

Individual Differences and Factors Affecting Male
Behaviour in Field Crickets

by

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A Thesis

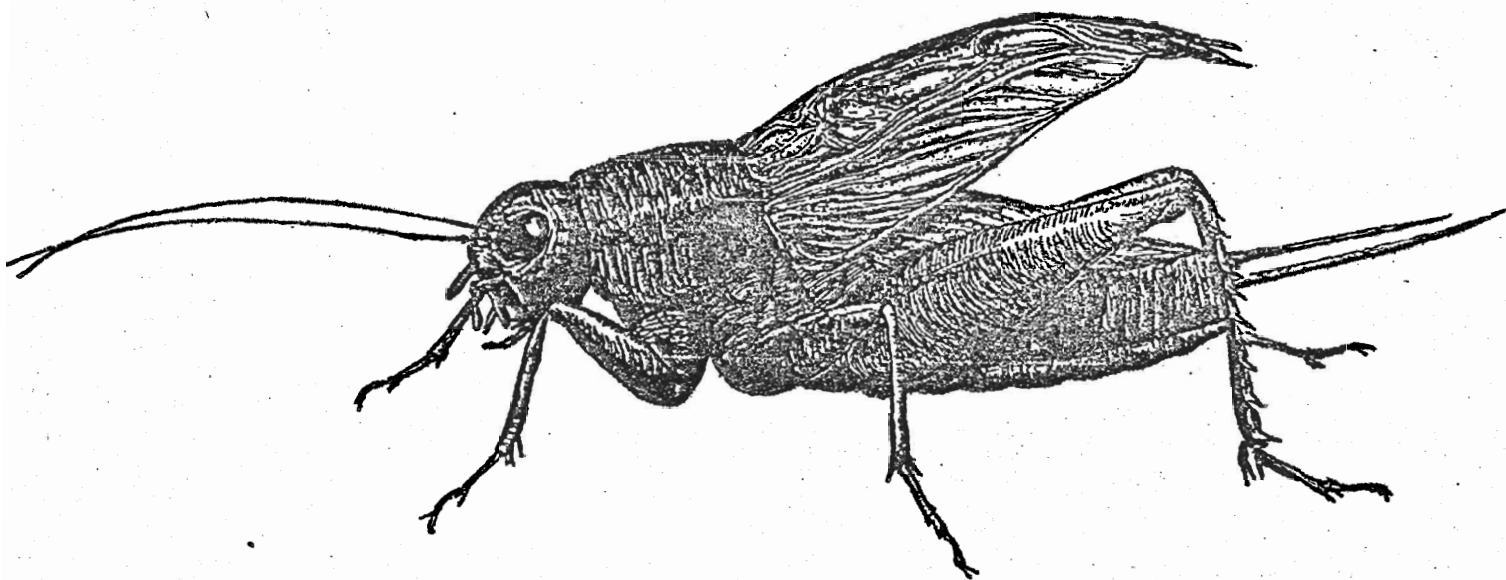
submitted to the Department of Biological Sciences
in partial fulfilment of the requirements for the
degree of Master of Science

November 1981

Brock University
St. Catharines, Ontario

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To Bernice, Gordon and Barbara



ABSTRACT

Individual differences in male sexual behaviour and the factors influencing calling behaviour were studied in the field crickets Gryllus integer and G. veletis. In a large (13m^2) outdoor arena individually numbered adult male G. integer started calling at three to five days of age but thereafter the age of individual G. integer males did not affect nightly calling duration. Calling also did not correlate with individual weight. In this study individual male calling was continuously distributed from 0 hrs. per night to 3.5 hrs. per night, on average. A temporal effect on the number of G. integer males calling was observed. The number of males calling through the night was uniform, but a sharp increase in the number calling was observed in the early morning. No difference in calling times was observed between the night and dawn callers. Also males calling at dawn usually did not call during the preceeding night.

Calling and reproductive success in 1979 demonstrated a negative logarithmic relationship while in the 1980(initial) population a negative linear relationship was observed. No relationship was seen in the 1980 high density population. The ratio of non-callers to callers also affected the mating of individuals in the 1979 and 1980(initial) densities: non-callers (males calling .5 hrs. per night, on average, or less) obtained more females when the population contained a high number of callers, this being a negative logarithmic relationship. No such relationship was observed in the 1980 high density population.

Individual displacement varied nightly and was not correlated to amount of calling or reproductive success of individual G. integer males. G. integer males were displaced more when in a higher density in the outdoor arena

Male G. integer and G. veletis behaviours were also observed in an indoor arena at different densities and, in G. veletis, with respect to female presence. When females were present in the arena, in G. veletis, male

calling was reduced. Males of both species called less, on average, when in a higher density, than when they were in a lower density. Male displacement of both species increased on average when in a higher density as compared to displacement in a lower density.

Aggression was measured by aggressive calling and fighting and was studied in regards to density. G. integer demonstrated less aggression in all but one comparison at higher density. No difference was observed in the ratio of aggressive calling to fighting comparison in G. integer. G. veletis demonstrated mixed results. No difference in aggression between densities was observed in comparisons. Less aggression did occur in higher densities when comparisons involved fighting behaviour.

Male behaviour represents a competitive strategy against other males, strategy being defined as a genetic (in part) alternative to other strategies. In this sense, the factors of time, density, male-male aggression, and female presence are conditions demonstrated to affect male behaviour in G. integer and G. veletis. Individual male differences and other considerations suggest that alternative male behaviours are represented by at least two conditional strategies. This possibility, and the transient or stable nature of genetic polymorphisms in field cricket behaviour are considered.

ACKNOWLEDGEMENTS

I would like to express my deep appreciation to Dr. William H. Cade for his unending guidance, encouragement, and confidence in me throughout the course of this study.

My appreciation is also extended to members of my supervisory committee, Dr. R.D. Morris and Dr. J. Rossant who provided needed criticism and ideas for this study.

I thank members of the shop at Brock University for their ideas and use of equipment for construction of the arena and other mechanical aspects of this study.

I would also like to thank Jina Chudzik, Kathy Graham, Patricia Hartman, George Melvin and Scott Sakaluk for their valuable assistance and discussion. A special thanks goes to Mike Nagel for valuable assistance in the preparation of the figures for this thesis. Also I thank Linda Vaughan for her excellent job of typing this thesis. Here a thanks should also go to those who helped in various ways without my realizing it (probably by staying out of my way).

