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ACOUSTICAL BEHAVIOR AND SPACING IN THE NEBRASKA
CONEHEAD NEOCONOCEPHALUS NEBRASCENSIS (BRUNER)-
(ORTHOPTERA: TETTIGONIIDAE).

Iowa State University, Ph.D., 1976
Zoology

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Acoustical behavior and spacing in the Nebraska
Conehead Neoconocephalus nebrascensis(Bruner)-

(Orthoptera: Tettigoniidae)

by

Andrew Jackson Meixner

A Dissertation Submitted to the
Graduate Faculty in Partial Fulfillment of
The Requirements for the Degree of
DOCTOR OF PHILOSOPHY

Department: Zoology
Major: Zoology (Animal Behavior)

Approved:

Signature was redacted for privacy.

In Charge of Major Work

Signature was redacted for privacy.

For the Major Department

Signature was redacted for privacy.

For the Graduate College

Iowa State University
Ames, Iowa

1976

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INTRODUCTION

Background Material

General range and habitat

The range of Neoconocephalus nebrascensis (Bruner) extends from the eastern seaboard across southern Canada and the United states as far west as Nebraska and Kansas and south to Tennessee and Arkansas (Froeschner, 1954).

The species has been reported occurring in a variety of habitats. For example, Thomas (1933) noted its occurrence in boggy spots in or near wooded areas and in sloughs and river-bottom marshes bordered by willows and other trees. He rarely found the species far from trees and approximately half of the males were singing from perches in woody vegetation. In Ohio, Alexander (1956) reported the Nebraska Conehead in marshy areas and along the border of swamp forest associations, in a blue grass pasture on a well drained slope, and in grassy and weedy fields. Froeschner (1954) located the species among tall coarse grasses on dry prairies.

Song and associated behavior

Calling song The song of N. nebrascensis has been described by Fulton (1928) as a "series of rasping buzzing notes each lasting a little over a second and separated by about equal intervals of silence". He recorded a total of

23 to 24 buzzing notes per minute at a temperature of 76°F. It was noted that the calling song is produced only at night.

Thomas (1933) described the song as containing notes lasting a little more than one second followed by a pause of a half-second or less, "the series of notes thus forming a rhythmical song which is continued for an indefinite period, thus: 'Bz-z-z-z-z-t, bz-z-z-z-z-t, bz-z-z-z-z-t,...'". He never heard the song before sunset.

The sound was described by Alexander (1956) as consisting of loud rather uniform buzzes produced at a rate of about one in 2-3 seconds. Buzzes were described as being slightly longer than the intervals. He was able to hear the song in the field at distances of 200-300 yards under proper conditions. He determined the pulse rate to be about 125/sec at 70-75°F. Although green and brown forms have the same basic sound, Alexander reported that the green forms have a stronger buzz with a somewhat different quality than the brown forms on some occasions.

Walker (1975) studied the mechanism of sound production in N. nebrascensis by the use of high speed, sound-synchronized, photographic studies. He found that phonatomes (the acoustical unit corresponding to a cycle of wing movement) were produced at a rate of 165/sec at 21°C. Series of phonatomes were started and stopped in a stereo-

typed fashion at a rate of 31/min. Walker's films of N. nebrascensis were not of good enough quality to give repeatable frame-by-frame measurements so that exact description of stridulatory movements and related sound could not be made. The species is thought to be comparable to N. melanorhinus which has opening movements of the wings occurring much faster than closing movements. Walker, using the terminology proposed by Morris and Pipher (1972), called the sound produced by the opening stroke a rapid-decay pulse and that produced by the closing stroke a prolonged pulse. The rapid-decay pulse was defined as a brief complex wave train of rapidly decreasing amplitude, while the prolonged pulse was described as a wave train of relatively longer duration and uniform or smoothly changing frequency that approximates a pure tone.

Courtship song No courtship sound has been reported for this species (Alexander, 1956). Alexander was able to get a caged male singing in the laboratory to "consistently split his buzz into two, more-or-less equal parts each time the screen" on which he was singing, "was jiggled slightly in an attempt to simulate the approach of a female". He noted that this kind of singing had never been heard in the field.

Chorusing and synchrony

Behavior Initial singing by N. nebrascensis males quickly develops into synchrony (Alexander, 1956, 1957). The first male to sing is joined by a second male that starts out with his first buzz synchronized with that of the first individual, and each successive individual begins in synchrony with the chorus. Thus, the initiation of song in the early evening is probably elicited by certain physical conditions of the environment (e.g., change in light intensity) and/or the sounds of conspecific males.

Alexander observed that singing males were usually not less than 6 - 8 ft apart. Twice males sang at about 2 ft apart. On both occasions, one male lagged slightly behind the other and when one male was induced to quit singing the other male stopped as well "after producing two or three songs alone" (Alexander's use of song probably refers to the 1- to 2-second buzzes produced by the species). Then, if the first began to call again, the second joined in almost immediately. This behavior was repeated by laboratory animals which were caged only 6 inches apart and sang readily.

Fulton (1928) characterized the species as being a "remarkable synchronist". In laboratory experiments it was found that coneheads maintained near perfect synchrony. Occasionally one male started a fraction of a second

ahead of the other, but they were never entirely separated.

Mechanism of synchrony The mechanism for synchrony in sound producing animals has not, on the whole, been studied extensively. Little mention of the tendency of N. nebrascensis to synchronize has been made. Fulton (1928) demonstrated the inability of the species to synchronize after removal of the auditory organ. Little descriptive information is available for elucidating the mechanism for the species per se. Most information concerning mechanism for synchronizing systems comes from other insect groups including cicadas, tree crickets and fire flies.

Individuals of the seventeen-year cicada Magicicada cassinii are remarkable synchronists especially during optimum lighting conditions (Alexander and Moore, 1958). Both visual and auditory stimulation are involved in this synchrony. Males were induced to begin ticking immediately after hearing recorded ticks played to them. Buzzes were produced slightly behind the buzz on the tape. Alexander and Moore hypothesized that hearing the cessation of the buzzing part of the congregational phrase stimulated ticking, and hearing the beginning of a buzz stimulated buzzing.

Dumortier (1963) offered a hypothesis for the mechanism of synchrony saying "the time gap between two chirps may be considered as a kind of refractory period characteristic of the species, during which the individual cannot emit

another chirp". The mechanism for bringing all individuals into synchrony apparently operates consequent to the effectiveness of the chirp produced by one individual in inhibiting sound production in surrounding singers for a time equal to their refractory period. Thus, the refractory period for all would end at the same time and all the individuals would stridulate together.

The Snowy Tree Cricket (Oecanthus fultoni Walker) uses two mechanisms to attain and maintain synchrony (average interval between buzz initiation of two males was: mean = 27 msec, standard deviation = ± 17) (Walker, 1969). Whenever the buzz of one male fell out of phase with that of the other male, the males attained synchrony by producing either long or short periods or a combination of the two. It was found that only two consecutive responses (L,L or S,L) were required for a cricket to achieve synchrony with any song like its own. These responses were graded responses to immediately preceding chirps of the chorus. Walker termed this proepisodic synchrony. Homoepisodic synchrony would require a method of reacting to a stimulus concurrent with the episode, i.e., sound production.

Studies by Buck and Buck (1968) on the firefly Pteroptyx malacca indicated a type of anticipatory synchrony. Pteroptyx synchrony was thought to be regulated by central nervous feedback from preceding activity cycles, as in the human sense of rhythm rather than by direct con-

temporaneous response to the flashes of other individuals. According to the authors, the mechanism would require a sequence discriminator to indicate the order of an individual's flash relative to its neighbors so that the proper response could be made. A method of modulation of the endogenous pacemaker would be required to maintain the rhythm of the group.

From work done with fireflies, Hanson, et al. (1971) suggested a single mechanism that would not require the animal to be able to discriminate the sequence of his act in relation to the acts of neighbors in the synchrony. In studies involving a pacer signal, it was found that the firefly's flash occurred at an interval following the pacer flash that was approximately equal to the firefly's normal free-run period. It was felt that the pacer signal reset the flash-timing oscillator in the brain, thus, providing a mechanism for synchronization.

Aggression and hierarchial relationships between males

Aggressive behavior Various workers have investigated aggressive behavior between males of the saltatorial Orthoptera. Two categories, contact and acoustical aggression, are important to this study.

Alexander (1961) investigated aggressive behavior in crickets, especially North American species of Gryllus.¹

¹Previously the genus Acheta

In addition to sounds termed aggressive, aggressive behavior was characterized by various forms of contact between males. Aggression was categorized into five levels depending on the intensity or kind of aggression exhibited. The first three levels of aggression were characterized by more or less casual meetings which provoked little or no aggression or mild to moderate one-sided aggression or as in the case of third level encounters mild reciprocal aggression. In fourth and fifth level contacts moderate to intense reciprocal aggression or sustained combat occurred. Most contacts were seen to involve aggressive behavior by one or both individuals and to terminate with the obvious retreat of one individual. If neither male retreated, then aggressive or courtship behavior occurred or they became immobile for several minutes. A male was more likely to court a male which approached him from behind than one met head-on. When males met head-on, courtship was rarely initiated unless one of the typically female responses occurred such as passivity or immobility.

Aggressive behavior consisted of one or more of several actions: in mild encounters there was either rearing of the forebody, lashing of the antennae, and shaking of the body, or else rearing of the hind body, kicking with the hind legs, and shaking of the body; in intense encounters, antennal lashing and rearing of the forebody were followed

by spreading the mandibles, stridulating distinctively, rushing forward, sparring with the forelegs, butting with the head, and grappling, wrestling, or biting with the mandibles. A male was often flipped back or thrown sideways, but mutilation as a result of fighting was rare, and only in the most intense encounters was the winner determined by what seems to be superior strength of fighting ability. The outcome of most encounters were determined by the relative tenacity of the two males, and the intensity of aggression exhibited was correlated with the length of the fight. Continued aggressive activity developed into increasingly severe combat until one male finally retreated.

Males almost always stridulated during combat. Fighting males seldom, if ever, stridulated together. Apparently both were inhibited from fighting and from stridulating during the time that the opponent stridulated. A winner of an encounter almost always stridulated afterwards, and the loser almost never stridulated afterward. The aggressive stridulation was distinct from sounds made in other situations. Dominant males stridulated during aggression more frequently than subordinate males.

Heiligenberg (1969) found a relationship between sound production and aggression in crickets. He attributed a higher level of fighting to attack readiness apparently elicited by a near-by male's chirps.

Zippelius (1949) reported contact aggression between males of Metrioptera roeseli (Hagenbach) and M. brachyptera (L.) under laboratory conditions. Morris (1971) reported M. roeseli fighting in the field. He also described contact aggression between conspecific males of Orchelimum gladiator Bruner, O. vulgare Harris, and Conocephalus nigropleurum (Bruner) (Morris, 1967, 1971). Aggressive behavior patterns were broken down into four phases: Approach, confrontation, grapple and withdrawal.

The approach phase consisted of the sudden departure by a male from his perch and movement toward another male. Stridulation apparently triggers the approach phase and serves as a navigational aid during its execution.

Confrontation occurred when one male moved within 30 cm or less of another. Both males would turn toward the other and slowly converge. Next, grappling usually ensued between the two males. Grappling, involving biting of the opponent's mouthparts and venter, as well as raking with appendages occurred between males of Orchelimum. In C. nigropleurum, grappling consisted of leg contact involving raking and kicking. Aggressive encounters usually ended with a silent rapid withdrawal of one of the two males. Withdrawal was considered terminated with the first obvious pause in rapid locomotion following an encounter. Abraham (1972) also observed grappling between O. vulgare males. She indicated

that aggressive males would be attracted to males producing song, but non-aggressive males would be repelled.

In O. gladiator, male-male aggression was reported as being associated with patterns of mating behavior (Morris, 1967, 1971). In one instance males coming together would rake the air for about 5 seconds with their abdomens curving and recurving. The tips were almost placed in contact several times. The final coming together of the two males ended in a markedly vigorous grapple.

Tremulation was observed in male-male interactions in both Orchelimum and C. nigropleurum. Tremulation, a series of up and down movements of the animal's body, has been described by Busnel, as producing a tactic response in females when employed by males (Busnel, et al. 1956).

Morris found that C. nigropleurum males often tremulated as they approached a stationary singing conspecific male. He concluded that its association with male aggressive interactions suggested it may not function exclusively in the attraction of a female, rather it could act as a gauge of the relative level of aggressiveness in two contending males.

Weih (1951) and Jacobs (1953) found no contact aggression in Acridids. Rather, a rival's song was produced which differed from the calling song in intensity, in the rate of stridulatory movement, or in some other song parameter. The distance between calling males seemed to determine the degree

of departure from the calling song. The distance between males when the calling song changes to the rival song may delineate the extent of the territorial area (Dumortier, 1963). If a male of the katydid genus Ephippiger produces sound and a second male enters into the song, the "rivalry" song is produced by an alternation in the rhythm of emission of both males (Busnel, 1963).

Spooner (1964) studying the Texas Bush Katydid (Scudderia texensis) found that when two males came in contact both produced a very erratic ticking which he called "crackling". "Crackling" was always followed by immediate separation of the two katydids.

Shaw (1968) described an aggressive call operating at distances of from 1 - 7 ft or less for the katydid Pterophylla camellifolia. His description was of an interaction characterized as the "increase in chirp length and decrease in solo chirp interval that occurs when katydids are 5 - 7 ft or less, from one another, and when the sound level of one katydid as recorded at the site of the other ranges between 69 and 80 dB".

Non-acoustical changes in behavior also occurred which could be related to aggressive calling. These changes included increase in antennal movement and antennal movement accompanied by erratic locomotor activity. At the end of such behavior, one male remained calling in his territory and the other silently left the encounter site.

Jones (1966a, 1966b) found that close proximity of Pholidoptera griseoptera males during singing provoked rivalry behavior in which long chirps were produced.

Morris (1967, 1971) and Abraham (1972) found that O. vulgare, which uses buzzes and ticks in the calling song, uses ticks and slurred ticks in aggressive interactions.

Young (1971) found evidence in Chorthippus brunneus for a change in rate of the rival song toward the end of a rivalry sequence. One male continues to sing and the other drops out. He postulated that the male that continues to sing may be the dominant male.

Dominate-subordinate relationships between males

Alexander (1961) studied hierarchial relationships among the cricket Gryllus. Crickets were kept in a small aquarium where they made numerous contacts. Most encounters ended with the clear retreat of one of the two males, thus, the dominant male could usually be easily determined. Records of encounters taken at irregular intervals and periods of time seemed to indicate a linear dominance hierarchy (Alexander, 1961, 1962).

Males won almost all encounters with males below them in the hierarchy and conversely lost bouts with males above them. The intensity of bouts and the number of encounters between males increased toward the top of the order. Furthermore, he found that dominant males stridulated more

often in aggressive situations than subordinate ones. After a highly intense aggressive encounter, the dominant male almost always produced chirps, whereas, the subordinate male rarely did.

Male grasshoppers, of the species C. brunneus, may be able to establish a hierarchial system based on sound interactions (Young, 1971). Dominant males are apparently able to bring about a change in rate of pulse repetition and thereby end a rivalry sequence.

In the tettigoniid genus Ephippiger, Busnel (1967) found that male dominance was established through acoustical interactions.

Territorial behavior

Alexander (1961) described territoriality as "characterized by association with a particular area". Territorial behavior in an animal may indicate a degree of sedentariness and attachment to a particular site as well as a method of warding off conspecific intruders. Animals within their territory characteristically are more dominant and as they leave their territory the inverse is true.

In an interesting study, Alexander (1961) found that G. veletis males placed in a small terrarium began to behave territorially after nine days. He found that less dominant males could successfully defend their territory against more dominant males.

Busnel (1955) marked males of O. pellucens Scop. and observed them for 15 consecutive nights. She found that individual males have territories within which they remain, and which they "tour" at intervals and "defend" against intruding males. Their territories covered about 30 to 50 cm².

Morris (1967) carried out investigations at three different field sites involving three species of Tettigoniidae (C. nigropleurum, O. gladiator and M. roeseli). He marked a total of 69 males all species combined. It was found that a large proportion of the population of singing males underwent little net displacement in 24 to 48 hr, but almost all singers moved more than 10 ft away after 120 hr. He concluded that it was unlikely that animals were associating with a given geographical area.

Of particular interest to this study is Alexander's statement that "the males in the Tettigoniidae and Gryllidae tend to remain in the same spot, that is, on the same plant, in the same part of the same tree, or by a rock, fencepost, or burrow, all their adult lives" (Alexander, 1956). Among species possessing this sedentariness were P. camellifolia, N. ensiger (Harris), N. nebrascensis, Microcentrum retinerve (Burmeister), O. nigripes Scudder, O. silvaticum McNeill, Amblycorypha rotundifolia (Scudder),

Conocephalus nemoralis (Scudder), and Oecanthus fultoni (niveus) (Walker). One species of Gryllus was heard in the same spot for over 30 days. Specimens were not marked, but it was felt that individuals could be recognized due to unique characteristics of their song and a nightly account of their location could be kept.

Male spacing behavior

The spacing of male saltatorians under natural conditions is probably due to a number of factors (e.g., plant and habitat preference, avoidance or aggregation of conspecifics due to visual or chemical communication, interspecific competition, and predator pressure). Behavioral aspects of conspecific interactions involving territorial behavior and establishing of dominant subordinate relationships has been investigated for many crickets, grasshoppers and katydids. Aggression involving contact and/or acoustical signaling appear to be important in maintaining territories and establishing hierarchial relationships. Avoidance of a conspecific singer may be an important non-aggressive aspect of spacing. Sound production may maximize male-female contact through spacing of males. And, as Walker (1973) proposes, sound may enhance utilization of the environment by attracting other animals to a favorable habitat.

Clark (1948) postulated that "sociable activity" may act to reduce the spreading out of grasshoppers and account

for a degree of concentration and localization. Stridulation was thought to be important in the aggregation of these insects.

Haskell (1958, 1961) proposed that grasshoppers having highly developed stridulatory behavior used sound to hold the colony together and, therefore, enhanced the chances of mating and allowed colonies to move in relation to major changes in environment without becoming dispersed. Young (1971) appeared to agree with Haskell.

Alexander (1956, 1961, 1968) has found that only on rare occasions have two singing males of the same species of Tettigoniidae or Gryllidae been found close together in the field, with the exception of a few species. The calling song apparently attracted males from some distance, but repelled those that were nearby. He indicated that males found together in the field usually produced sounds which varied somewhat from their usual song.

Males of O. vulgare, O. nigripes, and O. concinnum caged together in the laboratory usually produced only the ticking part of their buzz tick sequence. Alexander (1956) postulated that one part may attract females and the other part may be used to repel conspecific males.

Male field crickets tend to space themselves in the field, and to remain in one spot all their adult lives (Alexander, 1956, 1957). In describing the field crickets

habit of occupying burrows, he stated "permanent location of males at sites spaced so far apart as to be only within range of hearing maximizes the temporal and spatial size and continuity of the acoustical field available to the females of the species, and enhances the effectiveness of the calling songs of individual males as guides for sexually responsive females" (Alexander, 1961).

Males of various species of phaneropterine katydids apparently undergo kinetic movements resulting from conspecific male ticking (Spooner, 1964, 1968). Such ticking could be responsible for spacing in natural populations. There may even be interspecific interaction since many species that produced ticks also occurred in close proximity under natural conditions.

Morris (1967, 1971, 1972) has done extensive work regarding spacing and the mechanism for spacing in tettigoniids. Males of O. gladiator and O. vulgare had a tactic response to recorded songs of conspecifics. This response was associated with aggressive behavior and a guide in the approach phase. M. sphagnorum males changed their stridulation pattern at the approach of another male of the species (Morris, 1970). This was seen as an aggressive interaction.

Morris (1967, 1971) has quantitatively demonstrated a spacing within their habitat for O. gladiator and C. nigro-

pleurum. He set forth a behavioral model to account for this spacing. His contention was that conspecific stridulation within a critical distance of a singing male would elicit phonotaxis in that male. Fighting would result in silent withdrawal by one male leaving the other singing at the encounter site. Yielding males would usually withdraw to a distance greater than the critical distance necessary to evoke aggression. A dominant male would become more sedentary and tend to remain in the same spot. A subordinate male would repeatedly yield in subsequent encounters until they reached a position where their singing no longer provoked an attack. Silent males could possibly remain in the middle of the chorus as they would be ignored by calling males. In this manner the population was seen to be capable of remaining in equilibrium with regular spacing maintained by a continual exchange of acoustic information.

A subjective conclusion by Abraham (1972) for O. vulgare males indicated that they were evenly spaced within their habitat when the population was dense. This spacing accrued from calling song interaction when males withdrew so that the other male's song no longer inhibited its buzzes. Alternatively, males might fight to determine which will sing in the immediate area.

Scope and Emphasis of the Investigation

The spatial relationships of chorusing males of the Nebraska Conehead Neoconocephalus nebrascensis is the subject of this study. Males of the species produce sound and can be heard singing in the early evening, beginning soon after sunset. Chorusing, resulting from synchronization of sound bursts by two or more males, begins soon after the first male produces sound and may continue well into the night.

Cursory examination of a colony of katydids leads to the assumption that choruses are aggregations within the population. It is more difficult to predict if males within a single chorus are aggregated, randomly, or evenly spaced. Inter-animal distances of these males were measured and subjected to a statistical analysis that, according to Clark and Evans (1954), is capable of detecting significant departure from randomness and the direction of this departure.

Major emphasis is placed on elucidation of spacing mechanisms. Sound interactions seem to be the most likely mode of information exchange available to the animals for this purpose.

The literature provides little or no information concerning the ability of the species to produce any sound other than the calling song. A precise analysis of solo song provides the background for analysis of sounds produced in a variety of behavioral contexts. These sounds

and attendant behavior were important in determining the role of acoustics in spacing dynamics. The study investigates: a) song parameters and song related behavior, b) phonoresponse and chorusing, c) male aggressive behavior, d) dominant-subordinate relationships between males, and e) male sedentariness and spacing behavior. It is hoped that a clear concise record of these categories is provided and advancement toward solution of the spacing problem is demonstrated.

MATERIALS AND METHODS

Data were collected from July 17 to October 1973, July 17 to September 1974 and July 16 to September 1975. All field investigations were in Ames, Iowa; all laboratory studies were at Iowa State University. Some laboratory investigations involved adults raised from nymphs; otherwise, adults were collected in the field and transferred to the laboratory.

General Field Study

Field studies began each year on the night that males first began to produce songs. With the exception of diurnal observations made during the first few weeks each season, data was collected only at night. Time, temperature, general behavior, acoustical behavior and behavior pertinent to spatial relations of calling and non-calling males were recorded.

Investigation of Movement

Mark and location techniques

Twenty-six males were captured and marked between July 30 and August 12, 1974. No marked males were located after August 15, 1974.

Calling males located in the field with a flashlight were initially marked with both white paint (no. 2 Pactra

Namel gloss) and a system of tegminal clipping. Only the tips of the tegmina were clipped in an effort to minimize impairment of flight. This dual system was used for a short time to check the life of the paint under field conditions. Later, clipping was discontinued.

Animals were checked for movement after replacing them as near as possible to their original capture point. Some difficulty was encountered on warm nights when animals were particularly active. Animals would either crawl or fly away. These animals were retrieved and held loosely in a pocket of grass until little movement was observed. On cool nights, animals made little effort to escape.

After animals were marked and replaced successfully, a small flag was placed at the location. When marked males were located, a description of the markings and the surrounding area were recorded on a cassette recorder. A small flag was placed near the animal to mark its location. Since the intent of this study was to understand long term attachment to a site, no active attempt was made to relocate males on the same night that they were marked. The same general area was searched each night that calling occurred. Calling did not occur on all nights, possibly due to low temperatures, and no attempt was made to locate males on these nights.

Locations were made through careful stalking of calling males. Males that discontinued calling were nearly impossible

to locate. Little effort was made to locate them and, thereby, disturbance of the area was minimized.

Measurements to indicate the degree of movement of located males were made the following day when katydids are not normally active. The distance from a new flag to the permanent marker was determined with a 100 ft (no. 9589 J.C. Penney) measuring tape. The exact direction from the new point to the original point was determined using a PIC liquid-filled, Lensatic Compass. This compass has a sighting device for accuracy. Thus, magnitude and angle of polar coordinates were obtained for the new flag or position with reference to the permanent marker. Polar coordinates were converted to rectangular coordinates for ease of plotting on graph paper.

