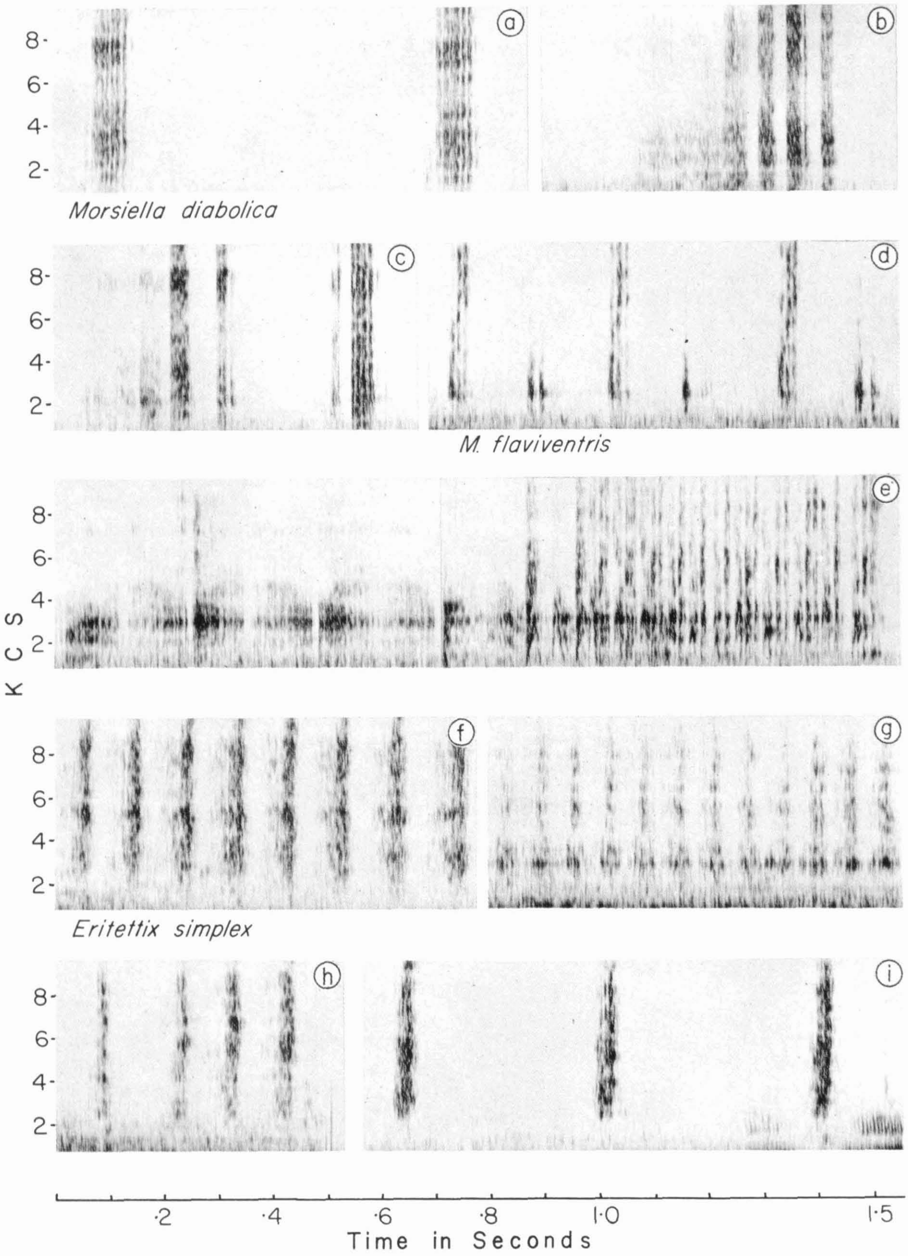

FIG. 13. Audiospectrographs of signals of various species of Acridinae: (a) *Morsiella diabolica* (Nayarit, Mexico), calling type of stridulation, 86°F; (b) same, stridulation by a male 0.5 inch from a female; he mounted the female soon after stridulating; (c) same, stridulation by a male as he touched a female; (d) *Morsiella flaviventris* (Nayarit, Mexico) calling? song of one male (antennating a female) followed in alternation by an aggressive song by a male eating nearby, 92°F; (e) same, courtship stridulation; first portion was produced while the male was stationary, and the second portion while rapidly advancing to the female; (f) *Eritettix simplex* (Monroe Co., Illinois) stridulation by an isolated male, 80°F; (g) same, courtship stridulation; (h,i) same, aggressive stridulation.

with the call of another male (Fig. 13d) and four times following the courtship sound of another male. Occasionally, pairs of closely spaced pulses were produced with each stroke.

Morsiella diabolica (Bruner)

This species occurs in western Mexico (Bruner, 1904). I found it at the same locality as *M. flaviventris.*

Pair Formation.—Two kinds of stridulation occurred in the field. One kind, type A (Fig. 13a), was common and on at least two occasions was produced by solitary males. The second sound, type B (Fig. 13b), was heard once in the field, but I did not determine the situation eliciting it. Both sounds were also heard in the laboratory. Eleven records of type A stridulation, all by males were obtained; in 10 cases, the males were stationary and more or less isolated from other individuals, and once the sound was produced by a male in antennal contact with a female. He did not attempt to mount either before or after this stridulation. From three to five pulses of stridulation were produced in each song. This sound probably has a calling function.

Courtship.—On seven occasions, both types of stridulation were produced in combination in a courtship context, type B always preceding type A (Fig. 13c): three times this combination was produced by stationary males, three times by males turning toward or approaching females, and once by a male in contact with females. One to three pulses of type A stridulation were produced each time. Type B stridulation was produced alone in eight instances: three times by males approaching females, and five times after males established contact with females. Males attempted to mount females only after producing this kind of stridulation. It is evident, therefore, that type B stridulation is associated rather closely with approaching and mounting. Type B stridulation was produced with one femur.

Aggression.—In one encounter between two males, one individual jerked his femora upward about five times in quick succession when he was touched by the other male (three jerks per second). A faint sound was produced during each jerk but it was not recorded.

GENUS *Eritettix* Bruner

Eritettix simplex (Scudder)

E. simplex occurs mainly on the prairies from North Dakota to Oklahoma (Newton and Gurney, 1956: 987). A few populations are found in relict prairies farther eastward: for instance, in the small prairie openings of southern Missouri and on hill prairies along the eastern bluffs of the Mississippi River in Illinois. It is apparently common along the eastern slopes of the Appalachian Mountains from Georgia to Connecticut (Newton and Gurney, 1956:987).

Pair Formation.—A few field observations were made on a hill prairie in southern Illinois by R. D. Alexander (pers. comm.). A male sang one to three songs, then walked about through the grass about a foot above the ground stridulating again. In 14 observations, the number of pulses per song varied between 11 and 21 (mean = 18.4). When a few years later I observed several males and females from this population in a terrarium, I recorded songs resembling these (Fig. 13f). The pulse number was somewhat lower, perhaps because several individuals were confined together and were responding to one another. Apparently all intermediates between calling songs with higher pulse numbers and aggressive songs with lower pulse numbers are possible.

Courtship.—I made the following observations on courtship (times indicate the duration of the various acts): A male followed a female up a grass stalk (5 secs.); when he was about an inch behind her, he rocked from side to side at about one cycle per second (10 secs.). Then, while stationary, he produced a burst of stridulation somewhat resembling the call (Fig. 13g) but with a much faster pulse rate (2 sec.), after which he rushed forward and attempted to mount. He failed to do so, however, and faced her from behind again (8 secs.). Rocking from side to side once more (7 secs.), he produced a short and long burst of courtship stridulation (2 secs.), but did not approach or attempt to mount after stridulating. During the first rocking motion the male's antennae were held straight down and during the second they were held straight forward. The bursts of stridulation were made with one leg at a time, but during each burst there was a switch in the leg producing the sound.

AGGRESSION.—No distinct alternation between the songs of males occurred, but the songs of one male seemed to cause other males nearby to stridulate. This latter stridulation was similar to the call but consisted of much fewer pulses (Fig. 13h). Males that were touched or approached by other individuals produced widely, and often irregularly, spaced pulses of sound (Fig. 13i). Once, when a male was approached by another male, he jumped away, then jerked his femora upwards several times about four times per second. This aggressive movement resembled somewhat that of *Syrbula* species.

GENUS *Syrbula* Stal

Syrbula admirabilis (Uhler)

S. admirabilis occurs over much of the eastern and central United States, and in the Southwest it reaches Arizona and northern Mexico. Of its habitat Blatchley (1920) said, "It frequents, for the most part, high, open uplands, where the soil is poor and covered with scanty vegetation, though it is sometimes found in timothy meadows and any roadsides." In Jackson Co., Ohio, Comanche Co., Oklahoma, and Hockley Co., Texas, *S. admirabilis* occurred in medium to tall grass, particularly in bunch grasses at the latter two localities. Stridulating males of this species were not conspicuous like stridulating males of *S. fuscovittata* and were difficult to locate. Also, unlike *S. fuscovittata,* males did not fly between songs.

PAIR FORMATION.—Calls of isolated males could be heard for a distance of several yards. These consisted of 15–63 pairs of pulses (Fig. 14a). Each pair appeared to be produced in a single stroke of the femur, and both femora appeared to move synchronously during each stroke. Throughout the call the ends of the femora were held just above wing level. Calls of males of *S. admirabilis* collected in San Luis Potosi, Mexico (55 mi. east of Cd. Valles) were shorter (8–10 pairs of pulses in four songs) and considerably faster in pulse rate. Whether these individuals should be considered geographic variants or members of another species cannot be decided without further investigation.

COURTSHIP.—Courtship in *S. admirabilis* is more complicated than that of any other species examined in this study. When males that had been calling became aware of females moving nearby, they produced stridulatory bursts of varying rate and duration (Fig. 14b, c). Such bursts of stridulation were also produced by males following retreating females. Several bursts were usually produced as males advanced toward females; the first bursts were usually shorter and had a faster pulse rate. In the vicinity of the female these bursts were usually longer, and the pulse rate slower. Stridulation of this sort was produced by males during each of 15 or more advances toward females. It was also produced when courtship was interrupted (see below). When females did not retreat, males took up a position parallel to and facing in the same direction as the females. Before mounting was attempted males proceeded through three phases of courtship. I saw eleven complete sequences involving individuals from southeastern Michigan, and the phases and events described below occurred during each sequence. Five times courtship was interrupted by the retreat of the female; on each occasion, the male emitted the same kind of stridulation he had produced during his initial approach towards the female (Fig. 14b). Bursts of such stridulation continued until the position parallel to the female was regained.

Phase 1. During the first phase, which lasted from 13–24 seconds, males produced stridulation that was somewhat similar to the call (Fig. 14d), differing mainly in that the femur nearest the female was held at about 45° while the other femur was held at about 60°. Most of the sound seemed to be produced by the femur nearest the female, and its intensity increased gradually at the beginning of the phase. Also, during this phase the antenna nearest the female was lowered in front of the female's face and waved up and down continuously. The other antenna was held at an angle of 180° from the near antenna and alternated in producing small waving motions and bursts of swings of fairly large amplitude (through approximately 90°). Each such burst consisted of 5–9 up and down swinging motions. The antennae were waved at the same rate as the femoral movements. During this phase, left and right sets of palpi were alternately raised and extended; as the right palpi were raised, the left palpi returned to a position next to the mandibles. Palpal movements were also produced in bursts, with right and left sets each reaching out twice. Each set was extended about once

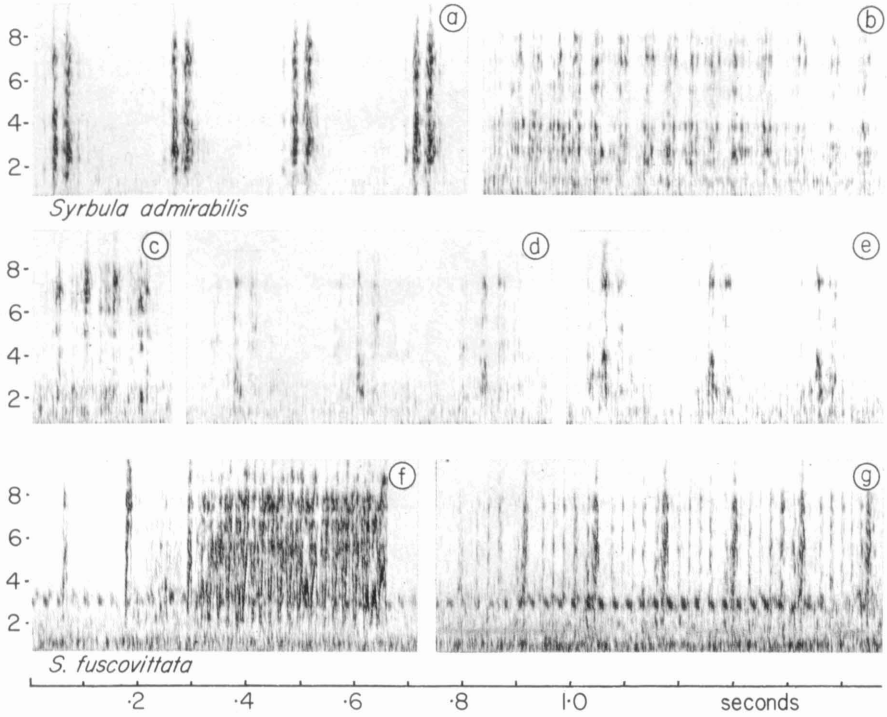

FIG. 14. Audiospectrographs of signals of *Syrbula* species: (a) *Syrbula admirabilis* (Livingston Co., Mich.), stridulation by a solitary male, 90°F; (b) same, stridulation by a male after loosing the female, 85°F; (c) same, stridulation by a male during the initial approach to the female, 85°F; (d) same, courtship stridulation during phase 1; (e) same, courtship stridulation during phase 3, (f,g) *Syrbula fuscovittata* (Hockley Co., Texas), two types of songs produced by solitary males, 73°F.

per second, or about one-fourth the rate of femoral and antennal motions. Successive bursts of palpi raising were separated by a two- to three-second interval. Bursts of palpal raising continued for the duration of phase 1. The palpi are marked with white and hence conspicuous against the black background of the face and mouthparts. Stridulation, antennal waving, and palpal waving stopped suddenly after about 20 seconds and did not occur during phase 2.

Phase 2. After a short interval the femora began to move up and down silently. These silent movements resembled those produced during phase 1 and continued for 11–25 seconds. Phase 2 lasted approximately as long as phase 1; when the latter was short, phase 2 was also short. Antennae and palpi were held motionless during phase 2, which ended with the cessation of silent femoral movements.

Phase 3. During the short third phase (1.0–2.5 seconds), femoral movements with sound were resumed as the male sidled up to the female as though to mount. As he approached her he lowered the end of his abdomen. Stridulation during the third phase resembled that of the first phase, but the stroke rate and the sound intensity were somewhat higher (Fig. 14e). Antennal and palpal motions were not observed during phase 3, but may have been present. Presumably males mount sexually receptive females after sidling up to them, but in this study females rejected males by raising the femur nearest the male to vertical and occasionally kicking out with the tibiae. Males never forcefully attempted to mount females.

Phase 4. When males were rejected they waved their antennae as in phase 1 and rocked their bodies forward and backwards about six times. During rocking, the abdomen was held in a lowered position. After body-rocking, males vibrated both femora silently and then appeared to spread both femora away from the abdomen and return them to the resting position in a very quick movement. Phase 4 lasted 3–4 seconds, and shortly after its end the sequence was resumed again, beginning with phase 1. On one occasion five full sequences were produced in succession, and at another time four sequences followed each other. When males aligned themselves on the right side of the female, the left femur and left antenna were lowered, and the right femur and right antenna were raised; when males were on the female's left side, the opposite occurred.

Aggression.—When males established contact or moved near one another, they sometimes exchanged signals which consisted of jerking both femora from horizontal to vertical three or four times in quick succession. A brief, soft sound was produced as the femora struck the forewings. Occasionally, the substrate was also struck. This signal resembled the call, but the amplitude of femoral movements was greater and the sound was much less intense. Aggressive males alternated in producing bursts of jerking, but alternation was not perfect, and a leader and follower could always be distinguished. Several times the roles of leader and follower were exchanged.

Syrbula fuscovittata Thomas

This species occurs mainly in the southwest United States and in Mexico; it is sympatric with *S. admirabilis,* at least in Texas. I found singing males of both species at the same locality near Lubbock, Texas. In Arizona (Ball et al., 1942) this species is most common in tall grass of the desert grassland but is also found in the denser growth of the northern grassland. In Hockley Co., Texas, and near Cd. Victoria, Tamaulipas, *S. fuscovittata* occurred in medium to tall grass.

Pair Formation.—The call of this species consisted of two kinds of sounds. One (Fig. 14f) began with a series of ticks produced by one femur; after the first or second tick, the other femur began to vibrate against the forewing. Ticking was produced throughout vibratory stridulation, and ended at about the same time. In the second sound (Fig. 14g), which followed the first after a short pause, males produced a series of widely spaced ticks with one femur (about 8 per second) and a series of closely spaced ticks with the other (about 50 per second). Most songs were made up of both sounds, and one to three bursts of the first kind preceded a single burst of the second kind. Both sounds sometimes occurred alone. The situations eliciting the various kinds of songs are unknown. In Texas and Mexico males often perched on top of vegetation and sang several songs (combining both kinds of sounds), then flew to another perch where they again sang a few songs. Flight between songs did not occur in *S. admirabilis,* which seems to be more secretive. The hindwings of *S. fuscovittata* are black, suggesting that they are involved in signalling.

Aggression.—The aggressive signal is similar to that of *S. admirabilis*: femora were jerked from horizontal to almost vertical position five times in quick succession at about six jerks per second, but no sound was detectable.

GENUS *Acantherus* Scudder

Acantherus piperatus Scudder

This species is known from the Big Bend region of Texas, from southern Arizona, and from Sonora, Mexico (Tinkham, 1948). According to Ball et al. (1942), it is usually found in tall grasses under spiny shrubs and trees. Near Imuris, Sonora, individuals occurred in tall grass by the roadside.

Pair Formation.—I did not make any observations on the behavior of this species in the field. In the laboratory a number of songs were sung in the presence of other individuals (Fig. 15a). In each song, pulses were usually grouped in threes, but a few bursts of two and four pulses each were also recorded. In five cases the total number of bursts per song varied from 10 to 28 (mean = 22.4).

Courtship.—On two occasions, males approached and mounted females. During each approach the male sang a song essentially identical to that described above; one song consisted of 13 bursts and the other of 12 bursts. As she was mounted, one of the females raised her femora to about 45° and from that position jerked them up and down a few degrees several times in quick succession (5 per second). The function of the movement is not known, for it was also produced during copulation.

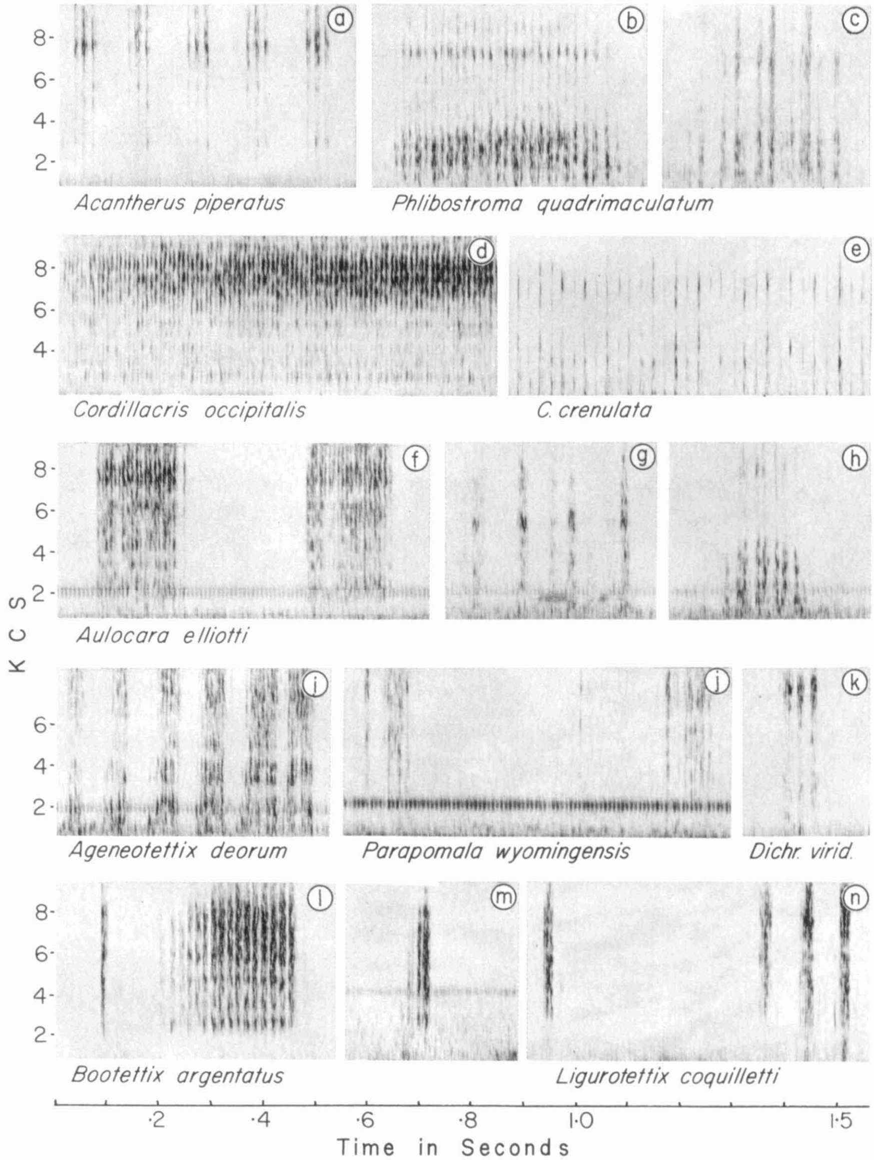

FIG. 15. Audiospectrographs of the signals by various species of Acridinae: (a) *Acantherus piperatus* (Sonora), stridulation by an isolated male, 94°F; (b) *Phlibostroma quadrimaculatum* (nr. Raton, New Mex.), aggressive stridulation, 90°F; (c) same, male produced this stridulation as he turned toward a female, 90°F; (d) *Cordillacris occipitalis* (Sherman Co., Kans.), stridulation of a stationary male in the presence of other moving individuals, 92°F; (e) *Cordillacris crenulata* (Pueblo Co., Colo.), stridulation by a stationary male in the presence of moving individuals, 90°F; (f) *Aulocara elliotti* (Sherman Co., Kans.), male aggressive stridulation, 90°F; (g) same, male courtship stridulation, 90°F; (h) female aggressive stridulation, 90°F; (i) *Ageneotettix deorum* (Sherman Co., Kans.), male aggressive stridulation, 90°F; (j) *Parapomala wyomingensis* (Wayne Co., Utah), stridulation by a more or less isolated male, 84°F; (k) *Dichromorpha viridis* (Monroe Co., Missouri), male aggressive stridulation, 85°F; (l,m) *Bootettix argentatus* (Brewster Co., Texas), stridulation by an isolated male, 70°F; (n) *Ligurotettix coquilletti* (Maricopa Co., Ariz.), stridulation by an isolated male, 95°F.

GENUS *Phlibostroma* Scudder

Phlibostroma quadrimaculatum (Thomas)

P. quadrimaculatum occurs chiefly on the shortgrass prairies from Canada to Mexico (Newton and Gurney, 1957:208). I collected it in very short grama grass with much bare ground between tufts near Marathon, Texas, on the high plains west of San Luis Potosi, Mexico, and on the high plains near Raton, New Mexico.

PAIR FORMATION.—I failed to observe pair formation in the field, but on the basis of laboratory observations this is likely to be similar to that observed in *Ageneotettix* and *Drepanopterna,* that is, males probably approach moving females.

COURTSHIP.—Mexico Population: Males produced only femur-tipping as they approached females. The femora were mostly tipped asynchronously, and often only one femur was tipped. In courtship males approached females from the side and slightly from the rear. New Mexico Population: Males produced three different movements while approaching females. Femur-tipping was the first signal produced in each courtship sequence. Two kinds of stridulation followed this (Fig. 15b, c). Sometimes series of tipping movements were interspersed with bursts of stridulation. Femur-tipping was fairly rapid (about 0.3 seconds); upstrokes and downstrokes were about equal in duration, and up to three tipping motions were produced in a row. In several sequences males tipped but did not stridulate.

AGGRESSION.—Mexico Population: Males produced bursts of vibratory stridulation when touched by other individuals (Fig. 15b). Females apparently rejected males by producing vibratory stridulation, and one female rejected a male by shaking her femora while they were held in the vertical position. Female stridulation was similar to the aggressive stridulations of males, only somewhat less intense. New Mexico Population: The aggressive behavior patterns of these individuals were similar to those observed in the Mexico population. One female raised her femora and jerked them in the raised position. Another female performed a movement similar to femur-shaking when she was touched.

GENUS *Cordillacris* Rehn

Three species belong to this genus: *Cordillacris grinnelli* Rehn and Hebard, *C. occipitalis* (Thomas), and *C. crenulata* (Bruner). I studied only the last two species.

Cordillacris occipitalis (Thomas)

C. occipitalis is a shortgrass prairie species that ranges from Montana to northern Texas. It also extends west of the mountains to Arizona, Nevada, and Oregon (Newton and Gurney, 1956: 884). In Arizona (Ball et al., 1942) it "occurs on shallow, sandy or gravelly soil covered with a scanty growth of short grasses and weeds . . ." I collected *C. occipitalis* in Sherman County, Kansas, near Denver, Colorado, and at Pueblo, Colorado. At the last locality it was intermingled with *Cordillacris crenulata.* At each locality individuals walked about on semi-open ground.

PAIR FORMATION.—Individuals apparently occur only on the ground. Although I heard many stridulations in the field, I did not determine the situations in which they were produced. In the laboratory similar stridulations were produced by more or less isolated males (Fig. 15d). It is possible that females are attracted to males by this call, but pair formation at least sometimes occurs in the absence of stridulation. In the field isolated males tipped their femora as they walked about on patches of open ground. Tipping was rapid (duration about 0.2 seconds), and the upstroke was faster than the downstroke. The antennae were raised and lowered and touched the substrate repeatedly as individuals walked along. In the field a disturbed female flew and alighted about 1.5 feet from a male, who promptly approached her, tipping his femora as he advanced. He stopped three inches short of the female and continued to perform femur-tipping motions at irregular intervals. About two minutes later the female moved, and the male immediately approached her and attempted to mount; she hopped away.