The Ontario Graduate Scholarship and an N.S.E.R.C. grant to Dr. Cade provided needed financial assistance which was much appreciated. Dr. Cade also assisted in data collection for this thesis.

Lastly, I would like to express my deep gratitude to Debra, David and Tara for their generous assistance and moral support (which was often needed) and most of all, the fun that was.

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INTRODUCTION

Sexual selection is differential reproduction within a sex which results from competition between individuals of that sex for possession of individuals of the opposite sex, and from mating preferences. Males usually compete for a limited number of females, and females choose from the available males (Darwin, 1871). The operation of these two modes of sexual selection are linked to parental investment. Parental investment is any investment which increases the survival prospects of offspring while decreasing the parents' capability of future investments. Examples of parental investment would include caring for young through feeding and protection, but exclude efforts in acquiring a mate (Trivers, 1972). Energies directed in mate acquisition, such as searching and provision of material benefits are classified as mating effort.

In the vast majority of species, male parental investment is minimal or non-existent whereas females invest heavily. Due to a male's low parental investment, males are selected to increase their reproductive success by mating with as many females as possible. A result is the polygamous matings resulting from some males outcompeting others. By mating with many females a male's reproductive success is, potentially, much greater than that of a conspecific female whose reproductive success is limited by the number and size of gametes she produces.

Intrasexual selection involves both precopulatory and postcopulatory competition between males. Precopulatory competition often takes the form of aggression between males in the context of territoriality or other dominance interactions. Aggressive competition often determines which males gain access to females (Emlen and Oring, 1977). In contrast, postcopulatory competition may involve competition between the sperm of different males for

an unfertilized ovum within a female. Sperm competition is common where females store sperm and mate frequently (Parker, 1970b). Such competition can take a variety of forms. Modes of competition include sperm blocking the female tract to other male's sperm (Parker, 1970b); sperm displacement (Parker, 1970a; Lloyd, 1975); and various polymorphisms of sperm within a species (Freilander and Gitay, 1972; Sivinski, 1980; White, 1973).

Females invest considerably more than males and their reproductive success may be enhanced by their own parental investment and by mating with the best male possible. Selection of a male is based on such facets as the investment a male makes toward feeding or protecting the female. In species where males don't invest parentally, female choice may be based on a potential mate's vigor, size, age, and behaviour. The intensity of a male's display may be correlated with his sperm supply and preparedness to transfer it (Halliday, 1978). Further, in some species females may observe males and discriminate amongst suitable genotypes. Female preference based on genotype should be more pronounced in areas where males congregate, such as the leks of birds and the choruses of acoustical vertebrates and invertebrates (Alexander, 1975; Borgia, 1979; Bradbury, 1980).

Male-male competition in acoustical insects, the subject of this thesis, has different modes of expression. One form is termed phonoresponding. Here, males calling in close association, change their song frequencies, structure, timing, and intensity and thus outsignal neighbouring males and make their songs more noticeable to females (Alexander, 1975; Otte, 1977). Silent males also occur in some species and intercept females attracted by the calling of neighbouring males. Alternative modes of acquiring females are known in other species (Hamilton, 1979; Howard, 1978; Thornhill, 1979, 1980; Wells, 1977a, 1977b; West-Eherhard, 1979), and may arise when males pursue individually different strategies, or when the same males switch their behaviour (Cade, 1980).

This study deals primarily with male-male competition in field crickets (Orthoptera: Gryllidae). The main objectives were to obtain information on individual differences in male sexual behaviour and to estimate the resulting reproductive success. Also, factors contributing to individual behavioural differences such as female presence and density were studied.

LITERATURE REVIEW

Acoustical Communication in Insects

Acoustical communication is common in the insect orders Orthoptera and Homoptera. Prolific sound production occurs in the Gryllidae (crickets), Tettigoniidae (katydids), Acrididae (grasshoppers), and Cicadidae (cicadas).

A variety of mechanisms are used to produce sound, with frictional methods predominating, particularly among Orthopterans. Stridulation is the production of sound by the rubbing together of two specialized body surfaces. A protrusion on one part of the body, the scraper or plectrum, is moved back and forth over a rigid surface, the file or pars stridulens, on an adjacent part. Katydids and crickets stridulate in this manner (Dumortier, 1963; Walker and Carlyse, 1975).

Tettigoniids live among herbage and trees from the tropics to the temperate climates. They are generally green with hairlike antennae and are active at night. The auditory organs are located on the base of the front tibia and song production is, as mentioned above, by stridulation.

Acridids range from tropical to temperate climates where they usually overwinter as eggs. Acridids inhabit a variety of low vegetation areas such as grasslands, although some inhabit trees. Their auditory receptors are located on the sides of the first abdominal segments. Sound production in Acridids involves the rubbing of the hindlegs against a wing or against each other.

Cicadidae are common in warmer areas of the world, although they are also found in the North Temperate Zone. They are found invariably in trees where they suck out plant juices. Cicadas receive sound through a well developed tympanum located on the ventrolateral wall of the second abdominal segment. Cicadas produce song by a tripartite apparatus which consists of the tymbal or acoustical tracheal air sac and the tymbal

muscle generating sound, the tensor muscle straining the tymbal, and the remaining accessory musculature altering the shape of the abdomen and controlling the intensity of sound produced (Alexander and Moore, 1962).

The Gryllidae or true crickets resemble the tettigoniidae but differ in the number of tarsal segments. Also females have straight, needle-like ovipositors. Most are nocturnal and reside in humid microhabitats during the days. The Gryllidae exhibit a large range of wing development. They are generally omnivorous and are found in a range of habitats from fields to caves (Alexander, 1968). Sounds are received by the tympana which are located on each front tibia and are made of sensory cells attached to a chitinous membrane (Dumortier, 1963). Crickets produce the purest sounds of any insect along with the simplest patterns (Alexander, 1962). Males raise their forewings and rub them together. During the closing movement a part of the posterior edge of the left wing or tegmen engages a toothed vein on the underside of the right tegmen resulting in a pulse of sound (Walker and Carlyse, 1975). Each pulse approximates a pure tone of the same frequency as the tooth contact rate. Opening movements are silent. These pulses are also temperature dependent.