This method reduced disturbance of the area to a minimum and allowed the use of simple mathematical procedures to deduce the distances traveled by the animal on successive nights.

Spatial Distribution of Calling Males

Statistical methods devised by Clark and Evans (1954) and Morisita (1954) were used in an effort to elucidate spatial relations between synchronous males of a chorus. The statistic R (Clark and Evans, 1954) is based on the ratio of observed to expected nearest neighbor distances

and is used as an index of the spatial arrangement of individuals within a population. The value of R depends on the pattern of distribution in the population. It approximates 1.0 in randomly spaced populations. Departure from 1.0 in a negative or positive direction may indicate respectively a clumped or uniformly spaced population. Maximal spacing produces an "even, hexagonal pattern" of individuals. When this occurs, the value of R reaches its maximum value of 2.1491.

For example, in a population of N individuals having a specified density ρ , the distance r from each individual to its nearest neighbor is measured. The mean observed distance is represented as $\bar{r}_A = \frac{\sum r}{N}$. The mean distance to be expected if the population is distributed at random, \bar{r}_E , can be shown to have a value equal to $\bar{r}_E = \frac{1}{2\sqrt{\rho}}$. The ratio $R = \frac{\bar{r}_A}{\bar{r}_E}$ is used as a measure of the degree to which the observed distribution approaches or departs from random expectation.

Classes of nearest-neighbor-distances were determined and compared to frequency distributions which would theoretically result if this same number of individuals were randomly spaced.

Methods presented by Morisita (1954) were used to compare frequencies of observed nearest-neighbor distances to those generated for a theoretical, randomly spaced,

population. If the occurrence of nearest neighbors is random relative to a center of measurement A, the probability of finding the closest individual to A, within the area set off by radii r and r' is: $e^{-[m(r')^2]} - e^{-[m(r)^2]}$. The variable m is defined as the mean number of individuals present in an area π . These probability calculations are based on the Poisson distribution.

Theoretical and observed distributions were compared with a χ^2 test to determine if the katydids' spatial distribution showed significant departure from randomness.

Data collection technique

Data was collected from two study areas in Ames, Iowa. The first area (SA-1) constructed in late July, 1974 was 45 ft by 50 ft and had an area of 2250 square ft. On July 25, 1974 all vegetation was removed, by a road construction crew, from the east and south sides of SA-1. Subsequently, on August 1, 1974 the total area was reduced, by the construction crew, to 1,630 square ft. Because of these changes in the surroundings, data were assumed to be from 3 populations. Sampling began on July 18, 1974 and was completed September 11, 1974. Thirty-one sample runs were made in 1974, and 113 nearest-neighbor-distances were recorded.

The 1975 study area (SA-2) was near SA-1 which had been completely denuded of vegetation. The new area was 65 by 45 ft with a total of 2925 square ft. Data was

collected from SA-2 from July 31 to September 11, 1975. Nine sample runs were made and 54 distances were recorded. An analysis of variance was applied to test for differences in R for the four populations according to procedures employed by Clark and Evans (1954).

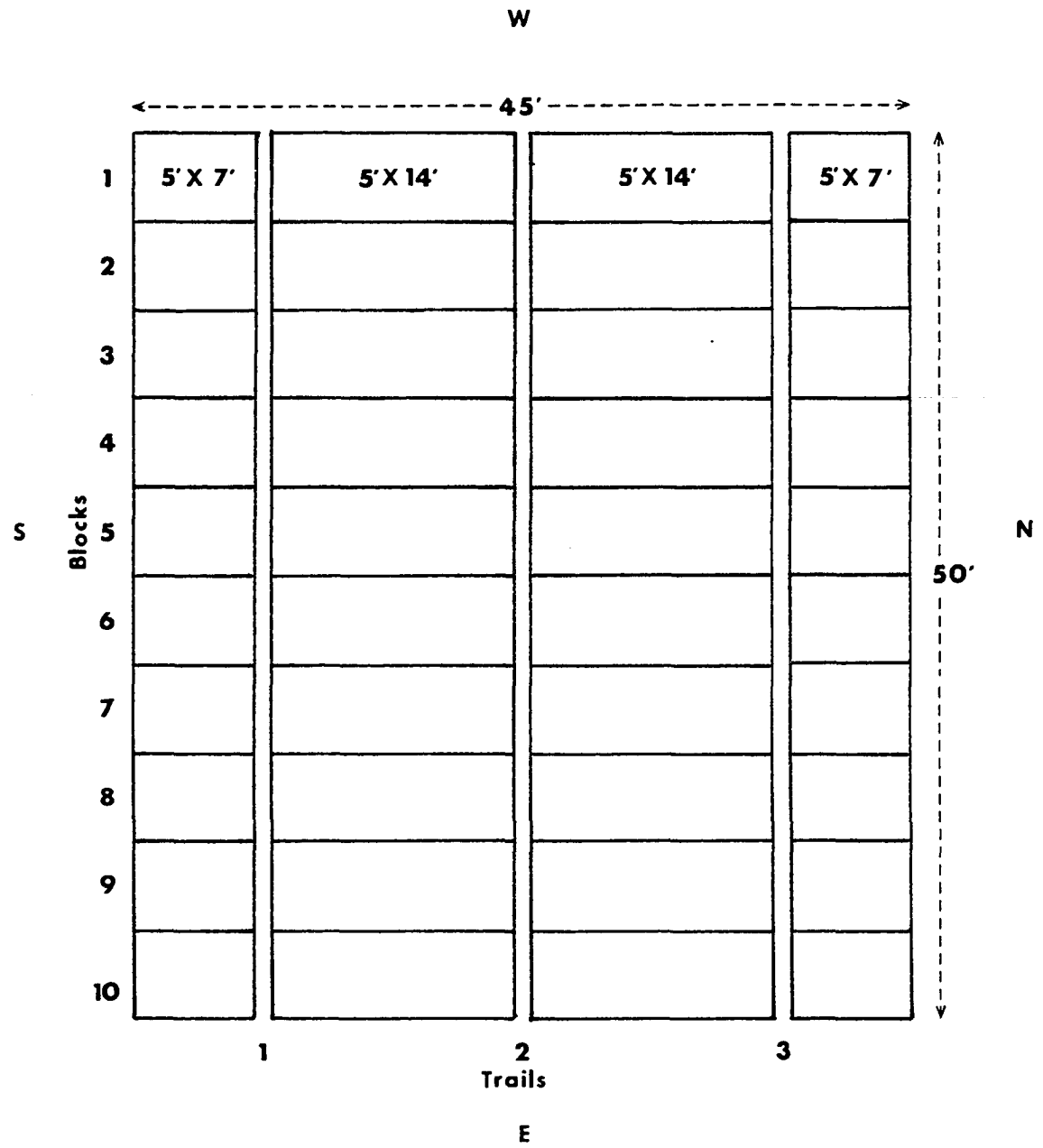
The original grid was constructed by marking off a large rectangle 45 ft wide and 50 ft long (Fig. 1). The 1975 grid was 65 ft long. Heavy gauge cotton string and lath sticks were used to make a sufficiently strong and long lasting structure. Cross strings were staked at 5-foot intervals that stretched across the rectangular area.

Three-foot wide paths were required as walkways for sampling. These were laid down lengthwise at intervals of 7, 22, and 37 ft from a side. Where cross strings intersected path strings, they were checked for five-foot accuracy, cut, and staked leaving the path open.

Cross strings were staked about 2 to 3 ft high so as to increase visibility. Path strings were stretched along the ground. The resulting grid provided 5 ft by 7 ft rectangular blocks along each side of the large rectangle with two rows of 5 ft by 14 ft rectangles on each side of the middle path.

Paths were labeled T-1 (one side), T-2 (middle), and T-3 (other side). A catgut fishing line was strung along

Figure 1. Diagram of 1974 study area.



each side of the path so that small rectangles (called blocks) could be labeled.

Sampling runs were made through T-1 back through T-2 in the opposite direction and then through T-3 in the original direction.

Only calling animals that were spotted with a 6-volt flashlight were recorded. The distance of the animal from the grid strings was determined through use of a fishing pole made into a T-shaped structure. The end piece was 2 1/2 ft wide and was marked off with white tape at 3 inch intervals. The long piece, 7 ft long, was marked with foot markers (wide tape) and at 3 inch intervals (narrow tape). Thus, an accuracy of approximately ± 3 inches was obtained from either direction.

The location of the katydid was recorded on a cassette recorder attached to the investigator's belt. For example, a location might be: T-1, B-3N 3.2 out, .6 in E. This indicates that the animal was north of the first path in block 3, 42 inches out from the path and 18 inches from the east line. These coordinates were transcribed into a field notebook. Time and temperature were recorded.

In order to determine inter-animal distances, the location of each animal was plotted on a large sheet of metric graph paper. Each mm was set as equal to 1 inch. Distances between animals were measured and nearest neighbor distances were extracted.

The size of the three paths did not appreciably affect the area size and were ignored in density determinations.

Laboratory Investigations

Song parameters

Nymphs were collected from the field in Ames, Iowa about 7 - 10 days before their final molt. These nymphs were kept in small 4" x 4" x 4" wire mesh cages. They were fed seeds collected from wild Bromus inermis and Agroslis alba plants. Water was provided in a small vial plugged with cotton.

Later, adults were collected from similar sites. Adults were caged and fed in the same way as nymphs. In 1974, eight adults raised from nymphs were isolated and later used in experiments to determine dominance relationships.

Tape recordings of sounds were made in an acoustic isolation chamber (Industrial Acoustic Co. Inc.). The walls were 4-inch steel perforated panels. The room has a floating floor on rubber vibration isolators. Its size is 15 ft by 17 1/2 ft with an 8 ft ceiling.

All recordings were made on a Nagra III tape recorder using a Shure Dynamic (Model 576) or an American electrodynamic microphone (Model D-33). Recordings were made at speeds of 3 3/4 or 7 1/2 ips on Scotch RB-7 or 206 (High output/low noise) tape.

Sound parameters were determined from oscillograms. Oscillograms were obtained by passing the tape-recorded sounds at $3\frac{3}{4}$ speed through a Krohn-Hite Band Pass Filter (Model 310-AB) and then into a Tektronix dual beam oscilloscope (Model 502A).

Sound produced traces were photographed at 50 mm/sec with a Grass kymograph camera (Model C4-k) on Kodak linagraph 1930 photographic paper. Sound lengths and intervals were measured from oscillograms by means of calipers accurate to 0.1 mm. Measurements of a series of phonatomes¹ or buzz, the intervening silent pause (interval), and the time lapse between initiation of buzzes (period) were taken for analysis and description of songs (Fig. 2). Songs range from one to several hundred buzzes and each buzz is separated by an interval of usually less than 1 second. Buzzes separated by 10 seconds or more were arbitrarily considered as two songs.

Phonoresponse

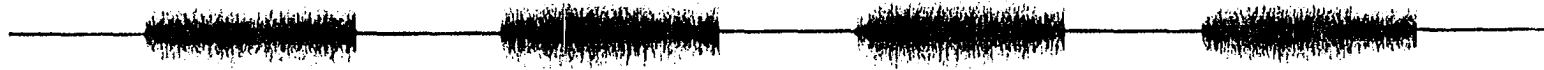
Investigations of katydid response to imitation sounds were begun in 1974 by connecting two Grass S-4 physiological research stimulators in conjunction with a driver speaker (Atlas Sound Corporation, Model PD5VH). In this system,

¹A phonatome is produced by one complete cycle of wing movement, i.e., a sound is produced during opening and closing of wings.

Figure 2. Acoustical repertoire of N. nebrascensis.
L - leader; F - follower; C - clicks.

NEOCONOCEPHALUS NEBRASCENSIS - male

CALLING SONG



buzz interval

SYNCHRONIZATION



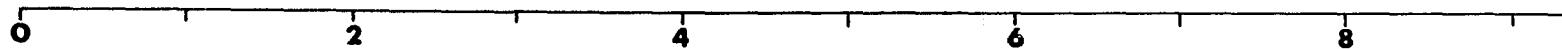
PRECOPULATORY SONG



CONTACT SONG



DISTURBANCE SOUND



TIME IN SECONDS

the output of one stimulator (the modulator) modulated the output of the other stimulator at predetermined sound lengths and intervals. The investigator attempted to imitate a sound which would approximate the buzz length and rate of a katydid at 25°C. The maximum imitation buzz length possible was 1 sec. This was slightly shorter than katydid buzz lengths which averaged 1.3 sec at 25°C. With only two stimulators, pulse and phonatome rate could not be reproduced. However, katydids appeared to respond to the electronic imitations in the same manner as to the sounds of other katydids. Flexibility of the set-up allowed playing of various imitation rates, or alternatively, single sound bursts manually produced at the investigator's discretion.

A manual switch was added to the equipment during 1975. This switch, which could be set for given lengths, served to modulate the S-4 modulator. Thus, imitation buzz length was determined by the switch setting and the S-4 modulator was used to set a pulse¹ rate of 150/sec which approximated the katydid's phonatome rate at 25°C. Therefore, in the imitation buzz, the length of one pulse was equivalent to the length of a 2-pulse phonatome in the song of the katydid. Katydids responded to and synchronized with imitation buzzes in apparently the same manner as to natural katydid sounds.

¹See Broughton (1963) for definition of pulse.

RESULTS

Solo Song

Neoconocephalus nebrascensis males begin calling as light intensity decreases after sunset. This calling usually begins with sporadic solo calling and rapidly develops into synchronous calling. Occasionally, however, calling does not develop into synchrony. Complete solo songs may be produced as males first begin to sing early in the season, or late in the season, as the number of males rapidly decrease.

Solo songs are occasionally produced in low density areas, especially between 11:00 P.M. and 1:00 A.M. Most animals are feeding during this period and do not readily call. Synchrony then resumes and if temperatures are above 20°C, full chorusing will normally re-develop and continue until about 3:00 A.M. After this the number of individuals calling begins to decrease and solo songs may again be produced prior to daybreak. The time at which synchrony begins to dissipate is temperature dependent, usually beginning as the temperature drops below 20°C. If the temperature falls to between 15-20°C prior to 3:00 A.M. for periods of up to one week or more, animals apparently accommodate and synchrony may again occur until around 3:00 A.M. although chorusing is less intense. When temperature drops below 15°C, regardless of the time of night,

the number of katydids calling rapidly diminishes and, if calling occurs, solo songs are most frequently produced.

Males kept at 24-26°C under laboratory conditions began calling about 30 to 40 min after they were placed in complete dark. Eleven males repeated songs lasting an average of 6 min 40 sec with 10 min intervals between songs. Repetition of solo songs usually lasted about 1 1/2 to 2 hr and then animals began to feed.

Diurnal solo song was heard during the first two weeks of the season in both 1974 and 1975. These songs were produced infrequently in the laboratory and the field from about mid-day until 6:00 or 7:00 P.M. This is the first known account of day singing in the species. Fulton (1928) and Thomas (1933) both reported that N. nebrascensis did not sing during the day.

Approximately 15-20 such solo songs were heard, consisting of 2 to 10 buzzes. It is likely that this is the first song produced by some animals because often it is the first song heard among adults raised from nymphs. The behavioral context under which the songs were produced is not known. Laboratory animals producing the sound were caged separately, although near one another, and the short songs seemed to be produced spontaneously (i.e., eliciting stimulus unknown). The possibility that males were stimulated to produce the songs by another male does

exist. A similar kind of song was often produced by males after contact with another male (see male-male contact song below).

Sound bursts of solo calling consists of a series of 2-pulse phonatomes. Phonatomes are repeated about 165 times per sec at 21°C to produce a buzz length of about 1 sec. Sounds must be separated by at least 100 msec to be distinguished as separate sounds by humans (Haskell, 1961), thus, a continuous sound is heard during the production of a buzz.

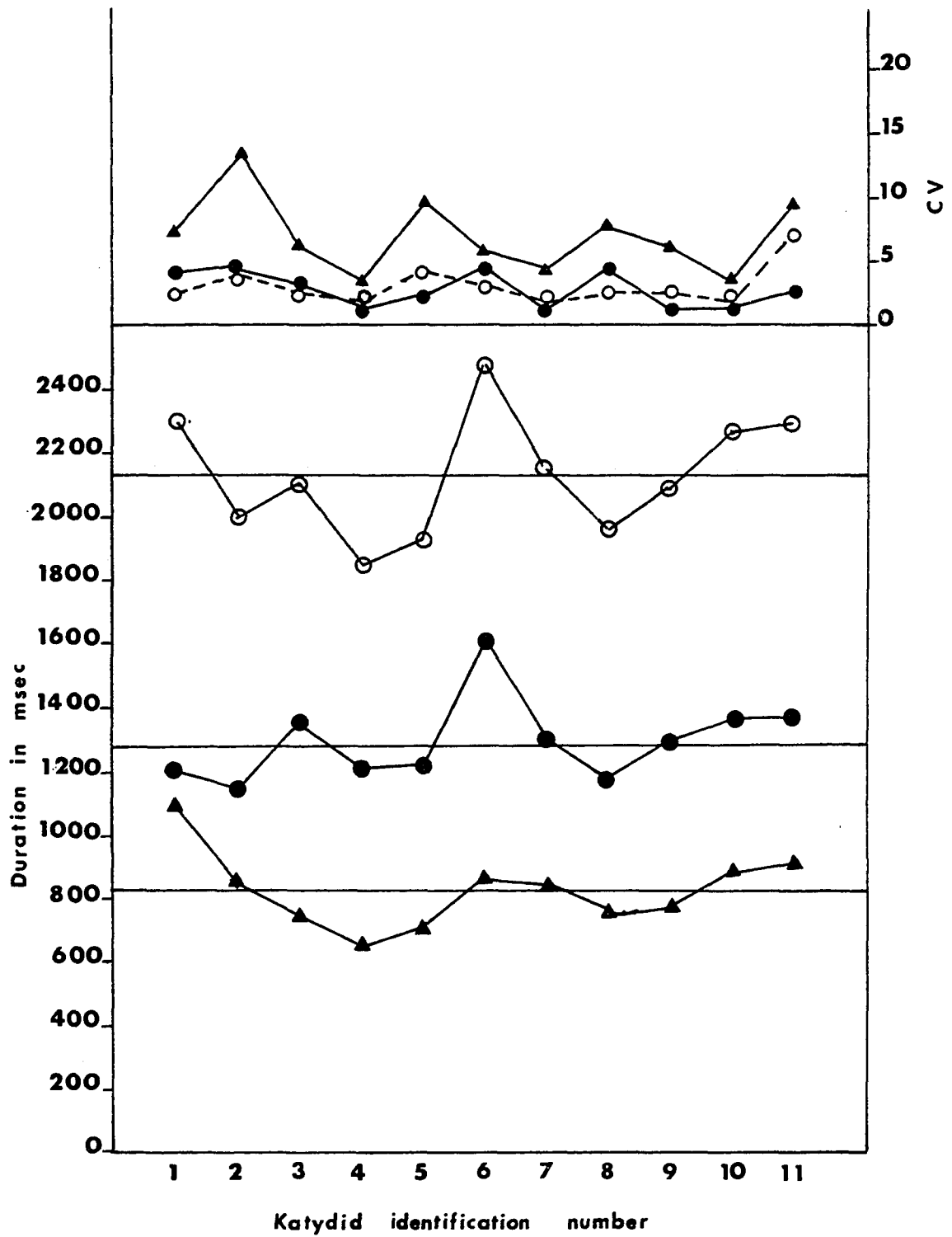
Portions of solo songs were taken for analysis from oscillograms. These never included the first 10 periods of calling because of frequent variability in parameter lengths at the beginning of the call (Fig. 4). The analysis always included measurements of 10 consecutive periods usually taken toward the middle of a song.

Solo calls of 11 males analyzed from oscillogram records made in both 1974 and 1975 produced a mean buzz length of 1296 msec and a mean interval of 835 msec at 24-26°C (Fig. 3). Determination of mean buzz rate from the mean period (2131 msec) gave a value of 28 buzzes per min.

Solos lasted from 5 to 7 min and consisted of 150 to 200 buzzes for males 2, 3, 4, and 5. These were the only males in which entire oscillogram records were available for determination of these parameters.

Figure 3. Analysis of solo calls for 10 consecutive periods of 11 katydids. Mean durations (msec) are plotted on the ordinate, identification numbers of katydids on the abscissa. Coefficient of variability (C.V.) for mean lengths of respective parameters are plotted on the upper right ordinate. Straight lines represent averages for each parameter mean.

●---buzz; ▲---interval; ○---period.



Buzz length was the least variable parameter (Fig. 3). Mean buzz lengths were all longer than mean intervals; buzz lengths were rarely exceeded by intervals within individual songs. The coefficient of variability (C.V.) for interval ($\bar{x}=8.0$) was always greater than that for period ($\bar{x}=3.1$) or buzz ($\bar{x}=2.8$).

Analysis of mean parameters for 11 males indicated a strong correlation of mean buzz and interval lengths to period length (B vs P: $r=+.78$, $t=3.74$, $p < .01$; I vs P: $r=+.73$, $t=3.2$, $p < .01$). Thus, males producing longer or shorter than average buzzes and/or intervals would be expected to have a slower or faster rate respectively.

In order to examine the nature of buzz and interval variation within songs of individuals, a correlation analysis was made from period parameters for males 2-7. Two tailed significance levels were used for all parameters (Table 1).

Individual variation seems to lie in the tendency for buzz lengths to be correlated to either interval or period. Males 6 and 7 had significant negative correlation of buzz lengths to interval and male 2 approached significance. Conversely, the buzz lengths of males 3 and 4 were positively correlated to period lengths and male 5 approached significance. Male 6 also had a positive buzz-period correlation, but was the only male not having significant interval-period correlation. Only male 6, which had an extremely long

Table 1. Within-song parameter correlations of solo song. Comparisons involve buzz versus interval (B vs I), buzz versus period (B vs P), and interval versus period (I vs P).

Parameter	Male no.	n	r^a	t^b
B vs I	2	20	-.42	- 1.96
B vs P	2	20	+.27	+ 1.19
I vs P	2	20	+.75	+ 4.81**
B vs I	3	20	-.04	- .17
B vs P	3	20	+.51	+ 2.52*
I vs P	3	20	+.84	+ 6.57**
B vs I	4	20	+.01	+ .04
B vs P	4	20	+.77	+ 5.12**
I vs P	4	20	+.65	+ 3.63**
B vs I	5	20	+.10	+ .43
B vs P	5	20	+.42	+ 1.96
I vs P	5	20	+.94	+11.69**
B vs I	6	60	-.64	- 6.34**
B vs P	6	60	+.80	+10.15**
I vs P	6	60	-.04	- .30
B vs I	7	85	-.64	- 7.59**
B vs P	7	85	-.16	- 1.48
I vs P	7	85	+.86	+15.35**

^a r = Correlation coefficient

^b t = Student's t-value

* $P < 0.05$

** $P < 0.01$

buzz length (Fig. 3), had significant correlation of the combination buzz to interval, and buzz to period.