In the laboratory, I recorded seventeen bursts of stridulation by stationary males. Each burst was produced by vibration of the femora against the forewings (duration: 0.5–0.9 seconds). Fifteen times males stridulated while at least several inches from other individuals and while other individuals were motionless. Twice a male stridulated shortly after he had briefly touched a female; both times the male courted the female after stridulating, once immediately following stridulation and once after a pause of 15 seconds. Seven stridulations were followed by femur-tipping; three stridulations were preceded by tipping, and seven stridulations were neither preceded nor followed by tipping.

Courtship.—In 6 of 8 approaches in the laboratory, males tipped their femora two or more times. In two approaches no signals were apparent. Femur-tips were usually performed in groups of 2–5 (at 2–3 per second). Usually the femora were tipped to 25° or 30° from the resting position. Before mounting, males assumed a position at right angles to the female. One male thrust his head against the female several times while facing at right angles to her.

Aggression.—Males usually tipped but sometimes raised their femora in encounters with other males. Females rejected males by raising their femora to near vertical, by kicking out with the hind tibiae, or by simply hopping away.

Cordillacris crenulata (Bruner)

Cordillacris crenulata is distributed across the short grass prairies and is widely sympatric with *C. occipitalis*. It occurs from Montana to the panhandle of Texas (Hebard, 1928, 1931a). Many individuals of *crenulata* occurred on the ground in an area sparsely covered with very short grama grass at Pueblo, Colorado, along with a few individuals of *occipitalis*. Near Raton, New Mexico, a few individuals of *crenulata*, but none of *occipitalis*, occurred among large numbers of *Drepanopterna femoratum* and a few individuals of *Phlibostroma quadrimaculatum*.

Pair Formation.—Individuals flushed in the field always alighted on bare ground. While I saw no interactions between individuals in the field, the overall similarity of *crenulata* with that of *occipitalis*, as observed in the laboratory, suggests that pair formation in the two species is similar.

Courtship.—Tipping is at least superficially similar to that of *occipitalis*. Usually three or four tipping movements were made in quick succession (repetition rate about 3 per second), and the downstroke was more rapid than the upstroke. Usually the tibiae swung through 60° from the resting position, which varied from 30° to 60° from horizontal. Each time the femora were tipped, the antennae were depressed in a quick short movement. Whether or not this dipping of the antennae serves any communicative function remains to be determined.

I saw males stridulate five times when another individual moved nearby. Twice males approached females after they stridulated, and three times they remained stationary. Stridulation was produced with both femora and resembled that of *C. occipitalis* except for a much slower pulse rate (Fig. 15e). The following sequence involving stridulation occurred two times: a female walked past a male. He remained stationary, tipped his femora several times in quick succession and then produced a single burst of stridulation. Then he tipped his femora as he advanced on the female.

Aggression.—Aggressive behavior is similar to that of *C. occipitalis*. Tipping seems to be the primary male-spacing signal, but males that were touched also raised their femora to vertical. Females raised their femora and made sharp upward jerks with their femora when touched.

GROUP AULOCARINI

This group of large-headed, ground-dwelling Acridinae includes *Ageneotettix* McNeill, *Eupnigodes* McNeill, *Zapata* Bruner, *Aulocara* Scudder, *Drepanopterna* Rehn, and *Heliaula* Caudell. I studied the following three representatives: *Ageneotettix deorum* (Scudder), *Aulocara elliotti* (Thomas), and *Drepanopterna femoratum* (Scudder).

GENUS *Ageneotettix* McNeill

Ageneotettix deorum (Scudder)

Ageneotettix deorum is widespread in grasslands of the United States and Canada but is apparently most abundant on the Great Plains. It is found among dry grasses, frequently where a considerable amount of bare soil is exposed among the scanty vegetation.

Pair Formation.—On sunny days on the George Reserve, individuals walked about or just stood motionless on bare patches of ground. Pair formation is apparently only achieved by males approaching moving females. Males also approached conspecific males, males and females of other grasshopper species, and even a tiger beetle. Solitary males frequently tipped their femora while walking about, but females did not do so.

COURTSHIP.—I saw more than 40 mounting attempts and six copulations by individuals from the George Reserve. The following descriptions of courtship apply to these individuals, but courtship of individuals from Sherman Co., Kansas, near Denver, Colorado, near Van Horn, Texas, and near Zion National Park, Utah, seemed to be similar to that of Michigan individuals. (1) When approaching other individuals, males tipped their hind femora repeatedly and synchronously from about 45° to nearly vertical. The movement was rapid (duration: about 0.2 seconds), the repetition rate varied considerably up to about 3 per second, and the downstroke was faster than the upstroke. Tipping was sometimes repeated continuously while walking, thus differing from the femur-tipping of the Oedipodinae, but it was also produced during momentary stops. Femur-tipping by courting males was faster and more precise than that by aggressive males. (2) The antennae of males were raised and lowered repetitively and rapidly as they walked about. The movement was made by both isolated and courting males, but seemed most pronounced when males had established contact with females. Shaking of the antennae was not continuous but was given in irregular bursts. (3) Before attempting to mount, the male always assumed a particular position with respect to the female. He stood behind one of the female's femora, facing her abdomen and also facing slightly forward. The male's antennae, and often his head, were in contact with the female's abdomen. As he moved into this position he tipped the femora and shook his antennae against the female.

Females rejected males by kicking them when they assumed the pre-mounting position, by raising their femora to vertical or tilting them forward from vertical, or by stridulating. Males did not attempt to mount females signalling in these various ways. One male and female exchanged stridulations as the male approached and then separated. Stridulation by females was similar to that of males but softer. The mean duration of six copulations was approximately five minutes.

AGGRESSION.—Males that were approached by other males raised their femora to vertical, or stridulated (Fig. 15i), or tipped their femora, or performed some combination of these. For instance, a copulating male raised his femora to vertical when he was approached by another male. Another copulating male only stridulated. In both cases the approaching male turned aside without touching the pair. I frequently saw two males approach one another in the field; they sometimes separated after exchanging only femur-tipping signals, and sometimes after exchanging both femur-tipping and stridulatory signals. Females also stridulated aggressively when touched by other individuals. Similar aggressive signals were produced by males collected in Kansas, but stridulation was absent in males and females from near Zion National Park, Utah. These latter individuals belong to the subspecies *A. d. curtipennis*. Femur-tipping was the most common aggressive signal produced by males and it was usually the only one performed. The movement was slower (duration 0.5–0.7 seconds) and less precise than that made by courting males. The femora often moved asynchronously. Males sometimes approached other males, first producing the fast, courtship type of femur-tipping, then switching to the slow type of femur-tipping in response to slow tipping by the male being approached.

GENUS *Drepanopterna* Rehn

Drepanopterna femoratum (Scudder)

This species occurs mainly in the shortgrass plains east of the Rocky Mountains, from Alberta to Texas (Newton and Gurney, 1956: 940).

PAIR FORMATION.—Pairing in *D. femoratum* is much like that in *Ageneotettix deorum*. I saw many individuals running about on sparsely-vegetated ground a few miles west of Van Horn, Texas, and between bunches of grama grass near Raton, N.M. No stridulations were heard at either locality. In Texas, a difference was noticed between the locomotion of *D. femoratum* and that of *A. deorum*, which might be involved in interspecific recognition. Males of *D. femoratum* moved across bare patches of ground in a series of small hops about two inches in length, whereas males of *A. deorum* walked without hopping. In New Mexico individuals of this species were intermingled with individuals of *Phlibostroma quadrimaculatum*, a superficially similar species.

COURTSHIP AND AGGRESSION.—Van Horn Population: Three kinds of femoral movements were made. (1) Several approaching males made tipping movements which were *slow* in duration and in repetition rate (duration, 0.4–0.7 seconds; repetition rate, 1.0–2.0 per second; upstroke slightly faster than downstroke). These movements may have an aggressive function; at least they resembled the tipping made by aggressive New Mexico males. (2) Males standing near females produced several *rapid* tipping movements in quick succession (duration less than 0.5 seconds; repetition rate, 4.0–5.0 per second; downstroke much faster than upstroke). This movement appears to have a courtship function. (3) Males that touched one another made 2–3 rapid upward jerks in quick succession (repetition rate, 2.15–4.16 per second), but, unlike New Mexico individuals, no sound was produced. Raton Population: Four kinds of femoral movements occurred. (1) Males made precise tipping movements with rapid downstrokes while approaching other individuals. (2) Males in close proximity to one another made slower tipping movements in which the upstroke and downstroke were nearly equal in duration and in which the two femora were sometimes alternately raised and lowered. This slower type of tipping was continued until the males separated. (3) Males that were mounted, touched, or approached jerked their femora upwards several times in quick succession and produced faint ticking sounds. (4) One male produced several faster femur-tips (see 1 above) and then two bursts of vibratory stridulation as he approached a female.

GENUS *Aulocara* Scudder

Aulocara elliotti (Thomas)

This species is distributed both east and west of the Rocky Mountains (Newton and Gurney, 1956:744) and it lives mainly on bare ground in areas of short grass (Brooks, 1958; Hebard, 1935; Buckell, 1922b). The species is quite similar in appearance to *Drepanopterna femoratum*. Individuals were observed and collected near Zion National Park, Utah; near Bicknell, Utah, and in Sherman County, Kansas.

PAIR FORMATION, COURTSHIP AND AGGRESSION.—Zion Population: Males wandered about on sparsely vegetated ground, stopped frequently, and stridulated occasionally. One male repeatedly (n=5) climbed onto small prominences and then stridulated. Between songs he walked about. Other males behaved similarly. When two males encountered they tipped their femora, then separated. Solitary males also occasionally tipped their femora while moving about.

Buckell (1922b) made the following observation on pair formation in British Columbia: "On several occasions from three to five males were observed following a female. In each case the female was hopping while the males were running rapidly behind, stopping occasionally to stridulate."

Bicknell Population: Individuals occurred on open ground and stridulation resembling that of the above population was heard. In five courtship sequences observed in the laboratory males silently and rapidly approached females and assumed a position similar to that assumed by courting males of *Ageneotettix deorum*. Females kicked the males each time and mounting failed. Aggressive stridulation was produced three times: (1) When two males attempted to mount a female simultaneously, they touched one another, and each produced several bursts of stridulation. (2) A male stridulated when he was approached and touched by another male. (3) A male produced 27 bursts of stridulation when he was touched while feeding.

Sherman County Population: Individuals were found wandering about on the ground along with individuals of *Ageneotettix deorum* and *Cordillacris occipitalis*. No stridulations were heard in the field. In 10 of 13 courtship sequences observed in the laboratory, males assumed a position similar to that in the above population when attempting to mount. In three instances they faced the female at right angles to the metathoracic region. Usually males only tipped their femora as they approached females, but in two approaches they also stridulated before mounting. Stridulation consisted of a series of short, more or less regularly spaced pulses of sound (Fig. 15g). Females rejected males by (1) raising the femora to vertical, when the male approached, (2) kicking out with the hind tibiae when males assumed the premounting position, (3) jerking both femora from horizontal to about 70° when mounting was attempted, and (4) stridulating when males assumed the premounting position (Fig. 15h). Sometimes several of these movements were performed in succession. Aggressive stridulation in females was heard only once and it seems to be quite distinct from that of males. When touched, males (1) produced one to three short bursts of stridulation (Fig. 15f), (2) tipped their femora, (3) raised their femora to vertical, or (4) jerked their femora from horizontal to vertical.

GENUS *Parapomala*

Parapomala wyomingensis (Thomas)

This species extends from Montana and Nebraska to Mexico (Newton and Gurney, 1957: 208). It evidently lives exclusively in clumps of grass throughout its range (Ball et al., 1942). I collected it near Bicknell, Utah. Individuals were reluctant to leave grass clumps, and clung to the stems with their very short fore and middle femora. When placed onto the ground, they either jumped or reached out laterally with the hind femora in search of a grass stem. If they grasped a stem they immediately pulled their bodies to it. Such behavior and the very short fore and middle legs indicate that the species is highly specialized for living on stems.

PAIR FORMATION.—Relatively isolated males stridulated in the absence of movements by other individuals (Fig. 15j). The number of pulses in five songs was 12, 15, 17, 18, and 28.

COURTSHIP.—A single acoustical signal was produced by approaching males. The femora were raised to vertical, and at the same time the tibiae were flung out to an angle of 90° from the femora. The femora then dropped to the horizontal position, were raised again to less than vertical, and then rubbed against the forewings as they were lowered for the second time. The whole movement was continuous and very rapid, and the stridulation produced was similar to the stridulation of isolated males. One to four strokes of stridulation were produced during each of three approaches. One male made courtship stridulations in the absence of other individuals and another approached a female along a grass stalk and mounted her without stridulating.

AGGRESSION.—In the only male–male encounter observed, one male jerked his femora from horizontal to about 20° and the other made no movements. An isolated male raised his femora slowly to about 70°, then dropped them rapidly; he repeated this movement several times. The significance of the movement is not known.

GROUP ORPHULELLINI

This group includes the North American genera *Orphulella* Giglio-Tos, *Dichromorpha* Morse, and *Clinocephalus* Morse. The first genus includes a large number of species distributed from the United States into Central America. The presence of large fore and middle femora in the males is a characteristic feature of this group. In this regard they resemble the Catantopinae and the similarity seems owing to similar pairing methods.

GENUS *Orphulella* Giglio-Tos

Gurney recognized four species of *Orphulella* occurring in the United States (1940b). *Orphulella compta* occurs in southern California and southern Arizona; *O. speciosa* occurs mainly in the central states from North Dakota to Texas and extends eastwards through the northern states to New England; *O. pelidna* is widespread throughout the United States; and *O. olivacea* occurs in coastal marshes along the Gulf and Atlantic coasts. In the present study only *O. speciosa* and *O. pelidna* were examined.

Orphulella speciosa (Scudder)

Orphulella speciosa is especially abundant in the central and eastern prairie region and extends eastward to New England. It also occurs along the Texas coastal regions (Newton and Gurney, 1957: 250). I observed the behavior of individuals from Livingston and Crawford counties, Michigan.

PAIR FORMATION.—The mating behavior of this species differs strikingly from that of the Acridinae examined above. On the George Reserve, many short (0.25 second) crepitating flights were heard. I saw a male walk about in fairly dense dry grass, then make short (1 foot) flights. He crepitated during each of several flights and walked about on the vegetation between them. I observed this behavior on one morning only, even though I frequently encountered this species at precisely the same locality. Whether or not this crepitation is involved in pair formation is not known.

Pair formation sometimes occurred in the following manner: males approached moving individuals slowly and stealthily, and when sufficiently close, pounced on them apparently without first signalling; thus, males appeared to stalk females and apparently did not inform them of the impending attempt to mount. More than ten approaches and mountings had the following elements in common: (a) Males advanced only when the individual being approached was moving—as soon as this individual stopped moving the approaching males stopped advancing. (b) Antennae were held straight forward during the approach. (c) Males moved their heads slowly from side to side several times, placed their hind tibiae well against the substrate, and then leaped onto the female. (d) There were no signals produced during the approach. In the laboratory I saw males mount conspecific females, conspecific males, and males of *Chloealtis conspersa* (a species which is quite different in general appearance).

AGGRESSION.—Males mounted by other males kicked out alternately with both hind tibiae; each tibia was kicked out two or three times in quick succession, producing a series of 4–6 ticking sounds as the forewings were struck. Similar movements were performed when they were touched by males of *Chorthippus curtipennis*. On one occasion a female accidentally jumped onto a male; the male kicked and struggled, the female hopped away, then both individuals produced a series of ticks (about 6) and became motionless. Males touched by other individuals also performed one or more of the following movements: jerking the femora up to near vertical, jerking their bodies, and spreading the femora to about 45° from the body. Three repelling movements were made by females: (a) raising one or both femora to vertical; (b) raising the femora more rapidly and kicking out with the tibiae; (c) kicking out both tibiae alternately and striking the ends of the forewings.

Orphulella pelidna (Burmeister)

Two subspecies are listed for this species by Gurney (1940b); *O. p. pelidna* occurs from Texas and North Dakota eastwards, and *O. p. desereta* occurs from northern New Mexico to Washington. Intermediates between these two forms are found in the intervening area. In the West the species occurs in moist grassy or weedy areas, and in the East it occurs in a variety of situations from dry to moist, grassy areas. I collected the species in moist grass along roadsides in Anderson County, Texas, and in Volusia County, Florida.

PAIR FORMATION.—Anderson County males performed very short crepitations like those of *O. speciosa* males in Michigan. One male also crepitated during a disturbance flight. The function of crepitation is not known.

COURTSHIP AND AGGRESSION.—Texas Population: Twice, I saw a male approach a female. On one occasion he approached slowly (as *O. speciosa* does) and then tipped his femora alternately (4–5 times per second); each femur was raised three times. This male did not continue to approach after these movements. On the other occasion, the same male slowly approached a moving female, his antennae pointing directly at her. When he touched her with his antennae, she raised her femora and tilted them forward, and he did not attempt to mount, nor did he lift his femora alternately as he had done in the first approach. Females raised their femora when males approached or when other individuals moved nearby. One female raised both femora when she was approached and from that position jerked her femora forwards several times through a few degrees. Another female tilted her femora forward when she was approached and touched by a male. I saw no interactions between males. Florida Population: I heard a single crepitation by a disturbed male and saw one courtship sequence in the field: Two disturbed males alighted within an inch of one another. For several minutes, they remained motionless, then one of them walked forward and began to feed on a blade of grass. The other male, seeing him move, turned toward him and slowly approached, advancing only while the feeding male moved. When they were within an inch of one another the approaching male pounced onto the feeding male; the pair struggled for a second or so and then separated. No signals were evident.

GENUS *Dichromorpha* Morse

Dichromorpha viridis (Scudder)

Dichromorpha viridis is the only species in the genus occurring in the United States and is distributed over most of the eastern part of the country (Newton and Gurney, 1956: 938). It is abundant in moist, dense grasses, often at the margins of woods (Morse, 1920; Hebard, 1931a; Coppock, 1962).

COURTSHIP.—Approaching and mounting are similar to those seen in *Orphulella* species; each of 7 approaches was stealthy and no signals were emitted before mounting.

AGGRESSION.—Copulating males stridulated (Fig. 15k) or raised their femora slowly when touched or when other individuals moved nearby. The degree to which the femora were raised varied; sometimes it consisted of only a slight upward tilt with almost no extension of the tibiae; at other times they were raised to vertical, with the tibiae extended to 90°; and at still other times they were tilted forward to almost head level, with the tibiae held parallel to the back. In this last position the tibiae made slight, slow, upward kicking motions. One male turned toward a copulating pair that moved about an inch away, pointed his antennae at the pair and then pounced onto them. After a brief struggle he departed. During this intrusion, the copulating male turned his head toward the intruding male and regurgitated a drop of brown fluid. He held his head turned in this position for several seconds with the drop clinging to his mouthparts, then he straightened his head as he withdrew the droplet again. Many species of grasshoppers regurgitate a brown fluid when handled, but apparently no other species is known to do so in interspecific interactions.

GROUP LIGUROTETTIGINI

This group consists of two monotypic genera, *Ligurotettix* and *Goniatron.* Both species, *L. coquilletti* McNeill and *G. planum* Bruner, are distinctive among the Acridinae in the shape of the head, which is rounded as in the Oedipodinae. Both species occur on the stems of desert shrubs and trees and are loud daytime stridulators. They were presumably placed in distinct genera because of the difference in size and because of differences in the forewing. *L. coquilletti* has a greatly enlarged costal area traversed by parallel and evenly spaced cross veins. *G. planum* has both the precostal and costal areas somewhat enlarged, but in the latter area the cross veins are thickened and may serve as scrapers in stridulation. The radial vein appears to be the scraper in *Ligurotettix.*

GENUS *Ligurotettix* McNeill

Ligurotettix coquilletti McNeill

This small gray grasshopper occurs in the deserts of southwestern United States, from southern Arizona to Nevada and southern California. Three subspecies of *L. coquilletti* have been described (Rehn, 1923): *L. c. coquilletti* McNeill from southern California, *L. c. cantator* Rehn from Nevada, and *L. c. kunzei* Caudell from southern Arizona. The species is found on the stems of bushes such as creosote, mesquite, *Lycium,* and *Atriplex* (Ball et al., 1942).

I encountered individuals on the gray stems of creosote bushes in western Arizona and southern California. All were faced upwards along the stems, and when disturbed, they moved around the stem and out of sight. Stridulation by males was heard emanating from nearly all bushes at both localities. Most stridulations consisted of single pulses of sound produced by single strokes of the femora. The interval between pulses was quite variable. Some two- and three-pulse stridulations were also produced (Fig. 15n), in which the intervals between pulses appeared to be constant. A total of 34 single pulse sounds, 17 double pulse sounds, and 11 triple pulse sounds were recorded. One femur was used to produce each burst of sound, but the femora sometimes alternated in producing successive bursts. Males frequently moved up and down the stem between stridulations, and even while descending they continuously faced upwards along the stem.

GENUS *Goniatron* Bruner

Goniatron planum Bruner

This species was not examined in the present study, but some observations on its behavior were made by Tinkham (1948). Like *Ligurotettix* it inhabits bushes or low trees. It is almost restricted to southern blackbrush *(Flourensia cernua).* Regarding its habits, Tinkham said, "In bright sunlight *G. planum* is inclined to hide in the foliage on top of its host plant. When cloudy or in the late fall it is often observed on the bare adobe soil, found where its host plant grows, perhaps to gain warmth from the soil or perhaps the females are seeking locations to lay their few eggs. The song of *Goniatron* commences as a rapid tk-tk-tk-tk-tk—*schick* followed by *schicks* at 30 to 60 second intervals. Usually after being disturbed . . . it produced a *shuck-a-shuk* . . . . It is not known whether the females stridulate but the similarity in the tegmen between male and female would suggest that perhaps they do answer the sounds made by the male."

GENUS *Psoloessa* Scudder

This genus consists of three small ground-dwelling species occurring in sparsely vegetated regions of western United States, western Canada, and northern Mexico. In his revision of this genus, Rehn (1942) recognized three species, *P. texana, P. delicatula* and *P. thamnogaea,* of which the first has three subspecies and the second has two subspecies. *P. texana* and *P. delicatula* are known to overlap extensively, but *P. thamnogaea* is evidently allopatric with them.

Psoloessa delicatula (Scudder)

This species occurs in the Great Plains and in the mountains of the West, extending from Mexico to Canada and from California and Oregon east to Texas and the Dakotas (Newton and Gurney, 1957: 226). In Arizona (Ball et al., 1942) it is "found in greatest abundance in short grasslands, usually where the growth is sparse and the soil thin." Near Williams, Arizona, and at Walsenburg, Colorado, *P. delicatula* and *P. texana* occurred together on the ground among clumps of scattered grama grass.

PAIR FORMATION.—In the laboratory I tape-recorded a single "calling" song by a male from near Williams. This song was sung by a motionless male and was not followed by courtship. Other individuals were confined in the terrarium with him, and the song may have been in response to their movement. Six (calling?) songs (Fig. 16a), similar to that of the Williams male, were performed by more or less isolated Walsenburg males.

COURTSHIP.—Two acoustical signals were produced in courtship contexts. The first signal was identical to the "call" but was shorter (Fig. 16a). Males produced this signal when other individuals moved nearby and just before advancing on these individuals. It was present in three of six approaches. The second courtship sound, consisting of two to four widely but uniformly spaced pulses of sound, was produced while advancing on females and just before mounting was attempted (Fig. 16b). Males did not tip their femora either while walking about or while approaching.

AGGRESSION.—Males produced a series of ticking sounds when touched by other males or in response to the "calling" song of another male (Fig. 16c). Twice a female produced a series of ticking sounds as a male mounted her. Since copulation did not ensue, and since the sounds were similar to the ticking sounds produced by aggressive males, I presume that they were repelling signals.

Psoloessa thamnogaea Rehn

P. thamnogaea evidently occurs only in southern California and does not cross the mountains into the deserts to the east. Rehn (1942) reports, "Dry surfaces in the neighborhood of patches or larger areas of short yellow sun-cured grasses are the preferred habitats . . . At Alamitos Bay and Miramar it was found on coastal dunes or immediately back of the same." I collected individuals on bare open ground at Alpine, California.

PAIR FORMATION.—All stridulations were apparently made in response to movements of other individuals. Pairing seems to be achieved largely by visual means.