The major properties of cricket songs are pulse, phrase, trill, chirp, frequency and intensity, where a pulse is the simplest element of amplitude.

Types of Song

Acoustical insects have six functional song types, not all of which, are present in all species (Alexander, 1961, 1962). These include the calling song, the courtship song, the courtship interruption sound, the aggressive sound, the postcopulatory song and the recognition song. Males usually produce the long, steady, rhythmical calling song which results in the attraction of sexually receptive females. Another result

of this song is to either stimulate or inhibit calling in other males.

The male courtship song is of much lower intensity and duration than the calling song. This song is elicited when a female is within antennal contact of a male and promotes copulation (Alexander, 1962). This song is produced during both the opening and closing strokes rather than just the closing strokes as in the calling song. The courtship interruption song is produced by males when normal courtship behaviour has been interrupted. This consists of a few chirps and it probably functions in reuniting the pair.

The aggressive sound is a brief, loud signal which accompanies fighting behaviour between two males. This song functions to reinforce dominant-subordinant relationships in that it signals the likelihood of overt fighting.

The postcopulatory song is a continuous signal produced at regular intervals which functions to keep a female in close proximity to her mate after copulation. The postcopulatory song also functions to prevent other males from courting the female. The recognition song also functions in keeping the females within the vicinity of a male. Alexander (1961) found that the recognition song kept females in the male's burrow in mole crickets. This recognition song is an irregular signal usually prevalent in burrowing acoustical insects such as mole crickets.

Of these songs, the calling songs are the most species specific. For example, in the Southern Mole cricket, Scapteriscus acletus, Forrest (1980) found that 177 out of 179 S. acletus females were attracted to 12 S. acletus males while only 2 were attracted to 12 S. vicinus males. Ulagaraj and Walker (1975) demonstrated that this specificity was due to differences in pulse rate and carrier frequencies of the two calls. Zaretsky (1972) studied Scapsipodus marginalis and found that the pulse interval pattern

was the only species specific characteristic of their calling song. Varying other parameters such as fundamental frequency and number of pulses per chirp could be drastically altered without affecting the phonotactic response.

Other studies concerned with species specificity in gryllids have been performed by Hahn and Paul (1977), Hoy and Paul (1973), Lloyd (1973), Paul (1976), Pollack and Hoy (1979), and Ulagaraj and Walker (1973).

Crickets Studied

Gryllus integer and G. veletis were the two species used in this study. G. integer is found in the southwestern United States, whereas G. veletis extends from southern Canada to southern Georgia.

G. integer adults occur from late April to late June, and from early July to mid October, with two generations each year (Alexander, 1968). G. integer males call for females in moderate to high density choruses. Also, silent or satellite males are present within aggregations of calling males. The precise behaviour employed by individuals throughout their lives is, however, largely unknown. Acoustically orienting flies, Euphasiopteryx ochracea (Tachinidae), parasitize calling males, while noncallers are generally not parasitized (Cade, 1975, 1979 a).

G. veletis has one generation each year with adults occurring from late May to early August, and overwintering as nymphs (Alexander, 1968). This species occurs in low density populations compared to G. integer, and there are no silent males and no acoustically orienting parasitoids in this species (Cade personal communication).

Parental Investment in Crickets and Other Insects

Male crickets usually contribute little or no parental investment. When it occurs, however, males may invest through control of resources and by feeding females. An example is shown by males in the order Mecoptera who mate with females after a prey arthropod is presented by the males

just prior to copulation (Thornhill, 1976a).

A major type of paternal investment in insects is in the form of nutrition. This consists of 3 major types (Thornhill, 1976b): Females may receive nourishment from a glandular product of the male; females may receive nourishment from food captured or collected by the male; and the male may be eaten. A male's ability to invest nutriment during copulations is important in determining his ability to attract and inseminate females.

An example of the first type is seen in some orthopterans where dorsal glands provide nourishment on which females feed before and during copulations (Alexander and Brown, 1963). A function of such secretions may be to occupy the female, prevent spermatophore removal, and thus allow full transfer of the contents of the spermatophore during copulation (Alexander, 1961).

Many adult female insects require proteinaceous food stuffs in order to produce eggs (Chapman, 1971; Engleman, 1970). Observations on Scorpion-Flies (Mecoptera) showed that the salivary secretions of the male may be of nutritional value. Thornhill (1976a) observed that as females ate the secretions of males, the males production of secretion increased. Also, if a male ran out of secretions before copulation was terminated, the female would move to another male who had secretions available.

Bell (1980) found in the Black Horned tree cricket, Oecanthus nigricornis, spermatophore and glandular feedings by females increased the number of eggs they produced. Boggs and Gilbert (1979) working with Heliconius butterflies and Friedel and Gillot (1977) working with grasshoppers (Acrididae) have shown that labelled spermatophore proteins are in part incorporated into eggs and ovaries. Also Toolson and Gwynne (in prep) demonstrated that labelled amino acids from katydid spermatophores are used in both eggs and somatic tissue.

Spermatophores may also be a significant nutritional investment on the part of mated males. Thornhill (1976b) hypothesized that large spermatophores may have evolved during intersexual selection in the context of female preference of males willing to make large paternal investments. No information is available on how females of such species select spermatophores. Sakaluk and Cade (1980) also hypothesized that females of the house cricket, Acheta domesticus, and the field cricket, G. integer, acquire nutrition by spermatophore consumption. Further, Mays (1971) demonstrated that in the ground cricket, Nemobius sylvestris, mating behaviour routinely involves the attachment of two spermatophores. The female removes and eats the first spermatophore, following which a second sperm filled spermatophore is transferred to the female by the male.

Gwynne (1981) found that spermatophores of male Mormon crickets, Anabrus simplex, are very large, constituting up to 27% of the male's body weight. Males only mate with heavy females as these are more fecund. The spermatophore proteins a male gives a female during copulation may greatly aid successful reproduction. This tests the sex role theory since males are discriminating when their parental investment is high.