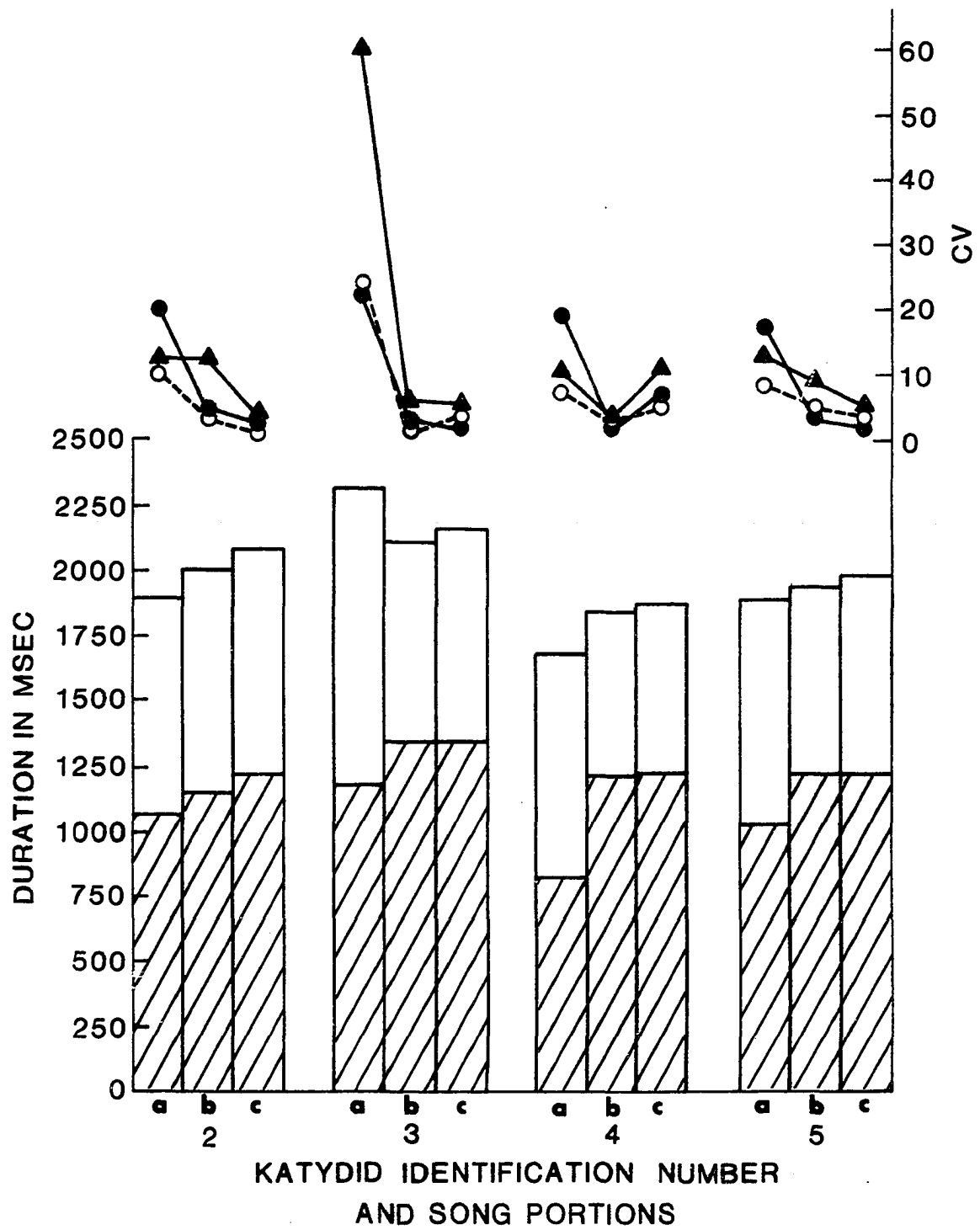
The incidence of positive correlation between interval and period might be predicted from Figure 3 which shows high variability of interval relative to buzz or period (i.e., one might reason that any change in buzz length would be compensated for by adjustment in interval length to produce a fairly uniform period). The extremely long buzz of male 6 (Fig. 3) appears to be consequential in increasing buzz variability, thus, buzz becomes an important factor in determining period variability.

Comparison of 10 periods from initial, middle and final portions of solo song from males 2-5 indicates a decrease in variability after the initial 10 periods for most parameters (Fig. 4). Except for interval of males 2 and 4, all parameters decreased in variability. Interval was more stable than buzz length for males 2, 4, and 5 during the first 10 periods.

Period means indicate a slowing of buzz repetition rate for 3 of the 4 males. The song of #3 showed a slowing trend from middle to final segments, but had a slower initial rate. This slower initial rate resulted from a long interval between the first and second buzz. Occasionally males include a long interval of about 1 1/2 to 2 1/2 sec in the first 10 periods. The long interval has often been

Figure 4. Comparison of 10 periods from initial (a), middle (b), and final (c) portions of solo song. Bar graphs indicate mean duration in msec for males 2, 3, 4, and 5. Shaded portions of bars indicate buzz length while open portions represent interval. Katydid identifying numbers and song segments are shown on the abscissa. Coefficient of variability (C.V.) is plotted on the upper right ordinate.

●---buzz; ▲---interval; O---period.



recorded after the first buzz and rarely after two or three buzzes.

Mean buzz length of the initial portion of solo calling was always shorter than mean lengths of the middle or final portions (Fig. 4). In contrast, interval means of the initial portion were longer except for male 2. Males normally increased buzz length and decreased interval length through the first 7-10 periods.

Males occasionally produced a barely audible, continuous buzzing (antecedent buzz) just prior to and continuous with the first buzz of calling allowing prediction of the first buzz in these instances. The sound had a noise-like quality and appeared to be produced by slowed passage of the stridulatory file over the scraper.

Male-male Contact Song (CtS)

Under laboratory conditions, males coming into antennal contact with another male may produce a short 1- to 6-buzz call (Fig. 2). The other male may reciprocate with a short song, but rarely synchronizes. When synchrony occurs, the song interaction may last several minutes with one male, the follower,¹ singing irregularly and discontinuing

¹The follower in synchrony always begins his buzz slightly behind the leader as buzzes are produced almost simultaneously.

song first. Clicks (apparently one phonatome) are often produced after buzzes within male-male CtS (Fig. 2).

Most male-male CtS consisting of one to two buzzes are similar in all parameters to the initial portion of solo calling. The length of initial buzzes of 1-buzz CtS, 2-6-buzz CtS, and solo song were subjected to an analysis of variance. No significant difference was found among buzz lengths ($F_{2,45} = 1.63$, $p < .05$).

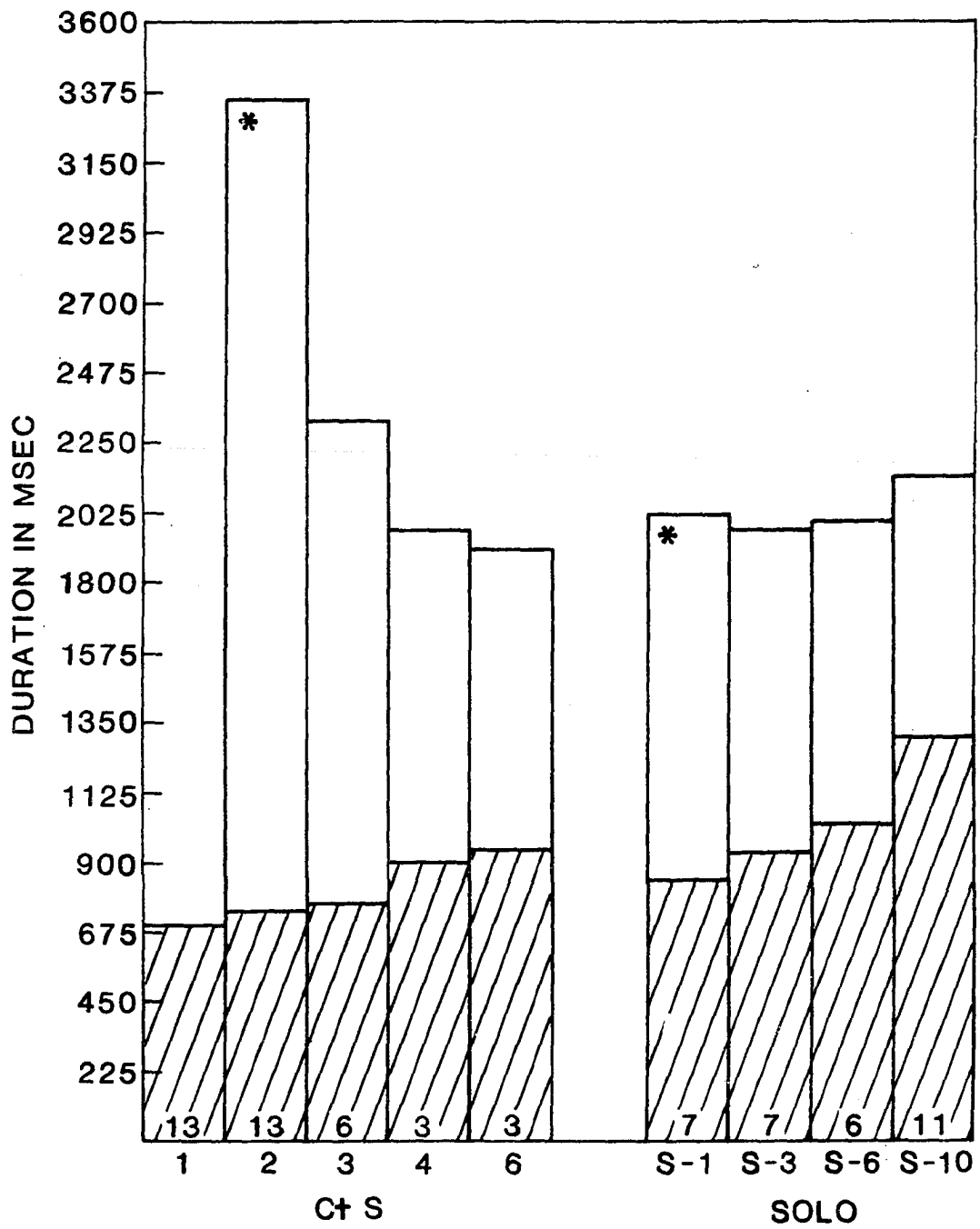
The number of 1-buzz CtS produced by different males were as follows: male #12-1, male #14-1, male #7-4, and male #13-7. The number of 2-buzz CtS were: male #6-1, male #14-1, male #15-1, male #7-5, and male #13-5. Three buzz CtS were produced by: male #7-1, male #16-1, male #17-1, and male #6-4. Only one 5-buzz CtS was recorded and was produced by male 7. Three 6-buzz CtS were recorded: male #1-1 and male #6-2.

The first 1-6 buzzes of solo song are averaged in Fig. 5 to compare to CtS having the same number of buzzes. The number of beginning periods averaged for males 2, 3, 4, 5, 6, 18, and 19¹ is indicated by the number following the symbol S (i.e., S-1 = 1 period, etc.). Mean parameters for normal solo song (Fig. 5, S-10) were included to show the longer buzz and shorter interval produced during stable solo singing. Male numbers and means are the same as in Figure 3.

¹Male 19 was not used in S-6 Fig. 5.

Figure 5. Comparisons of mean parameter durations (msec) of male-male contact song (CtS) and solo song. The numbers along the abscissa represent the number of buzzes in each CtS and each solo song used for comparison. Numbers within shaded bars give numbers of songs (CtS) or number of songs for which specific numbers of periods were selected (solo) for calculation of mean parameter durations (msec) given on the ordinate. Shaded portions of bars indicate buzz length while open portions represent interval.

* = simple mean.



Interval lengths for 2-buzz CtS were compared to interval lengths of first periods of solos (Fig. 5). Intervals between 2-buzz CtS appear to be consistently longer than the first interval of solo song although occasional short intervals between CtS buzzes and long intervals between solo song increased the variability of both in comparisons and no significant difference was found ($T_{(18df)} = 1.96$, $p < .05$).

Contact songs 3, 4, and 6 closely approximate the beginning of solo song (S-3, S-6) in Figure 5. Comparisons of both CtS and short solo sequences made to S-10 of Figure 5 indicate buzzes become longer and intervals shorter as more are produced. Period appears to remain relatively constant from beginning to end of all songs with the possible exception of the period of 2-buzz CtS.

In order to determine the behavioral context in which CtS were most often produced, tests were conducted in which males were allowed to contact males or females and the number of short songs produced were counted (table 2). The experimental set up included: 1) 4 males paired separately, 2) 4 males, each paired separately with a female, and 3) 4 isolated males, used as controls, placed in separate cages. Individuals or pairs were placed in 4" x 4" x 4" wire mesh cages with each cage at least 2 ft from another cage. Paired animals were parallel with 6 ft between them.

Table 2. Analysis of behavioral context for production of contact interaction songs (CtS). Males were paired with another male or female and controls were isolated. Short songs are categorized by the number of buzzes per song. The total number of CtS for each length were counted as animals were shifted through 30 min intervals of three light phases.

	Time: 8:00- 8:30 9:30-10:00	Time: 8:30- 9:00 10:00-10:30	Time: 9:00- 9:30 10:30-11:00	
	Dark phase	25 watt red light	Overhead lights	Total
<u>1-buzz</u>				
Male-male	6	8	19	33
Male-female	1	0	0	1
Control	0	0	0	0
<u>2-buzz</u>				
Male-male	10	1	8	19
Male-female	1	0	0	1
Control	0	0	0	0
<u>3-buzz</u>				
Male-male	6	1	2	9
Male-female	0	0	0	0
Control	0	0	0	0
<u>5-buzz</u>				
Male-male	0	1	1	2
Male-female	0	0	0	0
Control	0	0	0	0
<u>Total</u>				
Male-male	22	11	30	63
Male-female	2	0	0	2
Control	0	0	0	0

Test animals were subjected to three light conditions lasting 30 minutes each. Males were rotated through each phase twice. In the first phase animals were in complete dark. In the second phase activity was recorded under red lights and in the final phase the overhead lights were turned on. All CtS were counted. Controls were isolated under identical light and temperature conditions following the experiment with paired animals.

Males with males produced mostly 1- and 2-buzz songs under all light conditions. Males with females produced only two short songs compared to a total of 63 for males with males. Isolated males produced no short songs.

Parameters for calls initiated after contact with another male, or rarely with another female, do not appear to be appreciably different from beginning solo except for the shortness of the sequence and the occasional production of clicks. CtS were produced only after antennal or other contact, but often males separated slightly prior to production of the song.

Precopulatory Song

No detailed record of sounds associated with mating behavior for N. nebrascensis is available in the literature. Alexander (1956) postulated that a sound, that he characterized as a "split buzz", might be produced as a female approaches the male. An attempt was made to determine if

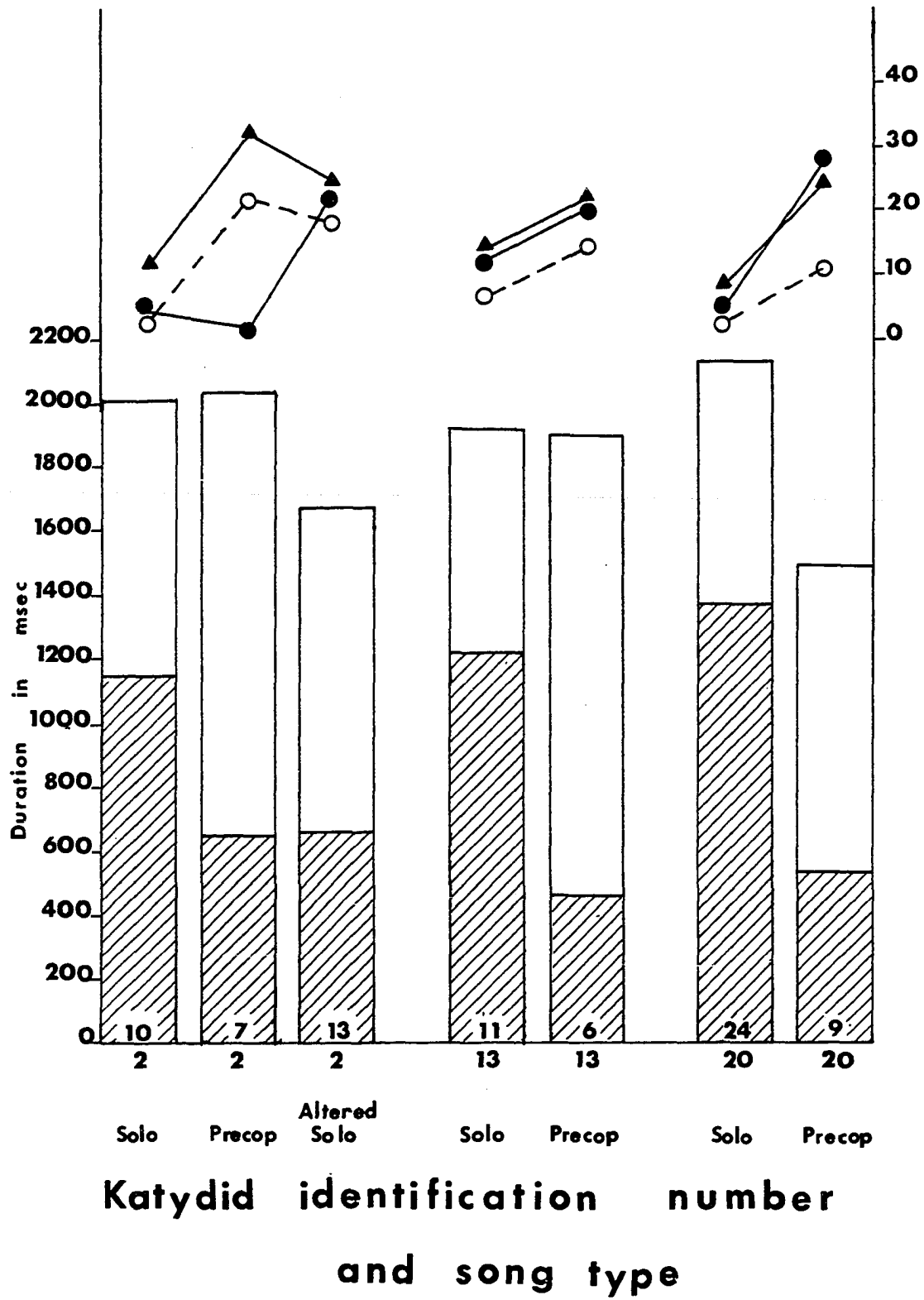
a "split buzz" could be elicited in a calling male and various experimental interactions between males and females were analyzed to determine if males either alter their song or produce a special song in response to females.

One male was placed with one to four virgin females in a large 13.5" x 14" x 15" cage consisting of a wooden frame, a glass top, a masonite bottom and front, and nylon mesh on sides and back. Grass placed in the cage provided a perch for the animals. The microphone was placed 2 in. from one side of the cage near the nylon mesh.

Parameters of seven songs produced by males just prior to or during attempts at copulation were analyzed from oscillograms. Temperatures were 24-26°C in all instances.

When placed in a female's cage, male 2, hopped close to the female and made head-to-head antennal contact and produced a precopulatory song. Buzzes of the song were shorter than the calling song and seemed to be of lower intensity (Fig. 6). The female began to tremulate and retained her position relative to the male. The male moved forward and parallel to the female as he laterally curved his abdomen toward her. The male continued to call until his parameres clasped the female's abdomen near its tip. The female then dragged the male 1-2 inches and they became stationary. Copulation lasted about 18 min and the female disengaged the male with her metathoracic leg.

Figure 6. Comparisons of mean parameter durations (msec) of solo, precopulatory song (precop) and altered solo. Numbers within shaded bars give the number of parameters used in calculating means. The remainder of the organization is the same as Figure 4.



The male produced 9 buzzes before copulation. The last 7 buzzes were recorded and are compared to male 2's solo produced under isolation prior to copulation.

Previously recorded solo song for male 2 had longer mean buzz lengths, while period means were about the same. All parameters except buzz were more variable for pre-copulatory song. Comparisons of means for buzz length and interval indicated a significant difference in the parameters (B: $t_{(15df)} = 25.03$, $p < .01$; I: $t_{(14df)} = 3.55$, $p < .01$) indicating shorter buzzes and longer intervals for precopulatory song.

Another male-female interaction occurred between male 13 and a female. This male produced a solo song prior to precopulatory song (Fig. 6). Three additional males were present at 4-12 feet as the solo and later precopulatory songs were produced. All males and one female were free to move about in the acoustic chamber, which had potted wild grasses and other plants to allow perching. The solo song was recorded at approximately 2:50 A.M. The pre-copulatory song was recorded 42 minutes later.

Both male and female were perched on the same grass plant when the interaction sequence was first noted. The male was producing short buzzes and the female moved a few inches upward and away from the male. She then turned and moved back down to within 2 inches of the male and became

stationary. The final six buzzes of the precopulatory song were recorded during the sequence which ended with the male moving up on an adjacent grass stem to bring his abdomen tip in contact with the stationary female. After 23 minutes, the female broke contact and moved away from the male. The male joined synchronous calling of two males about 10 min after copulation.

All parameters of the precopulatory song were more variable than those of solo calling (Fig. 6, 13). Precopulatory song buzzes were shortened, periods remained relatively constant and intervals were lengthened. A comparison of means for buzz and interval between solo song and precopulatory song indicated a significant difference (B: $t_{(16df)} = 11.86$, $p < .01$; I: $t_{(14df)} = 8.26$, $p < .01$).

Male 20 was introduced into the large cage described above with four females that had been housed in the cage for several days. After approximately 10 min the male began to produce calling sounds from the top of the cage with a stationary female about 6 inches away. A continuous record of song, after the first few periods, was analyzed (Fig. 6). The stationary female began movement toward the male during periods 15-20 of solo calling. The female's antennae apparently touched the side of the male. The male simultaneously altered his song (Fig. 6) and extended his abdomen laterally, as he turned toward the female. Both the male

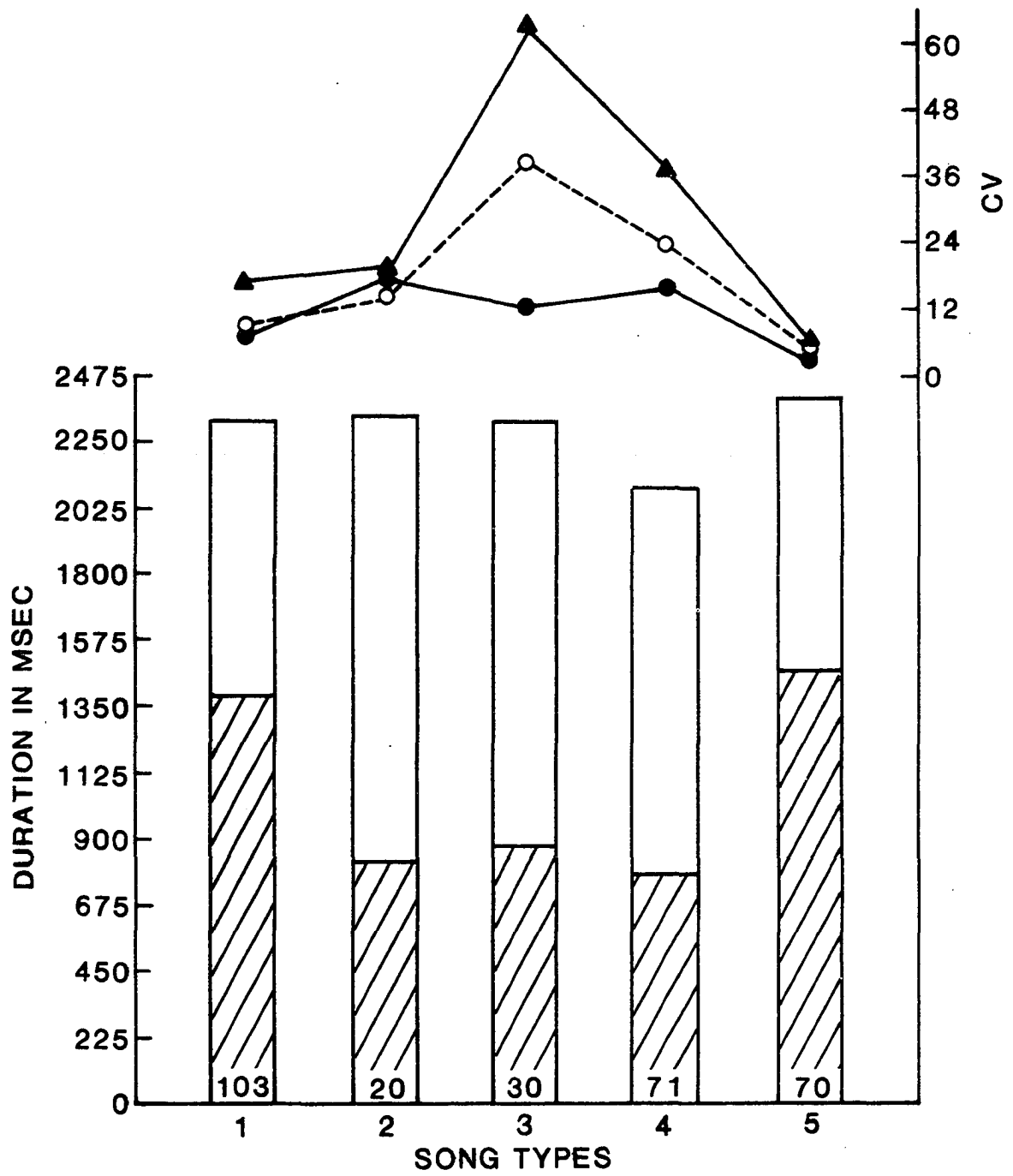
and the female moved forward slightly as the male contacted the tip of the female's abdomen with his parameres. The male discontinued calling immediately as contact was made. The female dragged the male a few inches and then became stationary. Copulation lasted 19 min.