COURTSHIP.—Four kinds of sound were produced in courtship: Type 1 stridulation consisted of groups of short sharp pulses and was produced 12 times by stationary males following movement by other individuals. Usually these pulses were grouped into twos and threes (Figs. 16d, h), but sometimes as many as eight pulses were produced (Fig. 16e). Type 2 stridulation (similar to the second courtship sound of *P. delicatula,* Fig. 16f), was produced after type 1 and while facing females, or each time that courtship was interrupted, e.g., following the escape of a female or following unsuccessful attempts to mount a female. Unlike *P. delicatula,* this sound was only produced by stationary males. One to three pulses with variable intervals were produced at a time. Type 3 stridulation, consisting of ticking sounds (first part of Fig. 16g), was

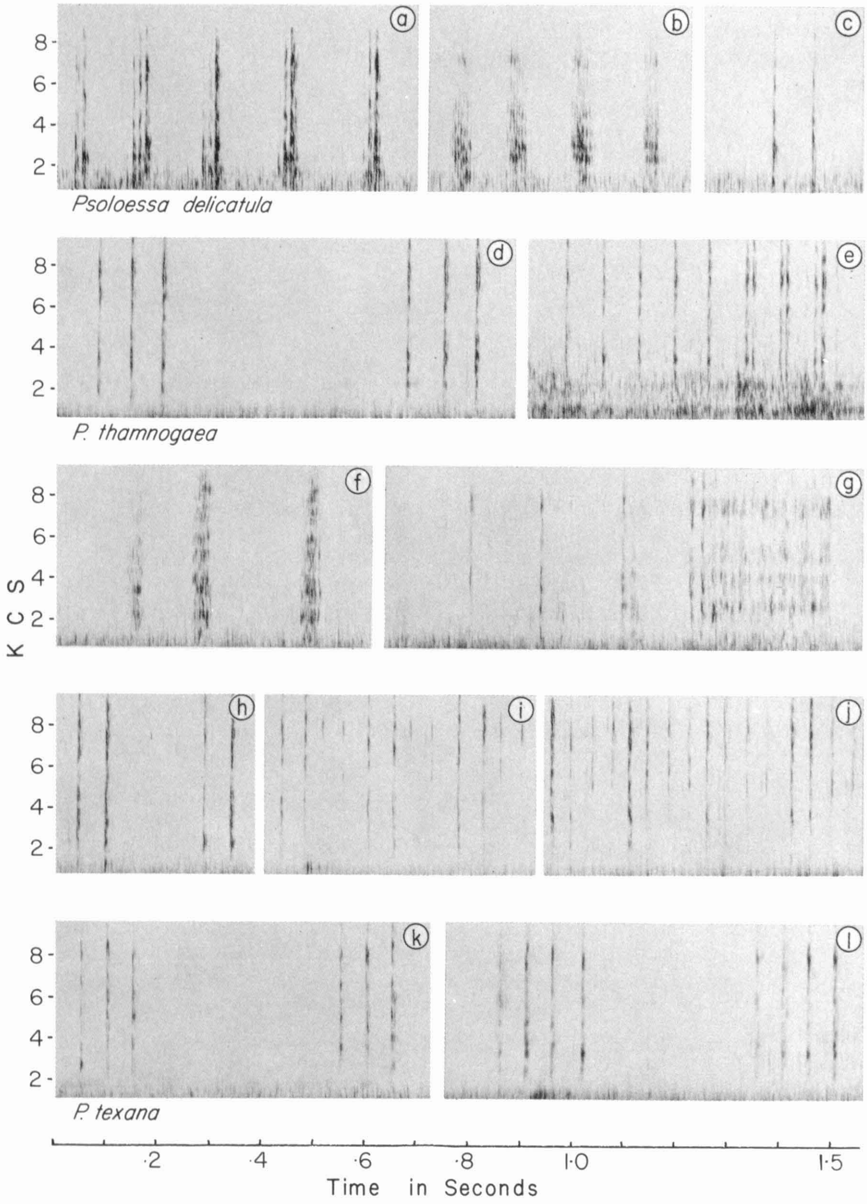

Fig. 16. Audiospectrographs of signals by *Psoloessa* species: (a) *P. delicatula* (Huerfano Co., Colo.), stridulation by a more or less isolated male, 93°F; (b) same, stridulation by a male approaching a female, 90°F; (c) same, aggressive stridulation, 93°F; (d) *P. thamnogaea* (Alpine, Calif.), calling stridulation?, 94°F; (e) same, stridulation by a male after movement by a female nearby, 94°F; (f) same, courtship stridulation while stationary before the female, 94°F; (g) same, courtship stridulation produced just before mounting the female, 94°F; (h) same, stridulation by a male as the female walked away from him, 94°F; (i) same, one male began to produce double pulse stridulations when a female walked nearby; soon after beginning, another male nearby began to alternate with him (softer two pulses), 94°F; (j) same, two males alternating almost perfectly in the production of two-pulse stridulations, 90°F; (k) *P. texana* (Cochise Co., Ariz.) calling stridulation?, 82°F. Temperatures were taken 3 inches above the substrate.

occasionally absent, but when present, was always immediately followed by type 4 stridulation, which was trill-like (second part of Fig. 16g). Type 4 stridulation always (five times) preceded a male's attempts to mount. Once this combination of type 3 and type 4 was produced by a male in the act of mounting. In summary, type 1 stridulation was elicited by the movement of other individuals; type 2 preceded actual advances towards females and followed interruption of courtship; and the combination of types 3 and 4 was made as males advanced on females and attempted to mount.

AGGRESSION.—Five times when a male began to produce type 1 stridulation, another male began to produce the same type of sound simultaneously, and the two eventually alternated with one another (Figs. 16i, j). All alternating stridulations consisted of pairs of pulses and the pulse rate was somewhat faster than in the normal song. In several male–male encounters femur-tipping signals were produced by both males. The femora were tipped through about 5° and the upstroke was jerk-like.

Psoloessa texana Scudder

P. texana occurs throughout most of the southwestern states except California and extends extensively into Mexico (Rehn, 1942). It occurs mainly on scantily covered sandhill areas or short grass areas with much bare ground (Ball et al., 1942). I collected this species near Sierra Vista in southern Arizona.

COURTSHIP.—In the laboratory, courting males produced three kinds of sounds. Type 1 stridulation (Fig. 16k, l) consisted of groups of three or four sharp tick-like pulses. Three songs consisted of 11, 15, and 17 such groups. In two cases, the stimulus for song was not known; three other individuals were present in the terrarium, but they appeared to be motionless prior to these songs. The third song closely followed movement by a female, and the male approached her after stridulating. A song consisting of only four groups of pulses was the only signal produced by a male that approached and mounted a female (Fig. 16-l). The signal is similar to type 1 courtship stridulation of *thamnogaea* but may also serve a calling function. Type 2 stridulation, similar to type 2 in *P. thamnogaea,* consisted of 1–3 irregularly-spaced pulses of sound made by stationary males. Seven times this stridulation was produced just prior to approaching the female, and twice it occurred immediately after courtship interruption. Type 3 stridulation consisted of a trill very similar to type 4 of *P. thamnogaea.* In 7 of 8 instances, this sound was produced during approaches and just before attempts to mount. It was also made by a copulating male as the female carried him about, by the same male after copulation ended, and by a male after an unsuccessful attempt to mount.

AGGRESSION.—I saw no encounters between males, but one of the males made sharp, upward jerks of his femora as he walked about. The only rejection movement performed by females was an upward jerking of the femora when males attempted to mount.

GENUS *Bootettix* Bruner

The genus *Bootettix* consists of two species, *B. argentatus* Bruner and *B. punctatus* (Scudder); these are small, green grasshoppers with pearly white markings that live almost exclusively on the green foliage of creosote bushes. Their color blends well with the foliage, and unless individuals move, it is extremely difficult to locate them. Tinkham (1948) remarks, "*B. argentatus* ranges over the entire Chihuahua Desert, from the valleys of the Pecos and the Rio Grande and Otero Basin south over the creosote sections of northeastern Mexico. It is common in southern Coahuila from the Sierra de Parras to 20 miles northwest of Saltillo. On the Sonoran Desert of Arizona, California, and Sonora, this species is replaced by its near relative *Bootettix punctata* Scudder."

Bootettix argentatus Bruner

In the vicinity of Big Bend National Park there was scarcely a creosote bush that did not contain one or more individuals, and those that were frightened from their perches returned to the same bush or to adjacent bushes within a matter of seconds.

PAIR FORMATION.—Two sounds are commonly produced by solitary males: a short *zick* sound and a longer buzzing sound. Frequently the two sounds were given in combination (Fig. 151) but sometimes they were produced individually. Males stridulated both in the daytime and at night, but I do not know when most stridulation takes place.

COURTSHIP.—In the field, short sounds were made by a male shortly after he dismounted from a female, and also by a male just before he mounted a female. Another male made similar sounds as he approached an individual that had just jumped onto the same bush. A combination of short and long sounds was made by a male perched on top of a female, of whom he may have been unaware. One male approached another that had just landed on a branch nearby, first making short sounds, then when one-half inch away vibrating his body and jumping towards the other twice; shortly after, they separated. The short sounds and body vibration, then, appear to be courtship signals, since they were both produced during approaching.

AGGRESSION.—No aggressive signals were seen or recorded.

Bootettix punctatus (Scudder)

This special, whose distribution is indicated above, also occurs on creosote bushes. According to literature records (Tinkham, 1948; Ball et al., 1942) it is entirely allopatric with *argentatus*. Near Lancaster, in southern California, I collected and recorded *B. punctatus* in creosote bushes. Stridulation resembled that of *B. argentatus* very closely.

SUBFAMILY ACRIDINAE: SUMMARY

PAIR FORMATION

CALLING OR FEMALE-ATTRACTING SIGNALS.—Most (42 of 51) species of Acridinae studied thus far are vegetation dwellers (Table 16); males of 39 of these species possess songs which are believed to have a female-attracting function and which are performed by more or less solitary males. Of the nine ground-dwelling species, four possess stridulation which may have a calling function. Pair formation among the ground-dwellers is probably achieved most often by males observing and approaching moving females. Calling stridulation is lacking in two vegetation-dwelling genera *(Orphulella, Dichromorpha).*

FEMALE ANSWERING STRIDULATION.—Females of some species answer the calls of males either with stridulation or with silent femoral movements. Fourteen species (Table 16) are known to stridulate in response to the calls of males. Regular alternation between the songs of males and females has been observed in seven European species by Jacobs (1953), Haskell (1958), and others. Answering stridulation or movements indicate female receptivity and allow males and females to pair rapidly (Loher and Huber, 1965).

INITIAL APPROACH.—Which sex approaches the other during initial stages of pair formation probably depends in part on the presence or absence of a calling song and on the presence or absence of female answering stridulation. In all species studied, i.e., those in which males possess a calling song (e.g., *Chorthippus montanus*) as well as those in which males do not stridulate (e.g., *Ageneotettix deorum*), males approach females at least during the terminal stages of pair formation and courtship, when visual contact has been established. In all species possessing a calling song and in which females do not answer males, females probably approach the males at least until the latter see them. In those species in which males possess a calling song and in which females have a well developed answering stridulation, either both male and female approach one another before visual contact is established *(Chorthippus montanus, C. bicolor)* or the male approaches the answering female *(Gomphocerus rufus, Chorthippus biguttulus).*

PAIR FORMATION.—The method of pair formation in the Orphulellini is unlike that of other members of the Acridinae but resembles closely the pair formation observed in Catantopinae. Males of the three species observed approach females stealthily and pounce onto the females without warning.

COLORED HINDWINGS.—Few of the Acridinae studied possess colored or contrastingly marked hindwings. This lack is correlated with a general lack of flight displays in this subfamily. *Syrbula fuscovittata* possesses black hindwings and flies from one perch to another after singing at each perch. The behavior of other Acridinae possessing black hindwings, e.g., *Pedioscirtetes maculipennis,* contrastingly colored hindwings, e.g., *Acrolophitus hirtipes,* or colored hindwings, e.g., *Goniatron planum,* has not been adequately studied, but it is likely that colored or brightly marked hindwings will be found to be associated with signalling flights.

TABLE 16

Behavior Patterns in Pair Formation, Courtship, and Aggression in the Acridinae[1]

SPECIES	HABITAT (G = ground-dwelling) (V = veg.-dwelling)	PAIR FORMATION				COURTSHIP						AGGRESSION				
			female answering													
		calling song by solitary male	stridulation	movement w/o stridulation	♂ and ♀ alternate in song	strid. by stationary ♂ in presence of ♀	advancing stridulation	mounting stridulation	femur-tipping	search sound	other	calling ♂♂ answering one another	special stridulation	alternation between stridulating males	femur-tipping	other
**Chrysochraon dispar*	V	+		+		+	+	+				+	+			
**Euthystira brachyptera*	V	+		+		+	+	+			body-jerking	+	+	+		
Chloealtis conspersa	V	+		+		+	+						+			
Neopodismopsis abdom.	V	+	?			+	+					+	+			
**Stenobothrus lineatus*	V	+	+		+	+	+						+			
**S. stigmaticus*	V	+	+			+	+			+		+	+			
**S. nigromaculatus*	V	+				+	+			+		+				
**Omocestus haemorrh.*	V	+				+	+	+		+		+	+			
**O. viridulus*	V	+	+		+	+	+			+	ticking	+	+			
**O. rufipes*	V	+	+		+	+	+					+	+	+		ticking
**Stauroderus scalaris*	V	+				+	+	+			wing-flapping		+			
**Chorthippus apricarius*	V	+	+			+	+	+		+		+	+			
**C. pullus*	V	+				+	+	+				+	+			
**C. vagans*	V	+				+	+			+			+	+	+	
**C. biguttulus*	V	+	+		+	+	+	+			body-rocking	+	+	+R		
**C. bicolor*	V	+	+		+	+	+					+	+	+		
**C. mollis*	V	+	+			+	+			+		+	+			

**C. parallelus*	V	+	+	+	+	+	+	+			antenna-	+	+			
**C. montanus*	V	+	+			+	+	+			swinging,	+	+			
**C. albomarginatus*	V	+	+			+	+				head-shaking,		+			
**C. dorsatus*	V	+	+		+	+	+	+			specific	+R	+	+		
C. curtipennis	V	+				+	+	+		+	orientation,	+	+	+R		
**Gomphocerus rufus*	V	+	+			+	+			+	silent leg	+R				
											movements					
**G. sibiricus*	V	+	+			+	+	+			head-nodding	+				
											sideways					
**Myrmeleotettix macul.*	V	+				+	+			+	body-rocking,	+	+			
**Arcyptera fusca*	V	+					+				femoral movem.	+	+			
**A. microptera*	V	+				+					tibial movem.,		?			
Pseudopomala brachyp.	V	+				+	+				abdomen up		+			
Mermeria maculipennis	V	+				+					and down,		+	+		femur-
M. intertexta	V	+				+	+				head shaking		+	?		shaking
Eritettix simplex	V	+				+	+				body-rocking		+			
											antenna-					
Syrbula admirabilis	V	+				+	+			+	waving,		+			
S. fuscovittata	V	+				?	?				palpi-waving,		+(no sound)			
Morsiella flaviventris	V	+				+	+				body-rocking,		+	+		
M. diabolica	V	+				+	+				silent femoral		+			
Acantherus piperatus	V	+				+					movements	?	?			
Parapomala wyomingensis	V	+				+					femur-raising	?	?			
Ageneotettix deorum	G								+		antenna-shaking		+		+	
Aulocara elliotti	G	+					+S		+				+		+	
Acrolophitus hirtipes	V	+				+						?	?	?	?	
Drepanopterna femoratum	G								+						+	
Phlibostroma quadrimac.	G						+		+				+			
Cordillacris occipitalis	G	?				+			+						+	
C. crenulata	G	?				+			+						+	
Psoloessa thamnogaea	G	?				+	+					+	+	+	+	
P. texana	G	?				+	+								+	
P. delicatula	G	?				+	+						+			
Orphulella speciosa	V												+			ticking
O. pelidna	V															
Dichromorpha viridis	V												+			

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[1] Key to symbols: +, condition present; +R, present but reduced or rare; +S, sometimes performed in this context; ?, presence or absence uncertain; blank, not observed. Species marked by * were studied by Jacobs (1953).

CREPITATION.—Crepitation occurs during flights by males of at least two *Orphulella* species and also of some species of *Acrida* (Uvarov, 1966). In both groups the hindwings are clear. Attraction of females has, however, not been demonstrated.

COURTSHIP

In most (45 of 50) of the species studied, males stridulate during courtship. Two of the species which do not do so are ground dwellers and three are vegetation dwellers which do not warn females of their impending copulation attempts.

INITIAL COURTSHIP STRIDULATION.—In the 41 species whose courtship has been adequately studied, a well-developed stridulation is performed by stationary males in the presence of females prior to advancing and attempting to mount. The term *Werbegesang* (courtship song) was used by Jacobs (1953) to designate this stridulation.

ADVANCING STRIDULATION.—Thirty-seven species possess a well-defined stridulation performed by advancing males just prior to mounting. Because this stridulation is produced during the final rapid advance, it has been termed *Anspringlaute* by Jacobs (1953). Advancing stridulation is species-specific and presumably allows females to discriminate between their own and other males.

MOUNTING STRIDULATION.—Males of 12 species are known to stridulate during mounting. These species also stridulate during courtship. In four sympatric species of Acridinae studied by Haskell (1957), mounting stridulation in the four species was quite similar while the advancing sounds were distinct. The mounting sound may therefore be of little or no significance in interspecific recognition.

SEARCHING SOUNDS.—Ten species, all vegetation dwellers with well-developed songs and courtship sounds, sometimes stridulate as they wander about in the absence of other individuals. These stridulations are quite distinct from calling, are usually short and quite faint, and have been termed *Suchlaute* (searching sounds) by Jacobs. Similar behavior occurs in some species of Oedipodinae. Why some species should possess this while others apparently do not remains unknown.

VISUAL SIGNALS.—Six species, all ground-dwellers, perform femur-tipping movements while advancing on females. Four of these species do not stridulate while advancing, and a fifth does so only occasionally. Each of these species and two other ground dwellers also tip their femora in aggressive contexts. Such silent movements may have originated from stridulatory movements. Males of a number of species possess other non-acoustical visual movements which are prominent in courtship situations. In some species only a single movement is apparent, e.g., femur-raising in *Parapomala wyomingensis* and body-rocking in *Eritettix simplex,* but in *Gomphocerus rufus* and *Myrmeleotettix maculatus* four different movements have been described by Jacobs (1953) and in *Syrbula admirabilis* five different movements are made. It is not known for certain, however, whether each movement is a signal.

AGGRESSION

(1) Males of 23 species are known to call in response to the calls of other males. As a result, bursts of calling by groups of males can be heard. Bursts of aggressive calling were heard when about six males of *Chorthippus curtipennis* were confined in a terrarium. In some species, silent males may approach calling ones and be stimulated to call themselves (Haskell, 1957). (2) Special stridulation produced only in aggressive contexts is known in 37 species, including four (and probably five) ground-dwelling species. (3) Alternation between songs of aggressive males is known in 12 species. In some species specialized aggressive songs are involved in alternation. In others one male produces aggressive songs in alternation with the calling song of another male. (4) Stereotyped, silent femur-tipping movements are rare in vegetation-dwelling species but are performed in aggressive contexts by seven of the nine ground-dwelling species.

SUBFAMILIES CYRTACANTHACRIDINAE AND CATANTOPINAE

GENUS *Schistocerca* Stal

Schistocerca lineata Scudder

This species extends from Texas to Montana and east through the northern states to New England. It lives and feeds on various low trees, shrubs and weeds (Hubbell, 1960).

Pair Formation.—Males evidently locate females by their movements. Once a female is located, males usually approach slowly and silently and without signalling. The female is evidently unaware of the male's approach. In 12 of 17 approaches in the laboratory males did not signal. But in five approaches, which followed aggressive interactions with other individuals, males continued to shake their femora. Stealthy approaches consisted of advancing only when females were actually moving, probably making it difficult for females to observe them. Males also moved their forequarters slowly from side to side during momentary stops in their advance and particularly just prior to pouncing. Presumably these movements permit males to gauge the distance to the female. While approaching, males also held their antennae close to one another and pointed them directly at the female. In ten successful mountings females struggled, either dislodging the male, or proceeding to copulate after a while.

Courtship.—While mounting and attempting to attach their genitalia (see above), males made one or more of the following movements: (1) wing-flipping, which consisted of flipping the wings out to about 45° from the abdomen; (2) femur-shaking or jerking, which consisted of holding the femora between the 45° and 90° positions and jerking them upward or forward through a few degrees (with the tibiae held at various angles up to 120° from the femora); and (3) body-jerking. Each of the movements was repetitive and the number of movements in a series was quite variable.

Twice, only wing-flipping was produced during mounting; three times, only shaking movements were made; twice, males shook their femora several times, then switched to wing-flipping; once, a male first jerked his body several times, then flipped his wings eight times and finally shook his femora five times; twice, no jerking or flipping occurred. The rate of wing-flipping varied from 2.5 to 4 per second. The rate of shaking was approximately 3 per second.

Aggression.—Males produced three kinds of leg movements when touched or approached by other males: (1) femur-shaking (similar to the shaking made by mounting males); (2) femur-raising (similar to the rejection movements of females); and (3) sparring with the forelegs (performed when males established head-to-head contact). Raising movements were most often made by copulating males when approached by other individuals. The rate of aggressive shaking varied from 1.0 to 4.5 per second, and bursts of shaking varied in duration up to 7 seconds. Females repelled males by raising their femora, tilting them forward, and kicking out with the tibiae. Males and females sometimes struggled for up to a minute before copulation ensued.

Loher (1959) studied courtship and aggression in *Schistocerca gregaria.* He found that males produced short and long sounds with the wings, the former shortly before and during mounting, and the latter (sometimes accompanied by short sounds) by males mounted by other males, or by copulating males approached by another male. Both pairs of wings were involved in producing sound, but they apparently do not possess a specialized stridulatory apparatus. Long sounds were accompanied by shaking of the antennae and palpi. Aggressive males made long sounds and shook the femora, antennae and palpi. Femur-shaking was also performed by unreceptive females.

GENUS *Melanoplus* Stal

Melanoplus confusus Scudder

This species is most abundant in the northern grasslands of the United States. In Michigan it lives in open fields covered with short grass. Adults emerge early in the summer (Cantrall, 1943).

Pair Formation.—I saw many approaches by males in the laboratory and two in the field. As in *Schistocerca gregaria,* these approaches were stealthy.

Courtship.—Five different males approached and mounted females as follows: (1) As a male mounted and attached his genitalia he jerked his femora repetitively; and after attaching he jerked his body from side to side repetitively. The repetition rate of both movements was about 1.3 per second. (2) After pouncing onto a female a male jerked both femora alternately forward and backward; and each femoral jerk was accompanied by a side-ways jerking of the body. The repetition rate of the movements was initially about 1.3 per second and eventually about 1.0 per second. After about a minute jerking stopped, but the sideways body movements continued a while longer. (3) For the first few seconds after mounting no jerking motions could be detected. About five seconds later, when the male began to attach, he jerked his body from side to side at about 1.0 per second. (4) A male pounced onto a female and began to jerk his body from side to side only after he had begun to attach his genitalia. He also bit at her pronotum each time that he moved his head from one side to the other. (5) A male mounted without jerking his femora or his body. Femur-jerking motions were usually performed with the femora held near vertical.

AGGRESSION.—Males spread their femora to about 45° from the abdomen (with femora held horizontally) and shook them in very close encounters with other males or when mounted by other males. Each burst of shaking consisted of 2–6 femoral strokes. The stroke rate was variable but usually about 7 per second (78°F). The burst rate was highest (about 3 per second) when males were in contact with one another. Males touched from behind either raised their femora to near vertical and shook them, or they raised them and kicked out with both tibiae.

Females displayed several kinds of repulsive movements: (1) They frequently swung the hind femur nearest the intruder forward to the head in a single swift sweep, when touched from in front or from one side. (2) They sometimes shook their femora when approached or in response to the shaking of another individual. (3) They raised their femora to about vertical and made mild kicking motions with the tibiae when approached. (4) They kicked out rapidly with the hind tibiae, sometimes several times in quick succession when approached from behind. On one occasion a male jumped onto a female even though her femora were raised. Following a bout of struggling the pair proceeded to copulate. One female raised her femora to vertical and rocked her body from side to side (as mounting males do) when approached by another female.

Melanoplus keeleri (Dodge)

This species is distributed over much of the northern and eastern United States (Newton and Gurney, 1956: 1150). On the George Reserve this species occurs in the dry upland areas, in areas also inhabited by *M. sanguinipes* and *M. confusus.* Adults emerge late in the summer (Cantrall, 1943).

PAIR FORMATION.—In this species, pair formation resembles that of *M. confusus.* No signals preceded five different mounting attempts.

COURTSHIP.—I observed two males mounting females. One female shook her femora and removed the male by kicking. The second female scarcely struggled and the whole interaction was as follows: As the male landed on the female he began to produce bursts of femur-shaking and to bite at her pronotum. He produced a series of six bursts, and a few seconds later, when the female moved, he produced a series of five bursts (burst rate, 1 per second; 7 femoral strokes per burst; stroke repetition rate, 21 per second). The female struggled when the male mounted and then produced four series of bursts after the male had attached his genitalia (burst rate, 3–4 per second; stroke rate, 100 per second; 4 femoral strokes per burst). This shaking by the female resembles aggressive shaking of males.

AGGRESSION.—Males shook their femora when approached or mounted by other males. This shaking was quite different from that produced by mounting males (burst rate, about 1.6 per second; femoral stroke rate, about 100 per second; 3 strokes per burst).These parameters could be determined fairly accurately because the femora struck a grass straw, producing sounds which could be tape-recorded. One male produced several series of bursts, spread his femora to about 60° from his abdomen and lowered the end of his abdomen sharply when mounted by another male. Males that jumped onto other males shook their femora after separation. Non-copulating females also shook their femora like aggressive males when either touched or approached. One female alternated in jerking her femora up and down through about 5° from the horizontal position (repetition rate, 2.5–3.0 per second) and jerked her body from side to side with each femoral jerk.

Melanoplus sanguinipes (Gab.)

This species is distributed practically across the entire United States (Newton and Gurney, 1957:50). In Michigan this species occupies the same habitats as *M. keeleri* and *M. confusus* and there is also overlap in the adult season between *sanguinipes* and each of these two species (Cantrall, 1943).

Pair Formation.—Males approached females slowly and inconspicuously, advancing only when females moved, and pointed their antennae straight toward the females. During the approach and usually just prior to pouncing, males moved their heads first to one side, then over to the other side and then back to the middle position, sometimes several times in succession.

Courtship.—In six approaches males did not signal; but in three approaches males shook their femora several times in succession. Males successfully mounted females four times, once in the field, and each time they produced bursts of femur-shaking immediately after landing on the female. Each burst consisted of about five femoral strokes. No sound was produced, hence the number of strokes and the rate of shaking could not be determined. Bursts were repeated at about four per second, and 9, 11, 15, and 50 bursts were produced in the four separate mountings. In each of the three successful copulations the female behaved differently. One female failed to remove the male by kicking him and eventually became quiet allowing the male to attach his genitalia. A second female shook her femora (at about 10 strokes per second) continuously for several seconds then intermittently for the next 25 seconds, then eventually became quiet. A third female apparently did not attempt to repel the male, but spread her femora to about 45° from her abdomen as the male mounted.

Aggression.—Males responded to being touched or approached by other individuals in several ways: (1) Copulating and non-copulating males alike shook their femora when touched or mounted by other individuals. Most shaking was in the form of bursts (4–6 strokes per burst; burst duration, 0.1–0.3 seconds; burst rate, 1.3–4.0 per second). Twice a male produced a single, long burst of shaking (duration, 0.5–1.0 seconds) when another male jumped onto him and next to him. (2) Males (and females) made sparring movements with the front and middle pair of legs when establishing contact with other individuals. (3) Males kicked out with their hind tibiae when touched from behind. (4) A copulating male produced bursts of shaking when another male jumped onto him. Each burst was produced as the male jerked his body from side to side. Unlike *Schistocerca lineata* and *M. confusus,* copulating males did not raise their femora to the vertical position when either touched or mounted by other males. Females repelled mounting males by raising their femora and kicking out with the tibiae, or with sharp upward jerks of the femora, and they sometimes produced bursts of shaking similar to those of aggressive males.