Male Reproductive Competition in Acoustical Insects

Low male parental investment generally leads to high male-male competition (Trivers, 1972). Male competition in Orthoptera often involves overt aggression and acoustical signals. In field crickets (Alexander, 1961), katydids (Morris, 1971, 1972) and acridids (Otte and Joern, 1975), these signals act as threats which indicate the possibility of physical attacks. Fighting is associated with territoriality, and often results in regular male spacing within choruses. Morris (1971, 1972), for example, observed that signalling males of several species of tettigoniids are spaced regularly within the environment. Morris found that males reacted

aggressively only when in close association to stridulating conspecifics. Silent males were ignored as were calling males outside a critical distance of 90 to 120 cm. Feaver (1977) produced similar findings on Orchelimum gladiator, O. nigripes and O. vulgare, with a minimum distance of approximately 70 cm. Cade (1981b) found similar results in three species of field crickets. In general, when fighting occurs between males, the result is the withdrawal of the defeated male, and the resumption of singing by the victor (Alexander, 1961; Morris, 1971, 1972).

Some male orthopterans adopt an alternate mode of behaviour in their mating competition. Alternate male behaviour should be common in species where male reproductive competition is high. Such alternatives are often displayed in the form of satellite or parasitic males (Cade, 1979a, 1980; Emlen and Oring, 1977). Satellites associate with calling males and apparently intercept females attracted by another male's calling. In part, adoption of satellite behaviour is dependent on density. In high density situations, defeated males have less chance to call without eliciting an attack. Alexander (1961) discussed the aspect of less calling at high densities. He hypothesized a higher incidence of random collisions at higher densities, and proposed that there were increased benefits for non-calling and searching for mates.

Otte and Joern (1975) studied male-male competition in three species of grasshoppers, primarily Liqurotettix coquilletti. When the population density was increased artificially by introducing a number of males from outside the study, the number returned to the previous level a few days later. Territories were maintained through repulsion of males by loud continuous stridulation and by fighting. Once a male was in possession of a bush he was sedentary. These bushes seemed to be the size which was likely to harbour females. Territoriality and low densities are thought to

increase male quota of females through competition (Otte and Joern, 1975). In the grasshopper, Goniatrum planum, calling male spacing was facilitated by clicks, but this species also had silent males around callers (Otte and Joern, 1975). Silent males intercepted females coming into a bush having a caller. Singing males in a bush apparently did not perceive satellites.

Otte (1972) reported that nonsinging males occurred in the grasshoppers, Syrbula admirabilia and S. fuscovittata, and that they become active when they hear a female answering a male's call. Satellites walk rapidly in the area and appear to search for the signalling female. In S. fuscovittata, mate stealing was witnessed when a noncaller mounted a signalling female.

Similar findings are reported in several katydid species where ticks produced by males seem to function in spacing (Spooner, 1968). Satellites also occurred here. Males call females with the females "tick" as a response. In the field, Spooner discovered noncalling males orienting to females answering male ticks.

Feaver (1977) observed sexually mature silent males as well as immature silent males in the katydid O. nigripes. Mature silent males were observed in the proximity of callers. Silent males were only observed when densities were highest, and they often called when an adjacent male stopped calling. Silent males never mated with a female. Intercepted females skirted around silent males and approached the callers.

Cade also observed that in G. integer some males were attracted to calling males and these remained silent and, in the vicinity of the caller, intercepted attracted females. Silent males also were observed to attack callers. Through this interference satellite males may increase their likelihood of copulation. The reproductive success of satellites is expected to be, on the average, equal or greater than that which satellites would obtain if they were to adopt territorial behaviour (Cade, 1979a, 1980).

Alexander (1961) in studying field crickets, G. veletis, found that caged males developed dominance hierarchies through fighting and intense acoustical calling. The dominant males established a territory and were spaced in the environment. Aggression resulted in territorial males usually monopolizing females. Some of these males acquired females by searching and attacking other callers.

In the acoustical insects described, males occur in aggregations where they signal with other males. Two types of mating choruses were noted by Alexander (1975). One occurs when males aggregate and compete for females where the females are already located. These include emergence sites, oviposition sites and feeding sites. Morris (1972) and Feaver (1977) showed that katydid males, O. vulgare, sing in the area of plant species which females use for oviposition. Other examples of males aggregating where females will appear are seen in wasps (Lin, 1963; West, 1969), other katydids (Spooner, 1968), and in dungflies (Parker, 1970a).

A second type of aggregation occurs where signalling males attract females from outside the group. In this case, the aggregation does not correspond to localized resources. An example is in the cicada, Cicada orni, where males called for females but not in association with any particular plant species (Claridge et al., 1979).

In cricket aggregations, soil moisture may be a resource which selects for clumping (Alexander, 1961). Females may prefer moist soil for oviposition due to more successful development of eggs and instars (Bate, 1971). Cade (1979a) noted that male and female G. integer had a preference for a damp area of an arena suggesting that mating assemblies in this species may be partially dependent on the distribution of nonfemale resources. In G. integer, however, other evidence indicates that these aggregations are non-resource based. Observations show males to be clumped even though

other suitable areas were nearby. These were shown to be suitable by broadcasting conspecific songs from these areas with males and females orienting and establishing normal chorusing (Cade, 1979a).

Males should form aggregations if increased reproduction is a likely consequence. Cade (1981b) found that females of G. integer were attracted more often to clumped loudspeakers than to single loudspeakers. Similarly, Morris (1978) observed that in the katydid, Concephalus nigropleurum, four times as many females would orient to a recording of two males close together than to a recording of a single male. No such preference, though, was shown in the grasshopper Syrbula admirabilis (Otte and Loftus-Hills, 1979). In both Cade's (1981b) and Otte and Loftus-Hill's (1979) study, however, when the average number of females per signal is looked at, isolated males equal the average clumped male, making the data rather inconclusive. This, however, may demonstrate a balanced evolutionarily stable strategy in the population.

Alternation of calls is a mode of male competition. Alternation occurs when one individual places his call between the calls of other individuals in the population. Shaw (1968) discussed alternation in the katydid Pterophylla camellifolia. Males singing alone have a faster chirp rate than those alternating with one another. Interactions consist of the entrainment of each katydid to a slower chirp rate because of inhibition by the other individual.