Variability of calling increased as precopulatory alteration of song occurred (Fig. 6, #20). Altered periods were shorter with shorter buzzes and longer intervals. Comparisons of means for solo and precopulatory parameters showed significant differences (B: $t_{(31df)} = 22.46$, $p < .01$; I: $t_{(30df)} = 3.32$, $p < .01$).

Male 11 was placed in the cage with three females. After about 5 min, the male moved to the female, located on the nylon mesh, and made head-to-head antennal contact. The male immediately tremulated three times. The stationary female did not respond and the male turned and moved away.

Within a few minutes, the male moved to a second female on a grass stem and made head-to-head antennal contact. The male tremulated twice, then backed away about 1/4 inch and turned around. The female remained stationary as the male moved 2-4 inches away. The male began to call from a grass stem about 1 min after the encounter. Total length of the song is not known; however, the last 102 periods (103 buzzes) were recorded and means are illustrated for all parameters in Figure 7, #1.

Figure 7. Comparison of mean parameter duration (msec) of solo and precop for male 11. Numbers 1-5 on the abscissa represent respectively: solo before copulation, precop during unsuccessful attempts at copulation, precop followed by copulation and solo after copulation. Numbers within shaded bars give the number of parameters used in calculating means. The remainder of the organization is the same as Figure 4.



All three females moved in an apparently disoriented manner along the cage and over the grass for most of the song. One female moved on to the grass stem from which the male was calling and became stationary. The male discontinued calling within a few periods and moved 3-4 inches over the top of the stem toward the female. Copulation occurred on the initial contact as the female was under the somewhat horizontal stem and facing the male. Both of the other females moved to the same stem and walked over the copulating pair within a few seconds after initiation of copulation, and knocked them to the floor of the cage where they remained stationary. Copulation lasted 15 min.

Five min after initial copulation, the male again initiated calling from the top of the cage on the glass surface. Repeated attempts at copulation occurred as the females approached the male and as the male moved toward the females. Both females could be seen to tremulate as they approached the male.

Portions of three precopulatory songs were recorded. Each song was followed by silent inter-song intervals of up to 1 min. Mean parameters of two unsuccessful and one successful attempt at copulation are shown in Figure 7 (song types - 2, 3, and 4). During all three songs the male moved toward one or both of the females and extended his abdomen, but seemed unable to correctly attach his parameres.

His abdomen tip frequently probed at the head, thorax or legs of the females as the females continued to move. Successful copulation occurred during song 4 after several unsuccessful attempts during the song. The female remained stationary as the male approached and discontinued calling just prior to successful attachment of the parameres. Copulation lasted 20 min.

Much of the song record of unsuccessful attempts at copulation was produced while the male was not in direct contact with the female. Interval lengths were increased, ranging from 2 - 4.2 sec, when the male touched a female with his extended abdomen. Mean buzz lengths were reduced during copulation attempts, as the mean period remained relatively constant. Coefficient of variability for recorded portions of songs 3 and 4 show increases in variability from solo for interval and period.

Similar reproductive behaviors and altered songs were observed in at least three other instances for males reacting to non-receptive females. However, no sound records were made of these encounters.

Figure 7, #5 shows mean parameters for a portion of solo song. The song was produced in isolation about 10 min after male 11's second copulation and is similar in variability and parameter means to solo prior to copulation.

Males, producing calling songs, shorten buzzes in response to gentle tapping of their perches. Buzz lengths resulting from such alteration appear very similar to those produced in precopulatory song. Tapping on the side of the cage caused an immediate response, while discontinuation of tapping resulted in resumption of normal solo song after one to two buzzes. In order to investigate relationships between precopulatory song, solo song, and altered song due to tapping, songs from each category for male 2 are compared.

Thirteen periods of altered song, due to tapping on the side of the cage during calling song, were produced at 24-26°C (buzz length: 658 msec, interval: 1019 msec, and period: 1677 msec). Comparisons between precopulatory song and alteration of solo due to tapping (Fig. 6) indicate a significantly longer mean interval for precopulatory song ($t_{(17df)} = 2.27$, $p < .05$). Other song parameters for these two categories of calling were not significantly different (buzz: $t_{(18df)} = .25$, $p < .05$, interval: $t_{(18df)} = 1.97$, $p < .05$). Variability for interval and period are similar, but variability for altered song buzz length increased compared to precopulatory buzz.

Solo parameters produced during tapping were compared to the unaltered solo song (Fig. 6). Buzz length and period for altered song were significantly shorter (buzz: $t_{(21df)} = 10.16$, $p < .01$, period: $t_{(21df)} = 3.10$, $p < .01$)

and there was no significant difference between interval lengths ($t_{(21df)} = 1.86$, $p < .05$). Variability for all parameters increased for the song portion altered by tapping.

Alexander (1956) was able to get a caged male to "split" his buzz each time the screen on which it was singing was jiggled. Although the song was not recorded and analyzed it was probably similar to the song and associated behavior of male 2. Although Alexander did not attempt to elicit this song change in the field; in this study, gentle tapping of perches shortened the buzzes of males under field conditions. Gusts of wind appeared to have the same effect.

The only apparent difference between song induced by tapping and precopulatory song was the behavioral context. Males producing the precopulatory song did so only after direct antennal contact with the female. It is possible, however, that tremulating females may induce males on the same perch to produce precopulatory song. After antennal and occasionally genital contact by the male, initiation of precopulatory calling, and separation of male and female by either male or female moving away, the male often produces several buzzes and the female remains stationary. Thus, the precopulatory song is unlike the song altered due to tapping because of the continuance of the precopulatory song devoid of vibrating movements by the female. The altered solo song returns to the normal solo length buzzes almost immediately.

There also appeared to be a lowering of intensity when the precopulatory song was produced; however, no objective quantification of the parameter was made.

One male, preconditioned by numerous contacts with a non-receptive female, began song similar to precopulatory song when the cage directly beneath him was tapped. The male extended his abdomen laterally and seemed to have a lowered intensity. He produced several buzzes after tapping was discontinued. The female had tremulated prior to the unsuccessful copulatory attempts by the male.

Many male-female interactions, apparently unsuccessful attempts at copulation, were not recorded. These interactions followed the general patterns of behavior as described above. Males rarely tremulated and rarely attempted copulation without producing the precopulatory call.

Male calling song appeared to be altered immediately after contact by the female; however, tremulation may play an important role in eliciting mating responses by the male. Precopulatory song appears to inhibit locomotion in receptive females at close range (within 1- 3 in).

Disturbance Sound

Disturbance sounds (Fig. 2) were produced under the following conditions: 1) cage tapping immediately after calling, 2) movement of vegetation on which males were perched in the field, and 3) prior to flight or hopping.

Direct observations of the wings indicate the sound is made during a single closure of the tegmina and is, therefore, one pulse of sound. Functional significance of the sound is not known.

Effect of Inter-animal Distance on Synchrony

The effect of inter-animal distance on synchrony was investigated with regard to 1) a distance at which synchrony could be maintained, 2) coefficient of variability (C.V.) for song parameters, 3) changes in parameter lengths, 4) mean song length for leader and follower, and 5) behavior associated with leader-follower relationships. A brief field investigation in August 1974 provided some information but the major part of the data is from a 1975 laboratory study.

In the laboratory, cages were suspended on a taut string located diagonally and about 4 ft above the floor of the acoustic chamber. Animals were placed at six different distances (stations 1-6) during the course of the experiment. Inter-station distances, determined by measuring from the center of cages, were 4 inches and 1, 4, 8, 14, and 20 ft. Red photographic masking tape (Scotch) was placed over the lens of a flashlight and used to view behavior with minimum disturbance of animals.

A different male was placed at station 0, the stationary position, for each new pair sequence. The other male was

moved outward through the series beginning with station 1 (4 in) or inward from station 6 (20 ft). Animals completed a synchronized song before they were moved. Oscillograms for 10 synchronized periods were analyzed and at least seven synchronous buzzes were allowed before recording began.

Placement of the recording mike closer to the follower facilitated analysis of oscillograms. It was mandatory for oscillogram measurements that the follower's buzz, which was overlapped by the leader buzz, be of greater intensity. The leader always began and ended his synchronous buzz before and after the follower (Fig. 2). Leader-to-follower phase differences averaged 118 msec for 24 songs and six different pair combinations of five katydids (s.d. = ± 75.77 , C.V. = 64.12, $n = 235$).

Four pairs of katydids (4-5, 5-3, 3-2, and 4-3) were moved through all stations. All records for all pairs, at all stations could not be analyzed because, in some instances, the follower buzz, falling within the leader buzz, could not be discerned. Two additional pairs (4-2, and 4-21) synchronized at a limited number of stations, and their records were added to the information for the four original pairs. Males 4 and 2 synchronized on successive nights at stations 1 and 6. Males 4 and 21 only synchronized at station 6. These songs were used in compiling parameter

means for the respective stations. Only three songs could be deciphered for station 5 for all katydid pair combinations.

Figure 8 is a comparison of 3 to 5 mean song parameter lengths for leaders and followers for six different pair combinations of five katydids. Mean song period of leaders remained relatively constant at each station. Change in period mirrored buzz length changes ($n=24$, $r=.94$, $t_{(22df)}=12.91$, $p < .01$). Mean coefficients of variability for leader parameters (Fig. 8) were consistent with those of solo calling (Fig. 3).

Follower mean buzz lengths were shortest at station 1 and became successively longer with increasing inter-animal distance (Fig. 8). Although the data suggest a significant difference between follower and leader period at station 1, the difference in these means is due to one pair of katydids. The follower (male 7) of the pair 8-7 became erratic in its calling and did not synchronize every buzz with the leader.

Buzz length variability of followers (range of C.V. = 6.4 - 21.7) is consistently higher than that of leaders at station 1. Follower buzz length variability decreases linearly with increased distance from station 1 to 5. Variability at stations 5 and 6 is near that expected for solo song (see Fig. 3 for comparison to solo C.V.).

Interval variability at station 1, usually greater for the follower, ranged from 6.3 to 58.6. One male (8) of the

Figure 8. Affect of inter-animal distance on leader and follower song parameters during synchrony. Parameters for synchrony at six distances (4 in - 20 ft) are shown on the abscissa for leaders and followers. Numbers within shaded bars indicate the number of means (10 parameters/mean) used to calculate the averages of means shown by bars. The remainder of the organization is the same as Figure 4.

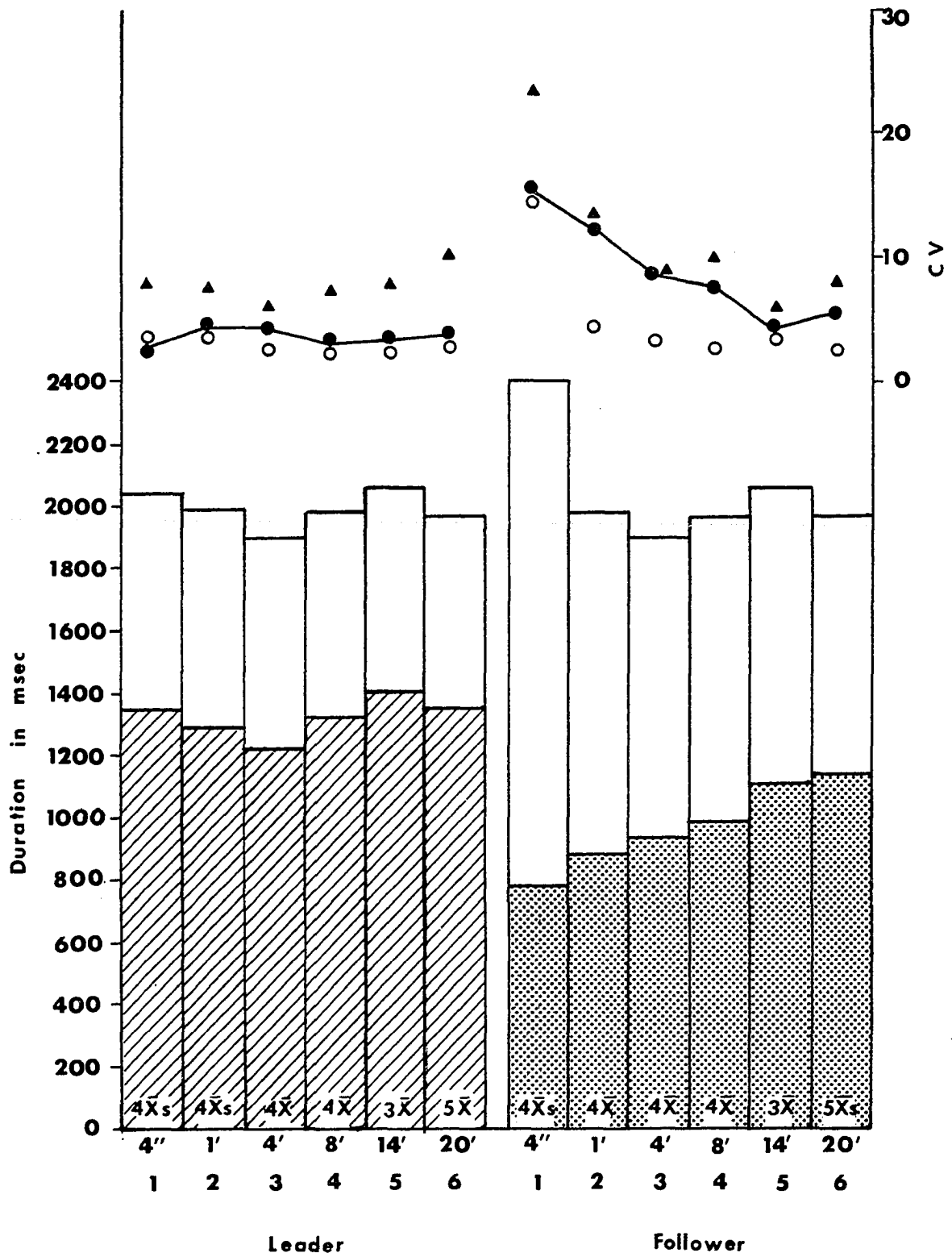


Table 3. The leader of synchrony at each station is shown for pair combinations used in 1975 synchrony experiments. See the text for an explanation of inter-animal distances at each station.

Stations Pairs							Solo		Solo		Rate Difference
	1	2	3	4	5	6	Male	Rate	Male	Rate	
4-5	5	4	4	4	5	5	5	31.0	4	32.5	1.5
5-3	5	5	5	5	5	5	5	31.0	3	28.5	2.5
3-2	3	3	2	2	3	3	2	29.9	3	28.5	1.4
4-3	4	4	4	4	4	4	4	32.5	3	28.5	4.0

pair 8-4 produced greater leader interval variability. At other stations, interval variability appears to be near that of the leader, but may be somewhat high at station 2.

Period variability at station 1 ranged from 2.9 to 45.5 for the follower. Two males (4, 1) produced about the same variability as the leaders (8, 4) and two males (1, 7) produced greater variability than the leaders (7, 8). The follower (male 7) that produced erratic synchrony was 20 times more variable than the leader. Another male (1) was slightly over twice as variable as the leader (male 7). At other stations leader and follower variability are similar.

Increased intensity with decreased distance between males could be the primary influence causing increased variability and decreased buzz length in follower synchrony. Mean sound levels of solo calling for males 2, 3, 4, and 5 ranged from 97.5 dB (s.d. = ± 3.22) at 4 inches to 66.5 dB (s.d. = ± 2.38) at 20 ft.

It seems likely that males with a faster buzz rate will usually lead synchrony. Both Shaw (1968) and Jones (1966a, 1966b) found leaders in alternating species of katydids have faster solo rates than followers. Evidence to support this assumption for N. nebrascensis was gained by comparing solo rates prior to synchrony to the eventual leader-follower relationships (Table 3). Male pairs 5-3,

and 4-3 with a rate difference of 2.5-4.0 buzzes per min were led by the faster male at each station. Male pairs 4-5 and 3-2¹ with slight rate differences of 1.4 to 1.5 buzzes per min switched from leader to follower depending upon which began synchrony first. Being the first male to sing did not appear to influence leader-follower relationships between males with the larger divergence in solo rates. The leader for pair 5-3 failed to initiate song 5 of 6 times (i.e., number of times initiated song at each of 6 stations) and male 4, a consistent leader of 3, never initiated song.

There did not seem to be any correlation between leader and last katydid to sing except at station 1 where the leader always sang last. Both leader and follower moved around their cages after termination of song (n=48) on all but 3 occasions involving 3 different males.

Thus, the data seems to indicate that males with faster rates tend to lead males with slower rates. When solo calling rates are closely matched, the male beginning synchrony appears to be more likely to lead. Contingent upon this assumption, rates may have important application to spacing dynamics. At inter-katydid distances of less than 1 ft, followers discontinuing song may move toward or away from the leader as the leader continues to call.

¹No information is available for the initial singer for male pair 3-2 at station 2.

Total time of song for leader and follower and duration of synchrony reflect the tendency for follower males to call for shorter periods of time when the inter-animal distance is less than 1 ft. Song lengths for leader and follower and the duration of first synchrony was recorded for all pairs at each station. If a follower re-engaged in synchrony, after termination of synchrony and subsequent movement around its cage, these additional songs were not included in the analysis of data.

At station 1, total singing time (20 min, 12 sec) was greatest for four leaders (range = 3 min 37 sec to 8 min 49 sec). Followers spent less time singing and the total for four males was only 6 min 8 sec (range = 5 sec to 3 min 38 sec).

The mean time spent in synchrony by all pair combinations was 2 min 47 sec (s.d. = \pm 1 min 9 sec, $n=24$). Mean song lengths for 24 leader and follower songs recorded at all stations were 4 min 5 sec (s.d. = \pm 1 min 26 sec) and 3 min 29 sec (s.d. = \pm 1 min 40 sec) respectively.

Analysis of variance indicated no difference in total singing time among stations for leader or follower ($F_{(5, 15)} = 1.86$ and $.61$ respectively, $p < .05$). Because of an unusually short song for one male at station 6, the variability was greater than expected at 20 ft. Another analysis was performed for followers excluding station 6 and the analysis indicated a significant difference among stations 1-5 ($F_{(4, 12)} = 4.78$,

$p < .05$). The largest mean song duration (4 min 10 sec at station 4) was within the range of inter-animal distances most often observed between males synchronizing in the field. Mean song duration at station 4 was compared to station 1 (\bar{x} = 1 min 52 sec) by the least significant difference method (Steel and Torrie, 1960). A significant difference was found at the .05 level for 12 degrees of freedom. Coefficient of variability for all parameters was low for both leader and follower at station 4 as compared to the follower at station 1 (Fig. 8). Low variability may lead to increase in duration of synchrony.

Paired comparisons of leader-to-follower song lengths were made separately for each station. Data suggest ($t_{(3df)} = 2.61$, $p < .05$) that mean song lengths of leaders are significantly different from followers at station 1. Mean song lengths of leaders and followers are not significantly different at any other stations.

Alexander (1967, 1968) has indicated that phonoresponding males chirp longer and more continuously than soloing males because of excitatory and inhibitory effects of the sound of one on the response of the other. The evidence presented above for synchronizing males indicates a possible inhibitory effect of synchrony on total song length. The mean song duration for leaders (4 min 5 sec) and followers (3 min 29 sec) was considerably shorter than mean solo song length for the same five katydids (\bar{x} = 6 min 3 sec).

An attempt was made in August 1974, to analyze the effect of inter-animal distance on synchrony. This study, conducted on an Ames golf course, was similar to laboratory studies previously discussed. Little information could be obtained from this study due to the reluctance of males to synchronize at more than one or two distances. Cool temperatures and lack of cover probably inhibited calling. Singing improved when oak leaves were placed over the cages, but only one pair of males, 13 and 22, produced synchrony at more than two distances and is the only pair analyzed. The temperature was 22-24°C for recordings.

Little data was available for comparison of solo rate to leader-follower relationships, but available data supports the postulate made from laboratory studies that leaders are males with faster rates. Male 22, the leader, had a rate of 29.3 buzzes/min based on three periods just prior to synchrony. The follower buzz rate determined about five min later from 2 periods was 26.7 buzzes/min.

Synchrony at an inter-animal distance of one foot was always led by male 22 which had a mean buzz length of 1390 msec. Follower buzz lengths were always shorter than the leader during synchrony ($\bar{x} = 839$ msec). The leader mean interval was 721 msec and the follower's was 1263 msec.

Males 22 and 13 sang simultaneously at 75 ft but could not remain in phase. There was marked increase in C.V. for

buzz, interval, and period for synchrony at 75 ft compared to synchrony at 1 ft and to solo calling at 24-26°C (laboratory conditions). Variability for solo, synchronous singing at 1 ft and asynchronous singing at 75 ft respectively for the follower were: buzz = 12.33, 11.17, and 18.75; interval = 13.52, 11.75, and 26.53; and period = 6.82, 6.79, and 17.64. Period ranges were as follows: solo = 1577 to 2042, synchrony at 1 ft = 1830 to 2480, and asynchrony = 1618 to 4181 at 75 ft.

Song parameter comparisons between 1 ft and 75 ft show mean buzz length increased from 839 to 1158 msec, interval increased from 1263 to 1357 msec and period increased from 2102 to 2515 msec.

Although male 13 responded to buzzes by male 22 at 75 ft, synchrony was often considerably out of phase. The animals would alternately produce normal, shortened, or long periods. Similar difficulty in synchronizing was observed under natural conditions in field studies. Such difficulty was estimated to occur at distances ranging from 60 to 100 feet depending upon ambient conditions. At distances very much further males did not appear to respond to the other's call. Males 13 and 22 produced solo songs simultaneously at an inter-animal distance of 150 ft, but made no response to the other's call.

In situations in which males were synchronizing with a distant chorus, they appeared to be able to synchronize at

somewhat greater distances (perhaps 5 to 10 ft), however, good synchrony was unusual beyond 60 ft. Isolated males were observed on many occasions, especially early in the evening, to make short flights toward a synchronizing chorus until they were able to maintain properly phased synchrony.

Response Mechanisms Involved in Synchrony

The stimulus-response mechanisms involved in maintaining synchrony were investigated using artificially produced stimuli. It was hoped that by playing stimuli to calling males the adjustments required to attain and maintain synchrony could be discerned.

Responses to 80 dB imitation buzzes played to seven calling males were recorded. A total of 166 imitations were played to the 7 katydids within periods called test periods (Fig. 9). The test series for individuals began after the initial ten buzzes of song. At least two buzzes were allowed for recovery after an imitation was played. Katydid parameter lengths were measured and analyzed from oscillograms.

Responses to randomly spaced imitation buzzes were pooled for all katydids by converting parameters to ratios. In order to convert to ratios, parameter means for all periods immediately preceding the imitation were calculated. The parameters within the response periods were recorded

Figure 9. Diagrammatic representation of the relative position of single electronic buzzes to natural buzzes played to soloing katydids.

a. Diagrammatic representation of a portion of solo calling to which a stimulus buzz was played.

b-d. The relative position of imitation buzzes to natural buzzes within and extending beyond the test period (TP).

B_{-1} , I_{-1} - Buzz and interval prior to TP.

B_0 , I_0 , B_1 , I_1 - Buzz and interval of response periods (RP_1 , RP_2).

BOS - Buzz overlapped stimulus.

SD - Stimulus delay.