Melanoplus femur-rubrum (DeGeer)

This species occurs across the entire United States (Newton and Gurney, 1956:1122). In the George Reserve it occurs mainly in moist places on tall weedy vegetation.

Pair Formation.—Approaching and mounting are similar to those of the above *Melanoplus* species. No femoral movements by mounting males or copulations were observed.

Aggression.—Males produced bursts of shaking when they established contact or moved near one another (burst rate, about 3 per second; 2–4 strokes per burst). Females repelled males by raising their femora and kicking out with the tibiae. After kicking a male one female shook her femora much as males do.

Melanoplus differentialis (Thomas)

This species is widely distributed in the United States, from the east coast to the west coast (Newton and Gurney, 1956:1091). On the George Reserve it occurs in thick tall grass, along the margins of marshes and in tall weeds.

Pair Formation and Courtship.—Three approaches and mounting attempts were like those of the *Melanoplus* species described above. Immediately after successfully mounting a female, one male produced bursts of femur-shaking (burst rate, 4.8 per second; 4 strokes per burst; stroke rate, 73 per second). A few minutes after attaching his genitalia he produced several more bursts. This male used his cerci to pull down the female's subgenital plate before he attached.

Aggression.—Males produced bursts of shaking when touched or when other individuals moved nearby (burst rate, about 1.5 per second; about 3 strokes per burst). Male shaking was similar to that of females (see below) but slower both in burst rate and in stroke rate than the shaking of mounting males. Copulating males did not raise their femora when touched by other males. In one copulating pair the female attempted to dislodge the male by tilting her femora forward and by kicking and pushing up at him with her hind tibiae. When this failed, she produced bursts of shaking for several minutes (burst rate, 2 per second; about 7 strokes per burst). Another copulating female also shook her femora in a similar fashion for about 10 minutes but did not attempt to remove the male by kicking. Similar shaking motions were produced by two other non-copulating females when they were touched by males. One of these females shook her femora while they were raised in the vertical position. The other female first shook her femora when touched, then rocked her body from side to side for several seconds. A few minutes later she only rocked her body from side to side when a male approached her.

Melanoplus bivitattus (Say)

This species ranges widely in the United States, from Oregon to California in the West, to Maine and South Carolina in the East. It occurs mainly in tall grasses and sedges in hydric situations.

PAIR FORMATION.—Pair formation is like that of other *Melanoplus* species described: males approach stealthily and jump onto females without first signalling.

COURTSHIP.—One male produced several lengthy bursts of shaking immediately after mounting the female and while attaching his genitalia (duration, 3–4 seconds; stroke rate, about 5 per second). Another male produced a similar long burst of shaking, then began a series of short bursts with a faster stroke rate (burst rate, about 3 per second; stroke rate, about 20 per second; 3–5 femoral strokes per burst). Two pairs of individuals each copulated about three hours. Males made no femoral movements as the females carried them about.

AGGRESSION.—Males and females produced short bursts of shaking, similar to the initial shaking produced by mounting males (duration, less than 1 second; stroke rate, about 5 per second), when touched. Females also swung one femur forward to the head when touched from the side or front. Copulating males held their femora at about the 40° position and did not raise them or shake them when other males moved nearby.

Melanoplus viridipes Scudder

I collected this species in grass and weeds in a wooded area in southern Illinois. Pair formation is like that of other *Melanoplus* species. During copulation the ends of the abdomens were turned sharply upwards and even bent over backward somewhat. Non-copulating males and females, chiefly the latter, often had the end of their abdomens curved sharply upwards, but not turned over backwards. The reason for this posture is not known. Aggressive movements are in general similar in males and females. They include: (a) sparring with front or middle legs; (b) raising femora to vertical; (c) kicking out with hind tibiae (sometimes repetitively up to 10 times and at about 5 per second); (d) femur-shaking, with one or both femora; (e) rocking the body from side to side (made by females, but not seen in males); (f) small upward jerks of the femora; and (g) lowering the end of the abdomen (by males that were pounced upon by other males).

Melanoplus dawsoni (Scudder)

This species was abundant in grasses and short shrubs under jack pine in central Michigan. Pair formation was like that of other *Melanoplus* species. Males jerked their bodies and made bursts of femur-shaking when they touched one another. When a male was mounted by another male he struggled until they were separated; then both began to produce bursts of femur-shaking. I did not see any interactions between males and females.

Paroxya hoosieri (Blatchley)

This species lives on tall marsh grasses and sedges in Michigan. Pair formation is like that of *Melanoplus* species, but nothing is known about femoral movements during mounting. In male–male encounters males shook their femora in bursts.

Paraidemona mimica Scudder

I collected this species in the grasslands of central Texas. Pair formation is very much like that of *Melanoplus* species, but the movements made by males on the backs of females were not recorded. I observed one male point and pounce onto another male. They separated again within a few seconds and began to produce bursts of femur-shaking. The male that was pounced upon spread his femora away from his abdomen as he shook them. Females repelled males by raising their femora and tilting them forward.

CYRTACANTHACRIDINAE AND CATANTOPINAE: SUMMARY

PAIR FORMATION

Pair formation in this subfamily appears to be achieved solely by visual means, that is, by males orienting on moving females. In the field, members of this subfamily did not behave in a way suggesting that another means of forming pairs might be involved. No flights other than disturbance flights were seen; the wings are always clear and flight is silent.

In all species, males appear to approach females stealthily and to jump onto the females without warning (Table 17). Struggling between male and female occurs frequently, sometimes resulting in the separation of the pair, other times in copulation. Associated with this type of pair formation are thickened fore and middle femora of males, which are considerably larger than those of females. They probably assist males in remaining mounted on struggling females.

COURTSHIP

Since communication between males and females occurs mainly after the male has mounted the female, courtship can be thought to occur after contact is established. Whereas females sometimes struggle before copulation ensues, there is reason to believe that they are capable of removing males. Presumably there are various levels of responsiveness, and struggling occurs when a female is unresponsive or only partially responsive. It is also possible that females struggle until they receive the necessary stimuli from the male.

Males usually make jerking motions with some part of their body after mounting. The hind femora are shaken or jerked, or the whole body is jerked from side to side, or the wings are flipped out. Males of two species bite at the pronotum of the female.

In some species a single kind of movement is performed by mounting males, e.g., *Melanoplus sanguinipes,* whereas in others, e.g., *Schistocerca lineata, M. confusus, M. keeleri,* several movements are performed, suggesting that while some sort of jerking is necessary the means of producing it are less significant.

Femur-shaking produced by mounting males is usually different from that produced in aggressive or repelling circumstances. This fact is consistent with what occurs in the Oedipodinae and Acridinae—that when one movement is produced in both courtship and aggressive contexts there seems to be selection for making the movements produced in the two situations different.

AGGRESSION

A number of graded repelling movements are produced by aggressive or repelling individuals. Males and females repel other individuals by swinging their femora forward to the head, by raising their femora to a near vertical position, by striking out with the fore and middle legs, by jerking the femora sharply upwards, and by kicking out with the hind tibiae.

Males shake their femora in a stereotyped fashion in interactions with other males. This movement is produced before contact is established. The movement is also usually distinct from that made by mounting males. Females of a species usually perform the same kind of aggressive movements.

SUBFAMILY ROMALEINAE

This subfamily comprises 46 genera, of which seven occur in North America (Rehn and Grant, 1961). One species, *Taeniopoda eques,* was investigated in this study.

TABLE 17

PAIR FORMATION AND SIGNALLING IN CYRTACANTHACRIDINAE AND CATANTOPINAE

Species	pair formation	post-mounting signals	aggressive signals
S. lineata	♂ approaches ♀ stealthily, without signalling	wing-flipping, femur-jerking, body-jerking	femur-jerking, femur-raising
Melanoplus confusus	"	femur-jerking, body side to side jerking (both at 1.3/sec) biting (sometimes)	femur-shaking (up to 3 bursts/sec) femur-raising
M. keeleri	"	bursts of f.-shaking (1.0/sec; slow stroke rate) biting	bursts of f.-shaking (1.6/sec; fast stroke rate)
M. sanguinipes	"	bursts of f.-shaking (4 bursts/sec)	bursts of f.-shaking (1.3–4/sec) body side to side jerking
M. femur-rubrum	"	?	bursts of f.-shaking (up to 3/sec)
M. differentialis	"	bursts of f.-shaking (4.8/sec)	bursts of f.-shaking (1.5/sec)
M. bivitattus	"	femur-shaking (duration 3–4 secs; stroke rate 5/sec), bursts of f.-shaking (burst rate 3/sec; stroke rate 20/sec)	longish bursts of shaking (stroke rate 5/sec)
M. viridipes	"	?	femur-jerking, femur-raising
M. dawsoni	"	?	bursts of f.-shaking, body-jerking
Paroxya hoosieri	"	?	bursts of f.-shaking
Paraidemona mimica	"	?	bursts of f.-shaking
**Podisma pedestris*	"	femur-shaking, body-jerking, biting, pulls end of ♀ abdomen up	femur-shaking (different from shaking during mounting)
**P. alpina*	"	body-jerking, pulls end of ♀ abdomen up	femur-shaking, body side to side jerking

*, species studied by Jacobs, 1953.

Taeniopoda eques (Burmeister)

T. eques is the only member of the genus which occurs in the United States. It is found from western Texas to southern Arizona and is broadly distributed in northern Mexico (Rehn and Grant, 1961). The other members of the genus occur in Mexico and Central America. *Romalea microptera,* a widespread species in the southeastern United States, similar to the species of *Taeniopoda,* was not studied. *T. eques* commonly feeds on bushes such as mesquite and low plants such as burroweed and succulent annuals (Ball et al., 1942). In western Texas many individuals occurred on open ground, but none was seen on vegetation. Individuals are aposematically colored.

They are mostly black but are colored bright yellow along the margins of sclerites. The hindwings are flame red and are raised during aggressive and disturbing displays. Individuals produced a hissing sound when handled.

PAIR FORMATION.—*T. eques* is capable of loud stridulation by rubbing the hindwings across the undersides of the forewings, but whether this sound is involved in pair formation is not known. The only stridulation heard was that produced in aggressive situations. Males paired with females, in the laboratory as well as in the field, by orienting on them visually and approaching them. In Big Bend National Park, Texas, I placed a female several feet from a male found walking across bare ground. The male turned toward the female, followed her and then attempted to mount her. He was repelled but continued to follow and made repeated attempts to mount and to attach his genitalia. He produced no visual or acoustical signals as he approached and jumped onto her.

COURTSHIP.—In the laboratory males approached females silently but not stealthily. They pointed their antennae straight towards females, as males of Catantopinae do. No signals were produced in seven such approaches. Males jumped onto females before touching them with the antennae. No stereotyped femoral movements of the sort produced in the Catantopinae were seen after mounting. Males were repelled each time they mounted females.

AGGRESSION.—Females repelled males in one of two ways. In the field, when a male attempted to attach his genitalia to those of a female, the female pushed the end of his abdomen away from the end of hers with her hind tibiae. The same slow deliberate movement was used to remove fecal pellets. In the laboratory, females rejected males by rocking their bodies vigorously from side to side. While the tarsi maintained contact with the substrate the sides of the body almost touched the substrate during rocking. Males made two kinds of aggressive movements. (1) They made sideways body-rocking movements, like those performed by females, when mounted by other males. (2) Sometimes they raised both sets of wings to about 45° and made short loud stridulatory sounds when touched by other males. The bright hindwings rendered this latter movement very conspicuous. Stridulation is caused by rubbing the hindwings across raised veins on the underside of the forewings (Uvarov, 1966). I elicited the same stridulation by touching males with my fingers. Individuals touched by others sometimes performed imprecise, graded femur-tipping movements. A hissing sound was produced when individuals were picked up but was not produced in interactions between individuals. Raising of the wings and stridulation, however, occurred frequently in aggressive interactions.

FAMILY PNEUMORIDAE

The members of this family are known only from southern Africa, where I observed them in 1965. Males have a stridulatory file on the third abdominal tergite, and their abdomens, which are inflated and bladder-like, probably act as resonating chambers. Males are long-winged, whereas females are short-winged or wingless. Females lack a stridulatory file and both sexes lack a tympanum.

Bullacris sp.

On the only two nights that males were heard in Natal, South Africa, stridulation began after midnight. The sound was very loud and could be heard perhaps as far as a half-mile away. Calls consisted of an initial lisping portion and a final loud squawking portion. The latter was fairly low in pitch (less than 2 kc per second) and had a fairly narrow frequency spectrum. I heard one male call repeatedly as he flew from tree to tree up a narrow valley. Although I could not see this flight, the sequences of sound suggested that he was producing one or two calls at each tree (trees were visible in the moonlight) and was then flying as much as 100 yards to the next perch. He remained a few minutes or less at each perch. He was also the only male singing in the valley. The means by which the wingless Pneumorid females indicate their presence to the male is not known, but they do not have the stridulatory file possessed by the male.

This group of night singing Acridoids presents a unique opportunity for testing various hypotheses concerning the distinctiveness of pair formation as contrasted to the distinctiveness of courtship (see Reproductive Isolation).

FAMILY PAMPHAGIDAE

This family is restricted in the Old World, the 30 or more genera being distributed in Africa, southern Europe, and Asia. Males and females usually possess tympana, and different kinds of stridulatory mechanisms occur in different groups (Dirsh, 1965). Individuals may have fully developed wings, or only very short wings, or no wings at all. Four genera contain wingless species; the tympanum in these species is either absent or vestigial. Winged species, including species in which the wings are very short and appear not to be used in stridulation, possess tympana.

Porthetis sp.

I captured males of a species of this genus in the Kruger National Park, South Africa. Individuals were long-winged and sang both during the day and at night. Stridulation was very loud and is apparently produced by rubbing the tibial spines across numerous parallel veinlets in the costal area of the forewing (Uvarov, 1966). At night males sang 1–3 songs, each lasting about 15 seconds, on one tree and then flew to another tree where they sang again. Since females are wingless they cannot stridulate as males do, and the method by which they inform males of their presence at night is not known. In Zululand I captured what appeared to be the same species. Females were wingless and were captured walking about on the ground. In this area I heard males singing only in the daytime. They were one of few animals that could be heard singing loudly during the heat of the day, and were considered by the natives to be the harbingers of hot weather.

Burtt (1946) states that in East Africa a species of *Saussurea* stridulates from about 10 a.m. to sunset, and that a species of *Lamarckiana* stridulates from about 5 a.m. to 8 a.m. and flies from bush to bush during this period.

INTERSPECIFIC INTERACTIONS AND REPRODUCTIVE ISOLATION

BEHAVIORAL INTERACTIONS

In grasshoppers the accidental coming together of individuals belonging to different species occurs frequently in the field, even between distantly related species belonging to different genera. Such interactions must have some important evolutionary consequences on the behavior of the interacting species. The accepted theory is that closely related species of animals are frequently capable of hybridization, but the hybrids are in one way or another inferior to homospecific offspring. Thus, individuals capable of recognizing members of other species and mating only with their own kind leave more descendants, and differences in communication which aid in interspecific recognition are therefore favored. Selection against interspecific sexual interactions such as those described below should be the chief cause for communicative differences.

A number of interactions between individuals of different species were observed in the field. These and comparable interactions between species observed in the laboratory are listed below. They are arranged so as to indicate the participants of each interaction and have been divided into seven categories according to the level of the interactions. For instance, the first category includes interactions in which males approached females partway but in which the interaction was terminated before contact was established, and the last category includes interactions in which interspecific copulation took place. Between these two extremes are categorized interactions of intermediate intensity. Interactions observed in the field are marked with an F, those observed in the laboratory are marked with an L. L+ and L– denote that the species involved in an interaction live together or do not live together in the field. The numbers in brackets indicate the number of times a particular interaction was observed. The categories could doubtless be improved, but since the information was not collected with such a classification in mind, certain additional data needed to improve the classification are lacking.

1) A male approaches a member of a different species but stops before contact is established. The individual being approached makes no repelling movements.

Arphia sulphurea–Pardalophora apiculata female, F
Arphia sulphurea–caterpillar, F
Ageneotettix deorum–tiger beetle, F
Ageneotettix deorum–Spharagemon collare male, F (2)
Ageneotettix deorum–Dissosteira carolina male, F
Spharagemon collare–Ageneotettix deorum male, F
Chorthippus curtipennis–Stethophyma gracile male, L+

Pardalophora haldemanii—*Metator pardalinus* female, L+
Melanoplus dawsoni—*Orphulella speciosa* male, L+
Dichromorpha viridis—*Trachyrhachys kiowa* male, L—

2) A male approaches but stops before establishing contact when the individual being approached escapes or makes repelling movements.

Arphia sulphurea—*Chortophaga viridifasciata* male, F
Arphia sulphurea—*Pardalophora apiculata* female, F
Arphia sulphurea—*Pardalophora apiculata* male, F
Arphia sulphurea—*Pardalophora apiculata* male, F
Pardalophora apiculata—*Arphia sulphurea* female, F
Pardalophora apiculata—*Arphia sulphurea* male, F
Spharagemon planum—*Dissosteira carolina* male, F
Spharagemon collare—*Melanoplus confusus* female, F
Spharagemon collare—*Ageneotettix deorum* male, F
Spharagemon collare—*Ageneotettix deorum* female, F
Spharagemon collare—*Dissosteira carolina* male, F
Ageneotettix deorum—*Spharagemon collare* female, F
Derotmema haydenii (2 males)—*Trimerotropis latifasciata* female, F (2)
Trimerotropis pallidipennis (4 males)—*T. latifasciata* female, F (2)
Pardalophora apiculata—*Arphia sulphurea* female, L+ (5)
Chortophaga viridifasciata—*Arphia sulphurea* female, L+

3) A male approaches and touches a member of a different species, then leaves. The individual being touched makes no escaping or repelling movements.

Arphia sulphurea—*Pardalophora apiculata* female, F
Arphia sulphurea—*Pardalophora apiculata* male, F
Arphia sulphurea—*Melanoplus confusus* female, F
Pardalophora apiculata—*Arphia sulphurea* male, F
Pardalophora apiculata—*Arphia sulphurea* female, F
Sphargemon collare—*Ageneotettix deorum* male and female, F
Spharageman collare—*Dissosteira carolina* male, F
Camnula pellucida—*Spharagemon collare* male, F (6)
Arphia sulphurea—*Chortophaga viridifasciata* female, L+ (2)
Chortophaga viridifasciata—*Arphia sulphurea* female, L+
Pardalophora haldemanii—*P. phoenicoptera* female, L—
Pardalophora phoenicoptera—*P. apiculata* female, L+
Spharagemon collare—*T. huroniana* female, L+
Spharagemon bolli—*S. collare* female L+ (3)
Spharagemon crepitans—*S. planum* female L— (4)
Trimerotropis huroniana—*Spharagemon collare* female, L+
Chorthippus curtipennis—*Orphulella speciosa* female, L+
Aulocara elliotti—*Ageneotettix deorum* female, L+

4) Male approaches and touches an individual of a different species, and the interaction stops when the approached individual makes repelling movements.

Trimerotropis pallidipennis—T. latifasciata female, F
Arphia sulphurea—Chortophaga viridifasciata female, L+
Chortophaga viridifasciata—Melanoplus confusus female, L+
Pardalophora apiculata—P. phoenicoptera female, L+
Pardalophora haldemanii—P. apiculata female, L+ (4)
Spharagemon bolli—Spharagemon collare female, L+ (3)
Spharagemon collare—S. bolli female L+ (2)
Spharagemon crepitans—S. planum female L+

5) A male approaches, touches, mounts and then dismounts without attaching or attempting to attach his genitalia. The individual being mounted does not make repelling movements.

Camnula pellucida—Spharagemon collare male, F
Chortophaga viridifasciata—Arphia sulphurea female, L+
Pardalophora haldemanii—P. apiculata female L+
Pardalophora haldemanii—P. phoenicoptera female, L—
Pardalophora apiculata—P. phoenicoptera female, L+
Pardalophora phoenicoptera—P. apiculata female, L+
Trachyrhachys kiowa—Dichromorpha viridis male, L—
Melanoplus dawsoni—Orphulella speciosa male, L+
Melanoplus sanguinipes—M. femur-rubrum female, L+

6) A male approaches, touches and mounts and is then repelled, or the individual being mounted escapes.

Melanoplus confusus—Chortophaga viridifasciata male, L+
Pardalophora haldemanii—P. apiculata female, L+
Orphulella speciosa—Chloealtis conspersa male, L+
Orphulella speciosa—Melanoplus dawsoni male, L+
7) A male approaches, mounts and copulates with a female.
Trimerotropis huroniana—T. verruculata female, F
Dissosteira carolina—D. longipennis female, F
Dissosteira carolina—Encoptolophus sordidus female, F
Pardalophora haldemanii—P. apiculata female, L+

It has been maintained that the more closely two species are related to one another the more likely they are to influence one another's behavior. If the number of congeneric and non-congeneric interactions is compared with respect to the level of interaction (Table 18), it appears that the level of interaction between species belonging to the same genus is significantly higher than it is for species belonging to different genera. Using the chi-square test, the differences in the level of interaction between congeners and noncongeners are highly unlikely to be owing to chance alone ($\chi^2=29.36$;

d.f.=4; $P<.005$). Since sexual interactions with other species are a waste of time and energy, it follows from the above figures that a species would be most likely to undergo evolutionary changes in its sexual behavior in relation to the more closely related species.

TABLE 18

NUMBERS OF CONGENERIC AND NON-CONGENERIC INTERACTIONS OBSERVED IN GRASSHOPPERS.

		interaction level[1]						
		1	2	3	4	5	6	7
Numbers of								
interactions	field		2		1			2
between	lab			9	10	5	1	1
congeners	total		2	9	11	5	1	3
Numbers of								
interactions	field	7	14	13		1		1
between	lab	4	6	7	2	3	3	
non-congeners	total	11	20	20	2	4	3	1

[1] For explanation of interaction levels, see text pp. 117–119.

If grasshopper species are more prone to accidents of pair formation than, for example, other groups of acoustical Orthoptera (and this seems likely, given the ease with which interactions between different species have been observed in the field) then there might be some fundamental difference in the ease with which reproductive isolation can be achieved and in the manner in which it is achieved. Perhaps it is on the average easier for newly formed species of nocturnal ensiferans to remain sympatric with one another than it is for grasshopper species to do the same. In ensiferans the call seems to be the prevalent means of pair formation, and a difference in the call would prevent most interspecific interactions; in grasshoppers, where pair formation is achieved by visual as well as by acoustical means, more than just a call difference would be needed. Extensive differences in courtship among closely related species, as contrasted to the lack of such pronounced differences among closely related species of crickets (Alexander and Otte, 1967), might be only one of several important consequences of the relative difficulty that grasshoppers may have in improving their system of pair formation. Important differences in distribution patterns and ecological relations between night singing insects and day singing insects might also exist as a consequence of the fact that more than one method of pair formation is possible in the diurnal species.

SEASONAL AND HABITAT ISOLATION

There is as yet little evidence to indicate that seasonal separation of the adults of different species has evolved as a reproductive isolating factor. The adults of the species of *Arphia* probably interact with one another less than do the adults of another closely related species, because they are for the most part separated either seasonally or geographically. Associated with this separation is the fact that courtship and pair-forming signals of the various species differ relatively little from one another, compared to the signals of other genera in which adults are not separated to the same extent, e.g., *Spharagemon, Trimerotropis.*

There is no evidence for the existence of differences in the daily activity cycles in the species I have studied. They all appeared to be active during warm, sunny periods of the day.

There is also little information on the ecological separation of closely related species. The species in the genus *Spharagemon* can be divided according to whether they inhabit open sandy areas (*collare, cristatum*), short grass prairies *(humile, equale),* or lightly wooded areas *(bolli, crepitans).* The members of the first and the last pairs of species appear to be largely allopatric with one another, but the geographical relations of the middle pair are poorly known. The members of each of the above pairs seem to be closely related, but perhaps the three ancestors of these pairs became adapted to different habitats during speciation. In the genus *Trimerotropis* the most similar species seem to inhabit similar habitats.

BEHAVIORAL ISOLATION

Much concerning species distinctiveness in pair-formation and courtship in grasshoppers tends to corroborate findings for other groups of animals. There is some direct evidence that acoustical signals have a pairing function and that they serve to coordinate the activities of potential mates. Most of this comes from work on European species of Acridinae (Jacobs, 1953; Perdeck, 1958; Haskell, 1958), where in a number of species calling by males and answering by females leads to pairing and copulation. I described several instances of females being attracted to acoustical-visual signals of males, e.g., *Chortophaga viridifasciata* and *Arphia simplex,* and of females answering the calling stridulation of males, e.g., *Chloealtis conspersa* and *Chorthippus curtipennis.* But there is as yet little direct evidence that the same signals serve as reproductive isolating mechanisms. Only one study, that of Perdeck (1958), showed convincingly that females of two grasshopper species, in this case *Chorthippus brunneus* and *C. biguttulus,* answer only the song of males of their own species.

The evidence that pairing and courtship signals serve as mechanisms for reproductive isolation is mostly indirect. Perhaps the most important observation is that pairing and courtship behavior tend to be very distinct and to differ greatly among closely related species, while other types of behavior (for instance, aggression and repulsion) remain relatively constant. The distinctiveness of the calls of European Acridinae facilitated the work on the taxonomy of that group (Faber, 1929). Thus, the situation existing in grasshoppers is quite similar to that existing in the Ensifera (crickets, katydids) and in anuran amphibians. There are, however, some notable differences in behavioral isolation which seem owing to the fact that grasshoppers are largely diurnal while ensiferans and anurans are largely nocturnal.