Asynchronous calling is another mode of acoustical competition in some species of Orthoptera. In asynchronous calling signals are temporally and spatially independent, resulting in the production of bursts of activity in aggregations of males (Otte, 1977). An example involves the grasshopper, Syrbula admirabilis, where a number of males may become active all at once and then remain quiet for a period of time (Otte, 1972). Experiments with tape recorded songs showed that two males singing at the same time and

within hearing range of females divide the females between them. The leading male may have a slight advantage over a "following" male (Otte and Loftus-Hills, 1979). Also, two songs emanating simultaneously from the same loudspeaker are not more or less effective than a solitary song emanating from another speaker opposite (Otte and Loftus-Hills, 1979). Hence, as Otte (1977) reported males may attempt to interfere with other male's songs by making it more difficult for females to orient. The adaptive value of this simultaneous singing may lie in the ability of a male to cause females to remain available for a longer period.

Alternate Male Behaviour

Many of the previous examples indicate that conspecific males may pursue alternative reproductive behaviours. A general framework for viewing these alternatives is provided by the concept of Evolutionarily Stable Strategies (E.S.S.). Maynard-Smith (1976) put together previous ideas on game theory and formalized the concept of E.S.S. Although initially used in studies of aggression, it has lately been applied to a variety of situations.

An E.S.S. is a strategy which, when a certain frequency of the population adopts it, is superior reproductively compared to a given set of alternatives. A strategy can be defined as a genetically determined behaviour which can be judged only in relation to natural selection of alternatives (Dawkins, 1979). An individual exhibits one reproductive strategy, although it might take different forms depending on environmental circumstances.

Individuals can have different pure strategies with a stable polymorphism existing. Individuals may have a single mixed strategy and spend a certain proportion of time in one behaviour and then switch to another behaviour. In a mixed strategy, this shift in behaviour does not correspond

to any environmental or individual factor such as age or female availability. Individuals may also have a single conditional strategy and change their behaviour to a particular form in response to environmental or social conditions. Thus it is possible to have an equilibrium of two or more strategies in a population which are evolutionarily stable against each other. When these strategies are genuine functional alternatives which co-exist in a population for an appreciable amount of time they must, on average, be equally successful reproductively (Cade, 1979a, 1980; Gadgil, 1972).

In a consideration of pure strategies and stable polymorphisms, Gadgil (1972) described a theoretical model which explained how two alternative strategies can reach an equilibrium. It was reasoned that either alternative strategy has its benefit arising from a given amount of investment. Simultaneously, the cost or survival probability decreases as investment increases. Males that invest more relative to other males in the same population will increase their mating frequency. Males avoiding competition mate less, but live longer. A cost-benefit trade-off would exist with each strategy representing a given cost and a given benefit. For example, territoriality involves large risks and expenses, but probably results in the insemination of more females than would otherwise be the case. Satellite behaviour is relatively inexpensive to perform, but does not give immediate returns in fitness. Satellites may, however, live longer and thus be able to attempt future matings.

An example is seen in Hogan-Warburg's (1966) and Van Rhijn's (1973) studies on the ruff, Philomachus pugnax. Territorial males are darkly coloured, and satellites are white and resemble females in colour and behaviour. Satellite males rarely show aggressive behaviour and can

peacefully co-exist on a territory with the resident. An exception occurs when females are present on the territory. At this time satellites may be attacked by the resident. On a large lek satellites performed only 10% of the matings while on a small lek they represented 28% of the matings. These strategies may represent a trade off if territory holders obtain more females than satellites and if satellites live for a longer period of time. Data comparing longevity and mating success for this species are not available.

A mixed strategy is a second possible situation characterizing species with males behaving in different ways. An animal switches from one strategy to another, regardless of other conditions (Cade, 1980; Dawkins, 1979). All stimuli which affect an organism, however, may not be perceived by observers and environmental conditions may affect behaviour in an unknown way (Cade, 1980). Mixed strategies are therefore hard to demonstrate conclusively. Nonetheless, a possible example of a mixed strategy, although not a male example, is seen through the detailed observations of Brockman et al. (1979) on the Great Golden Digger Wasp, Sphex ichneumoneus (Hymenoptera: Sphecidae). Females provision excavated tunnels with paratized katydids upon which one egg is laid. Part of the normal nesting involves the digging of a burrow, but some females do enter pre-existing burrows. If the burrow is already occupied, both the digger and the enterer will provision the nest until they meet and fight. The result is that the losing wasp leaves. No individual tendency to dig or enter is seen, thus ruling out a stable polymorphism. A mixed strategy is suggested by evidence that females entering a pre-existing hole cannot distinguish occupied nests from unoccupied ones, and nests seem to be abandoned for no apparent reason. More importantly, the total number of eggs laid by females who had begun

sequences by digging or by entering are roughly equal when time differences are considered. Females may therefore partition their time into two behaviours based on the probability of reproductive returns which, in some fashion, is programmed genetically, and hence a mixed strategy could exist within individuals.

Conditional strategies are the easiest to demonstrate and probably represent most cases. Here an individual behaves a particular way if certain conditions prevail. These decisions can be reversible or non-reversible. Size, age and population density are conditions often important in making behavioural decisions. For example, Howard (1978) studied age specific mating in the bullfrog, Rana catesbeiana. Males have three modes of mating: they may hold a territory and attract females by calling; satellite males may intercept females attracted to callers; and males may call from sites they don't defend and leave if challenged. These behaviours depend on the age and size of males. Territorial males are the largest and oldest, satellites the youngest and smallest, and opportunists or non-territorial calling males intermediate between these two. Mating success increases with body length for callers, so that the territory holders may have the highest fitness. Satellite mating success is not known, however, in this species. Perril et al., found that 40% of satellites in The Green Tree Frog, Hyla cinerea, achieved amplexus.

Size is seen as a factor in Alcocks' (1976, 1979) studies on the bee Centris pallada (Hymenoptera: Anthophoridae). Here, eggs are laid in the ground and males emerge before females. Large males patrol the ground for emerging females. Smaller males hover above, catching females that large males miss. Patrolling males defend areas against other males, and are generally more successful reproductively than hoverers. Small males, however, probably

maximize their success by hovering as they lose fights with large males. These size differences are due, in part, to the size of the brood chamber and the food fed them as larvae. There may be, however, genetic differences as well. Males behave according to the condition "if small hover" may be "making the best of a bad job" in that they salvage whatever fitness is possible (Dawkins, 1979).

The effect of population density was described previously in Otte and Joern's (1975) study of grasshoppers. They stated that as density increases, the amount of effort invested in defense also increases. When the cost of territoriality exceeds the benefits, non-territoriality becomes the expression of the same strategy.