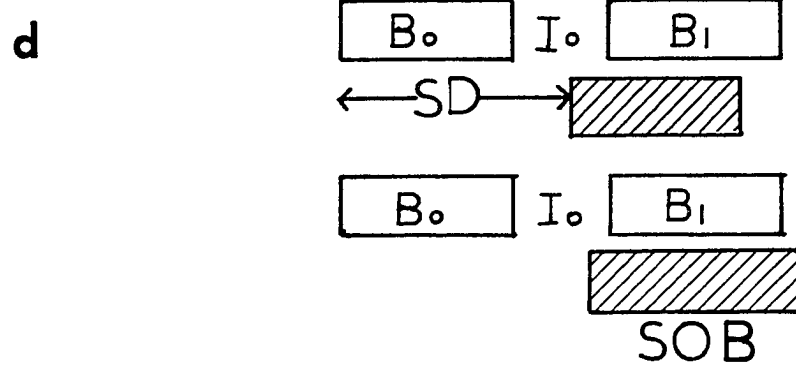
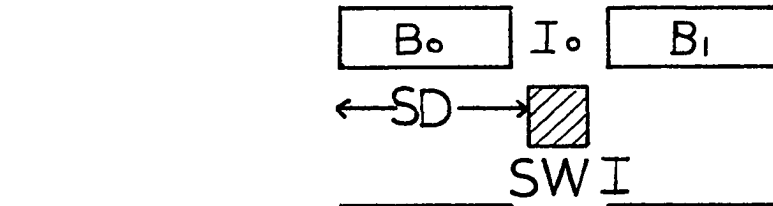
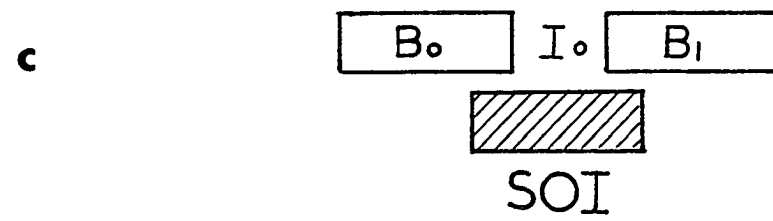
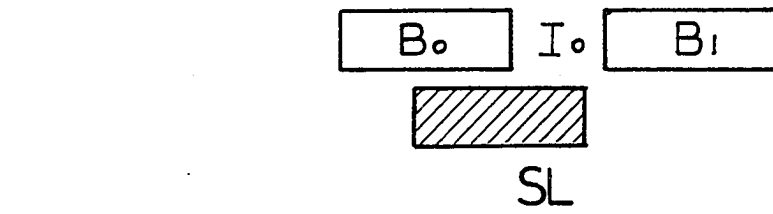
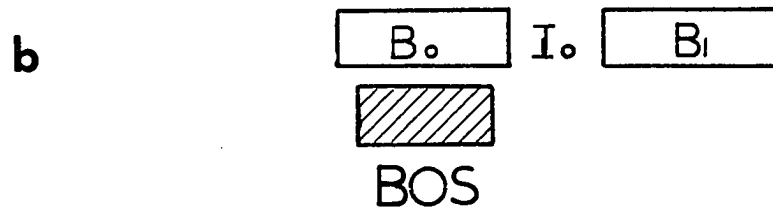
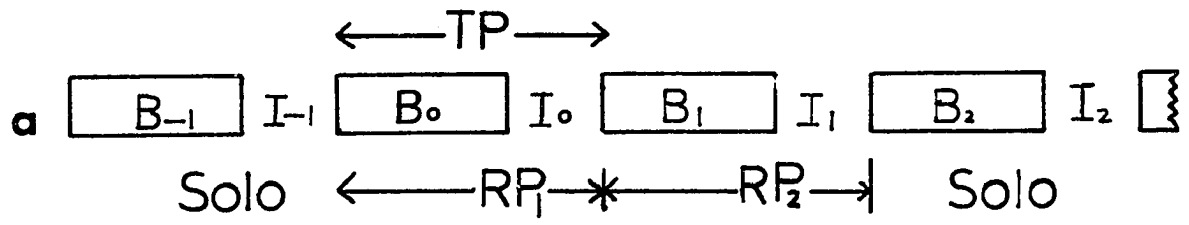
SL - Stimulus lag.

SOI - Stimulus overlapped interval.

SWI - Stimulus within interval.

SOB - Stimulus overlapped buzz.

////// - Stimulus buzz.



as a fraction of pre-test means for each parameter. These ratios were plotted against stimulus delay (SD) and stimulus lag (SL) (for an explanation of these terms see Fig. 9).

Stimulus delay was converted to a ratio by using the katydid buzz within the experimental period as the denominator (SD/B_0). Thus, a value less than one indicated the imitation began within the buzz (B_0) (Fig. 9-b, c). Ratios larger than one indicate an imitation beginning within the interval (I_0) (Fig. 9-c, d). Stimulus lag, always within I_0 or I_1 , was converted to a fraction by using the mean of all intervals just prior to the test period as the denominator ($SL/\bar{x}I-1$). The mean ratio, referred to as normal for the parameter, is 1.00 for both buzz and interval (s.d. = .04 and .09 respectively, $n=166$) and is based on the mean for B_{-1} and I_{-1} (Fig. 9-a).

Twenty-seven stimuli ranging from 424-1371 msec were played within the katydid's buzz as illustrated in Fig. 9-b. Little or no alteration of parameters occurred within RP_1 and RP_2 (Fig. 10). I_0 appears to be slightly more variable than normal, but no definite trend can be detected.

Fifty-four stimuli ranging from 424 to 1371 msec were used. Stimuli extending into RP_1 (Fig. 9-b) affected I_0 (Fig. 11). I_0 usually increased after SL reached 40% or more of the normal interval; variability of I_0 was high

Figure 10. Katydid's response to electronically-produced imitations of their buzzes. Katydid buzz and interval responses are shown for RP_1 and RP_2 after situations in which the buzz overlapped the stimulus (BOS) within the test period (TP) (see the diagramatic representation of BOS in part a). Magnitude of the katydid's response expressed as a ratio of the pre-test mean for the parameter is on the ordinate (pt. a-d) and the initiation of the stimulus (SD) is expressed as a ratio of B_0 on the abscissa (pt. a-d).

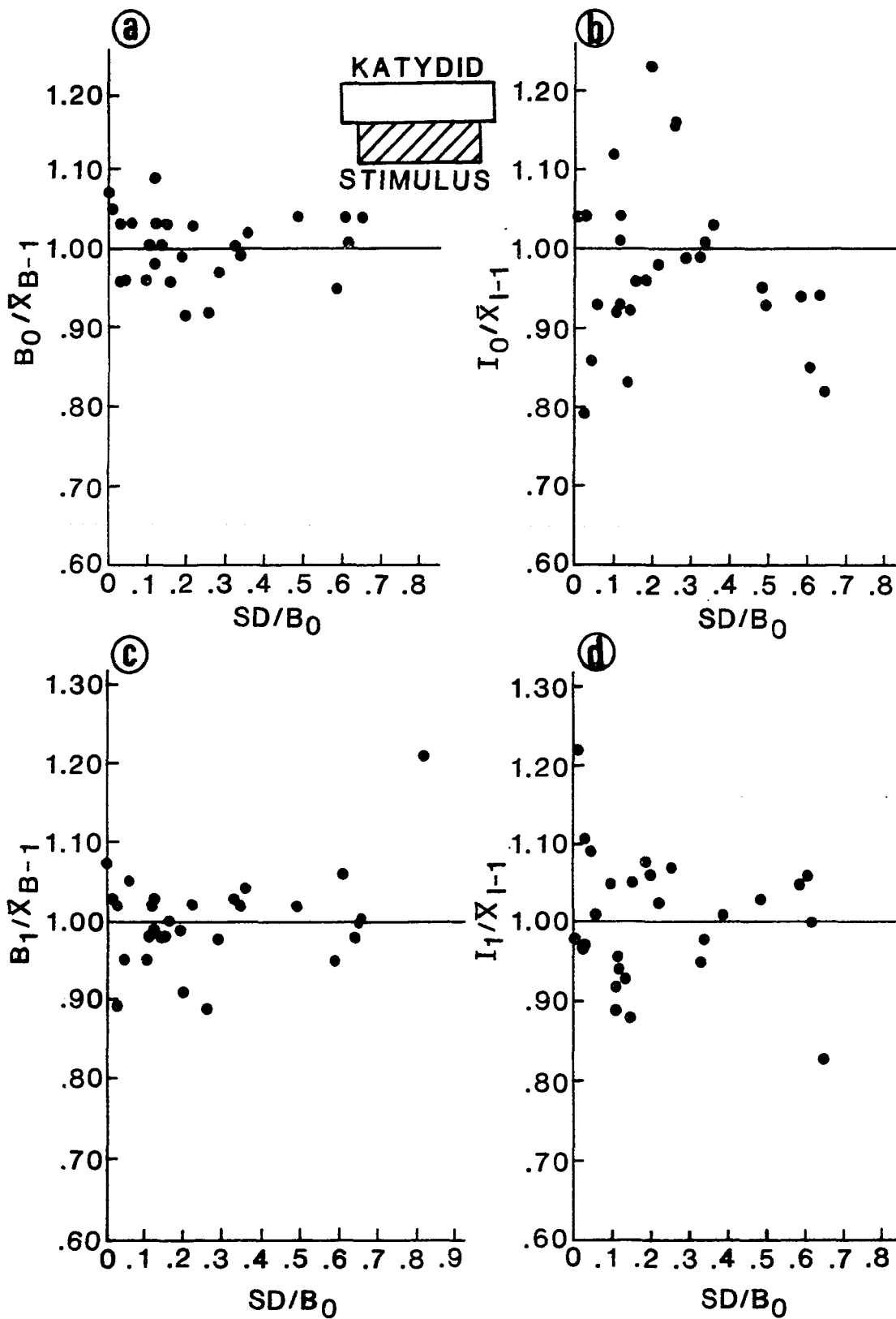
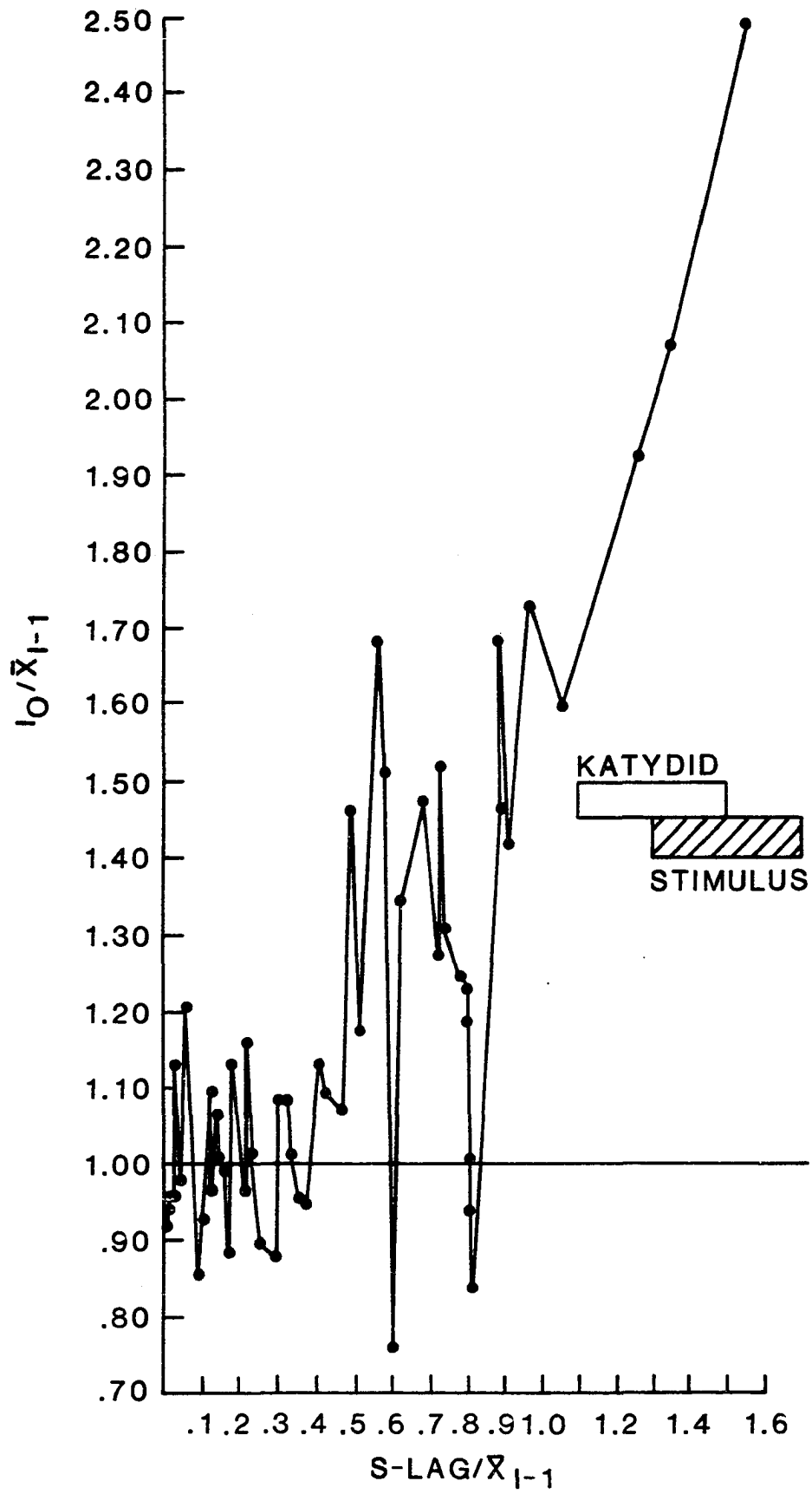


Figure 11. Katydid response to electronically-produced imitations of their buzzes. Adjustment of I_0 to imitations that extended from B_0 into I_0 are plotted. Magnitudes of each response is plotted on the ordinate as a ratio of I to the pre-test means ($I_{-1}\bar{x}$). Stimulus-lag (SL) is plotted as a ratio of $I_{-1}\bar{x}$ on the abscissa.



when stimulus terminated at a point less than 40% of the normal interval. No pattern of adjustment was found for parameters within RP_2 .

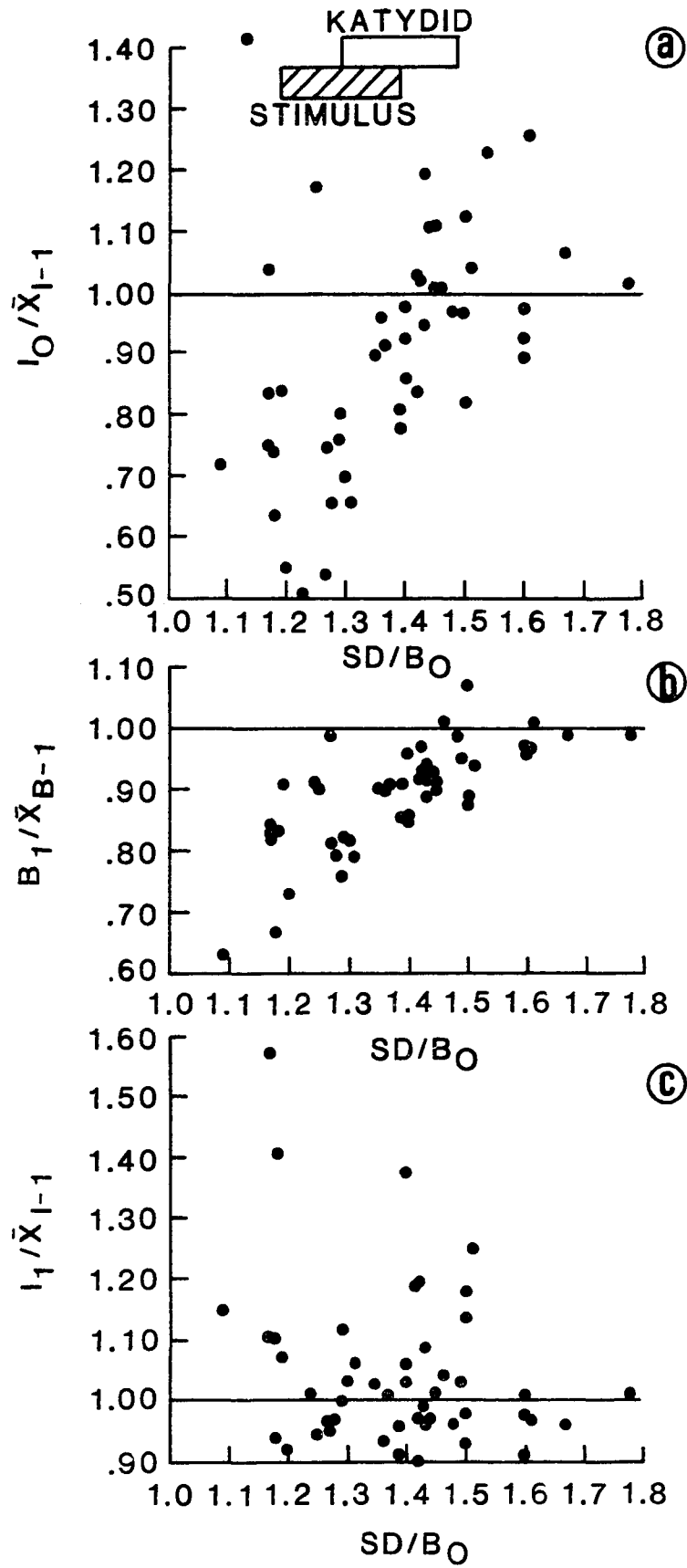
The overlapped I_0 and the following B_1 were shortened when stimuli of 1272 to 1880 msec completely overlapped I_0 (Fig. 9-c). Nineteen intervals were overlapped by stimuli for five katydids producing shorter than normal I_0 's (ratios: $\bar{x} = .84$, s.d. = .1). All 19 B_1 s within RP_2 were shortened (ratio: $\bar{x} = .76$, s.d. = .09). The SD/B_0 ratio ranged from .22 to .99 for stimuli producing the shortening response.

Four stimuli ranging in length from 425 to 1290 msec fell entirely within I_0 . I_0 was longer for these four periods (ratio: $\bar{x} = 1.74$, s.d. = .49).

Forty-seven stimuli, ranging from 424-1371 msec were played so that the stimulus began within the test period, but extended part way into (B_1) as illustrated in Figure 9-d. These stimuli, initiated prior to the katydid's buzz, produced either a shortening, (most frequent effect), no effect, or lengthening of I_0 and a shortening (most frequent effect) or no effect on B_1 (Fig. 12-a, b). I_1 had all normal values except for approximately 9 sample points which were long.

Fourteen stimuli beginning in I_0 ended in I_1 . Stimulus length ranged from 1271 to 1880 msec. I_0 varied from shorter than normal to longer than normal as B_1 stimulus delay in-

Figure 12. Katydid response to electronically-produced imitations of their buzzes. Katydid I_0 , B_1 , and I_1 responses are shown following a situation in which the stimulus was initiated in I_0 and extended into B_1 (see diagram in pt. a). The remaining organization is the same as Figure 10.



creased (Fig. 13-a). B_1 was always shorter than the normal value (Fig. 13-b). All but one I_1 was longer than normal (Fig. 13-c).

Response to constant rate imitations

Katydids were exposed to 10 1-sec imitation buzzes produced at constant rates ranging from 23.5 to 46.2 buzzes per min at 30-32°C. One katydid, exposed to the full range of imitation rates, was unable to match the imitation rate at 23.5 and 46.2 buzzes/min (Fig. 14). The male's solo calling rate was 29.35 periods/min. Leaders in natural synchrony do not deviate significantly from their solo rate when synchronizing, however, followers match the leader rate. This male was unable to match the imitation rates that varied from the solo rate by +57.24 and -19.83%. Oecanthus fultoni, a synchronizing tree cricket, had limits for solitary rate matching of +31 and -51% (Walker, 1969).

The katydid switched from leader to follower during series 1, 2, 6, 8, 9, 10, and 12 and led all stimulus repetitions during series 3, 4, and 5 (Fig. 14). It followed the stimulus during series 7 and 11.

Katydid adjustments to both manually-timed stimuli and continuous-rate stimuli appear to be identical. There does not appear to be any response to stimuli falling within a buzz (BOS) (Fig. 15-B), but definite responses were elicited

Figure 13. Katydid response to electronically-produced imitations of their buzzes. Adjustment of I_0 , B_1 , and I_1 to imitation buzzes that extended from I_0 to I_1 are plotted. Stimulus lag (SL) in part c is plotted as a ratio of $I_{-1}\bar{x}$ on the abscissa. The remaining organization is the same as Figure 10.

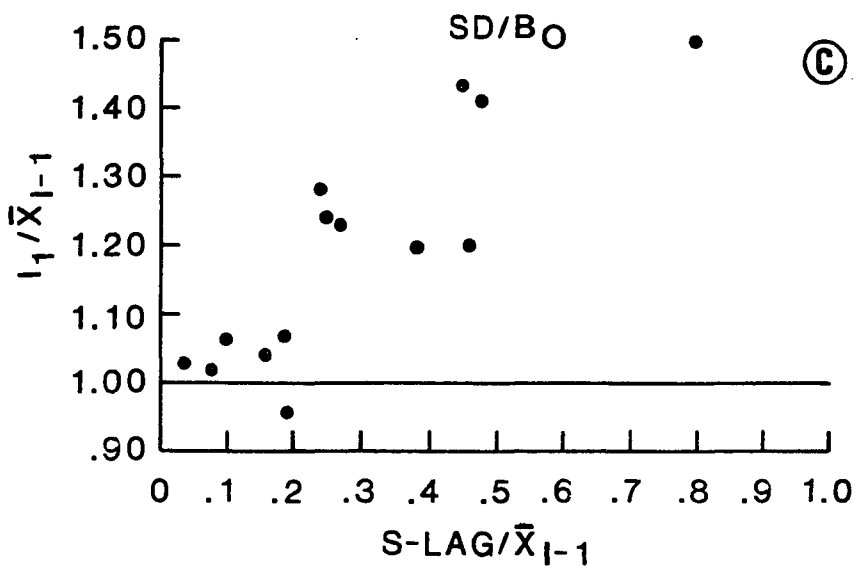
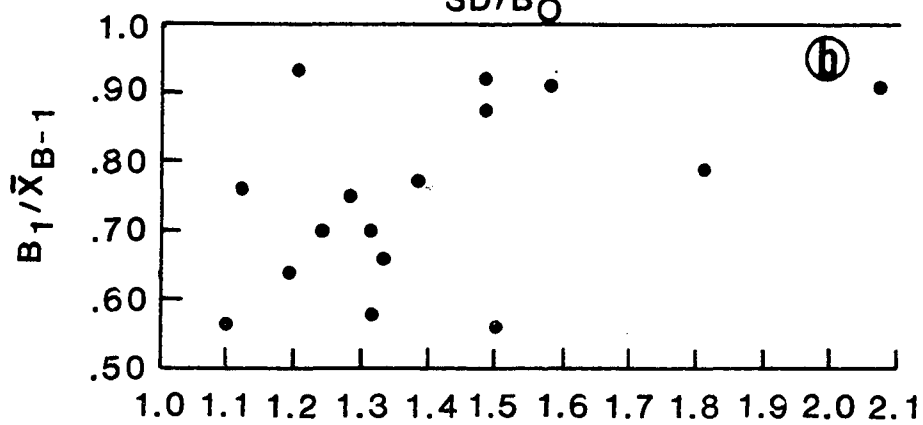
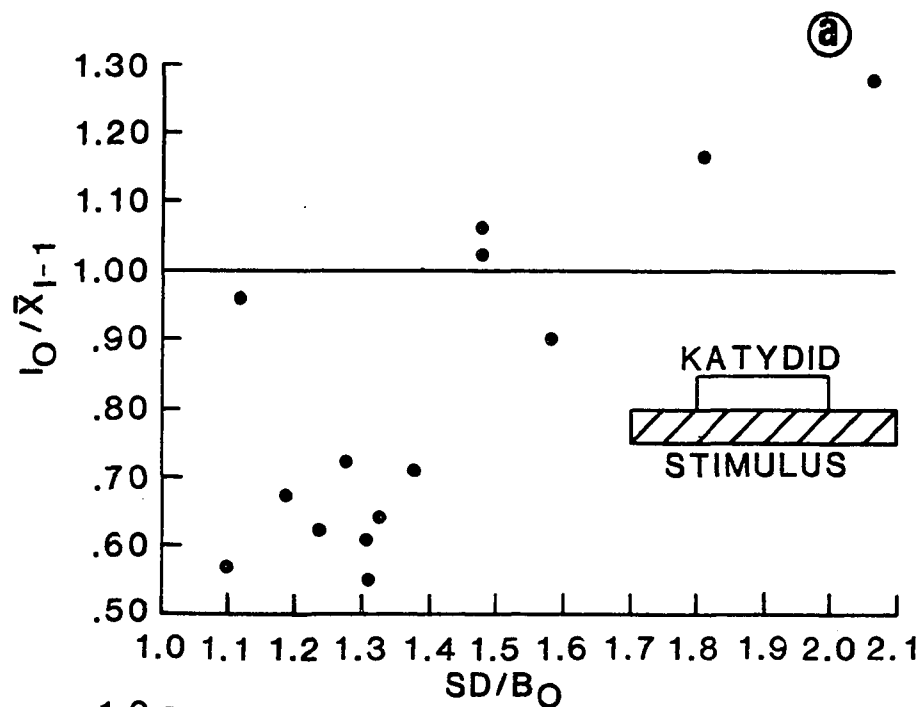