PAIR FORMING SIGNALS.—Differences in the crepitation patterns of species living together probably serve as reproductive isolating mechanisms when the species are closely related. But even if two species are incapable of crossmating, the differences in crepitation could serve to reduce the number of needless interactions, however short they may be. Since males often approach individuals of the wrong species, even individuals of distantly related species, it follows that selection should be operating continuously to increase the ability to distinguish between individuals of one's own and other species. In southern Colorado and northern New Mexico, several oedipodine species live together in various combinations. The crepitation of each species is distinctive (Fig. 17) with the possible exception of one pair of species, *T. campestris* and *S. humile,* and individuals of the various species are active at the same time. Other combinations of these species exist; for instance, the species *A. pseudonietana, S. humile, T. pallidipennis* and *T. campestris* were found within a few feet of one another near Denver. Even though these species may have acquired their particular patterns of crepitation before establishing the present sympatry and may be more or less distantly related to one another and incapable of crossmating, the differences in crepitation patterns probably reduce the number of accidental pairs formed and are therefore probably maintained, or even improved upon to some extent, by natural selection. In addition to the species listed, there are non-crepitating species which occur in the same region, e.g., *Derotmema haydenii, Trachyrhachys kiowa, Mestobregma plattei* and *Hadrotettix trifasciatus.*

I have encountered three cases where species that are partially sympatric have very similar rates of crepitation. Populations of *Arphia xanthoptera* (Ohio) and *A. pseudonietana* (Michigan) have similar crepitation rates. But *xanthoptera* has yellow to orange wings and *pseudonietana* has red wings. It is not known whether this difference in wing color is involved in any way in the prevention of wasteful interactions between these two species where they are sympatric. Also, no comparison between crepitation rates in areas of sympatry has been made. Crepitation of *Spharagemon bolli* (Michigan) is very similar both in rate and duration to that of *S. saxatile* (Pennsylvania). The wing coloration of the two species is similar. Courtship, however, is quite different. *Spharagemon humile* and *Trimerotropis campestris* appear to be broadly sympatric in southern Colorado and northern New Mexico and both have been collected at the same locality. Crepitation rate and wing coloration in these two species are similar, but again, courtship is very different.

There have apparently been no studies showing that color or pattern differences result in reproductive isolation in grasshoppers. These characters are usually quite similar among closely related species, at least among Oedipodinae. There is sometimes a striking polymorphism in wing color

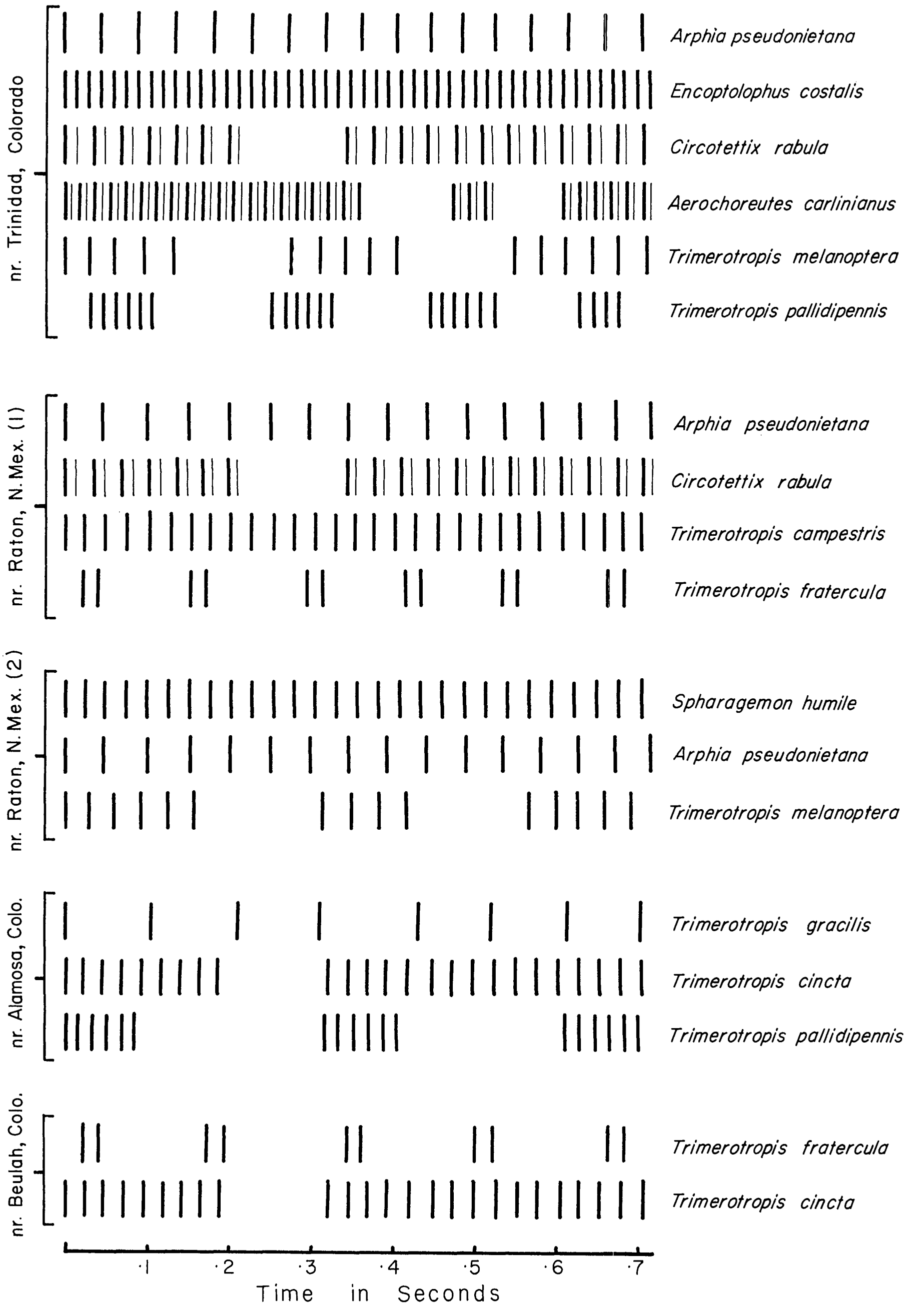

FIG. 17. Crepitation patterns of Oedipodinae at five localities in southeastern Colorado and northeastern New Mexico.

within a species, e.g., *Arphia xanthoptera, Derotmema haydenii,* suggesting either that the differences in wing color are mostly selected for on some other basis or that differences in wing color are not so easily acquired as reproductive isolating mechanisms as are other differences. The members of the Acridinae and Cyrtacanthacridinae tend to be more varied from species to species in body coloration than the Oedipodinae. Some color differences must be owing to selection for cryptic coloration in different habitats. However, it seems probable that in the Cyrtacanthacridinae and Catantopinae, where there is no exchange of visual or acoustical signals between males and females, and where males hop onto females without first signalling their approach, color differences may be relatively more important as cues in pair formation than in the Acridinae and Oedipodinae.

COURTSHIP SIGNALS.—Several differences between closely related species might tend to restrict crossmating, but there appears to be selection for perfecting those isolating mechanisms operating earlier in a sequence of interaction (Alexander, 1967). According to Alexander, "diverging selection on later events would cease when early events become completely effective." If this is true, one would expect pair-forming signals to become more efficient isolating mechanisms than courtship signals. But as Alexander points out, courtship signals "may be selected as reproductive isolating mechanisms in cases in which the chance of accidental pair formation is high." In grasshoppers the great diversity of courtship signals correlates with a seemingly high incidence of accidents in pair formation. Differences in courtship may, as Alexander indicates, be the result of selective action on the calling signal when the motor patterns of calling and courtship signals are similar. Some of the species-specificity in courtship in the Acridinae may have arisen in this manner; but in the Oedipodinae, where the method of pair formation and courtship is quite different, selection operating on pair-forming signals would not be expected to change courtship signals, and therefore selection must have operated directly on courtship differences. Thus, courtship differences can, in some groups at least, also be expected to distinguish all the species in a situation where the species have become adjusted to one another.

While courtship signals appear to be as species-specific as pair-forming signals, I know of no method for determining whether courtship differs more, overall, among different species, than pair formation. It is apparent, however, that these two aspects are much more species-specific than other aspects of mating behavior that occur later in the mating sequence, such as mounting, presenting behavior by females, and copulation. Haskell (1957), for instance, points out that in four sympatric species of Acridinae stridulation produced by the male approaching the female is highly distinctive, whereas the stridulation of the male mounting the female is quite similar. Figure 18 illustrates some changes that have probably occurred in the courtship patterns of various species and lineages of Oedipodinae. The primitive condition probably consisted of the production of ordinary stridulation during courtship. In various species vibratory stridulation,

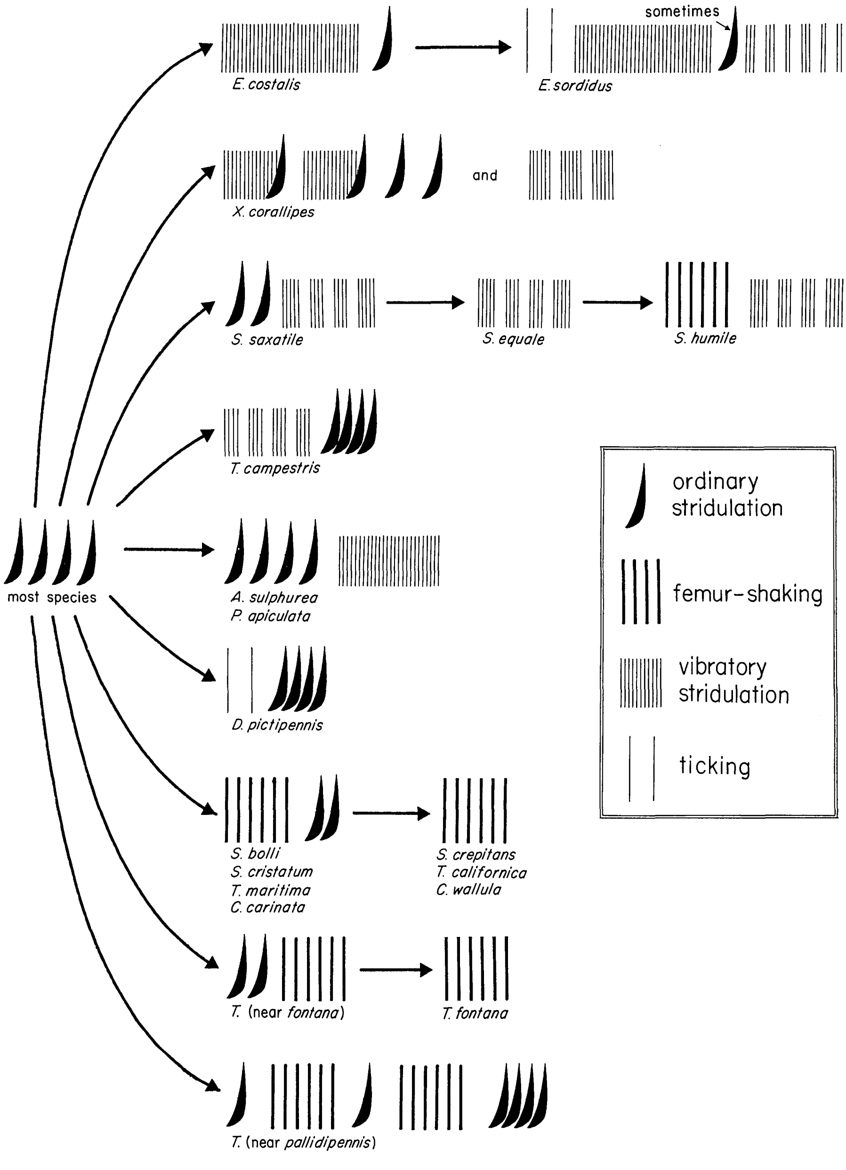

FIG. 18. Qualitative changes in courtship in the subfamily Oedipodinae. Arrows indicate the probable direction of evolution. The postulated primitive condition, on the left, is possessed by a large majority of species including congeners of most of the species on the right. A number of different courtship patterns were evidently derived from this original condition. Thus, vibratory stridulation and femur-shaking were apparently incorporated into courtship independently a number of times. This was evidently followed, in several lineages, by the loss of ordinary stridulation.

femur-shaking, and ticking became incorporated into courtship and in some species stridulation was evidently lost entirely (but the stridulatory apparatus remains). Among the Acridinae and Catantopinae courtship changes are largely quantitative, involving changes in rates, in intensity, and in numbers of movements.

In the Acridinae aggressive behavior tends to vary between species almost as much as courtship behavior. This may be owing to the fact that aggressive movements and courtship movements are very similar (they use similar neuromuscular apparatus) and, consequently, when calling or courtship changes occur, there is necessarily a change in aggressive signals as well.

There seems to be no other explanation for the considerable diversity in courtship signals than that there has been strong selection for behavioral differences which promote intraspecific recognition and reduce the number and extent of interactions between species. Among the Oedipodinae there has evidently been little if any selection for distinctiveness in aggressive signals, perhaps because it is not important for a male to be able to discriminate between males of his own species and those of other species. In each case the separation of the males is advantageous. It is even possible that if pairing mistakes, in which a male of one species approaches a male of another species, occurred frequently, there would be selection for similarity of the aggressive signals of different species.

OLFACTION.—Chemical differences seem to be important in interspecific recognition when contact between individuals has been established. Males of one species often turn away from females of another species only after contact between them has been established. No repelling movements need be made. Chemical differences among species of Catantopinae may be relatively more important than visual differences because interactions between the sexes occur mainly after male and female have established contact with one another.

MECHANICAL ISOLATION

It was once believed that genitalic differences were effective isolating mechanisms, but a growing number of people maintain that behavioral or other premating differences function as isolating mechanisms and that genitalic differences are incidental byproducts of selection for increased efficiency in coupling and have not been selected in the context of reproductive isolation. This opinion is based on the great similarity that exists among the genitalia of closely related species and on experimental evidence indicating that even species with different genitalia can cross-mate (Mayr, 1963; Alexander and Moore, 1962; Alexander and Otte, 1967).

The situation found in certain grasshoppers suggests that the question is not yet resolved. Genitalic differences are very distinct among the species of Catantopinae and have been widely used by taxonomists to distinguish them. Among the Oedipodinae and Acridinae, however, the differences are much less pronounced and have not been used for taxonomic purposes.

They are hardly owing to chance, however, for these are large groups, each containing hundreds of species. In the Catantopinae no signalling is apparent before the male has mounted the female. Interspecific recognition probably occurs partly as a result of chemical and mechanical-tactual signalling between male and female *after* the male has mounted the female. Males frequently mount unreceptive females, males of their own species and (in the laboratory) males and females of other species. Furthermore, females sometimes struggle vigorously before copulation ensues. It seems quite likely, therefore, that genitalic differences have been favored because they prevent interspecific matings. In the Acridinae and Oedipodinae visual and acoustical signals are exchanged *before* contact between males and females is established and males seldom mount unreceptive females, males, or individuals of other species.

A very similar situation exists in certain fruit flies (Spieth, 1968). Males of *Scaptomyza* species "assault" females and mount them without first producing the relatively complicated courtship patterns that one observes in drosophilids. After mounting, however, males vibrate one or both wing as they attempt to attach their genitalia. Both males and unreceptive females are sometimes mounted in this fashion and they usually struggle until the mounting male departs. In this genus the genitalia are highly species-specific and need to be examined in order to correctly identify the species. In the drosophilids, which possess premounting courtship signals, genitalic differences are evidently not nearly so pronounced. Spieth concludes (p. 176): "It is reasonable to assume that each female [of *Scaptomyza*] receives multiple and specific stimuli resulting from the complex and unique genitalia plus other stimuli involved by the male's mounting activities."

ORIGIN AND EVOLUTION OF SIGNALS

Different species may be similar owing to convergence, but by and large, they are alike because they retain some of the characters of a common ancestor. Furthermore, characters in the descendant species evolve at different rates, so that in some species they may be like those possessed by the common ancestor, whereas, in others the same character may have evolved into something quite different. These two facts, (1) similarity owing to common descent and (2) differential rates of evolution in different lineages, permit one to determine (within limits) not only the ancestral condition but also the course of evolution in a character. I have used the following criteria for determining the primitive states and the direction of evolutionary change in a character (Maslin, 1952; Simpson, 1961): (1) characters possessed by many or most members of a taxon are likely to be more primitive than characters possessed by one or only a few members of the same taxon; (2) if, however, the minority condition resembles a condition in members of related taxa of the same rank, this condition may be primitive; (3) if a character appears sporadically among the members of taxa of comparable rank, then its presence in the various members is likely to be the result of convergence.

Ordinarily a receptor system must exist before a signalling system can evolve. Acoustical and visual signals probably developed from existing movements, which originally served functions other than communication, after a receptor system became operative. Those aspects of an animal, e.g., its position, its structure, or its behavior, which indicate to other individuals something else about that animal, e.g., its physiological state, an impending behavioral act, etc., assume a signalling function when the information is emitted for purposes of communication. In other words, the emission of information is initially an incidental effect of some other function, but later it may be adapted for communication. For example, movement, form, color, odor, or sound may initially be merely signs indicating the whereabouts of an individual, but when these become elaborated as communicative devices, or when they are used for communication rather than for some other function, then they become signals. This relationship is illustrated in the following diagram, where A is a behavior pattern, (X) is its original evolved function, S is a sign, and (S) is a signal:

$$\begin{tikzcd}
& A(X) + S \arrow[d] & \\
& A(X) + (S) \arrow[dl] \arrow[dr] & \\
A(X) & & A'(S)
\end{tikzcd}$$

A serves function X, but also acts as a sign; emission of information is incidental to function X.

A serves function X, but it is also used to communicate; emission of information is evolved and is therefore at times not incidental.

A′ is a ritualized behavior with a signalling function.

Darwin (1872) was the first to investigate the origins of communicative signals. During the past 30 years much more attention has been given to the subject. For discussions of this topic and for additional references, see Daanje (1950), Armstrong (1950), Tinbergen (1952), Morris (1956, 1957), Blest (1961), and Smith (1969). Signals are currently thought to have originated from several kinds of non-communicative movements and to have become ritualized to various degrees, sometimes to the extent that the source of the signal is obscured.

In grasshoppers, signals have evidently originated (1) by ritualization of various non-communicative activities—for instance, certain orientation and locomotive movements seem to have assumed a signal function in some species, (2) through structural changes of pre-existing signals, so that one signal may give rise to two or more different signals, (3) through functional changes of pre-existing signals—for instance, a signal may undergo a change in function from aggression to courtship, or (4) as a more or less sudden appearance of a new motor pattern.

ORIGIN FROM NON-COMMUNICATIVE MOVEMENTS

FLIGHT SIGNALS.—The ancestor of all grasshoppers (Acridoidea) was probably a winged insect without brightly colored wings that did not signal during flight and that flew only as a result of disturbance or during dispersion or displacement. The evidence for this is, first, that most fossil grasshoppers were winged, as are most Ensifera, the group from which grasshoppers are presumed to have been derived (Zeuner, 1939, 1942), and secondly, that most grasshoppers are clear-winged and are not known to perform elaborate flight displays.

It seems likely that ritualized approaching flights evolved from unspecialized approaching flights, and that calling flights by solitary males evolved from ritualized approaching flights (Table 2). Listed below are conditions of flight and wing morphology in various species. These conditions probably represent some of the possible stages in the evolution of female-attracting flights.

a) Flight not associated with pair formation; hindwings colorless; no flight sounds. Example: most species of Catantopinae.

b) No female-attracting flights; males occasionally approach females by flying (unspecialized approaching flights); hindwings colorless; no flight sounds. Example: *Camnula pellucida.* (In this species this condition may have been derived from a more elaborate one.)

c) No female-attracting flights; males frequently approach females by flying; hindwings brightly colored; no flight sounds. Examples: *Heliastus azteca, H. benjamini, Derotmema haydenii.*

d) Short (female-attracting?) flights by solitary males occur, but only rarely; few or no approaching flights; hindwings brightly colored; no flight sounds. Example: *Pardalophora apiculata.*

e) Flights by solitary males infrequent; approaching flights frequent; hindwings brightly colored or conspicuously banded; flight crepitation distinct. Examples: *Trimerotropis maritima, Conozoa carinata.*

f) Female-attracting flights performed by solitary males; approaching flights with crepitation; crepitation distinct; hindwings not brightly colored or contrastingly marked. Example: *Chortophaga viridifasciata.* (This condition is probably derived from the condition described in (g) because faint tracings of markings in the related genera, *Arphia* and *Lactista,* can be discerned.)

g) Female-attracting flights performed by solitary males; approaching flights; crepitation loud; hindwings brightly colored and contrastingly marked. Example: *Arphia* species, some *Spharagemon* species.

Secondary reductions have probably occurred in several species. For instance, in *Spharagemon collare* approaching flights sometimes occur, males sometimes crepitate during disturbance flights, the hindwings are brightly colored and contrastingly marked, but female-attracting flights do not occur, there is no crepitation during flights, and approaching flights appear to be rare or absent.

To summarize: in most species of Acrididae flight is probably not a communicative signal. Flights probably became elaborated into communicative signals (through modification of wing patterning and flight noises) only *after* males began to approach females by flying. With the evolution of such species-specific flights, sexually receptive females could be attracted to males flying toward them or toward other individuals. This was probably followed by the performance of conspicuous flights by *solitary* males to which females were attracted.

WING-FLAPPING.—This movement is perhaps universal among winged grasshoppers. The movement consists of a burst of wing-flapping lasting a fraction of a second. Its function in most species is not clear. It is performed by species whose wings are too short to permit flight, and in long-winged species there does not seem to be a close relation between flight and this movement. In the great majority of species it does not seem to be of communicative significance because it is not performed with particular reference to other individuals. Wing-flapping may be a so-called "autonomic response" or "comfort movement" and be somewhat analogous to piloerection in birds or to stretching in mammals. The movement has, however, assumed a courtship function in a few distantly related species. It is part of the courtship sequence in *Bryodema tuberculata* (Oedipodinae) and *Stauroderus scalaris* (Acridinae) (Jacobs, 1953) and in *Schistocerca lineata* (Cyrtacanthacridinae). In the latter species the movement differs from ordinary wing-flapping, in that the wings are flipped out only once, and hence may not be the same as that occurring in most species. In view of the near-universality of this behavior in winged grasshoppers, it is surprising that it has not been developed as a display more often.

SIDEWAYS BODY-ROCKING.—In three species, *Myrmeleotettix maculatus, Chorthippus biguttulus* and *Eritettix simplex,* males move their bodies from side to side repetitively, without shifting the positions of their legs, at a certain point during the courtship sequence. This movement has evidently been derived from the non-communicative, orientational, "body sideways" movement performed perhaps by all species. In *Eritettix* the display appears just shortly before the male rapidly approaches the female, that is, at the same time that the orientational movement from which it may be derived probably occurred. It is of course possible that the movement is not a display, but this seems unlikely since it differs greatly from the sideways movement observed in most species and since it appears only in this context.

In all *Melanoplus* species observed, the sideways movements of the head and forequarters are made by males about to jump onto females or about to jump to another perch. Similar, but more pronounced, movements are performed by males of *Melanoplus confusus* and *M. keeleri* shortly after mounting the female and by females of *M. differentialis* apparently as a repelling signal. Sideways rocking motions were also performed by copulating males of *Taeniopoda eques* (Romaleinae) when they were disturbed by other individuals.

TICKING.—This signal is probably derived from kicking, a movement which it resembles closely. It differs from kicking in being highly stereotyped and in that the tibiae strike the forewings. Ticking is produced by males of five distantly related species of Oedipodinae: *Encoptolophus sordidus,* and *Dissosteira pictipennis* in the United States, and *Aiolopus thalassinus, Bryodema tuberculata,* and *Psophus stridulus* in Europe. It is a courtship display in all but *Psophus stridulus,* where, according to Jacobs (1953), it is an aggressive display. It is also produced by three species of Acridinae, *Omocestus viridulus* and *Omocestus rufipes* in Europe, and *Orphulella speciosa* in the United States; it is produced by courting males of the first species and by aggressive males of the last two species.

FEMUR-JERKING.—This is a graded disturbance or repelling movement performed by individuals touched by other individuals. It is evidently ancient, perhaps having occurred in the ancestor to the Caelifera, for it is performed by all five species of Tetrigidae and by all species of Acrididae which have been carefully studied. Jerking is somewhat similar to the small upward movements performed by walking individuals and may have been derived from such locomotory movements.

FEMUR-RAISING.—This graded repelling movement is performed by all the species of Tetrigidae and Acrididae examined so far, and evidently also by a species of Tridactylidae (*Tridactylus madecassus*) examined by Wickler (1966). In species studied more thoroughly, all gradations from a simple raising and lowering of the femora to raising and holding the femora in a raised position have been observed. (The femur-raising movement is apparently lacking in crickets.) Although a given movement can usually be readily classified either as femur-jerking or as femur-raising, intermediates between the two sometimes occur. Whether femur-raising arose as a modification of femur-jerking or had some other source is difficult to determine. In many species the movement is also performed before bodily contact between individuals is established, so that it seems to prevent such contact from taking place. It has therefore become a visual signal as well as a tactual signal. Femur-raising also seems to be quite ritualized and to have developed a "typical intensity" (Morris, 1957), perhaps owing to its evolution as a visual signal.

ORIGIN THROUGH STRUCTURAL CHANGES OF PRE-EXISTING SIGNALS

FEMUR-SHAKING.—This signal is performed by all but one of the 79 species of Oedipodinae and by all Cyrtacanthacridinae and Catantopinae studied to date. It has evidently been derived from femur-jerking, because (a) femur-jerking is possessed by all species which possess femur-shaking and is therefore probably ancient; (b) within some species (*Pardalophora apiculata, Arphia granulata,* three species of *Lactista, Trimerotropis maritima, Derotmema haydenii, Circotettix rabula, Trachyrhachys kiowa, Spharagemon saxatile, Melanoplus sanguinipes* and *Podisma alpina*), intermediates between single jerks and femur-shaking occasionally occur; (c) among the various species of a single lineage all intermediates between single strokes of femur-shaking and multiple strokes of femur-shaking occur —for instance, in the genus *Arphia*, the number of strokes per burst of shaking varies from 1 to 4 in *granulata* and from 3 to 9 in *simplex;* and (d) the difference between femur-jerking and femur-shaking is basically one of definition only; femur-shaking, aside from being stereotyped, consists merely of repetitive femur-jerking. Three basic kinds of femur-shaking are known: silent shaking, shaking with wing-striking, and shaking with substrate-striking. Because femur-jerking is silent and is produced by individuals in contact with other individuals in all species, femur-shakng probably originated as a silent movement produced by individuals when touched.

In three species of *Pardalophora* and in *Xanthippus corallipes* the signal is silent and is performed only when contact is established. In *Chortophaga* species and all of the examined species of Catantopinae it is silent and is produced both before and during contact. In the group Arphiae (which, in my opinion, includes *Lactista* and *Platylactista*) both *Chortophaga* species shake silently, both *Encoptolophus* species strike the substrate, and *Arphia, Lactista,* and *Platylactista* strike the wings. Females of *Arphia sulphurca* shake silently. Wing-striking and substrate-striking both probably evolved from silent shaking. Aggressive femur-shaking in *Platylactista, Lactista,* and *Arphia granulata* has been reduced to single strokes.