Variables such as age can affect male behaviour. In terms of reproductive value the costs of signalling should decrease with increasing age. Nielsen and Dreisig (1971), working on the bush cricket Tettigonia viridissima found that individuals increased their calling time relatively steadily over the first two weeks of adult life with a sharp increase occurring in the third week. After this point the calling remained relatively constant. Alexander (1961) reported anecdotal evidence that old isolated and unmated crickets are highly susceptible to stridulation when movement is sensed nearby. No actual data were reported in Alexander's case.

Another factor affecting acoustical behaviour is the time of day. Many crickets call only at night, while other individuals call during the day (Alexander and Merril, 1967). Other crickets, for example, G. campestris, call mainly during the daytime with a peak at 15:00 hr. Cade (1979a) reported the phenomenon of dawn calling where a population of crickets increased the amount of calling during the dawn hours.

Calling songs are also inhibited for some time after copulation (Huber, 1962, 1965). Huber, in studying G. campestris, found that stridulation is not resumed after mating until a new spermatophore is produced. In this species, singing males which copulate one night produce very few calls and resume calling behaviour the next night.

The presence of females also affects male calling. Alexander (1960) observed that males of the katydid, Microcentrum rhombifolium, would produce a shuffling sound after a ticking response by the female to the males normal calling. Spooner (1968) found that several species of katydids either reduced their calling or changed its composition altogether after a female acoustically responded.

Another factor inhibiting stridulation is temperature. Nielsen and Driesig (1971) found that temperatures below 12°C inhibited calling in T. viridissima, while 100% of the individuals called at temperatures over 15°C. They also noted that rain inhibited calling.

Hunger was also found to be a factor. Nielsen and Driesig (1971) found that hunger enhances locomotion while inhibiting stridulation.

Female Choice in Acoustical Insects

Acoustically communicating insects identify conspecific mates by song. Various workers (Cade, 1979a and 1981b; Forrest, 1980; Morris et al., 1978 and Ulagaraj and Walker, 1975) have found that females prefer males calling at higher intensities than those calling at lower intensities. Also, females of the katydid, Scudderia texensis, orient to males who increase the intensity at the end of their song (Spooner, 1968). Signal quality is the cue that may indicate the best male in these cases.

A further possibility is to maximize the fit between the pattern of one's song and that favoured by females. This can be accomplished by

producing the appropriate pattern and minimizing its loss of distinctiveness due to nearby singers (Alexander, 1975). An example is seen in the synchrony of periodical cicadas such as the 17 year cicada, Magicicada cassini. Long periods of synchrony are due to visual stimuli, whereas short periods of synchrony result from auditory stimuli (Alexander and Moore, 1958). Such synchrony may be sufficient in attracting cicada females.

A second situation occurs where the song consists of a series of short chirps. To keep the song effective a male should place his chirps between those of neighbouring competitors so the important within chirp elements are least likely blurred. Thus there would be a minimizing of signal overlap with more information being available for the female to choose from. Such behaviour is witnessed in the cricket, Scapsipedus marginatus, where chirps are widely spaced with intermediate pulse rates (Zaretsky, 1972).

METHODS OF STUDY

The research was performed in St. Catharines, Ontario. An outdoor arena was used to study Gryllus integer from mid-July to early September, in 1979 and 1980. G. integer and G. veletis were also studied in two indoor arenas from January to mid June, 1979 and 1980.