Figure 14. Katydid synchrony with electronically-produced continuous rate buzzes. Each response series on the abscissa is a mean rate for at least 10 repetitions of imitation and katydid buzzes.

x = imitation, o = katydid

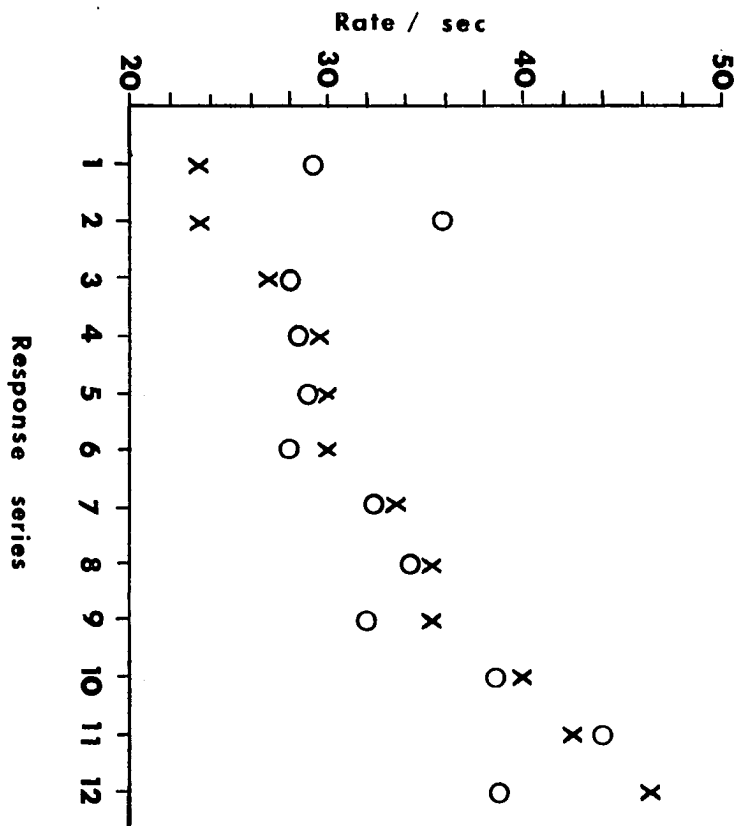
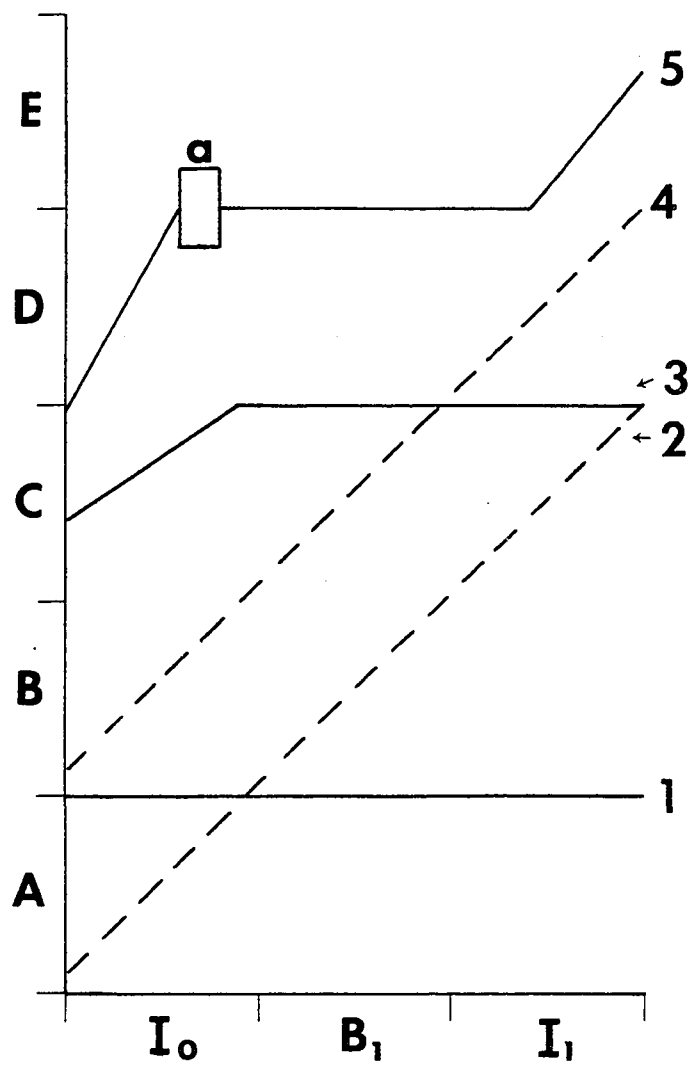


Figure 15. Idealized model of katydid responses involved in synchrony. The distance from line 2 to line 4 represents the .8 sec duration of an imitation stimulus. Letters on the ordinate each represent a duration of .8 sec and katydid song parameters are indicated on the abscissa. As the imitation is moved diagonally through I_0 , B_1 , and I_1 , the resulting effect on katydid buzz lengths (line 1-3), interval length (line 3-5) and period length (line 1-5) can be noted. Point a represents an area of either increase or decrease in period length due to the effect of initiation of the imitation at this point in I_0 .



when stimuli began or extended into intervals. A marked increase occurred when SL extended beyond 300 to 400 msec into I_0 (Fig. 15- I_1).

Occasionally, the stimulus overlapped the interval (SOI) (Fig. 9-c). This caused a shortening of I_0 and B_1 . It is not known if the shortening responses can be attributed to SD or SL. It is likely, however, that SL elicits the response because there is no clear trend for shortening of I_0 by BOS situations. If this type response occurred naturally between katydids, the male causing the overlap would be delayed by B_1 of the leader and the two would likely be in phase on the next buzz.

Natural or imitation buzzes beginning less than 150 to 250 msec prior to a katydid's buzz do not seem to cause much change in the follower's I_0 , but B_1 is usually shortened slightly (Fig. 15- I_0). Generally, stimuli beginning beyond 150 to 250 msec before the following katydid caused a shortening of both I_0 and B_1 (Fig. 15- I_0); however, there was a point of either lengthening or shortening of I_0 that began about 150 msec prior to B_1 and extended to about 350 msec into I_0 (Fig. 15- I_0 , pt. a).

A situation, very much like one buzz of natural synchrony, occurred when stimuli overlapped buzzes (SOB) (Fig. 9-d). Stimuli beginning in I_0 may shorten this interval and B_1 while the extent of SL into I_1 affects the length of I_1 (Fig. 13).

It is interesting to note that males can follow a continuous rate stimulus for long periods using only short responses (I_0 and B_1) (Fig. 14). The katydid can be driven at much faster rates than its normal solo rate. If the imitation rate is increased sufficiently the katydid's capacity to shorten is exceeded and both shortening and lengthening responses are elicited as the stimulus begins to fall irregularly within the katydid's period (Fig. 16-I). When this occurs the katydid's rate falls due to the long responses (I-a) and release from shortening or lengthening due to BOS (I-c). On the other hand, as stimulus rate is decreased, there is a point at which katydids return to near normal rates, then decrease rate and finally exceed normal rate (Fig. 14). Slowing of katydid rate in response to decreased imitation rate appears to be due to the delaying effect of SL. The katydid rate is increased at very slow imitation rates due to interspersed normal parameter and shortening responses (Fig. 16-II). In instances where stimuli fall irregularly within the katydid's period, the rates may be faster than solo song because the magnitude of the short responses are greater than the long responses.

The natural interplay of responses postulated from experiments with artificial stimuli can be seen from careful study of Figure 17. This figure is a visual illustration of leader-follower relationships for 20 periods of

Figure 16. Katydid response to electronically-produced continuous rate buzzes. Katydid rate and stimulus rate are shown on the ordinate. Duration in msec for buzz and interval is written above each parameter for periods a-d. Imitation lengths are 1 sec.

////// = imitation buzz.

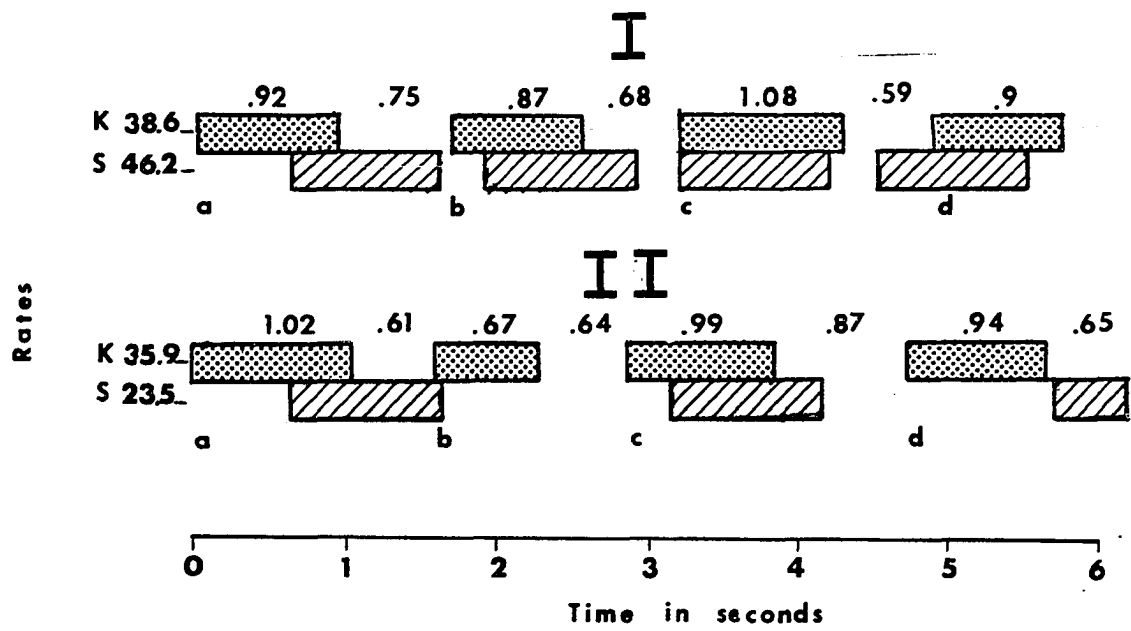
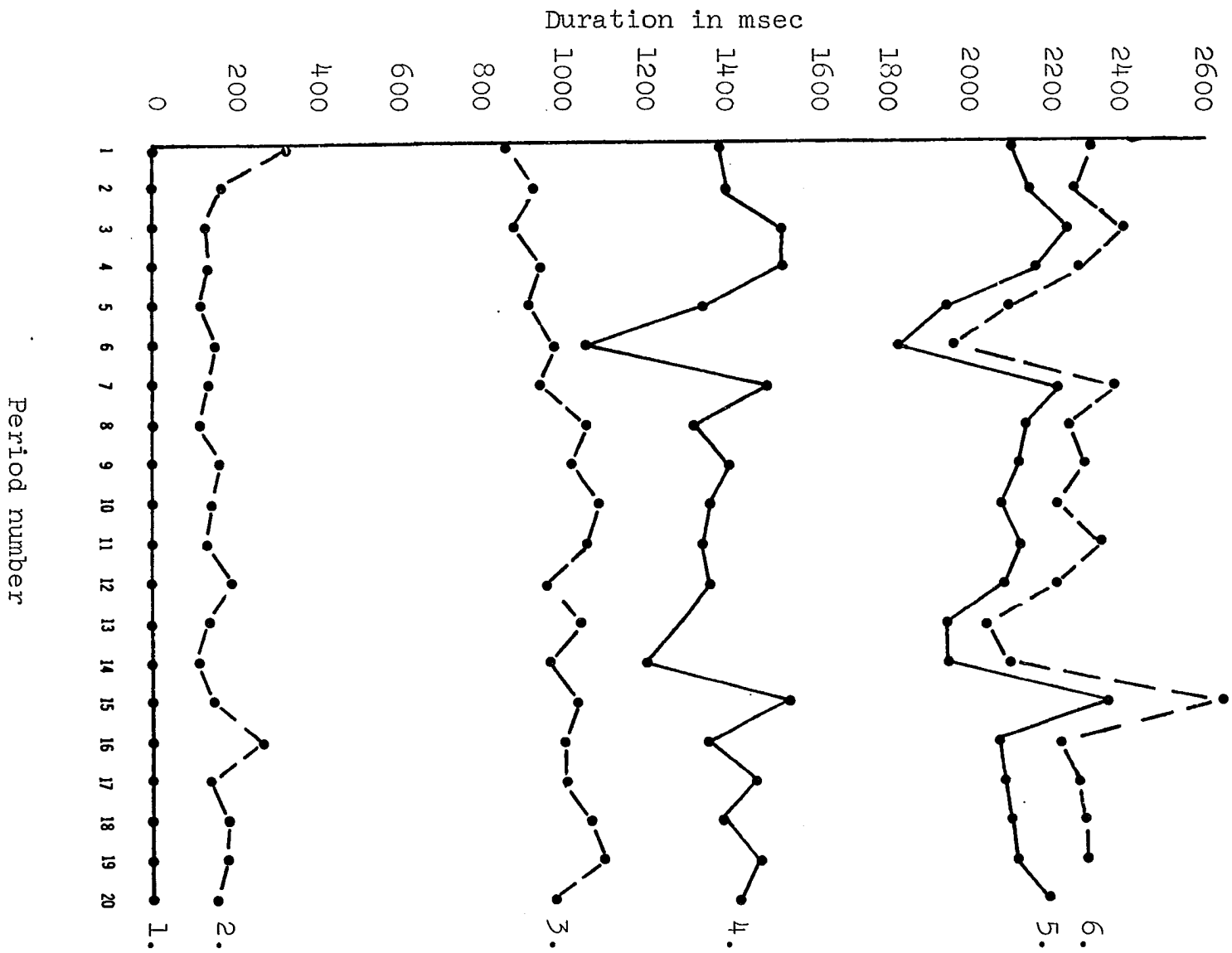


Figure 17. Analysis of leader-follower relationships in natural synchrony. Twenty periods of synchrony are indicated along the abscissa with parameter duration (msec) indicated on the ordinate. A series of points representing initiation or termination of a particular parameter is indicated by numbered lines on the right ordinate: 1) initiation of leader buzz, 2) initiation of follower buzz, 3) termination of follower buzz, 4) termination of leader buzz, 5) leader period length and 6) beginning of a second follower buzz.



synchrony at 1 ft distance between two animals. Increase or decrease in duration of leader-to-follower buzzes (line 1 to line 2) is reflected in an increase or decrease in buzz length for the follower ($r = -.70$, $t_{(18df)} = 4.16$, $p < .001$). Leader periods (line 5) mirror changes in leader buzz lengths (line 4) ($r = +.88$, $t_{(18df)} = 7.86$, $p < .001$). Similar correlation of buzz length to period length was found for some males during solo calling (Table 1).

The distance between line 2 and line 6 represents follower period lengths. The degree of matching between lines 1-2, and 5-6 indicates an ability to remain in close phase during synchrony (mean leader to follower differential = 163 msec, $n = 20$, C.V. = 33.0). Points 6-7, and 14-15 on line 6 indicate a capacity for rapid change in follower period length, without a corresponding change in prior phase relationships, i.e., points 7 and 16 respectively on lines 1-2. Note, however, the close correspondence of leader buzz lengths to increased follower intervals.

The following mechanisms appear to be operating as katydids attain and maintain synchrony: 1) leaders appear to be males with faster rates, 2) follower buzzes do not affect leader buzzes unless they get out of phase, 3) synchronous phase relations are attained by either shortening I_0 and B_1 or shortening B_1 and lengthening I_0 , and 4) synchrony is maintained through use of the short and long responses by the follower.

The Snowy Tree Cricket (Oecanthus fultoni) shows a similar lengthening of I_0 , but occasionally the following B_1 would also be lengthened (Walker, 1969). Walker did not report immediate shortening of I_0 , rather, stimuli played in I_0 caused B_1 and I_1 to shorten. He termed this type of synchrony proepisodic, i.e., responses were thought to be elicited by preceding episodes (stimuli or natural buzz).

No apparent excitatory effect on buzz rates following natural or artificial synchrony was found. Walker (1969) did not find a post-synchronous excitation effect in analysis of synchronization of snowy tree crickets; however, Shaw (1968) found post-inhibitory excitatory effects in the alternating true katydid. Jones (1966a, 1966b) found that the alternating bush cricket (Pholidoptera griseoptera) has post-excitatory effects lasting several minutes after alternation has ended.

Inter-species interruption

Inter-species interruption of song occurred when N. nebrascensis and N. ensiger sang within approximately 10 ft or less of one another under both natural and laboratory conditions. N. ensiger's normal song (Fig. 18-I), consisting of closely spaced bursts of sound, became patterned much like that of N. nebrascensis during song interaction. N. nebrascensis shortened buzzes when N. ensiger sounds immediately preceded buzzes (Fig. 18-II, a).

Figure 18. Simultaneous singing of N. nebrascensis (n) and N. ensiger (e). Part I was recorded at 18°C. Part II was recorded at 25°C. a, b, c, - N. nebrascensis short buzz, short interval and long interval respectively.

I

NEOCONOCEPHALUS ENSIGER

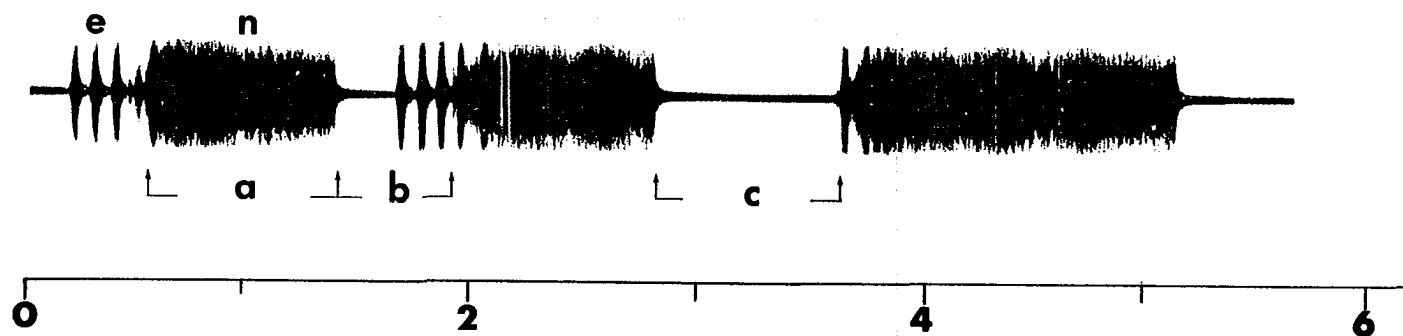
CALLING SONG



II

N. NEBRASCENSIS - N. ENSIGER

SONG OVERLAP

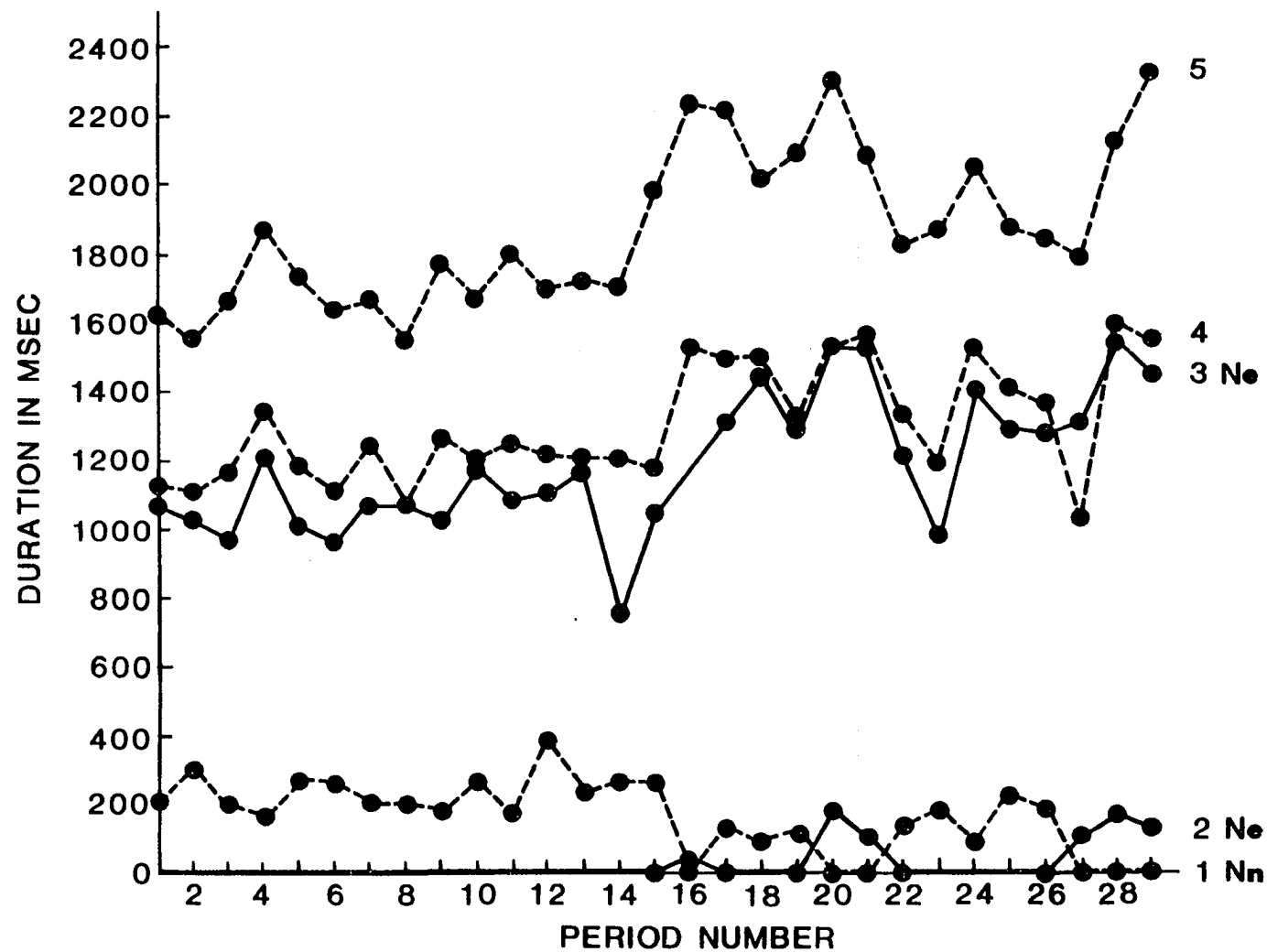


Intervals were either shortened as in Figure 18-II, b or lengthened as in Figure 18-II, c.

Figure 19 indicates the expected shortening of N. nebrascensis I_0 and B_1 when the buzz of a conspecific began 200-300 msec prior to the follower (pts. 1-15). Subsequent lengthening of B_1 and I_0 occur as the lead is switched or when the distance between line 1 and line 2 is decreased (pts. 16-24). The long I_1 at point 27 is probably caused by N. ensiger sound lagging into I_1 . During this interaction, N. ensiger discontinued calling as N. nebrascensis continued. N. ensiger resumed calling when the near-by N. nebrascensis discontinued calling.