Most members of the Hippisci shake silently, but two species, *Pardalophora haldemanii* and *Leprus robustus,* strike the substrate. In these species, particularly in the former, shaking with substrate-striking has almost certainly evolved from silent shaking. Silent shaking with occasional substrate-striking—a possible intermediate condition—occurs in *P. apiculata.* Femur-shaking with wing-striking is not possessed by any members of this group, but *P. apiculata* occasionally strikes the wings, thus displaying a possible intermediate condition between silent shaking and shaking with wing-striking.

In the group Trimerotropi (*Trimerotropis, Conozoa*) most species strike the substrate. Only two species shake their femora silently; they probably acquired this condition secondarily. In California, *Trimerotropis verruculata* strikes its wings, but in Utah and Michigan it more commonly strikes the substrate. *T. fratercula, T. pallidipennis,* and *T. huroniana,* also strike the substrate but occasionally strike the wings. Another species, *T.* (near *pallidipennis*), apparently only strikes its wings. Thus, it is evident that wing-striking has been derived from substrate-striking in this group.

In the group Bryodemae, *Circotettix rabula* and *Bryodema tuberculata* only strike the substrate, *C. shastanus* usually strikes the substrate but occasionally strikes the wings, and *C. thalassinus* always strikes the wings but occasionally strikes the substrate at the same time. The apparent close relationship between the Bryodemae and the Trimerotropi suggests that wing-striking evolved from substrate-striking in this group also.

In the Catantopinae shaking is always silent. In some species single jerks are produced which differ from ordinary femur-jerking in being stereotyped; in other species shaking is repetitive and is produced in bursts of varying rate and duration.

To summarize: femur-shaking probably evolved from a femur-jerking movement by becoming stereotyped and repetitive; it is least stereotyped in those species in which it is performed only when contact is established. Shaking with wing-striking probably evolved from silent shaking in the Arphiae and from substrate-striking in the Bryodemae and Trimerotropi. In the Hippisci substrate-striking probably evolved from silent shaking, and in the Trimerotropi it probably evolved secondarily from shaking with substrate-striking.

FEMUR-TIPPING.—In the Oedipodinae this signal appears to have been derived from either a femur-jerking or a femur-raising movement. In *Pardalophora apiculata, P. haldemanii* and *Chortophaga viridifasciata,* movements intermediate between jerking and tipping and between femur-raising and tipping are produced by males and females. Femur-tipping has probably evolved at least twice, once in the Oedipodinae and once in the ground-dwelling Acridinae. It appears to have been derived from stridulation in some of the ground-dwelling Acridinae, because (1) tipping is rare among the Acridinae, being present only in the ground-dwelling forms; (2) when tipping is prominent, stridulation is reduced or absent, e.g., *Ageneotettix, Drepanopterna, Cordillacris;* and (3) faint stridulatory sounds were produced during tipping-like movements by individuals of *Drepanopterna femoratum* from a New Mexico population, but no sound was produced during similar movements by individuals from a Texas population.

There is now considerable diversity in the form of femur-tipping among the various species, most of it owing to rate differences. Some of the variations are of particular interest. In four species—two Oedipodinae *(Mestobregma plattei, Trachyrhachys kiowa)* and two ground-dwelling Acridinae *(Ageneotettix deorum* and *Drepanopterna femoratum)*—males perform two kinds of femur-tipping, each in a different context. In these species, rapid, precise femur-tipping motions are performed by males approaching females, and slower, less precise motions are found in male-male interactions. Males of *Dissosteira carolina* also exhibit two kinds of femur-tipping. One movement is silent, and during the other the wings are struck. Both movements are performed by aggressive and courting males, and in both situations silent femur-tipping precedes acoustical femur-tipping. However, acoustical femur-tipping has a higher repetition rate in courtship than in aggression.

ORDINARY STRIDULATION.—The origin of ordinary stridulation in the Oedipodinae is less clear than that of some of the other signals. In European Tetrigidae soundless femoral movements (*Singbewegungen*) are performed by males as they approach females (Jacobs, 1953). In *Chortophaga, Arphia, Lactista,* and *Pardalophora* species, stridulatory movements are essentially very similar to femur-tipping movements, and in *Arphia* species both femur-tipping and stridulation are a regular part of courtship. Hence, it is likely that in the Oedipodinae stridulatory movements are derived from silent tipping motions. Repetitive, silent raising and lowering of the femora occur during the courtship of *Trimerotropis rebellis*. In this species these movements are sometimes silent, sometimes accompanied by sound that may range from barely perceptible to intense. Thus, if we look at grasshoppers as a whole, we have all the intermediate stages between tipping and ordinary stridulation necessary to postulate that ordinary stridulation is derived from visual, tipping-like motions.

Many evolutionary modifications in rate have occurred, as well as modifications in the form of the leg stroke and in the sound produced. Two very distinct kinds of ordinary stridulation with no intermediates are produced by *Trimerotropis caerulipes* and *T.* (near *pallidipennis*). In both species the two kinds of stridulation have a very definite place in the courtship sequence.

Ordinary stridulation has evidently been lost entirely in *Chortophaga australior, Pardalophora haldemanii, Spharagemon crepitans, Trimerotropis californica* and *T. fontana*. It has been partially lost in *S. bolli, S. cristatum, T. maritima* and *T. cincta*.

CREPITATION.—The evolution of certain patterns of crepitation can be reconstructed with considerable confidence because of the existence of intermediate states. Taken together, the species studied so far display five different kinds of crepitation patterns. These are (1) single, continuous bursts of crepitation (most species, including *Arphia, Spharagemon, Chortophaga,* and *Encoptolophus* species), (2) series of bursts of irregular duration and spaced by intervals of irregular length, e.g., *Trimerotropis cincta, Circotettix rabula, Aerochoreutes carlinianus,* (3) series of bursts of regular duration and spaced by regular intervals, e.g., *Trimerotropis pallidipennis, T. verruculata, T. fratercula,* and *Dissosteira pictipennis,* (4) single long bursts consisting of two different wing-beat rates (in *Dissosteira carolina* the rate is much faster during the first half of the burst than during the second half), (5) sound is not produced with each stroke of the wings as in the four patterns above, but only during every third or fourth stroke, e.g., *Arphia simplex, Trimerotropis gracilis.* The second pattern is easily derived from the first and the third is easily derived from the second, but I have not found conditions intermediate between the fourth or fifth patterns and any other.

ORIGIN THROUGH FUNCTIONAL CHANGES OF PRE-EXISTING SIGNALS

While there are examples of slight changes in the function of some grasshopper signals—for instance, from informing a female of one's approach to attracting a female with the same display—the most dramatic changes in function involve signals which, in an ancestral species, probably had an aggressive function and which subsequently assumed a courtship function. At least three different signals have evidently undergone such a change in function independently several times.

Femur-shaking.—Of the 73 species in which both aggressive behavior and courtship behavior is known, 57 species shake their femora only in aggressive situations, 11 species shake femora both in courtship and aggressive situations, and 5 species shake only in courtship situations. In three of the 11 species that shake in both situations, shaking is similar in the two contexts but is reduced or occurs only rarely in aggressive encounters and may be in process of being lost; in three other species courtship and aggressive shaking are distinctly different from one another; and in the remaining five species courtship shaking and aggressive shaking are the same except that during courtship, shaking is combined with stridulation. These relationships are summarized in Table 19. Femur-shaking seems to have been incorporated into courtship about 13 times among the species studied by me. Table 19 also shows that when this happens, stridulation tends to be lost. Thus, during courtship, 9 of the 16 species that shake do not stridulate, whereas 55 of the 57 species that do not shake also stridulate. The figures indicate that courtship stridulation tends to be less prevalent among the species in which femur-shaking has assumed a courtship function.

TABLE 19

Femur-Shaking in Aggression and/or Courtship in the Oedipodinae[1]

	Total No. of species	femur-shaking in aggression reduced	Number of species showing femur-shaking in aggression not reduced		stridulation present in courtship	no stridulation in courtship
			courtship and aggressive shaking same	courtship and aggressive shaking diff.		
femur-shaking present in aggression and courtship	11	3	5*	3	5*	6
femur-shaking present only in courtship	5	not applicable			1, 1R	3
femur-shaking present only in aggression	57	not applicable			55	2

[1] R = reduced expression; * = same species.

The probable evolutionary steps leading up to the condition in which femur-shaking is performed only by courting males and courtship stridulation has been entirely lost can be determined by comparing the various stages reached by different species. In Table 20 I have indicated some stages represented by the contemporary fauna.

The picture emerging from the analysis of this signal is, first, that its incorporation into courtship is a fairly common method by which different

TABLE 20

STAGES IN INCORPORATION OR LOSS OF FEMUR-SHAKING AND STRIDULATION IN COURTSHIP AND AGGRESSION[1]

	COURTSHIP			AGGRESSION	
most species	*T*	OS	–	T	SH
S. bolli *S. cristatum* *T. maritima* *T. cincta*	*T*	OS*	SH	T	SH
L. (near punctatus)	*T*	–	SH_1	T	SH_2
P. haldemanii *T. californica* (Calif.)	*T*	–	SH	T	SH*
T. californica (Ariz.) *T. fontana* *S. crepitans*	*T*	–	SH	T	–

[1] Key to symbols: T = femur-tipping; *T* = Femur-tipping usually present; OS = ordinary stridulation; SH = femur-shaking; SH_1 and SH_2 denote that shaking in the two situations is different. An asterisk indicates reduced occurrence.

species have acquired specific distinctiveness in the context of reproductive isolation. Second, once this happens there is selection for making aggressive behavior distinct from courtship behavior. This has apparently been achieved by (a) a loss of shaking in aggressive contexts, (b) production of a distinct type of shaking in aggressive contexts, or (c) a combination of shaking and stridulation. Third, when shaking becomes incorporated into courtship it becomes the primary signal, because it is nearly always present in a sequence while other courtship signals tend to be reduced or to be completely lacking.

FEMUR-TIPPING.—In some species tipping appears to be a regular part of courtship, e.g., in *Arphia sulphurea* and *Spharagemon bolli.* In other species it is only occasionally performed by approaching males. Because tipping is sometimes present during approaching in most species, and because there seem to be few differences among the species in the form of the movement, it is probable that it usually serves only an aggressive function, i.e., it elicits aggressive behavior from males that have been approached accidentally.

In some species femur-tipping is the only courtship signal produced, e.g., in *Chortophaga australior, Dissosteira carolina* and *Heliastus azteca. C. viridifasciata,* a close relative of *C. australior,* never tips its femora in courtship situations. In this pair of species, therefore, there has probably been an adjusting of the function of tipping in the context of reproductive isolation. In a number of species of both Oedipodinae and Acridinae where femur-tipping is a regular part of both aggressive behavior and courtship behavior, tipping performed during approaches is different from tipping produced in male-male interactions. This occurs in *Trachyrhachys kiowa, Mestobregma plattei, Dissosteira carolina, Drepanopterna femoratum* and *Ageneotettix deorum.* Thus, some of the same trends observed in femur-shaking are also apparent in this behavior: (1) tipping has sometimes assumed a courtship function in addition to an aggressive function, and (2) where it has done so, the nature of the movement in the two situations has become different.

TICKING.—This signal seems to fit the same pattern as the two discussed above. It may have been derived from an aggressive movement (kicking) and changed by ritualization. The movement is a courtship signal in four distantly related species of Oedipodinae: *Encoptolophus sordidus, Dissosteira pictipennis, Aiolopus thalassinus,* and *Bryodema tuberculata.* In one species, *Psophus stridulus,* the movement is an aggressive display. Among the Acridinae ticking is performed only by courting males of *Omocestus viridulus* and only by aggressive males of *Omocestus rufipes* and *Orphulella speciosa.*

ORIGIN THROUGH THE APPEARANCE OF NEW MOTOR PATTERNS

It is possible that femur-jerking originated as a new motor pattern. In this movement the hind femur strikes encroaching individuals. The movement is therefore a mechanical means for removing or repelling other individuals and may have had a signal function right from the beginning, because an avoidance response to being struck must have already existed in the receiving animals before femur-jerking appeared.

SUMMARY

Figure 19 summarizes some aspects of the origin and evolution of three kinds of signals: shaking, tipping, and ticking. The variations of these signals appear to be the result of diversification of a few basic movements. This diversification has probably involved several of the following steps: (1) the performance of a signal in one context only, (2) the performance of a signal in two or more contexts, e.g., in aggressive and courtship contexts, (3) the gradual evolution of structural (motor pattern) differences in the movements performed in the different circumstances, and (4) the subsequent loss of a signal from the original context. In Figure 19 the diagonal lines indicates such structural changes and the horizontal connecting lines indicate a change in function only. As an example, males of *Dissosteira carolina* possess three kinds of tipping movements. In encounters with males they initially perform *silent tipping* and eventually *tipping with wing-striking;* when courting, males perform a *rapid tipping with wing-striking.* In the ancestry of this species stereotyped tipping probably evolved from a graded femur-raising movement (which is still retained but performed by males only when they are touched by other males) and subsequently "speciated" or differentiated to form two aggressive movements, one silent and one acoustical. The acoustical signal later assumed a courtship function and underwent a further structural change, an increase in repetition rate. (Ordinary stridulation, now lacking, was probably the primitive courtship

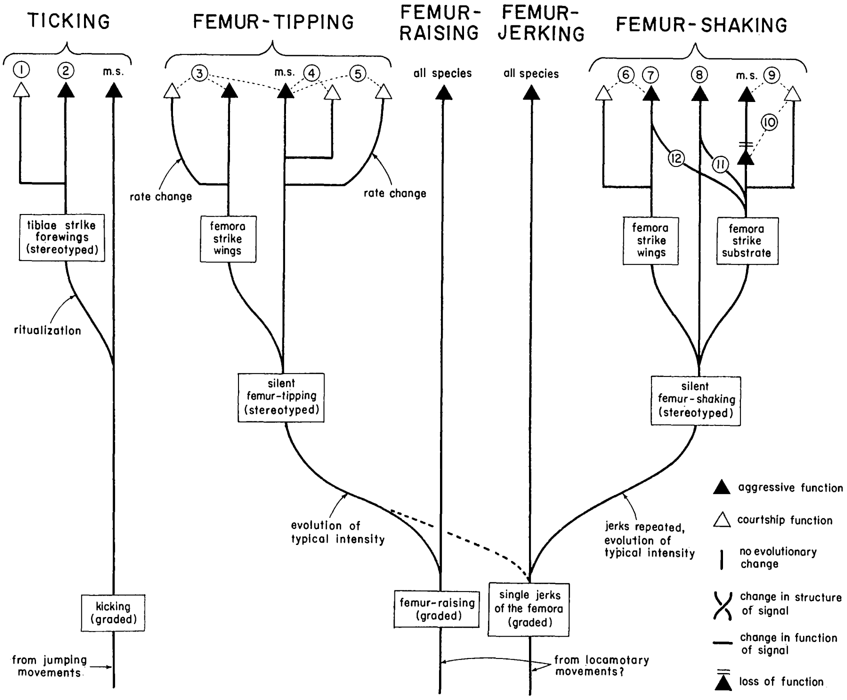

FIG. 19. Probable evolution in three kinds of communicative signals in grasshoppers: ticking, femur-tipping, and femur-shaking. Numbers refer to species possessing each condition: (1) *Encoptolophus sordidus, Aiolopus thalassinus, Bryodema tuberculata, Dissosteira pictipennis,* and *Omocestus viridulus;* (2) *Psophus stridulus, Orphulella speciosa,* and *Omocestus rufipes;* (3) *Dissosteira carolina;* (4) *Chortophaga australior;* (5) *Trachyrhachys kiowa, Mestobregma plattei;* (6) *Lactista* (near *punctatus);* (7) *Lactista* species, *Arphia* species, *Circotettix thalassinus*; (8) most Hippisci, *Trimerotropis fontana;* (9) *Spharagemon bolli, S. cristatum, Trimerotropis maritima, T. californica* (Calif.); (10) *Spharagemon crepitans, T. californica* (Ariz.); (11) *Trimerotropis fontana;* (12) *Circotettix thalassinus, Trimerotropis verruculata* (Yosemite National Park).

sound.) In the ancestry of *Spharagemon crepitans,* shaking probably served an aggressive function, but today it is performed only in courtship contexts. In its closest relative, *S. bolli,* shaking is still performed in both courtship and aggressive contexts. Table 21 lists various signals and indicates their present function, their probable sources, and changes they may have undergone.

GENERAL CONCLUSIONS

PAIR FORMATION

KINDS OF PAIR FORMATION.—Grasshoppers are quite diverse in regard to the methods used in pair formation. The following types of pair-forming behavior have now been observed in Europe (Jacobs, 1953) and in North America:

(1) *Males see and approach moving females.* This general method of pairing is probably employed by most grasshopper species. Exceptions might occur in night singing grasshoppers, for instance, among the Pamphagidae and Pneumoridae. This is evidently the exclusive means of pair formation in many Oedipodinae, e.g., *Mestobregma plattei, Derotmema haydenii, Heliastus benjamini, H. azteca, Lactista punctatus,* and *Spharagemon collare,* some ground dwelling Acridinae, e.g., *Ageneotettix deorum, Drepanopterna femoratum, Cordillacris occipitalis,* and *C. crenulata,* some vegetation dwelling Acridinae, e.g., *Orphulella* and *Dichromorpha* species, and perhaps all Catantopinae, e.g., *Melanoplus* and *Podisma* species.

(2) *Females hear and approach solitary stridulating males.* This method probably exists in most species of Acridinae in which stridulation by solitary males occurs. It is known to occur in *Stenobothrus lineatus, Omocestus viridulus, Chorthippus brunneus, C. parallelus* and others (Haskell, 1958; Jacobs, 1953). There is also some evidence that males of these species form choruses to which females are attracted (Haskell, 1957). Females of these species answer the stridulation of males with silent femoral movements or with stridulation as they approach stridulating males. Of the few species in which pair formation has been studied in detail, no species is known in which females do not answer the male with either silent movements of the femora or with stridulation. This method also appears to be present in at least one species of Oedipodinae *(Dissosteira carolina).*

(3) *Females answer the stridulation of solitary males; the male then approaches the female.* This method has been observed in *Chorthippus brunneus* and *Gomphocerus rufus* (Jacobs, 1953). In both species pair formation is also achieved by females approaching stridulating males. The method may also occur in some Oedipodinae, e.g., *Cibolacris parviceps, Pardalophora apiculata,* and *Arphia sulphurea.* In the last two species females may answer the courtship stridulation sometimes produced by solitary males wandering about in the field. This method probably exists among the night-tipping Pamphagidae, e.g., *Porthetis* sp., and Pneumoridae, e.g., *Bullacris* sp., in which males fly from tree to tree at night, singing one to several songs at each perch. Females are presumed to be sedentary because they are wingless or have only very short wings. How females make their presence known to the males is not clear, since in both groups they lack the stridulatory apparatus possessed by the male. Also, the Pneumoridae lack a tympanum so that the mechanism of hearing remains to be discovered.

(4) *Females hear, see, and approach flight displays performed by solitary males.* This method is known to exist in a few species of Oedipodinae, e.g., *Chortophaga viridifasciata* and *Arphia simplex,* but probably exists in all oedipodines in which solitary males perform flight displays. Such flight displays are rendered conspicuous either by the flashing of brightly colored wings or by crepitation noises produced with the hindwings, or both.

TABLE 21

PROBABLE ORIGIN AND CHANGES IN STRUCTURE AND FUNCTION OF COMMUNICATIVE SIGNALS IN GRASSHOPPERS

Signal & type of signal	Present Function	Probable Origin	Structural Changes	Changes in Communicative Function	Taxon
femur-jerking (mechanical)	aggression	locomotory movement? new motor pattern?	?	none	most species
femur-raising (mechanical, visual)	aggression	locomotory movement? new motor pattern?	exaggeration	none	most species
kicking (mechanical)	aggression	locomotory (jumping) movements	position of femora	(see 'ticking')	most species
femur-tipping (visual)	aggression (most) courtship (some)	femur-jerking or femur-shaking (Oedipodinae) stridulation (Acridinae)	became stereotyped and ritualized, femoral color changes	aggression to courtship	Oedipodinae, some Acridinae
femur-shaking (visual?, acoustical, mechanical)	aggression (most) courtship (some)	femur-jerking	became stereotyped, became acoustical in some species	aggression to courtship	Oedipodinae
ticking (visual, acoustical)	pairing, courtship, aggression	kicking	became stereotyped, acoustical, and iterative	aggression to courtship	some Oedipodinae some Acridinae
wing-flapping (visual, acoustical)	courtship	comfort wing-flapping	?	none?	*Bryodema, Schistocerca*
ordinary stridulation (acoustical, visual?)	courtship, pairing?	femur-tipping	became iterative, and acoustical, evol. of different patterns	none	Oedipodinae
vibratory stridulation (acoustical)	courtship	new motor pattern?	evol. of different patterns	none	Oedipodinae
flight display (visual, acoustical)	pairing	locomotory flight (e.g. approaching flight)	acquisition of colored wings and crepitating noises	none	Oedipodinae

TABLE 21—(Continued)

Signal & type of signal	Present Function	Probable Origin	Structural Changes	Changes in Communicative Function	Taxon
wing crepitation (acoustical)	pairing	incidental flight noises	exaggeration of noises, evolution of diff. patterns	none	Oedipodinae
body sideways-rocking	courtship, aggression	orientational, or distance gauging movements	ritualization, exaggeration	none	*Eritettix, Melanoplus*
body forward-rocking (visual?)	courtship		ritualization, exaggeration	none?	*Syrbula admirabilis*
antenna-waving (visual)	courtship		ritualization, exaggeration?	none?	*Syrbula admirabilis*
palpi-waving (visual)	courtship		exaggeration?	none?	*Syrbula admirabilis*
wing-raising (visual, acoustical)	aggression, aposematic (warning display)	?	exaggeration	none?	*Taeniopoda*

(5) *Males approach solitary flight displays performed by females.* This method has been reported in only one species, *Trimerotropis agrestis gracewileyae.* Tinkham (1960) reported that undisturbed females flew and crepitated upon alighting, thereby attracting males. Males flew silently towards females and then walked the remaining distance. No solitary flights by males were observed.

Several Pair-Forming Methods Possessed by one Species.—Some species employ more than one method of pair formation. Males of all diurnal species which attract females with stridulation or with flight signals probably also approach females in the absence of calling signals, after having merely seen them move, e.g., *Chortophaga viridifasciata. Dissosteira carolina* possesses two signals which probably attract females: stridulation by solitary, stationary males and hovering flights by solitary males. *Chorthippus brunneus* females answer males with stridulation and approach males, or they simply answer males and allow the males to approach them (Haskell, 1958).

Species Specificity in Pair-Forming Signals.—The vast majority of species possess pair-forming signals distinct from those of other species. A few instances have been encountered in which two members of a genus possess similar pair-forming signals where the two species are allopatric, but the signals have not been studied in the region of overlap, e.g., crepitation rate in *Spharagemon bolli* and *S. saxatile; Arphia pseudonietana* and *A. xanthoptera; A. sulphurea* and *A. granulata.*

AGGREGATIONS.—Five kinds of aggregations of individuals appear to occur in grasshoppers:

(1) *Individuals aggregate in areas of suitable habitat.* Individuals of *Dissosteira carolina* aggregate on bare patches of ground, and individuals of *Bootettix argentatus* aggregate on creosote bushes. These aggregations are relatively permanent, although in the former species individuals appear to move at night into thicker or denser vegetation, where they are probably less susceptible to predation. An area such as a bare patch may be suitable for aggregation because it constitutes the best place to find food or oviposition sites, or because it is in such areas that pair formation is most likely to occur, or it may be suitable for a combination of reasons.

(2) *Males approach moving individuals.* Males of some species approach moving individuals presumed to be females. The aggregations are usually of relatively short duration, lasting a few minutes at most. When females are approached the aggregation may last until the female escapes or until one male copulates with her. When a male is accidentally approached by other males, the aggregation is usually of short duration and breaks up when aggressive signals are exchanged. Such aggregations occur frequently in dense, natural populations of *Arphia pseudonietana, Camnula pellucida,* and *Ageneotettix deorum.*

(3) *Sexually responsive females approach displaying males.* Loose aggregations of this sort have been observed in *Chortophaga viridifasciata* under artificial conditions. It seems doubtful that they occur frequently under natural conditions because it is unlikely that there would frequently be a number of females, all sexually responsive, ready to approach a displaying male at the same time.

(4) *Males approach another displaying male.* Such aggregations occur frequently in *Dissosteira carolina.* Similar aggregations have not been discovered in other species. Such aggregations, some of them involving seven or more males, were of short duration, and males tended to disband soon after exchanging aggressive signals. The hovering display of *D. carolina* probably attracts females, and males flying toward a hovering male may on occasion find females that had been attracted to that spot. From the standpoint of a sexually responsive female such an aggregation of males would ensure her of a mate.

(5) *Displaying males form a chorus.* Whether males of Oedipodinae approach other displaying males and then display themselves so as to form a chorus is not known for certain. Such aggregations occur and are well-developed in periodical cicadas (Alexander and Moore, 1962). *Circotettix rabula* appears to occur in loose aggregations, and bursts of crepitation involving several males occur frequently. It seems highly probable that crepitations by one male stimulate other males to crepitate as well, but

whether the aggregation occurs because males are attracted to one another or simply because they find suitable habitat conditions is not known.

Males of some European Acridinae frequently approach other stridulating males and begin to sing, so that a chorus of singing males, all within a few inches of one another, is formed. When the males are disturbed they can be triggered to sing again by a playback recording or by the song of one of the males (Haskell, 1957). Presumably such choruses attract females, and a male's chances of mating are improved if he sings in a chorus.

Behavior of Males in Response to Displays by other Males.—Males respond differently to the pair-forming signals of other males. Four types of responses are known to occur in grasshoppers:

(1) *Remaining passive.* In many species, particularly among the Oedipodinae, no responses can be detected on the part of males when other males display nearby. This occurs in *Chortophaga viridifasciata, Arphia* species, and *Trimerotropis* species.

(2) *Approaching the performer.* Males of *Dissosteira carolina* frequently fly toward a hovering male. After exchanging aggressive signals the males separate. This behavior may have been selected because of the opportunity of encountering a female that has been attracted to a performing male.

(3) *Signalling at the same time.* Males of *Circotettix rabula* and perhaps also males of *Arphia pseudonietana* are triggered to signal by another signalling male. Thus, bursts of loud crepitation produced by several males of *C. rabula,* all active at the same time, can frequently be heard in the Rocky Mountains of Colorado.