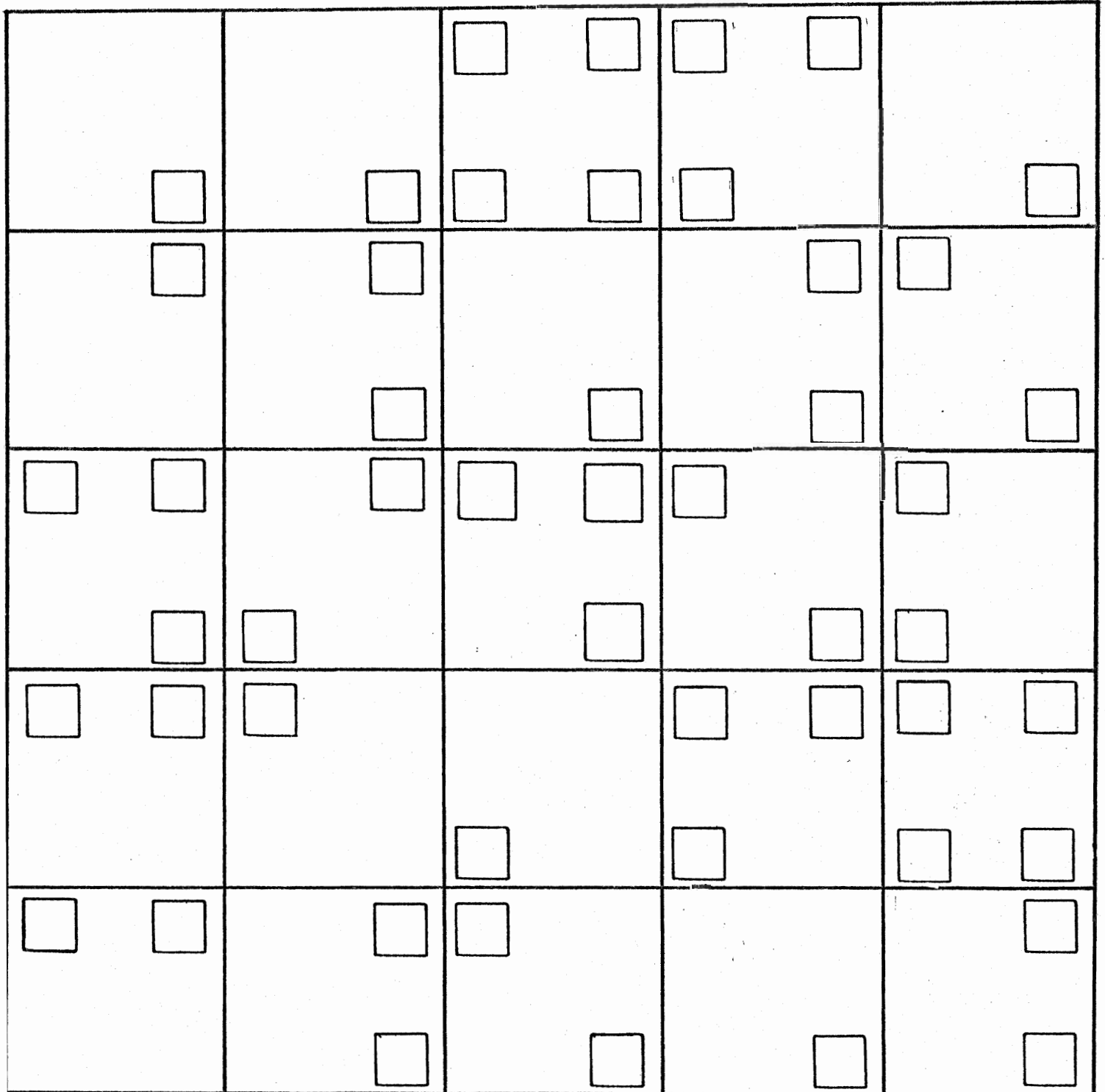
Study Insects

G. integer were collected in Austin, Texas and G. veletis in the Niagara Region. Cultures of both species were established and housed in 20 gallon plastic garbage cans with screened tops. Purina Cat Chow^R, water and egg cartons for shelter were provided. Cultures were maintained on a 12:12 light dark cycle, at approximately 23 - 31°C. Containers were checked daily for adults. Adults were removed on the day of the final molt. Males were used in observations, or isolated in jars until needed. Females were housed together in a terrarium. Each male was weighed with an Oertling Analytical Balance. Males and females used outdoors were marked by glueing a small numbered sticker on the pronotum (Graze Bee Supply), and by painting the femurs with fluorescent Day Glo^R paint for easy location outdoors by a blacklight (see outdoor arena). Males studied indoors were marked with different combinations of white liquid paper on the pronota and femurs. Females used indoors were not marked.

Outdoor Arena

An outdoor arena was constructed in the spring of 1979 to observe acoustical behaviour, movement patterns and mating behaviour in a semi-natural environment. The arena consisted of a 13 m x 13 m area fenced by galvanized steel, 1 m in height, as well as Frost fencing. The top of the arena was covered by chicken wire to exclude birds. The base of the arena was planted with grass sod, and divided into 25, 2.6 m x 2.6 m

Figure 1. Map of the Brock University outdoor arena indicating the 25 quadrants and the randomly located cricket shelters.



← 13 m →

quadrats. Quadrats were numbered and marked with a flag. Fifty shelters consisting of a 12 cm x 6 cm hole in the ground covered by a plywood block were placed randomly in the arena (Fig. 1).

Crickets were introduced into the arena in daytime and allowed one day to acclimate. Observations were usually performed at night from 2200 to 0600 hrs (E.D.T.). For six days in 1980 observations were extended to 1000 hrs. During this time four full checks of the arena were made at regular intervals, (2200, 0100, 0400 and 0600 hrs), to ascertain the location of individuals. In these checks crickets were located by walking through the arena with a Burgess ultraviolet lantern model 165/3. The painted legs of crickets were readily visible and their locations were recorded on a scale map of the arena. Also, every 15 min the presence or absence of calling from a particular male's location was recorded. When a song was heard from a location where a male had not been previously observed, his identity was determined. In addition, song intensities were measured at irregular intervals throughout the night by a General Radio Sound Level Meter (1565-B) held approximately 18 cm from the caller.

In 1979 G. integer was studied at a density of 16-19 males and 10-12 females. This was maintained by adding new crickets of known age to replace dead or missing crickets. Crickets missing for more than three consecutive nights were replaced.

In 1980, G. integer was studied at two densities, an initial density of 18 - 21 males and 10 - 14 females and higher density of 37 males and 10 to 14 females.

To estimate male reproductive success the number of times each male was seen with a female was scored in 1979. In 1980, females were recorded as mating with a male when a spermatophore was attached and a male was present.

These methods were performed to study the effects of age, weight and

density on the reproductive success, calling behaviour and displacement¹ of individual males.

Indoor Arena

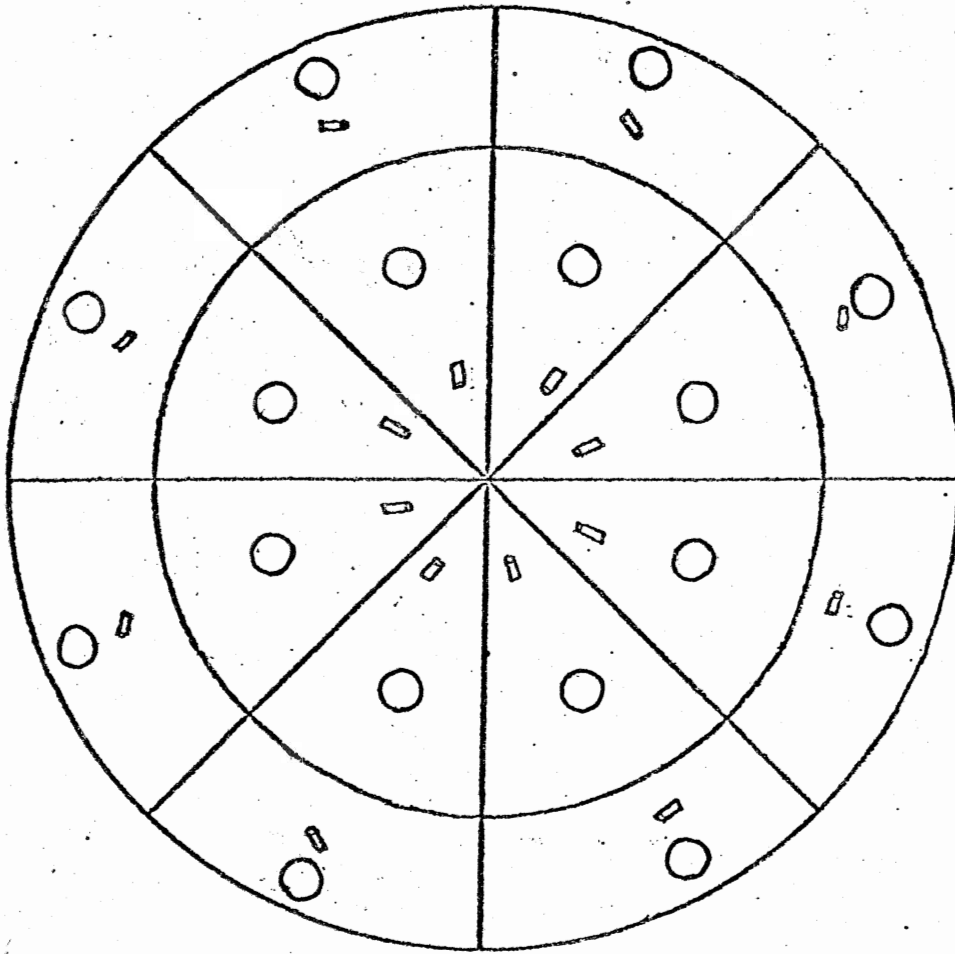
To study the effects of density on cricket behaviour two indoor arenas were used. The arenas were 7.6 m in circumference with a diameter of 2.4 m. The walls were made of galvanized steel 0.9 m in height. The base was covered with approximately 8 cm of sand and vermiculite, and it was divided into 16 sectors of equal area by string suspended 2.5 cm above the base. Four, 25 watt, incandescent, red bulbs were suspended over the arena. Each sector contained cat chow, water in cotton plugged test tubes, and an inverted petri dish cut on the sides for shelter (Fig. 2). The soil was moistened daily. Indoor arenas were on a photoperiod of 8:16 hrs (dark:light), opposite that of the ambient photoperiod. Observations began one hr into the dark period and continued for six hours.