McNeill, according to Rehn and Hebard (1914), stated that N. nebrascensis begins song earlier in the evening than N. ensiger and that N. nebrascensis choruses continuously. Thus, chorusing by N. nebrascensis may inhibit calling by N. ensiger. This investigator has observed that N. ensiger calls sporadically in areas where N. nebrascensis is chorusing. Later at night, after the number of N. nebrascensis males calling decreases, N. ensiger has often been heard to begin calling in the same area. Chorusing appears to be important in species isolation between these closely related species. N. ensiger males in the immediate area of chorusing N. nebrascensis might encounter difficulty in attracting a mate through use of their calling

Figure 19. Analysis of interspecific acoustical interaction. Leader-follower relationships for 29 periods are shown for N. nebrascensis (Nn) and N. ensiger (Ne). Organization is the same as Figure 17.



song. This could lead to reduced number of progeny in the area and possible emigration by the species most effected by the interaction. Separation of the species would reduce fortuitous meetings between interspecies members of opposite sex.

Other species may have the capability of disrupting calling by N. nebrascensis. In field observations, it was noted on several occasions that calling was disrupted by calls of O. vulgare and that N. nebrascensis males subsequently moved away from the O. vulgare colony.

Aggression and Hierarchical Relationships between Males Aggressive behavior

Field observations Apparently, contact aggression between conspecifics is relatively rare. Apparent contact aggression in which two males grappled was observed only once in the field. Both males, facing in opposite directions, were laterally extending and curving their abdomens toward each other and raking toward the other male with their forelegs. After spotting the males with the flashlight, they immediately moved apart presumably in response to the light.

Five instances of mutual or one-sided antennal contact were observed in the field. On one occasion, a male (male 1) was observed calling in a horizontal position from a mat of grass a few inches above the ground. A second male (male 2) that had previously been marked was observed about 1 ft

from the calling male. Male 2 had been the only male in the immediate area for the previous 7 days. This male was not calling, but was crawling toward the calling male 1. Male 1 discontinued calling shortly after the light shone on him. This male then began to crawl toward male 2. Both would pause briefly and tremulate and then continue slowly toward the other. Tremulation consisted of two or three up-and-down movements. Each male tremulated two or three times. As they came into antennal contact, the second male immediately turned and produced two short bursts of sound. Both males moved apart slightly as male 2 paused then produced another short burst of sound followed by a 1-2 sec pause, a short burst of sound, a short pause, and another short buzz. During the sound production sequence both males moved until they were about 6 in apart. Male 1 then produced two closely-spaced, short buzzes a few seconds after male 2. Male 2 immediately produced two closely-spaced, short buzzes followed by a 1-2 sec pause and then called continuously. Male 1 moved during Male 2's calling to a perch about 1.5 ft. away, remained stationary for a period of time, then hopped away (flight may have followed the hop, however, this could not be observed due to darkness). Male 2 remained in the area, but discontinued calling. Male 2 was relocated in the area five nights later, but had moved to a chorus about 50 ft away. No male called from the original area for the remainder of the season.

On three occasions males were seen to come into mutual antennal contact while synchronizing within a few inches of one another. In each case both moved away from contact and continued to synchronize. The leader of synchrony maintained a more stationary position and continued to call when the follower dropped out. In all three instances, the follower in synchrony crawled or flew away from the encounter after discontinuing calling.

On one occasion a calling male lashed his antennae up-and-down touching the side of a silent male. The silent male immediately flew (the effect of the light on the male could not be ruled out as a causative factor in the flight, although the encounter was about 10 ft away at the time it was observed). The remaining male continued to call from a stationary position.

Additional situations were observed that might have included contact aggression, but no detailed analysis could be made due to the rapidity of occurrence, the difficulty of spotting animals in tall dense grass in the dark, and the disturbance necessary for observation.

On several occasions the grass stem on which a male was calling was tapped gently. Males usually flew; however, on four occasions the male continued calling¹ and moved 6 to

¹Alteration of song similar to that discussed previously (Fig. 6-2) occurred.

12 inches to the investigator's finger. The male then either flew or turned and moved back down the stem. Two males returned to the point of tapping several times.

Laboratory situations Under laboratory conditions when males were allowed to synchronize within 4 to 8 in from one another, the follower male always discontinued calling first and moved around in its cage. Such activity was recorded seven times. At greater distances, it did not seem that one male continued calling more often than another. Moving around the cage after calling was characteristic for both leader and follower. The actual distances that a male moved after an encounter was never measured: however, many times silent males were located within a few feet of calling males under field conditions.

Male-male interaction behavior was observed under simulated field conditions by placing seven males in the acoustic chamber which had been provided with potted grasses and other herbaceous plants for perches. Four, 25-watt, red light bulbs covered with red photographic masking tape (Scotch) were used to view behavior. The acoustic chamber was maintained at 24-26°C and behavior was observed from approximately 9:00 P.M. to 3:00 A.M. on August 17 and 18, 1974.

Males, perched within 1-2 ft of each other, tended to move together after they began synchrony. In three cases in which the leader could be discerned, it was found that

the follower was the first to discontinue calling and crawl or fly away. The displaced male occasionally returned to the same plant and continued synchrony. On one occasion the returning male gained the lead in synchrony as it moved to within a few inches of the other male and remained stationary as synchrony continued. After a few minutes the follower dropped out and flew.

Closely-spaced, synchronizing males rarely made contact, but one or both usually moved back and forth on a stem, alternately moving closer and further apart, while remaining on the same stem or bush. Eventually one male would move several feet away or discontinue calling and remain silent 1-3 ft away.

During one sequence of synchrony males made head-to-head antennal contact. One of the males moved forward and to the side of the other as the second male remained stationary. Both males extended and curved their abdomens laterally and toward the other. They raked weakly with their fore-legs making contact with the other's legs and abdomen. One male eventually moved away and the other remained stationary. Rarely synchronizing males remained on the same plant (1-3 ft apart).

Movement by silent males within the same plant seemed to elicit movement by calling males which would first move toward and then away from the movement as they continued

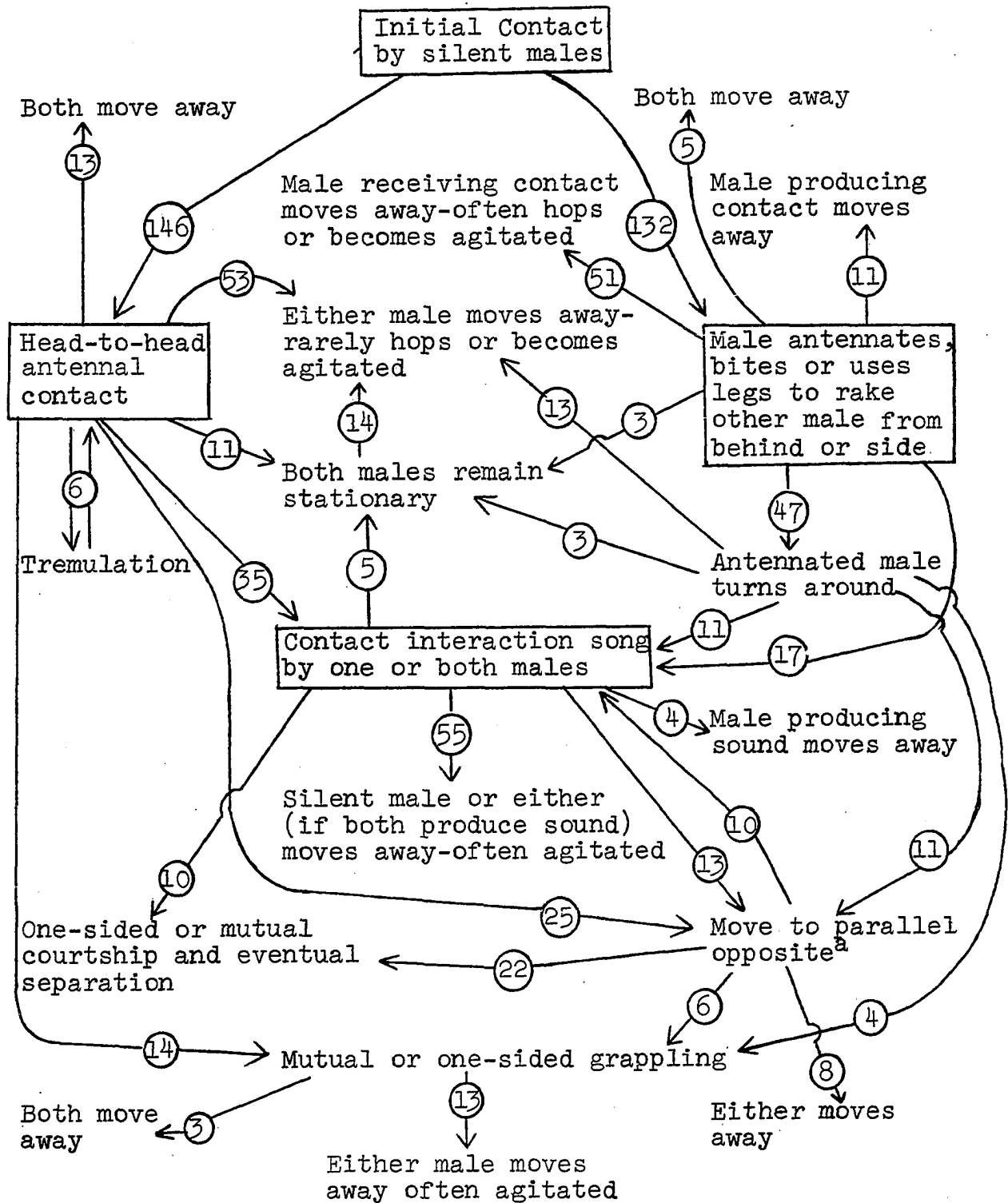
calling. The calling male usually became stationary eventually and continued calling.

Silent males occasionally made contact as a result of movement after cessation of calling. Head-to-head, mutual, antennal contact often resulted in turning away by one or both males. At times a CtS was produced by one or both participants and some grappling and abdomen extension occurred. These actions usually resulted in movement by one male as the other remained stationary. One silent male moved to and antennated a second silent male from behind. The first male simultaneously turned and produced a five-buzz CtS and the second male crawled away. The first male followed briefly then turned and moved back to approximately his original position.

In another instance, males reciprocated mutual head-to-head antennal contact and when one male moved forward under the other male, both raked at the other with their fore-legs from opposite sides of the same grass stem. A burst of sound was heard and one male immediately turned and moved down the stem as the other remained stationary.

Analysis of contact interactions Contact interactions were studied by pairing males in a small empty wire mesh cage (4" x 4" x 7"). A total of 43 different pairings involving 18 males resulted in 278 different male-male contacts. Each pair of males made from 4-10 contacts in 10-30 min before observations were terminated. Observations were made in the

Figure 20. A diagram of the kinds of interactions between adult male katydids. Numbers indicate the number of times paired events occurred.



^aIncludes only instances when males became stationary

acoustic chamber. Illumination for behavioral observations was provided by a 7 1/2-watt red light in 1973 and a 24-watt red light covered with red photographic masking tape in 1974. Only contacts made by non-calling males were analyzed.

The largest portion of initial contacts were head-to-head antennal contacts (Fig. 20). Almost as many contacts were initiated from the side or behind.

Males placed together usually moved away from initial contacts without noticeable response to the other male. One of the pair often became stationary soon after initial contact and the other continued to move around coming into repeated contact with the stationary male. Repeated contact with a stationary male usually led to one or more of the following: 1) agitated movement (side-to-side vibration and increase in walking speed) by the active male, 2) rarely, hopping by the active male, 3) mutual or one-sided grappling, 4) CtS by the active or inactive male, 5) courtship behavior, 6) prolonged inactivity by both males, or 7) possible movement by the stationary male. Figure 18 gives the frequency of pairing of specific acts.

Males contacting the side or rear of another male often raked the other male with their fore-legs or appeared to bite or butt the tip of the other male's wings. Males contacted in this way usually moved away or turned to make antennal contact with the agitating male. Often males, approached from the rear or side, became agitated and crawled or hopped

away. CtS' were often produced by one or both males after they antennated one another head-to-head.

Males turning to make head-to head antennal contact or those moving directly to this position often moved forward slightly to a position opposite and parallel to the other katydid. From a parallel and opposite position one of the males frequently produced a CtS. One-sided or mutual courtship (abdomen extension and or tremulation) was the most frequent activity occurring after males assumed this position, although males often had mild to intense grappling bouts, or simply moved away without noticeable overt activity.

Hierarchial relationships

Maintenance of inter-animal distance may depend upon aggressiveness by males, particularly at high density levels. Although overtly aggressive behavior is rarely seen under field conditions it may be important in brief encounters during establishment of the chorus in early evening as males often fly from spot to spot within the group. Aggressive interactions may increase distance between males that have moved into close proximity during feeding periods.

It was not known if males actually varied in their degree of aggressiveness. Eight males reared from nymphs were used in studies of hierarchial

relationships. They were individually marked and isolated from sounds of other males. Observations were made on three consecutive nights.

Each animal was paired with every other animal by simultaneously placing a pair of animals into a neutral cage. Twenty-seven rather than 28 male-male interactions were analyzed due to the death of one male before its final bout. A total of 187 contacts were made between all males with an average of 7 contacts per male. Observation periods were from 10-20 min and each male was allowed at least 1 hr between bouts.

The neutral cage (4" x 4" x 7") used in the experiment was small enough to force encounters between males. It was placed on a wooden stand about 3 ft from the floor and illuminated with a 24-watt, red light bulb. Notes were taken on a tape recorder and later transcribed to a field notebook.

Categories of behavior were established as either aggressive or submissive. Behavior considered as aggressive included: 1) grappling, 2) producing CtS, and 3) biting. Behavior classified as submissive included: 1) moving away from an encounter, 2) becoming agitated (quicken movement and vibrating weakly from side to side), and 3) hopping in response to any interaction with the other male. Pluses were given for aggressive acts and minuses for presumed

submissive acts. The animal accumulating the more positive score was considered the winner of the bout.

Twenty-seven of 28 possible pairings indicated a linear hierarchy (Fig. 21). Thus, males showed a propensity for performing certain acts with enough consistency to be hierarchically ordered respective of other males.

Extent of Movement

Limited movement within and defense of a particular site is important in spacing dynamics. An attempt to determine if males remain in a restricted area was investigated by marking males and following their movement for an extended period of time.

Records for 14 of the original 26 marked males were obtained. Movement by males ranged from 4 ft 7 inches to 260 ft 11 inches (Table 4). One to eight days lapsed between the time of marking and relocation except for male 14 which was relocated about 1 hr after marking. This male had moved 39 ft 11 inches from the site of marking.

Total amount of movement did not appear to increase with time. Although considerable movement between successive relocations occurred, movement did not usually remove a male from a particular area (Fig. 22).

Figure 22 indicates the pattern of movements for 4 males selected from Table 4. Male 2, observed periodically from July 30 to August 8, was located in a chorus of about 8 males

Figure 21. Hierarchial relationships among adult male katydids. Scores from bouts to determine relative aggressiveness among eight males are shown. Dominant males head vertical columns with their scores listed above the score of subordinate males. Subordinate male numbers are at the left of rows. A flow diagram of the hierarchial order is shown below. Dominant males are circled. The dashed line represents a postulated relationship (death precluded experimental determination of the bout).

Dominated Subordinate		1	2	3	4	5	6	8
1			+3	0	+4	0	-5	+2
			0	-5	-2	-3	-12	-5
3			+4		+4	+1	+1	
			-6		-1	-2	0	
4			+1			+3	-4	
			0			-4	-11	
5			+1					
			0					
6			+2			+1		
			-2			-8		
7		-4	+2	0	*	+4	0	+2
		-8	-2	-7		-5	-5	-8
8			0	-1	+1	+3	+4	
			-1	-5	-5	-2	-4	

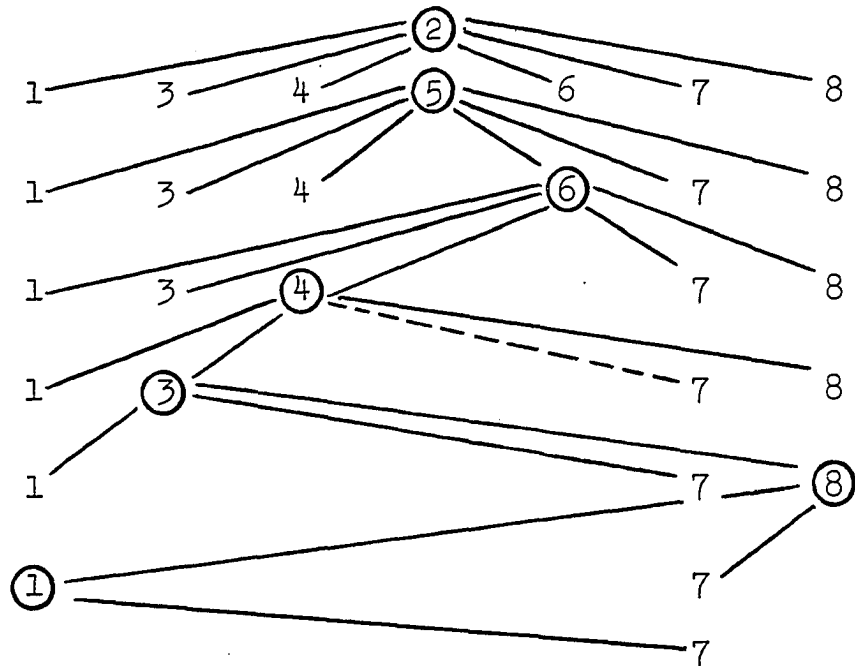
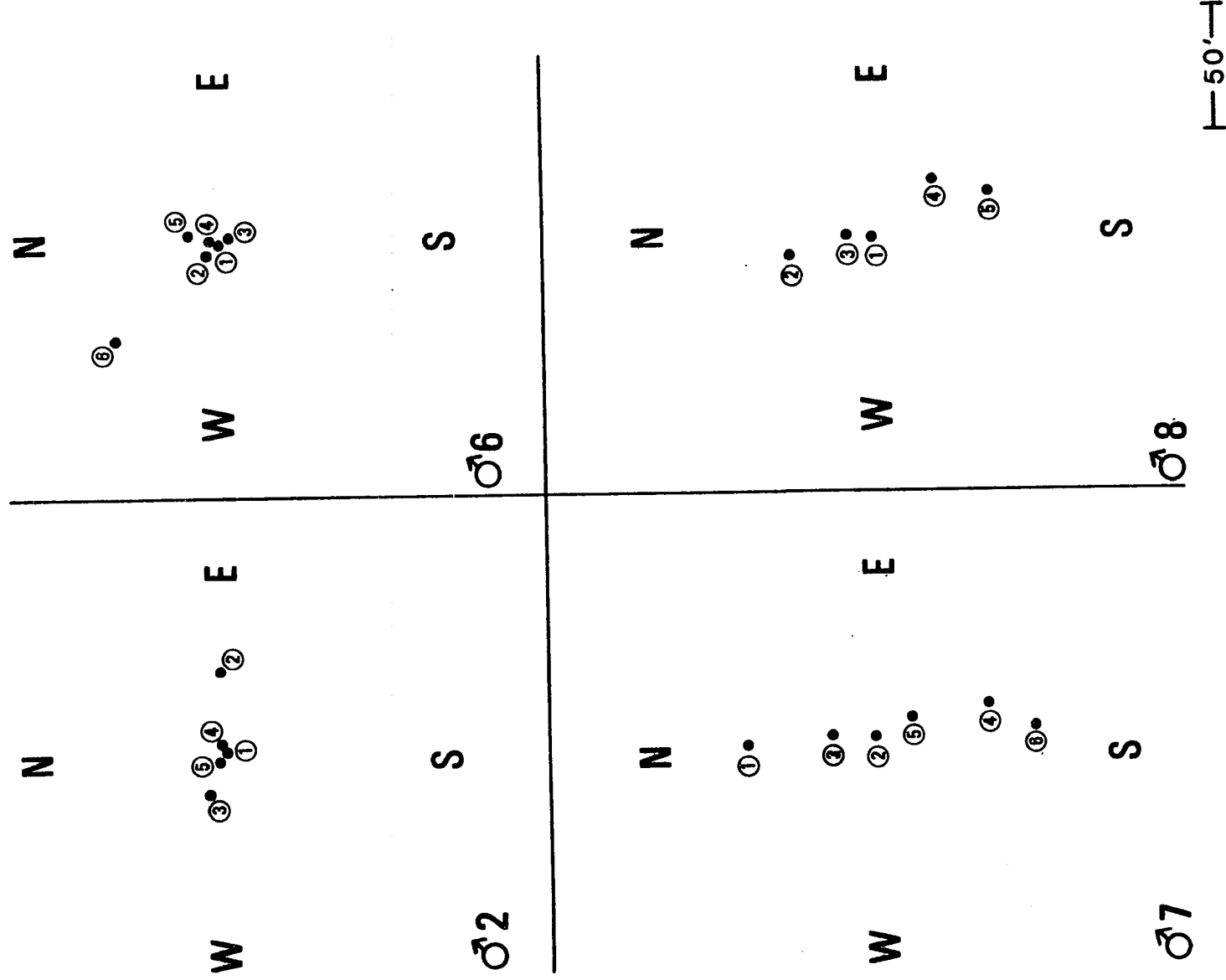


Table 4. Distance between successive locations for marked katydids. Location numbers indicate the chronological order of locations.

Katydid field number	Time lapse between locations in days	Location numbers	Distance between successive locations
14	0	1-2	39' 11"
2	1	1-2	33' 2"
2	1	2-3	49' 8"
4	1	2-3	10' 9"
6	1	1-2	6' 6"
6	1	3-4	6' 7"
7	1	2-3	17' 11"
8	1	1-2	32' 6"
2	2	4-5	6' 7"
6	2	4-5	8' 6"
10	2	1-2	9' 0"
7	3	4-5	29' 10"
7	3	5-6	46' 10"
8	3	3-4	43' 6"
19	3	2-3	165' 0"
2	4	3-4	18' 2"
6	4	2-3	4' 7"
7	4	3-4	62' 0"
8	4	2-3	22' 0"
1	5	1-2	14' 3"
6	5	5-6	48' 9"
7	5	1-2	50' 7"
11	5	1-2	70' 3"
13	5	1-2	260' 11"
23	5	1-2	24' 6"
4	6	2-3	32' 8"
24	6	1-2	5' 2"
18	7	1-2	44' 0"
19	7	1-2	22' 7"
8	8	4-5	20' 6"

Figure 22. Degree of spatial displacement of adult males from a fixed geographical site. Patterns of movement for representative males selected from Table 4 are presented. Point 1 represents the site of original release after marking. Subsequent numbers indicate successive locations of males after at least one day had passed. Refer to Table 4 for accurate distances traveled between points.



located along the north edge of a wooded area. The male changed its position, but remained within the chorus during its observation period.

Male 6 was the only calling male within about 40 ft of a small cottonwood tree from July 30 to August 7. On August 7, an additional male called from the area. No calling was noted from the area on subsequent nights. Male 6 was located in another chorus five nights later on August 12. The male had moved 48 ft 9 inches from point 5 to the new chorus (Figure 22).

Males 7 and 8 were located in separate choruses along the same fence running north and south. Both males were observed from July 30 to August 15 and both remained within their respective choruses, but moved around exchanging places with members of the chorus.

Male 13, marked on August 4, was relocated five days later 260 ft 11 inches away from the original site. The male was not in a chorus when marked, but there were 4 choruses closer to the male than the chorus in which it was subsequently found. This male was only located twice.

Male 19 was initially located within a chorus on July 5 and subsequently located with the same chorus on July 12. The male was located 165 ft away in a new chorus on July 15.

Males 3, 5, 9, 12, 15, 16, 17, 20, 21, 22, 25, and 26 were not relocated after marking and are not listed in Table 4.

Continuous field observations of males from dusk until dawn and marking and relocating techniques indicate much more activity by males than that envisioned by Alexander (1956). Isolated males tend to remain in a more restricted area for extended periods than males within a chorus, but none of the several hundred males observed in field observations were known to remain on the same perch night after night.