(4) *Approaching the performer and displaying at the same time.* Males of some European species of Acridinae approach calling males of only their own species, and when in close proximity begin to stridulate in alternation with the first male, or synchronously with him (Haskell, 1957). Such choruses may remain intact for extended periods. Haskell found that males kept isolated for a few days tended to approach singing males and to sing more readily than males kept with other males for the same period. Such behavior seems to be analogous to the formation of choruses in periodical cicadas. Presumably a chorus of males is capable of attracting females better than a single male, and a male's chances of finding a female are enhanced if he is a member of a chorus.

COURTSHIP

Kinds of Courtship.—It is difficult to classify courtship because of the great variety of types that exist. The following broad classification includes only American species and is modified slightly from that given by Jacobs (1953) for European species.

(1) *Melanoplus-type.* Males hop onto females without first signalling, then produce species-specific movements before, during, or after attaching their genitalia (similar to *Podisma-type* of Jacobs). This condition appears to be common among the Cyrtacanthacridinae, e.g., *Schistocerca lineata,* and

Catantopinae, e.g., *Melanoplus* species. It is also possessed by the species of *Orphulella* and *Dichromorpha* (Acridinae) that have been studied. Females frequently struggled before copulating, perhaps until the species-specific movements of their own males were felt.

(2) *Arphia-type.* Males approach females by walking, hopping, or flying and produce visual or acoustical signals as they advance or during momentary halts in their advance (similar to *Oedipoda-type* of Jacobs). This condition may be almost universal among the Oedipodinae, and it is also present in some ground-dwelling Acridinae, e.g., *Ageneotettix deorum, Drepanopterna femoratum, Cordillacris occipitalis,* and *Phlibostroma quadrimaculatum.*

(3) *Acrolophitus-type.* Males stridulate in the vicinity of the female and then attempt to mount. Example: *Acrolophitus hirtipes, Acantherus piperatus,* and *Mermeria maculipennis.*

(4) *Chloealtis-type.* Males produce one courtship signal while stationary in the vicinity of the female and another as they rapidly advance on the female (similar to the *bicolor-type* of Jacobs). Examples: *Chloealtis conspersa, Neopodismopsis abdominalis, Chorthippus curtipennis, Mermeria intertexta,* and *Psoloessa* species.

(5) *Syrbula-type.* Males produce one kind of courtship sound during the initial approach, orient themselves in a certain way to the female, then produce a more or less elaborate sequence of movements before attempting to mount. If repelled, the same sequence is repeated before the next attempt to mount (similar to *maculatus-type* of Jacobs). Examples: *Syrbula admirabilis, Eritettix simplex.*

Simple vs. Elaborate Courtship.—The reasons for differences in elaborateness of courtship between species (for instance, between *Syrbula admirabilis* and *Orphulella speciosa,* which occupy relatively similar habitats, and between *Chortophaga viridifasciata* and *Encoptolophus sordidus* which also occupy similar habitats), are not known. If only reproductive isolation were involved, then merely changing some parameter of a signal should suffice to make courtship of different species distinct and courtship should not have to become more complex. Perhaps greater complexity in courtship is owing mainly to selection for increased efficiency in mating within populations and is influenced only in a minor way by interactions with closely related species.

Relative Lack of Species Specificity in the Behavior of Females.—Females are species-specific in the selection of potential mates, but aside from such a selection, the behavior of females in the presence of males seems to differ relatively little among related species. Species specificity in female behavior ought to be most pronounced in those cases where females attract males to themselves by signalling. Among the Acridinae silent femoral movements and stridulatory movements which are produced in alternation with the calls of males tend to be species-specific (Jacobs, 1953).

Species Specificity in Courtship Signals.—Courtship signals are highly species-specific, evidently as much so as pairing signals and much more so than aggressive signals. Courtship tends to vary more among closely related species of grasshoppers than among closely related species of crickets (Alexander and Otte, 1967). This diversity of courting behavior is associated with a seemingly high incidence of accidents in pair formation. Such accidents seem in turn to be owing to the role played by vision in pair formation. It appears that males are unable to discriminate visually between members of their own and other species in the absence of specialized movements or sounds until they are very close to one another, and they may not be able to do so even then. Selection which causes different species to be visually distinctive might occur. However, such selection could be countered by selection for cryptic coloration. But even in the absence of predation long-range discrimination in animals is more easily achieved by acoustical means than by visual means (Marler and Hamilton, 1966).

COURTSHIP INTERRUPTION.—Males of some species possess sounds that are characteristically produced only when courtship is interrupted, for example, when a female escapes or is lost, e.g., *Arphia sulphurea, A. simplex, Pardalophora apiculata.* Males of other species, when courtship is interrupted, produce the same sounds produced before courtship was interrupted, e.g., *Psoloessa* species, *Chloealtis conspersa, Chorthippus curtipennis.* Still other species do not signal at all in the same situation. The reasons for these differences are not yet clear. (See also *Suchlauten* in Jacobs, 1953.) It would seem that the most likely function of a signal produced by males when a female is lost would be to aid in the reestablishment of the pair.

AGGRESSION

Grasshoppers do not fight. While it is possible that individuals are occasionally damaged when kicked by other individuals, physical contact between non-copulating individuals is very brief and only rarely involves physical damage. The term "aggression" in this study denotes any behavior which causes the separation of individuals.

REPELLING MOVEMENTS COMMON TO MOST SPECIES.—Femur-raising, femur-jerking, and kicking are movements produced by disturbed individuals of perhaps all species of Acrididae and Tetrigidae. These movements function chiefly as mechanical devices which separate individuals that have established contact. Femur-raising is, however, commonly produced before and after contact is established and has, therefore, assumed a true signalling function. These movements are graded, varying in intensity with the intensity of the stimulus, although femur-raising may have already developed a "typical intensity" (Morris, 1957). The above three movements also grade into one another so that in a given movement components of all three basic movements can sometimes be discerned.

KINDS OF RITUALIZED AGGRESSIVE MOVEMENTS.—Different types of aggressive behavior are possessed by the three subfamilies that were studied in greatest detail.

(1) *Oedipodinae Type.* Femur-tipping and femur-shaking movements are characteristically produced by both sexes and cause the separation of individuals. The movements are stereotyped (they have developed a typical intensity) and have probably been derived by ritualization from femur-jerking and femur-raising (Fig. 19). These movements, especially femur-tipping, seem to be mainly visual signals, but in some species the movements function as acoustical signals as well. Femur-tipping is of two kinds: silent movements (observed in most species) and movements in which the forewing is struck (as in *Dissosteira carolina).* Femur-shaking is of three kinds: silent femur-shaking (most Hippisci), femur-shaking with substrate-striking (most species), and femur-shaking with forewing-striking *(Arphia* and *Lactista* species). In all species of Oedipodinae in which both movements function as aggressive signals, i.e., in most species, femur-tipping precedes femur-shaking in an interaction. In some of these species shaking is produced only after contact between individuals has been established, e.g., in most Hippisci.

Femur-tipping is also produced in aggressive contexts by some ground-dwelling Acridinae, e.g., *Ageneotettix deorum, Aulocara elliotti, Drepanopterna femoratum,* and *Cordillacris* species, but ritualized shaking has not been observed among the members of this subfamily. *Ageneotettix deorum* and *Aulocara elliotti* produce femur-tipping movements in addition to stridulatory aggressive signals typical of most Acridinae.

(2) *Acridinae Type.* In males of most species of Acridinae the main aggressive signal is stridulation of one kind or another, but silent movements similar to and perhaps derived from stridulatory movements are performed by males of some species, e.g., *Ageneotettix deorum, Drepanopterna femoratum.* Usually aggressive stridulation is similar to and is probably derived from the normal calling song, e.g., *Chorthippus curtipennis, Neopodismopsis abdominalis, Pseudopomala brachyptera,* but in some species it is quite different, e.g., *Syrbula fuscovittata.* In some species all gradations exist between the normal calling song, produced by solitary males, and aggressive stridulation, produced by males touched by other males, e.g., *Chorthippus curtipennis, Neopodismopsis abdominalis, Psoloessa thamnogaea;* while in others no gradation whatever seems to exist, e.g., *Syrbula* species, *Pseudopomala brachyptera,* and *Chloealtis conspersa.* Aggressive stridulation among the Acridinae usually consists of pulses or songs or both which are shorter than those produced in the calling song (see, for instance, *Chloealtis conspersa,* and *Neopodismopsis abdominalis).*

Ageneotettix deorum possesses both femur-tipping typical of the Oedipodinae and stridulation typical of the Acridinae. Stridulation is produced by males and females that are very near one another or that are touching one another; tipping is produced in the same situations but it is also produced when individuals are separated by greater distances.

(3) *Catantopinae Type.* Femur-shaking or ritualized femur-jerking were the only aggressive signals observed among the Catantopinae and

Cyrtacanthacridinae. Alexander (1960) recorded mandible snapping sounds in *Paratylotropidia brunneri* which may serve as aggressive signals. Femur-shaking in this subfamily is quite similar to that of the Oedipodinae but is always silent.

SPECIES SPECIFICITY IN AGGRESSIVE BEHAVIOR.—Aggressive behavior is very similar among the species of Oedipodinae. Where marked differences in aggressive behavior have arisen, the differences seem owing to the fact that the aggressive signals have become functional in courtship contexts (Table 20). Among the Acridinae aggressive signals tend to be species-specific, probably owing to the fact that they are modified calling songs and change as calling songs change. The general lack of species specificity in aggressive behavior is probably due to the fact that natural selection is not operating directly to produce or enhance differences in aggressive behavior between species as it is in pairing and courtship behavior. Selection may sometimes even cause species to be more alike in aggressive behavior so that recognition between males of different species is as easily achieved as between males of the same species.

DISTINCTION BETWEEN AGGRESSIVE AND COURTSHIP SIGNALS.—Aggressive signals are generally quite distinct from courtship signals. In several species, aggressive signals such as femur-shaking, femur-tipping and ticking have assumed a courtship function but have retained their aggressive function; the signal produced in courtship contexts, however, is different from that produced in aggressive contexts, e.g., femur-tipping in *Trachyrhachys kiowa, Mestobregma plattei, Dissosteira carolina, Ageneotettix deorum,* and *Drepanopterna femoratum,* and femur-shaking in *Lactista* (near *punctatus*) and in species of Catantopinae. In some species, where such a change in function from an aggression to courtship has evidently occurred, it has been complete and the signal is no longer produced in the former aggressive context, e.g., femur-shaking in *Spharagemon crepitans* and in *Trimerotropis californica* from Arizona. It seems that there has been selection for making differences in the "intent" of males obvious by making the signals in the different contexts distinctive.

SEXUAL RECOGNITION.—Differences between movements and between the odor of males and females seem to be the chief means of sexual recognition. Size, color, and shape differences are either of no importance or of limited importance in sexual recognition, perhaps owing to the considerable similarity between the sexes in these characters. In most species one or two movements are characteristically performed by interacting males. Such signals are also performed by solitary males and may inhibit approaching or courting by other males that happen to see them. Courtship and pair-forming signals are also involved in sexual recognition. Males producing such signals are evidently not approached by other males (see, however, *Dissosteira carolina*) and they elicit aggressive responses on the part of males being approached by courting males. Females of some species perform aggressive signals indistinguishable from those of males. The performance of these signals inhibits courtship and approaching by males (see, for instance, *Encoptolophus sordidus* and *Melanoplus confusus).*

The reason for the existence of special male aggressive signals which are distinct from courtship signals may be that a single signal, even though it is responded to differently by males and females, is too ambiguous. It is not a reliable indicator of intent. In a certain situation such a signal may be broadcasting either the message: "I am a male, do not approach me," or the message: "I am approaching, prepare to be mounted." Since the signal is ambiguous the female's responses may be inappropriate.

ALTERNATION IN THE PRODUCTION OF AGGRESSIVE SIGNALS.—The production of aggressive signals by one male in alternation with the stridulation of another male occurs in a few species. In *Psoloessa thamnogaea* there is sometimes nearly perfect alternation between the signals of two males; that is, no leader and follower can be detected during the alternation. In *Syrbula admirabilis, Chorthippus curtipennis,* and *Pseudopomala brachyptera* a leader and follower can be detected, i.e., the stridulation of one male follows that of another male closely but never occurs at the same time. In other species the signals of two males do not seem to bear any constant relationship to each other and the two males may signal at the same time. In *Chorthippus curtipennis, Morsiella flaviventris, Psoloessa thamnogaea,* and *Pseudopomala brachyptera,* one male alternates in producing aggressive signals with the calling signals of another male. In species where there are sizeable gaps between successive pulses or between groups of pulses in a song, alternation is between pulses or groups of pulses (Fig. 13d, 13j). In species whose songs are without distinct silent gaps, alternation is between successive songs, e.g., in *Pseudopomala brachyptera, Chorthippus curtipennis,* and *Neopodismopsis abdominalis.* In these species the aggressive song is usually shorter than the calling song.

TEMPORAL AND ECOLOGICAL ISOLATION.—Members of the same genus sometimes possess different life cycles such that there is little or no overlap in the adult breeding seasons, e.g., in *Arphia* and *Melanoplus.* Whether or not these differences evolved in the context of reproductive isolation is not certain. No differences in the daily sexual activity cycle were observed in this study.

BEHAVIORAL ISOLATION.—No experiments were carried out in this study to determine whether sound differences have an isolating value, but the fact that species possess distinctive pairing signals or courtship signals, while other behavior patterns remain very much alike, is evidence that selection has been operating to make pairing and courtship signals distinctive. Studies on a few European Acridinae have indicated that some differences are sufficient to isolate different species (Perdeck, 1958).

Courtship differences have probably been selected to reduce interactions between members of different species that have accidentally come into close proximity. The greater uniformity of courtship among related species of nocturnal Orthoptera may be due to a low incidence of accidents in pair formation. In crickets pairing is brought about mainly by females actively seeking out calling males, and vision probably plays no part in this search. I think it is reasonable to assume that interactions which require physical contact must occur less frequently by chance than interactions which merely require the establishment of long distance visual contact. Examinations of nocturnally active grasshoppers, such as the Pneumoridae, and more intensive studies on both diurnal and nocturnal Tettigoniidae would be desirable to test this hypothesis further.

Haskell (1957) has indicated that while the initial courtship songs of four species of Acridinae occurring together in the field are quite distinct, the mounting sounds are quite similar. Presumably the discrimination necessary to keep the species from copulating occurs before mounting is attempted.

MECHANICAL ISOLATION.—Genitalic differences are relatively slight among the Oedipodinae and the Acridinae, and they have not been reliable as cues of specific distinctiveness in taxonomic studies. Among the Catantopinae, however, genitalic differences are pronounced and are successfully used to distinguish between species. This distinctiveness of genitalia among the Catantopinae is correlated with a peculiar type of courtship. Males mount females without first signalling and perform species-specific signals only after mounting and while attaching. The female usually struggles for shorter or longer periods before copulation is finally achieved. The number of mountings involving males of this subfamily is also higher than that of other subfamilies. In this group, therefore, where a large part of interspecific recognition evidently takes place only after the male has mounted the female, genitalic differences may have been directly favored by natural selection to reduce copulations and to reduce interactions between species.

LEVEL OF INTERACTION AND DEGREE OF RELATIONSHIP.—Behavioral interactions between members of different species occur frequently in the field. The observation that the level of interaction between more closely related (congeneric) species is greater than that of more distantly related (non-congeneric) species (Table 18) is consistent with the general view that the behavior of a species should diverge most with respect to closely related species, with whom the chances of interbreeding are greatest, or whose members are so confusingly similar that they are likely to elicit the most energy-consuming courtship behavior.

STEREOTYPED VERSUS GRADED BEHAVIOR

Both graded and stereotyped signals are common communicative responses of grasshoppers. While it can be shown that graded or stereotyped signals are more prominent in some situations than in others, the reasons for the differences are not yet clearly understood.

Some signals in grasshoppers vary little in form. The responses have acquired "typical" or even "fixed intensities" (Morris, 1957); that is, with an increase in the intensity of the stimulus there is little or no change in the response. Examples of relatively fixed signals include most stridulatory movements. There is, however, considerable variation in stridulation from species to species. In some species, individual femoral strokes are very constant but the number of strokes and the stroke rate are quite variable; that is, the response can be varied by changing the pulse repetition rate and the total number of pulses produced, e.g., ordinary stridulation in *Arphia sulphurea.* In other species, pulses, pulse rates, and the intervals between groups of pulses are constant, but number of pulses per burst and the total number of bursts varies with the intensity of the response, e.g., in *Trimerotropis pallidipennis.*

Femur-tipping and femur-shaking signals are also relatively constant in form in most species. While these signals are quite stereotyped, different intensities of the response are indicated either by the repetition rate of the signals or by the total number of signals performed. Crepitation flights are quite constant in the rate of crepitation but different intensities of the response are likely indicated by the length of flights and the repetition frequency of flights.

In most Oedipodinae males produce two stereotyped signals in aggressive contexts. One, femur-tipping, operates over greater distances; the other, femur-shaking, operates over short distances and when individuals have established contact. As males are approached only femur-tipping is produced at first; then, as the distance between males is decreased femur-shaking is given in combination with femur-tipping. As the distance between males becomes still smaller, the frequency of femur-shaking increases while that of tipping decreases until eventually shaking signals are almost exclusively produced. Thus, even though the signals are highly stereotyped the aggressive response itself is graded.

Repelling movements by individuals touched by others tend to increase in intensity directly as the intensity of the stimulus increases; these movements have not developed a typical intensity. Examples of highly graded responses include femur-jerking and kicking. Femur-raising, while it varies somewhat with the intensity of the response, seems to have developed a typical intensity. Presenting by females during courtship is also a graded response with various behavioral elements being included as the intensity of the response increases.

In general, signals operating over a distance, i.e., acoustical or visual signals, and courtship signals (where interspecific recognition is important) tend to have stereotyped elements. But signals produced while in physical contact with other individuals and which have a repelling function tend to be graded. An exception to this is presenting behavior performed by females in the presence of courting males. Since this signal varies little from species to species it is probably not important in interspecific recognition and therefore has not become highly stereotyped.

It can readily be appreciated that when interspecific recognition is important signals with stereotyped elements will evolve. However, some aggressive signals, in which specific distinctiveness does not seem to be important, are also stereotyped. Perhaps what has been selected in this case is an unambiguous response. According to Morris (1957), the evolution of stereotypy results in a loss of information at the same time that it results in more unambiguous responses.

MODES OF COMMUNICATION

ANCESTRAL CONDITION.—Grasshoppers and mantids are the only largely diurnal Orthopteroids and are for this reason believed to have evolved from a nocturnal ancestor. Grasshoppers probably evolved from the ensiferan lineage which then, as today, was probably largely nocturnal in habit (Zeuner, 1936, 1939, 1942). There is no evidence that the probable ancestor of the Acridoidea (the Lucustopsidae) stridulated with the forewings as do many modern ensiferans (Zeuner, 1936). The present condition of the Acridoidea suggests that ancestors to the Acridoidea possessed neither a tympanum nor a mechanism for stridulation (Table 3). Nocturnal ancestors probably communicated to a large degree by olfactory and tactual signals, and perhaps by signals transmitted through the substrate. Such mechanisms still appear to be the most important modes of signalling in cockroaches (Roth and Willis, 1952) and in non-acoustical Ensifera (Alexander and Otte, 1967).

EVOLUTION OF VISUAL AND ACOUSTICAL SIGNALS.—When grasshoppers became diurnal and long range vision was possible, the stage was set for two classes of movements to evolve into visual signals: (1) tactual movements already serving a communicative function, such as jerking or repelling movements of the hind femora, and (2) other non-communicative movements such as locomotory movements (flight, walking movements), orientation movements, and comfort movements. It is likely that several such movements became visual signals independently. A tympanum was apparently acquired early and evidently only once by grasshoppers. More important, however, is the fact that it probably preceded most of the sound-producing mechanisms we see today. This is shown by the facts that (1) very many silent species, including practically all the members of some large subfamilies (Table 3), possess a tympanum, indicating that it can be *maintained* in the absence of specialized sound production and suggesting that it could have *evolved* in the absence of specialized sound production, and that (2) while the tympanum is very similar even among widely divergent taxa, the sound-producing mechanisms of the same taxa are very different, suggesting that they were acquired independently.

With a hearing organ already existing, visual signals could repeatedly, with slight modification of movements, become acoustical signals. The great variety of sound-producing mechanisms in grasshoppers suggests that visual signals and perhaps also various tactile movements become acoustical signals independently when the parts of the body involved came to rub against one another. (Accidental rubbing of parts of the body occurs frequently in movements that are normally silent.) Specialization of these body surfaces resulted in the various mechanisms we see today.

Figure 20 illustrates the above hypothesis concerning the evolution of visual and acoustical signals. The Catantopinae and Cyrtacanthacridinae seem to rely more on chemical and tactile signals, since individuals interact mainly after contact has been established. In these regards they may represent a more primitive condition. (In their method of pair formation, however, they appear to be specialized.) The Acridinae and Oedipodinae interact mainly before contact is established, exchanging both visual and acoustical signals, and probably represent a more specialized condition.

BEHAVIOR AND MORPHOLOGY

Given only the morphology of a species, much can be said about its behavior. For instance, to mention but a few obvious examples, its feeding habits can be discerned by an examination of its mandibles (Isely, 1944), the do not have such flight displays. Therefore, in the absence of behavioral indicates whether the species lives on vegetation, and the coloration of the animal often indicates the background color of its habitat. The following correlations between morphology and behavior illustrate how sexual behavior can in part be determined by an examination of morphology:

(1) *Hindwing coloration.* Conspicuous hindwing coloration is very common in species possessing flight signals but absent from species which do not have such flight displays Therefore, in the absence of behavioral information the presence of colored hindwings would ordinarily suggest that the wings are used in communication.

(2) *Hind femur coloration.* Among the Oedipodinae the insides of the hind femora are usually contrastingly marked with light and dark bands. The presence of this coloration is correlated with the presence of visual signals produced with the hind femora.

(3) *Thickened anal veins.* Thickened anal veins of the hindwings, such as occur in *Circotettix, Aerochoreutes, Bryodema,* and some *Arphia* species, are associated with the production of loud crepitation noises. While not all crepitating species possess conspicuously thickened veins, e.g., *Chortophaga* species, their presence indicates that crepitation probably occurs.

(4) *Thickened femora.* In all Catantopinae and Cyrtacanthacridinae the fore and middle femora are conspicuously enlarged, being much thicker than those of females, e.g., in *Melanoplus* and *Podism*a species. Thus far, there is a perfect correlation between the presence of enlarged femora and the nature of the pairing process: males approach females stealthily, pounce onto them, and sometimes hang onto them even though the female struggles considerably. In the two genera of Acridinae (*Orphulella, Dichromorpha)* in which the pairing process occurs in the same way, the femora are also enlarged. I expect, therefore, that whenever there is a pronounced difference in femoral size between males and females a similar pairing or courtship process will be found.

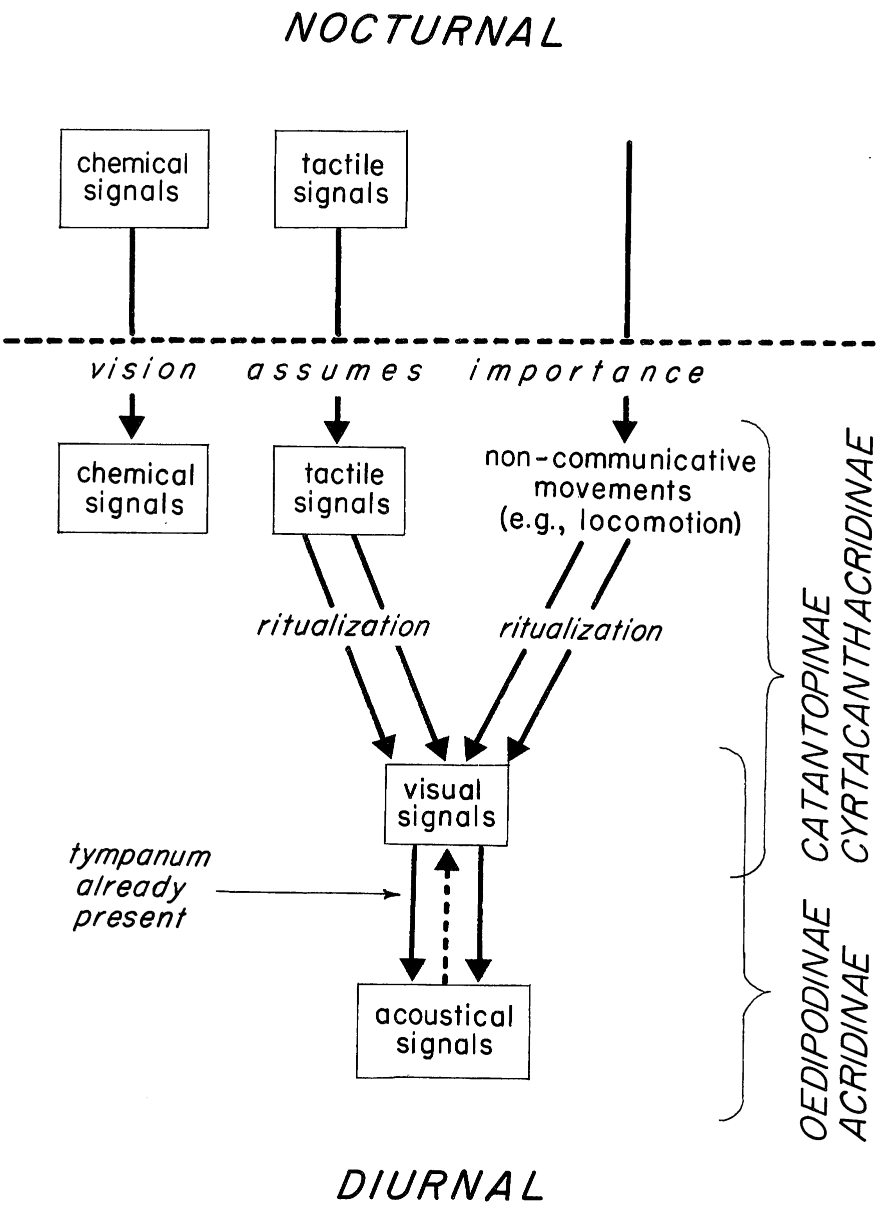

FIG. 20. Probable evolution of visual and acoustical signals in grasshoppers. The Oedipodinae and Acridinae employ mostly visual and acoustical signals, although tactual and chemical signals are also employed. The Catantopinae and Cyrtacanthacridinae employ chemical, tactual, and visual signals. The dotted arrow indicates a secondary loss of sound.

(5) *Stridulatory files.* The presence of stridulatory files normally indicates that a species produces acoustical signals in intraspecific interactions. In the two species of *Orphulella* that I studied, however, pairing is like that in Catantopinae and the stridulatory pegs found on the inside of the femora are apparently never used in sound production. Also, in the ground-dwelling species *Ageneotettix deorum curtipennis* no sound is produced even though stridulatory pegs are present. In this species visual signals have evidently secondarily replaced acoustical signals.

THE INFLUENCE OF HABITAT ON BEHAVIOR

EVOLUTION OF VISUAL SIGNALS.—The extent to which communicative behavior of animals is influenced by physical parameters of the environment has been little explored. Observations on the behavior of grasshoppers from various habitats suggest that there is a greater tendency for species living on sparsely vegetated ground to evolve and employ visual signals than for vegetation-inhabiting species to do so. Stereotyped, visual signals are almost universal among the Oedipodinae (a mainly ground-dwelling group) and less prevalent among the Acridinae (a mainly vegetation-inhabiting group). However, in the Acridinae visual signals are more common among the ground-living species than among the species inhabiting vegetation, and, in at least one species *(Drepanopterna femoratum),* acoustical signals may have been lost entirely. Table 22 indicates the greater prevalence of visual signalling in ground-dwelling species.

TABLE 22

PREVALENCE OF VISUAL SIGNALS IN VEGETATION-INHABITING AND GROUND-DWELLING ACRIDINAE

	Total number of species	species without courtship signals	species possessing visual courtship signals	species possessing only visual courtship signals	species possessing stereotyped visual aggressive signals
Vegetation-inhabiting species	41	3	9	0	1
Ground-inhabiting species	9	0	6	2	7

SUMMARY

1. Acoustical, visual, and tactual communicative signals were compared in the pair-forming, courtship, and aggressive interactions of 117 species of grasshoppers—71 Oedipodinae, 31 Acridinae, 10 Catantopinae, 1 Cyrtacanthacridinae, 1 Romaleinae, and two African species in the families Pneumoridae and Pamphagidae. The results are compared with the information obtained by Jacobs (1953) and Faber (1953), on European grasshoppers.

2. Pair-forming and courtship signals are species-specific, apparently as a result of selection in the context of reproductive isolation. Interspecific behavioral interactions occur frequently in the field and indicate that even distantly related species, belonging to different genera, might strongly influence one another's behavior.

3. Courtship signals in grasshoppers, unlike those of Ensifera, are frequently as distinctive as pair-forming signals. The difference between these two groups is presumably owing to the higher incidence of mistakes in pair formation among grasshoppers, resulting from the role played by vision.

4. Grasshoppers do not fight. Aggressive signals caused the spacing of males and tended to differ little among species, particularly in the Oedipodinae where evolutionary changes in pair-forming or courtship signals are not usually accompanied by a change in aggressive signals.

5. While the diversity in communicative signals seems to be due primarily to interspecific interactions, the habitats of species also influence their communicative behavior in important ways. In the Acridinae, for instance, visual signals are best represented in the ground-dwelling species and poorly represented among vegetation-dwellers. The reverse is true for acoustical signals.

6. In all diurnal species examined, vision evidently plays an important role in pair formation. In some Oedipodinae, females are attracted to the flight displays of males, while in other species, pairing is initiated when males observe moving females. In vegetation-dwelling Acridinae, females are evidently attracted to solitary stridulating males; in some ground-dwelling species, pairing is initiated by males orienting on moving females. Males of Catantopinae and Cyrtacanthacridinae also orient on moving females.

7. In all Oedipodinae and most Acridinae, males signal with visual, acoustical or substrate-vibrating movements as they approach females, and little or no signalling follows mounting. In a few Acridinae, and all Catantopinae and Cyrtacanthacridinae, males do not signal while approaching; instead, they advance stealthily and females seem to be taken by surprise. Species-specific signalling, mostly of a tactual nature, evidently occurs only after the male has mounted.

8. Genitalia do not vary greatly among the Oedipodinae and Acridinae and have scarcely been used in taxonomic studies. In the Catantopinae, genitalia tend to be highly distinctive, perhaps because species recognition involves the detection of genitalic differences.

9. Communicative signals in grasshoppers seem to have evolved through (a) structural modification of pre-existing signals, (b) functional changes in pre-existing signals, (c) ritualization of non-communicative movements, and perhaps (d) appearance of new motor patterns.

10. Female-attracting flight displays, performed by solitary males, evidently evolved from ritualized approaching flights, which in turn may have evolved from unspecialized, locomotory approaching flights. Each of three

different kinds of aggressive movements has been incorporated into courtship several times. A number of signals are unique to certain species and may have originated as new motor patterns.

11. The nocturnal (?) ancestor of grasshoppers probably communicated chiefly through chemical and tactual means. When grasshoppers became diurnal and vision became important, both tactual and non-communicative movements could become ritualized into visual communicative signals. The great diversity in sound-producing mechanisms in grasshoppers is apparently owing to the fact that various visual signals independently became acoustical.

12. Observations on communicative behavior, by and large, substantiate the current taxonomy of grasshoppers. Several inconsistencies have come to light, however, indicating that the status of certain groups needs to be reconsidered.

APPENDIX

Crepitation temperatures were taken at waist level; other temperatures were taken 3 inches above the substrate.

Arphia sulphurea

Crepitation rate:

32.0—33.3/sec	n = 2	undisturbed	75°F	Livingston Co., Mich.
29.2—32.1	n = 5	undisturbed	81	Livingston Co., Mich.
47.1—48.1	n = 4	disturbed	76	Livingston Co., Mich.

Duration of crepitation: averages less than 2 seconds

Duration of stridulation pulses: 0.04—0.06 secs

Femur-shaking rate and # strokes/burst:

25.0—33.3/sec	(3–7)	n = 30	94°F	Livingston Co., Mich.
24.0—33.2	(5–8)	n = 6	82	Lincoln Co., Okla.

Duration of femur-tipping: 0.5—0.8 secs

Arphia simplex

Crepitation rate:

11.07/sec	undisturbed	78°F	Adams Co., Ohio
14.40	undisturbed	78	Ripley Co., Mo.
12.50	undisturbed	85	Calcasieu Par., La.
12.25	undisturbed	86	Burnet Co., Texas
15.30	disturbed	94	Randolph Co., Ark.
13.10	disturbed	90	55 mi. w. Cd. Valles, Mex.

Duration of crepitation: 1.5—6.0 secs Adams Co., Ohio

Duration of stridulation pulses: 0.04—0.07 secs

Femur-shaking rate and # strokes/burst:

29.4—31.3/sec	(4–6)	n = 3	90°F	Adams Co., Ohio
25.0—33.3	(3–9)	n = 10	82	Calcasieu Par., La.
19.0—20.0		n = 3	81	Burnet Co., Texas
23.1—30.0	(4–7)	n = 4	83	Gillespie Co., Texas

Arphia xanthoptera

Crepitation rate:

23.1/sec		undisturbed	88°F	Hocking Co., Ohio
20.7—23.8	n = 5	undisturbed	70°F	Laclede Co., Mo.

Duration of crepitation: up to 5 seconds?

Duration of stridulation pulses: 0.08—0.13 secs
Femur-shaking rate and # strokes/burst:
17.2—22.0/sec (3–5) n = 6 80°F Morgan Co., Tenn.
16.9—18.0 (5–8) n = 5 84 Laclede Co., Mo.

Arphia granulata (Alachua Co., Fla.)

Crepitation rate:
33.3—35.0/sec n = 4 undisturbed 94°F
Duration of crepitation: frequently more than 2 seconds
Duration of stridulation pulses: 0.05—0.06 secs
Femur-shaking rate and # strokes/burst:
15.0—21.5/sec (1–4) n = 64 90°F

Arphia pseudonietana

Crepitation rate:
21.2—23.5/sec n = 4 undisturbed 86°F Livingston Co., Mich.
24.3—25.0 n = 3 disturbed 86 Livingston Co., Mich.
21.9 ? 76 Livingston Co., Mich.
25.0, 26.6 70 Livingston Co., Mich.
18.7—21.4 n = 4 undisturbed 82 nr. Van Horn, Texas
21.0 disturbed 71 nr. Marathon, Texas
18.3 undisturbed 80 nr. Imuris, Sonora, Mexico
Duration of crepitation: up to 5 seconds?
Duration of stridulation pulses: 0.05—0.07 seconds
Femur-shaking rate and # strokes/burst:
18.0—30.0/sec (2–6) n = 12 85°F Livingston Co., Mich.
15.5—26.7 (2–5) n = 12 92 nr. Van Horn, Texas
15.4—15.8 (3–4) n = 4 87 nr. Marathon, Texas
Duration of femur-tipping: 0.65—0.75 secs nr Van Horn, Texas

Arphia conspersa

Crepitation rate: 33.3/sec disturbed 82°F nr. Williams, Ariz.
Duration of stridulation pulses: 0.04—0.06 secs
Femur-shaking rate and # strokes/burst:
27.0/sec (4) 88°F nr. Williams, Ariz.

Chortophaga viridifasciata

Crepitation rate:
45.4—51.7/sec n = 4 undisturbed 85°F Washtenaw Co., Mich.
50.0 undisturbed 65 Livingston Co., Mich.
41.6—42.5 undisturbed 85 Union Co., Illinois
57.0 disturbed 90 Tulsa, Okla.
60.0 disturbed 88 Hocking Co., Ohio
59.1 disturbed 78 Ripley Co., Mo.
Duration of pulses of stridulation: 0.05—0.07 secs Washtenaw Co., Mich.
Femur-shaking rate: 70/sec 93°F Washtenaw Co., Mich.
Femur-tipping duration: 0.2—0.3 secs n = 7 93°F Washtenaw Co., Mich.

Chortophaga australior

Crepitation rate:
73.3/sec disturbed 94°F Gulf Co., Fla.
68.4/sec disturbed 94°F Alachua Co., Fla.
Femur-shaking rate and # strokes/burst:
66.6/sec (11) 78°F Alachua Co., Fla.
53.0 (10) 86 Alachua Co., Fla.
Femur-tipping duration: 0.23—0.26 78°F Alachua Co., Fla.

Encoptolophus sordidus (Washtenaw Co., Mich.)

Crepitation rate:
48.0/sec undisturbed 66°F
48.0 undisturbed 76
Interval between ticks: 0.26—0.85 secs n = 8 80°F
Number of ticks per series: 2—4
Interval between ticks and trills: 0.24—0.32 secs n = 4 80°F
Length of trill: 0.8—2.0 secs n = 6
Interval between trill and stutter: 0.8—3.7 secs n = 7
Length of stutter: 0.4—1.6 secs n = 10
Femur-shaking rate: 49.0/sec 76°F
Femur-tipping duration: approximately 0.5 seconds

Encoptolophus costalis (Las Animas Co., Colo.)

Crepitation rate:
62.5/sec disturbed 80°F

Lactista gibbosus (Alpine, Calif.)

Stridulation period lengths (within bursts): 0.21—0.95 secs 85°F n = 19
Femur-shaking rate and # strokes/burst:
8.4—10.0/sec (2-4) n = 7 85°F
Femur-tipping duration: 0.4 secs 85°F

Lactista punctatus (33 mi. N. Elota, Sinaloa, Mexico)

Stridulation period lengths: 0.20—0.31 secs 85°F
Femur-shaking rate and # strokes/burst: 5.0—15.5/sec (2-3) n = 5 85°F

Lactista (near *punctatus*) (25 mi. W. Cd. Valles, Mexico)

Courtship femur-shaking rate and # strokes/burst:
13.3—16.6/sec (3-8) 94°F
Aggressive femur-shaking rate and # strokes/burst:
6.6—12.5/sec (2) (usually only single strokes were given) 88°F
Femur-tipping duration: 0.6—0.8 secs 80°F

Platylactista azteca

Crepitation rate:
55.5—58.3/sec n = 2 disturbed 78°F Imuris, Sonora, Mex.
Stridulation period lengths (within bursts):
0.18—0.26/secs n = 12 86°F Sutton Co., Texas
0.22—0.40 n = 5 92 Imuris, Mexico
Femur-shaking (intervals between successive strokes):
0.15, 0.12, 0.10, 0.10 secs 85°F Imuris, Sonora, Mex.
0.08, 0.09, 0.06, 0.06 86 Sutton Co., Texas
Femur-tipping duration: 0.75 seconds 86°F Imuris, Sonora, Mex.

Pardalophora apiculata

Stridulation rate:
between 6.5 and 20/sec 98°F Livingston Co., Mich.
Duration of vibratory stridulation:
0.55—1.25 secs n = 5 88°F Livingston Co., Mich.
Male femur-shaking rate and # strokes/burst:
29.0—35.0/sec (14-19) n = 5 88°F Livingston Co., Mich.
32.0—36.7/sec (13-25) n = 4 90°F Ozark Co., Mo.
Female femur-shaking rate:
40, 90/sec (presenting female) 90°F Ozark Co., Mo.
40.8 (presenting female) 88 Livingston Co., Mich.
35.0 (copulating female) 90 Ozark Co., Mo.
(durations of shaking about one second)

Femur-tipping duration:
male: 0.5—1.0 secs n = 4 80°F Livingston Co., Mich.
female: 0.6—2.0 secs n = 4 80°F Livingston Co., Mich.
Duration of pulse of stridulation:
0.07—0.11 secs n = 8 88°F Ozark Co., Mo.

Pardalophora phoenicoptera

Duration of pulse of stridulation:
0.04—0.05 sec (type II) n = 4 88°F Ozark Co., Mo.
0.09 (type I) n = 4 88 Ozark Co., Mo.
0.05—0.14 (type I) n = 8 94 Hocking Co., Ohio

Spharagemon collare

Crepitation rate:
41.7/sec disturbed 86°F Livingston Co., Mich.
42.1 disturbed 86 Livingston Co., Mich.
52.6 disturbed 78 Livingston Co., Mich.
50.0 disturbed 80 Presque Isle Co., Mich.
39.5 undisturbed? 76 Crawford Co., Mich.
Stridulation rate:
8.0—16.6/sec mean 9.5 n = 27 98°F Livingston Co., Mich.
Femur-shaking rate and # strokes/burst:
26.0—40.0/sec (9–29) n = 6 80°F Livingston Co., Mich.
34.4 (16) 105°F Livingston Co., Mich.

Spharagemon cristatum

Crepitation rate:
37.7/sec undisturbed 90°F Anderson Co., Texas
42.3 disturbed 85 Cass Co., Texas
Courtship femur-shaking rate and # strokes/burst:
28.5—38.1/sec (8–17) n = 16 80°F Anderson Co., Texas
35.1 (16) 90°F 55 mi. W. Cd. Valles, San Luis Potosi, Mexico
Interval between shaking and stridulation:
0.07—0.41 secs mean = 0.20 n = 15 80°F Anderson Co., Texas
Aggressive femur-shaking rate and # strokes/burst:
34.4/sec (15) 80°F Anderson Co., Texas
33.3 (20) 90 San Luis Potosi, Mexico

Spharagemon bolli (Livingston Co., Mich.)

Crepitation rate:
40.0/sec n = 3 76°F
Courtship femur-shaking rate and # strokes/burst:
28.5—35.0/sec (9–24) n = 14 98°F
Interval between femur-shaking and stridulation:
0.02—0.33 secs mean = 0.17 n = 16 98°F
Stridulation period length (within bursts): 0.05—0.10 secs n = 28 98°F
Number of pulses/burst of stridulation: 1—7
Aggressive femur-shaking rate and # strokes/burst:
33.3—37.1/sec (13–26) n = 8 98°F
28.8 (18) 87°F Colfax Co., New Mexico

Spharagemon crepitans (Marion Co., Fla.)

Crepitation evidently occurs but was not heard or recorded
Femur-shaking rate and # strokes/burst:
17.8/sec (9) 78°F
22.2 (9) 86°F
Femur-tipping duration: 0.5 secs

Spharagemon saxatile (Bedford Co., Pa.)

Crepitation rate: 43.3/sec 78°F
Femur-shaking rate and # strokes/burst:
25.0—33.3/sec (6–12) n = 3 80°F

Spharagemon equale (Sherman Co., Kansas)

Crepitation was not heard
Vibratory stridulation burst duration:
0.05—0.15 secs mean = 0.09 n = 18 87°F
Intervals between bursts of vibration of a series:
0.04—0.12 secs mean = 0.07 n = 16 87°F

Spharagemon humile (Colfax Co., New Mexico)

Crepitation rate: 38.4/sec 80°F

Dissosteira pictipennis

Crepitation rate, crepitation burst rate, and # snaps/burst:
73.3/sec 5.6—6.2/sec (3) 98° Yosemite National Park, Calif.
Length of interval between ticks within a burst and # ticks/burst:
0.05—0.12 secs (3–5) n = 12 90°F Monterey, Calif.
Stridulation rate and # pulses/burst:
6.6—7.7/sec (3–6) 90°F Monterey, Calif.
Interval between last tick and stridulation:
0.55—0.85 secs 90°F Monterey, Calif.

Scirtetica marmorata (Alachua Co., Fla.)

Crepitation rate: 50/sec undisturbed 92°F
Femur-shaking rate and # strokes/burst:

35/sec	(9)	91°F
35	(15)	85°F

Tropidolophus formosus (Brewster Co., Texas)

Crepitation rate:
Stridulation rate: 7.7/sec 91°F
Femur-shaking rate: 47.0/sec 91°F

Psinidia fenestralis

Femur-shaking rate and number of strokes/burst:

29.0/sec	(21)	93°F	Gulf Co., Fla.
22.0	(20)	91	Gulf Co., Fla.
20.0	(11)	82	Gulf Co., Fla.
26.6	(11)	90	Berrien Co., Mich.
36.1	(23)	90	Anderson Co., Texas

Femur-tipping duration:

0.6—1.0 secs	n = 7	85°F	Gulf Co., Fla.
0.7		87	Berrien Co., Mich.

Trimerotropis pallidipennis

Crepitation rate, burst rate, and # snaps/burst:

55.5/sec	5.0/sec	(4, 5)	88°F	Lordsburg, New Mexico
58.3—58.8	4.7—4.8	(4—6)	82°F	Jeff Davis Co., Texas
57.1	3.8	(4—6)	73°F	Lubbock, Texas
60.0	4.9	(4, 5)	72°F	Warner Springs, Calif.
66.6	4.3	(6)	65°F	San Luis Potosi, Mexico
70.3	4.6	(5)	101°F	nr. Azusa, Calif.
66.5	5.0	(4—6)	80°F	Las Animas Co., Colo.

Stridulation rate and burst interval length:
16.0—17.5/sec n = 2 0.22 secs 85°F Albany, Texas
10.0—11.1 n = 4 0.24 secs 76°F Sutton Co., Texas
14.3—15.3 n = 3 0.17—0.22 85°F Lordsburg, New Mexico
10.7—11.5 n = 4 0.18—0.23 93°F Alpine, Calif.
13.3—16.6 n = 7 0.17—0.21 92°F Warner Springs, Calif.

Number of strokes of stridulation/burst:
7, 11 Albany, Texas; 3, 4, Sutton Co., Texas; 4—7, Lordsburg, New Mex.
5—14, Alpine, Calif.; 5—9, Warner Springs, Calif.
Femur-shaking rate and # strokes/burst:
37.5/sec (15) 76°F Sutton Co., Texas
40.0 (15) 93°F Alpine, Calif.
24.0 (17) 92°F Warner Springs, Calif.

Trimerotropis huroniana (Gd. Traverse Co., Mich.)

Crepitation rate and burst rate: 66.6/sec, 4.3/sec disturbed
Stridulation rate and # pulses/burst:
12.0—18.1/sec (4—8) n = 11 86°F
Length of burst interval: 0.13—0.20 secs n = 10
Femur-shaking rate and # strokes/burst:
35.5—40.0/sec (13—15) 86°F

Trimerotropis californica

Crepitation rate:
37.5/sec disturbed 95°F nr. Gila Bend, Ariz.
36.1 disturbed 101°F nr. Azusa, Calif.
37.5 undisturbed 100°F nr. Lancaster, Calif.
Femur-shaking rate and # strokes/burst:
25.0/sec (19) 90°F Benson, Ariz.
36.6 (13) 85°F nr. Lancaster, Calif.
36.6 (15) 85°F nr. Azusa, Calif.

Trimerotropis melanoptera

Crepitation rate, burst rate, and # snaps/burst:
31.2/sec 3.5/sec (4—6) 80°F Colfax Co., New Mexico
28.5 3.4 (4, 5) 86°F Las Animas Co., Colo.
30.3 3.0 (5—7) 80°F Las Animas Co., Colo.
Femur-shaking rate and # strokes/burst:
23.5/sec (11) 90°F Pueblo Co., Colo.

Trimerotropis maritima

Crepitation rate:
43.0/sec 86°F St. Clair Co., Mich.
44.5 86°F St. Clair Co., Mich.
38.4 92°F Jackson Co., Fla.
43.3 90°F Volusia Co., Fla.

Femur-shaking rate, # strokes/burst, and length of interval between shaking and stridulation:
25.0—30.0/sec (7—22) 0.04—0.38 secs n = 9 80°F Ipperwash, Ontario
33.3—40.0 (12—16) 0.07—0.16 n = 4 90°F Berrien Co., Mich.
26.3 ? 0.05 n = 1 86°F St. Clair Co., Mich.
28.0—35.0 (8—17) 0.12—0.32 n = 3 96°F Jackson Co., Fla.
36.4 (15) 0.15 n = 1 95°F Pinellas Co., Fla.
32.0 (13) No stridulation 90°F Ormond Beach, Fla.
25.0 (10) No stridulation 84°F Horry Co., S.C.
24.0 (14) No stridulation 77°F Comanche Co., Okla.

Trimerotropis agrestis (Alamosa Co., Colo.)

Crepitation rate: 32.7/sec 72°F
Femur-shaking rate: 21.7/sec 95°F

Trimerotropis campestris (Colfax Co., New Mexico)

Crepitation rate: 40.0/sec 78°F
Femur-shaking rate: 33.3/sec 85°F

Trimerotropis gracilis

Crepitation rate:
10.4/sec 85°F Taos Co., New Mexico
10.0 65°F Alamosa Co., Colo.
Femur-shaking rate and # strokes/burst:
38.0/sec (11) 90°F Alamosa Co., Colo.

Trimerotropis verruculata (Mich.)

Crepitation rate and crepitation burst rate:
45.4/sec 5.9—7.1/sec n = 7 85°F Chippewa Co., Mich.
45.4 5.5—6.6 n = 7 85°F Chippewa Co., Mich.
50.0 6.6—8.3 n = 7 82°F Manitoulin Isl., Ont.
Stridulation rate:
10.0—14.2/sec n = 17 80°F Chippewa Co., Mich.
Femur-shaking rate and # strokes/burst:
36.4/sec (11) 80°F Chippewa Co., Mich.
Number of one-, two-, three-, and four-pulse stridulations recorded:
1 (151), 2 (127), 3 (11), 4 (0)

Trimerotropis suffusa (= verruculata?)

Crepitation rate, crepitation burst rate:
42.8—47.0/sec 5.0—7.6/sec 86°F Kane Co., Utah
44.5 5.5—7.6 92°F Vail, Colo.
37.5 2.6 69°F Yosemite National Park
Stridulation rate:
8.0—10.0/sec n = 9 95°F Kane Co., Utah
10.7 Yosemite National Park
Femur-shaking rate and # strokes/burst:
32.0—33.3/sec (9–13) 95°F Kane Co., Utah
Number of one-, two-, three-pulse etc stridulations recorded:
1(10), 2(20), 3(7), 4(1) Kane Co., Utah
1(15), 2(21), 3(44), 4(10), 5(5), 6(1), 8(1), 10(1) Yosemite National Park

Trimerotropis fratercula

Crepitation rate, crepitation burst rate, and # snaps/burst:
52.6/sec 7.8/sec (2) 78°F Colfax Co., New Mexico
47.6 6.2 (2) 79°F Pueblo Co., Colo.
Femur-shaking rate, and # strokes/burst:
22.8/sec (22) 90°F Pueblo Co., Colo.

Trimerotropis cincta

Crepitation rate: 39.0/sec 79° Pueblo Co., Colo.
Femur-shaking rate and # strokes/burst:
29.4/sec (15) 90°F Alamosa Co., Colo.

Trimerotropis calignosa

Crepitation rate: 36.1/sec disturbed 69°F Yosemite National Park

Trimerotropis thalassica (San Diego Co., Calif.)

Femur-shaking rate and # strokes/burst: 25.0/sec (20) 88°F
Femur-tipping duration: 0.25 secs 88°F

Trimerotropis albescens (nr. Warner Springs, Calif.)

Crepitation rate and crepitation burst rate:
44.4/sec about 5/sec 72°F
Femur-shaking rate and # strokes/burst:
30.0/sec (17) 93°F

Trimerotropis fontana (Cuyamaca State Park, San Diego Co., Calif.)

Crepitation rate: 55.5/sec 70°F
Femur-shaking and # strokes/burst: 30.0/sec (21) 90°F

Trimerotropis bilobata (nr. Bicknell, Wayne Co., Utah)

Crepitation rate: 13.3/sec 82°F

Conozoa carinata

Crepitation rate:

66.6/sec	85°F	nr. Douglas, Ariz.
71.4	98°F	nr. Bumblebee, Ariz.
67.0	98°F	nr. Bumblebee, Ariz.
60.0	78°F	nr. Imuris, Sonora, Mexico
67.0	78°F	nr. Imuris, New Mexico

Number of wing snaps/burst of crepitation: 4—16

Conozoa wallula (Bigpine, Inyo Co., Calif.)

Crepitation rate: 55.0/sec 95°F

Circotettix rabula

Crepitation rate:

34.0/sec	78°F	Colfax Co., New Mexico
30.0	78°F	Pueblo Co., Colo.
28.6	80°F	Las Animas Co., Colo.

Circotettix thalassinus

Crepitation rate: 18.7/sec disturbed 80°F nr. Bigpine, Inyo Co., Cal.

Aerochoreutes carlinianus

Crepitation rate: 53.1/sec 86°F Las Animas Co., Colo.

Heliastus sumichrasti

Femur-shaking rate and # strokes/burst:

20.0/sec	(12)	78°F	nr. Tequila, Jalisco, Mex.
16.0		78°F	nr. Tequila, Jalisco, Mex.
17.5		96°F	Tampico, Tamaulipas, Mex.

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