Individual males characteristically quit calling and fly without apparent disturbance during the first one to two hours of synchrony at temperatures of around 18-20°C or above. Males have been observed to fly from a few feet to as much as 20 feet in a direction away from its position in a chorus. These flights are usually somewhat semi-circular and males usually begin calling almost immediately after landing. Calling from the new position is usually brief, a minute or less, followed by one or more flights that eventually return the male to closer proximity of the chorus. Other flights involving males within the chorus occasionally bring males into close proximity or, on rare occasions, actual contact. One or both males synchronizing in this manner may move up and down on their perch as they call, eventually returning to a stationary

point. From laboratory and field observations, it appears that the follower drops out of such interactions when inter-animal distances are less than one foot, flies to a greater distance, and resumes synchrony. The male that stops singing may remain in the area. There is, however, almost always some movement after cessation of calling. The male may simply move up and down on its perch or move through the grass a short distance. Rarely both males have been observed to discontinue calling and fly.

Choruses appeared to stabilize a few hours after dark, the rapidity of which seemed to be linked to 1) time of season and 2) temperature. Flights tended to decrease with duration of the season and could have been due to temperature change as well as age. Stable choruses seemed to be set up shortly after dark in late August to the end of the season. At this time males could be more easily approached soon after dark, even at warm temperatures. Similar behavior was observed early in the season, if temperatures were much below 20°C. Males tended to move short distances after calling even when flights did not occur.

Choruses were noted to form in areas where large numbers of nymphs were noted prior to calling. These choruses remained in the area unless disturbed. Presumably, these choruses were basically composed of the same males throughout the season although the males changed places within the chorus becoming sedentary late in the evening and early morning.

Spacing Analysis

Distances between males of a single chorus were measured. These inter-animal distances were subjected to a statistical analysis to determine the field distribution (Table 5).

Males were evenly spaced within chorusing groups in both 1974 and 1975. The Clark and Evans index R was 1.17 in 1974 ($C=3.568$, $p < .01$, two-tailed test), and 1.41 in 1975 ($C=5.766$, $p < .01$, two-tailed test).

The first study area (SA-1) constructed in late July, 1974 was 45' x 50' and had an area of 2250 square feet. On July 25, 1974, a road construction crew removed all vegetation from 2 sides of the area. Subsequently, on August 1, 1974, the total area was reduced to 1,630 square feet. Thus, SA-1 had three different conditions for sampling. R values were obtained for the area under each of the three conditions. A test for differences among R_1 , R_2 , R_3 , and the 1975 R value showed no significant difference ($F_{3,163} = .012$, $p < .01$).

Nearest neighbor distances were divided into eight classes in 1974 and six classes in 1975 (Table 6). χ^2 comparisons of observed and expected frequencies indicated that the two populations were not randomly distributed (1974: X_6 , $.005 = 18.55$, $p < .005$; 1975: X_4 , $.005 = 14.9$, $p < .005$).

A representative six member chorus plotted from SA-2 is shown in Figure 23. Males were synchronizing when measured at 9:30 P.M. on August 14, 1975 at 19°C. In

Table 5. Data from nearest neighbor analysis.

NEAREST NEIGHBOR ANALYSIS			
Parameter	1974	1975	Comment
n	113	54	Two runs per night were made in 1974. One run per night in 1975.
NND \bar{X}	13.73'	15.57'	
NND range	3"-39'	7"-69'	
Chorus size \bar{X}	3.66/r	6.00/r	r = run (one sampling)
Chorus size range	2-8	2-11	
Statistic R	1.17**	1.41**	Random distribution: R = 1.0 Uniform distribution: maximum R = 2.1491 producing "hexagonal pattern" (Clark and Evans, 1954).

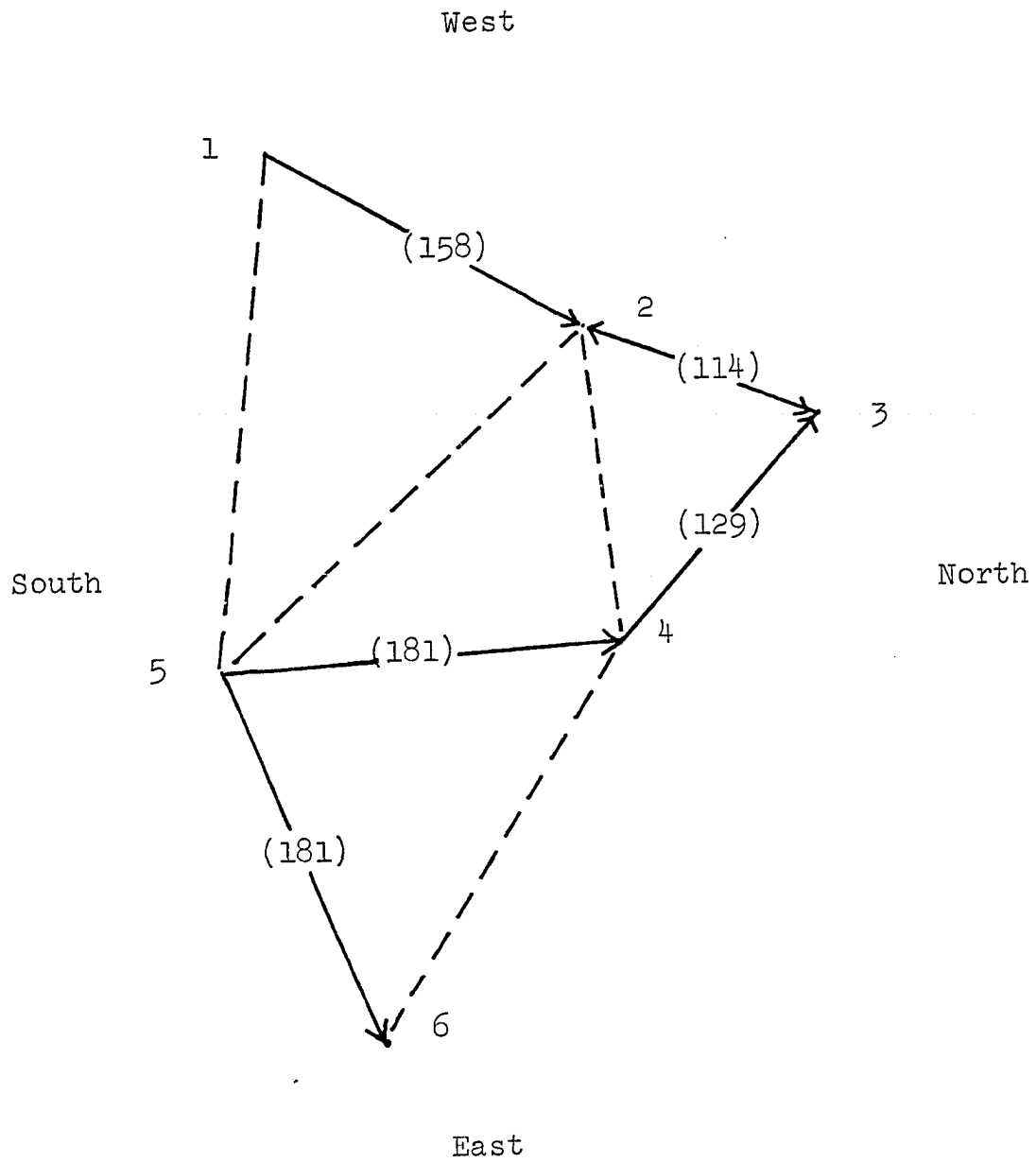
**P < 0.01

Table 6. Frequency distribution for a randomly spaced population compared to observed values.

<u>Class</u>	<u>Distance inches</u>	<u>Obs.</u>	<u>Prob.</u>	<u>Exp.</u>
Date: 1974				
1	0-20	12	0.0154	1.7399
	20-50	6 } 18	0.0770	8.7044 } 10.4443
2	50-75	8	0.1036	11.7085
3	75-105	18	0.1519	17.1696
4	105-140	14	0.1845	20.8491
5	140-175	12	0.1627	18.3836
6	175-220	11	0.1519	17.1602
7	220-280	9	0.1052	11.8866
8	280-340	10	0.0365	4.1230
	340-	13 } 23	0.0113	1.2751 } 5.3981
Date: 1975				
1	0-48	4	0.0980	5.2904
2	48-96	8	0.2400	12.9596
3	96-144	9	0.2667	14.4009
4	144-192	13	0.2033	10.9756
5	192-230	8	0.0984	5.3122
6	230-300	6	0.0759	4.0991
	300-	6 } 12	0.0178	.9613 } 5.0600

this plot, as with others not shown, males often positioned themselves in a more or less straight line. For example, because measurement error was ± 3 inches a relatively straight line might be projected through points 3, 4, and 6, points 1, 2, and 3, and with less certainty through points 1, 5, and 6.

Figure 23. Chorus structure. The relative locations of six calling males are shown. Numbers in parentheses are nearest neighbor distance in inches.



DISCUSSION

Aggregations of calling males forming choruses appear each year within the larger population of an area. These colonies usually form in moist areas associated with woody vegetation and dense grass cover as indicated by Thomas (1933) and Alexander (1956). Froeschner (1954) and Alexander (1956) also indicated the species could be found in drier areas, in grassy and weedy fields. In this study, animals were found in all of the above mentioned areas; however, they were always near woody vegetation that exceeded the surrounding herbaceous plants in height. The species feeds on grass seeds such as Bromus inermus and Agrostis alba, which are usually relatively dense through the area. It is not known why the species is found in these areas unless the shade is required for protection from desiccation during daylight. Males apparently remain immobile during the day as they drop to the bottom of the grass cover and remain stationary in a head down position.

Choruses usually appear in areas where large numbers of nymphs were located earlier in the season. A few choruses around the fringe of the colony appear in areas where nymphs are not usually found. Obviously, there is emigration of males into peripheral areas. It is interesting to note that females were never found in most of these areas. Choruses tend to remain in the same area for most or all of

the season provided external conditions remain relatively stable. If grasses are destroyed in an area, the chorus merges with near-by choruses.

Males within a chorus begin to synchronize their sound bursts as light intensity decreases. Initial singers apparently induce singing in near-by males (Alexander, 1956, 1957, 1967; and Dumortier, 1963). This is apparently true for N. nebrascensis during early evening as light intensity falls, but at low temperatures, during feeding periods, during day soloing, and early morning many males do not respond to calling of other males. In addition, Alexander (1967) suggested that phonoresponding males chirp longer and more continuously than soloing males because of excitatory and inhibitory effects of the sounds of one on the response of the other. Mean song durations, for individual Nebraska coneheads involved in two-male synchrony, was shorter by approximately 2 min from solo and at distances less than 1 ft there was statistically significant reduction in mean follower song.

One study with N. nebrascensis indicated that song duration is not reduced during chorusing involving more than two males. In this study, 7 males were placed in the acoustic chamber and allowed to move freely to perches on potted plants. Chorusing involving up to 6 males occurred with a combined singing time of 7 hr 46 min. If a male was involved

in at least some synchrony, the duration of its song was recorded (\bar{x} =7 min 46 sec, n =66). This is close to solo song duration (\bar{x} =6 min 40 sec, n =11) for 11 males recorded in 1974 and 1975 at separate times from the above study. In the chorusing study, intervals between songs averaged 10 min, but staggering of calling by individual katydids produced periods of 1-2 hrs of continuous chorusing. This increased mean song duration, for individuals in chorusing groups, may be biased due to individual males with a tendency to produce longer songs repeating their songs more often.

Calling males within a chorus were found to be non-randomly spaced with a tendency toward a uniform distribution. This structure within the chorus might result from a number of behavioral mechanisms. For example, territorial behavior might be important in a regular spacing. Alexander (1961) described territorial animals as being those that associated with a particular geographical location. He found that G. veletis exhibited territorial behavior which included attachment to a site and defense of that area. He listed N. nebrascensis as being a sedentary species (Alexander, 1956). Morris (1967) found conspecific fighting occurred among four species of tettigoniids (O. gladiator, O. vulgare, C. nigropleurum and M. roeseli), but concluded that the animals probably did not have fixed geographical territories. The results of this study indicate that N. nebrascensis frequently change position, this disagrees

with Alexander's observation that the species is sedentary, i.e., N. nebrascensis males do not occupy specific territories.

Fighting involving actual contact of N. nebrascensis males is rare under field conditions and its use in defense of a particular site is uncertain. Fighting, involving reciprocal raking with forelegs, biting or butting, and sound production occurs frequently when males are caged together in the laboratory. Mutual or one-sided abdomen extension and tremulation sometimes occurred during these interactions. Morris (1967) observed similar behavior in O. gladiator and C. nigropleurum in both the laboratory and field. N. nebrascensis usually exhibited this type of behavior after repeated contacts between two males; one male usually made the majority of contacts. Dominant males may repel subordinates in this manner during feeding periods when silent males come into contact. However, in most cases subordinate males are probably repelled after brief antennal contact. Synchronizing males rarely made contact under either laboratory or field conditions. Singing males were not approached by silent males in the same cage or on the same perch; however, singing males usually approached silent males moving on their perch.

Certain behavioral acts appear to occur in both male-male and male-female interactions and to have different functional significance in each context. CTS produced when silent males come into contact, probably serve to increase

distance between males and there-by reduce fighting and/or homosexual activity between males. Several investigators have found that sounds produced during fighting between tettigoniid males appear to function in increasing distance between males (Morris, 1967, 1971; Abraham, 1972; and Spooner, 1964, 1968). In N. nebrascensis, the CtS (Fig. 5) is similar to precopulatory song (Fig. 6) in mean buzz lengths, therefore, it is reasoned that the song may serve as a recognition song. Consequently, if a male produces the CtS when a receptive female is contacted, the female's responses stimulate continuation of the song. The CtS then becomes a precopulatory song which may continue and be quite long even when the male and female are not in direct contact (Fig. 7). The female may become stationary, tremulate, or move to a parallel opposite position relative to the male. Chemical or visual communication could play some role, but nothing is known with regard to these modalities.

Tremulation often occurs during courtship. The female most often tremulates, but occasionally the male may do so as well. Morris (1967, 1971) theorized that tremulation might act as a gauge of the relative level of aggressiveness in two contesting males. However, N. nebrascensis males rarely tremulated in the presence of another conspecific male even in highly intense aggressive bouts.

Morris (1967, 1971) has described aggressive behavior between males of O. gladiator as being "associated with patterns of mating behavior". Normal male-female mating behavior included spreading of the males parameres and curving of the abdomen. He described a mutual homosexual encounter as one in which two males "respond to each other's presence by executing the movements characteristic of males in normal male-female mating" (Morris, 1967). An aggressive homosexual encounter was described as one in which a clearly sexual response on the part of one male to the presence of another was repelled aggressively by kicking or grappling. During grappling, N. nebrascensis males occasionally extend their abdomens toward another male. The abdomen extension, as with O. gladiator, is similar to mating behavior in appearance except that the abdomen is often mis-directed and may contact any portion of the other males body. When males extended their abdomens to receptive females they most often make contact with the genital region of the female without contacting other portions of her body. Males attempting to copulate with non-receptive females do make contact with various parts of the body. A basic difference in male-female and male-male interactions is that the male almost always produces the precopulatory song when the abdomen is extended toward a female (receptive or non-receptive). The precopulatory song has not been recorded in male-male

interactions. In male-male interactions, both CtS and use of the abdomen in grappling may be considered aggressive behavior because they aid in repulsion of another male.

Vibrations of a calling male's perch caused by either a male or female (tremulation or walking in either case) apparently elicits movement in the direction of the vibration, a shortening of buzz length and increase in buzz rate. If a female is contacted the male's song may continue as a precopulatory song. If the disturbing animal is a male, it may be inhibited from singing (possibly by the high intensity and rate of the song) and be repelled from the perch as contact is initiated by the calling male. If the male is not repelled and both become stationary the original male will immediately return to his original buzz length and rate.

When males synchronize within a few inches of one another, as might occur if the agitated male begins to call or if another male flies within close proximity of the first and begins to synchronize, the follower is likely to discontinue song first. Males discontinuing song almost always move around the perch and often hop or fly. If a male discontinues song and moves on the perch, a repeat of the behavior described above in response to vibrations would be expected.

Shortened song by follower males occurs when synchronizing males are 1 ft or less apart. Three important changes occurred

in follower males song and song parameters as they were moved from a distance of 8 ft to points closer together: 1) \bar{x} buzz lengths decreased linearly, 2) \bar{x} buzz variability increased linearly, and 3) \bar{x} song duration at less than 1 ft was significantly less than leader song (see Fig. 8 for \bar{x} buzz length and C.V.). The mean phase differential between leader and follower (118 msec) did not change with decreased distance. One can theorize that increased intensity due to animals being in close proximity produced the shortened buzzes. This could be tested by playing imitation buzzes with a wide range of intensities to stationary calling males to determine the effect on buzz lengths.

It appears that the short buzzes and high variability are indicative of some influence (possibly increased intensity due to close proximity of singers) on the mechanisms of synchrony. Imitations played immediately after B_0 cause shorter I_0 and B_1 than those initiated just prior to B_1 (Fig. 12). The shortened follower buzz allows increased lag by the leader¹ which usually caused delay in onset of the following buzz. This may further increase variability in song parameters and reduce song lengths. This type of song length reduction would likely increase distance between males because males usually move away from such interactions after termination of their song. During field observations,

¹The leader's song parameters do not appear to be altered by the follower (Fig. 8).

six males were observed to fly to within 1 ft of another male and following synchrony, one male flew away. Little evidence exists to show significant decrease in follower song length at distances of 1 ft or more; however, variability may be above normal at distances up to 8 ft and it appears likely that followers produce shorter songs when variability is high. Again, this may cause shorter songs, increased locomotion, and increased distance between leader and follower. The spacing mechanism appears to be dependent upon one male maintaining the lead in synchrony.

Alteration in calling song has been noted by various workers. Acridids may, for example, produce a song called a rival's song that has a higher intensity and rate of stridulation (Weih, 1951 and Jacobs, 1953). The distance between calling males seems to determine the degree of departure from the calling song. Dumortier, (1963) has suggested that the distance between males when the calling song changes to the rival song may delineate the extent of the territorial area. Young (1971) suggested that in a species of grasshopper (C. brunneus), one male increases the rate of the rival song causing the other male to drop out. He suggests that the male which continues to sing may be the dominant male. Busnel (1967) has suggested that tettigoniid males establish dominance through acoustical interactions.

In certain alternating species of tettigoniids, males produce longer chirps as inter-animal distance is reduced (Shaw, 1968; Jones, 1966a, 1966b). These were considered aggressive calls that were thought to effect spacing between males. A trilling species (M. sphagnorum) was found to produce a variation of its song as the distance between males was reduced (Morris, 1970). Abraham (1972) suggests that calling males of O. vulgare inhibit the buzzes of conspecific males and that the males inhibited from calling move away from other males until their buzzes are no longer inhibited.

Occasionally, males calling 60 ft or more from a chorus were unable to maintain synchrony. These males would usually fly toward the main body of the chorus. This appeared to be a phonotactic response. Morris (1967, 1972) was able to get males of two species of Orchelimum to move toward the broadcast sound of a nearby conspecific male. Many others have postulated that sounds function to produce aggregations of males in both grasshoppers, and katydids (Clark, 1948; Haskell, 1958, 1961; Young, 1971; Alexander, 1956; Abraham, 1972; and Spooner, 1964, 1968).

Thus, the regular spacing of calling males within a chorus appears to accrue from adjustments on position required for stimuli (e.g., sound level of neighbors sound) necessary to facilitate synchronous song. Males that are near one another may be inhibited from producing sound or

the variability in their song may be increased so that shorter songs are produced and movements are increased at shorter inter-animal distances. Males too distant from other calling males are also likely to produce unstable songs. These males may be attracted toward the chorus. Eventually males become positioned in optimum chorusing positions and the structure of the chorus is maintained until feeding periods when the structure is likely to break down as males move around in order to obtain food. After feeding, singing is usually sporadic until daylight when males drop to the bottom of the grass and become immobile. The cycle of adjustment and positioning within the chorus again becomes evident as chorusing begins again each evening. During late August and early September the choruses become more sedentary and much less flying and readjustment of position occurs.

The maintenance of the chorus structure is apparently important in enhancing male-female contacts. It may also be important in attracting other males to favorable habitats. Walker (1973) suggests that species of crickets are attracted to other males in favorable habitats. In N. nebrascensis, chorusing appears to be important in maintaining the cohesiveness of the species in favored habitats. It also provides a means of excluding a closely related species by inhibition of the calling song of that species. For example, N. ensiger, appears to move away from areas densely populated by N. nebrascensis.

SUMMARY

1. Male Katydid (Neoconocephalus nebrascensis) produce five types of sounds: a) solo song, b) synchrony, c) contact interaction song, d) precopulatory song and e) disturbance sound. Each category was analyzed (excluding disturbance sound) in an attempt to accumulate a base line knowledge requisite to proper analysis and prediction of mechanisms involved in intra-chorus spacing dynamics.
2. Contact interaction songs (CtS) are often produced by silent males coming into head-to-head antennal contact. This song is rarely produced when males contact females and is comparable to beginning solo in parameter length and production rate. Unlike solo, clicks are often produced after each buzz. Excluding the clicks, males produce precopulatory sounds that have similar parameters, just prior to attempts at copulation. The short contact interaction song may serve the dual function of male-female recognition and repulsion of less aggressive males. Receptive females remain stationary or move forward slightly upon reception of soft short buzzes and may tremulate, whereas, males usually move away.
3. The nature of synchrony was examined by analysis of oscillogram records of pairs of males synchronizing at various distances and by analysis of the response of individual males to imitation sounds. Synchrony is

characterized by slight phase separation (118 msec) between leader and follower and a shortening of follower buzz length and lengthening of interval. Leaders are apparently males producing a faster rate of solo calling or, when rates are closely matched, the leader may be the male initiating synchrony. Males appear to be unable to maintain stable synchrony at distances greater than 60 ft or less than 8-12 inches. At 8-12 inches, followers drop out of synchrony. At 60 ft or more, either male may discontinue calling.

4. Katydids respond to randomly placed electronic imitations in the following ways: 1) by shortening I_0 and B_1 when the stimulus is initiated in I_0 , 2) increasing I_0 when stimulus lag extends beyond 40% into I_0 , and 3) shortening of I_0 and B_1 when stimulus overlaps I_0 . These responses are used to maintain synchrony when one katydid produces a buzz out of phase or when there is a change in rate of imitation sound. Leader rates and other parameters do not appear to be altered significantly from solitary calling during natural synchrony.

5. Chorusing by N. nebrascensis inhibits calling in N. ensiger a closely related species. It is postulated that chorusing is important in inter-species isolation. Chorusing may be important in maintaining the continuity of the species specific signal when it is subject to alteration by the calling of other species.

6. Male contact aggressive interactions are rare in the field. Although antennal contact is most frequent, occasional contact is made by abdomen extension and raking the opposing male with an appendage. Silent males may engage in brief aggressive bouts during feeding periods. Usually one male moves away from such encounters. In the laboratory, males repeatedly forced into contact initiated fighting behavior with the final retreat of one male. Males were artificially arranged into hierarchial categories based on relative aggressiveness.

7. Males were marked and relocated to determine their degree of association with a fixed geographical area. Males appear to remain within a chorusing area, but exchange positions within the chorus. Calling males tend to become sedentary during late night or early morning and late season.

9. The inter-animal distances between males of a chorusing group were subjected to a nearest neighbor analysis. Calling males were found to have a uniform spatial distribution. It is postulated that spacing depends upon calling males remaining within optimum chorusing distances. Males fortuitously positioned at shorter or greater than optimal distances (approximately 8 ft and 60 ft respectively) probably reposition themselves to facilitate synchronous calling.

Males landing or moving onto a perch with a calling male are likely to elicit contact interaction from the other male and one (either) moves away.

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ACKNOWLEDGMENTS

I would like to thank my major professor Dr. K. C. Shaw for his advice and assistance during the investigation and during the preparation of this manuscript. Assistance was provided by Dr. R. W. Pohl in identification of plants, by Donald Brice in assembling electronic equipment, and Paul A. Dubose in the statistical analysis.

Special thanks is extended to my wife, Bobbie, for her understanding, forbearance and assistance and to my parents for their encouragement and support during this project.