A density of six G. integer males were studied for a period of 10 days. Six more males were then added, and all 12 were studied for 10 days. The second set of six males were then removed, and the original six were observed for five days. In all the above cases no females were in the arena.

In all cases observations were made on individual male calling, movement, and on various aspects of aggressive encounters. Observations on a male's calling were made by timing the duration of each call each male made with a Marson electronic stopwatch. This stopwatch had a lap timer, allowing two males to be timed simultaneously. When needed a second stopwatch (Brenet no. 30) was used. Mean calling times per male per day were calculated.

1 The difference between the initial position of a body and any latter position. (Webster's Seventh New Collegiate Dictionary. Gand C. Merriam Co. publishers.)

Figure 2. Diagram of the indoor arena indicating the 16 quadrants and cricket shelters.



Displacement data were obtained in the same manner with each time the cricket moved in the arena being timed from start to finish of the movement.

When crickets encountered each other in a meeting the watch was started and was stopped when the crickets departed. In these meetings one or two of three events would occur: 1) nothing, the crickets meet then leave shortly thereafter without calling or fighting; 2) aggressive calling between the two was exhibited. When this happened the time it took to start calling was noted. The third alternative in a meeting was fighting with aggressive calling. A fight was classified as such when crickets made physical contact, usually with mandibles and/or legs. The times fights started and stopped since the crickets first met was noted. In such cases calling was also involved and the times that aggressive calling started and stopped in the meeting was also noted.

In G. veletis, densities of three, six and 12 males were studied in the same manner as G. integer for five days each. Here an initial three males were studied, after which three additional males were added. This density of six was studied for 5 days then split into two, three male density groups, which were studied simultaneously. In the results section, and on figures, the initial three are referred to as 3_0 , while the latter two sets of three are 3_1 and 3_2 . The 3_1 individuals corresponds to the initial set of three (3_0), after the six density study, while the $3_{(2)}$ refers to the initial set of three while in the six density. Following the above studies the same six crickets and an additional six were introduced into one arena and studied.

To test the effects of females on male behaviour five male G. integer were introduced and observed for one day. Eight females were then added and along with the five males were observed for one day, to note any

changes in male behaviour. A similar study was performed on G. veletis with three males and six females.

Statistical comparisons between two samples were made using the Mann-Whitney U test in the case of independent samples and the Wilcoxon Match-Pairs Signed Ranks test when the samples were dependent. These tests are not sensitive to the distribution of data (Siegel, 1956). In the case of three sample comparisons, one way Analysis of Variance was used to compare sample means using a TI59 calculator and statistical package. A one way Analysis of Variance was used as directionality was predicted in all comparisons. The .05 level of significance was used as the minimum designation for a significant relationship. Non-parametric tests were used with two samples since the equivalent parametric analysis, the t test, is especially sensitive to departures from normality. By comparison, the parametric ANOVA was used since the test is less sensitive to departures from normal (Snedcor and Cochran, 1967; Scheffler, 1969), and can be machine calculated. In addition, raw data for use in ANOVAs were first log transformed to homogenize variances between samples.

RESULTS

Results from behaviour studied in the outdoor arena are presented first, followed by the findings from the indoor arena study. Raw data on the behaviour of individual males are in the Appendix.

Outdoor Arena

Figure 3a and b shows the mean time calling by individual G. integer of known age in the outdoor arena in 1979 and 1980. Males started calling at an average of 6.3 days of adult age in 1979 and 1980 ($N = 37$, $SD = 7.9$, Range = 4 to 19 days of age). After six days of age, calling time did not differ significantly with increasing age in 1979 or 1980 (Anova; $F = 1.3$, $P > 0.5$, and $F = 1.47$, $P > .05$).

Figure 4a, b and c is a frequency distribution of mean calling time per night for individual G. integer males in the outdoor arena in 1979, 1980 (initial density), and 1980 (high density) populations. These data are from observations over 22:00 to 06:00 hrs. Males included for statistical analysis in this study were observed for at least five days and were between 5 and 19 days of age. The average calling time in 1979 was .74 hrs/night ($N = 17$; $SD = .87$; Range = 0 to 2.77 hrs/night). In the 1980 population at the initial density, males called an average of .63 hrs/night ($N = 20$; $SD = .58$; Range = 0 to 1.6 hrs/night). In the 1980 high density population males called an average of .47 hrs/night ($N = 37$; $SD = .75$; Range = 0 to 3.5 hrs/night). The mean calling time was significantly less in the 1980 high density population (U test $Z = 2.9$; $P < .01$), compared to the 1980 initial density. Calling time in 1979 was significantly more than in the 1980 initial density population (U test $Z = 2.12$; $P < .05$). Also, the 1979 population called significantly more than the 1980 high density population (U test; $Z = 1.5$; $P < .01$).

Figure 3. The mean calling time per night of individual G. integer males of known age in the outdoor arena in (a) 1979 and (b) 1980 (sample sizes and standard errors are shown).

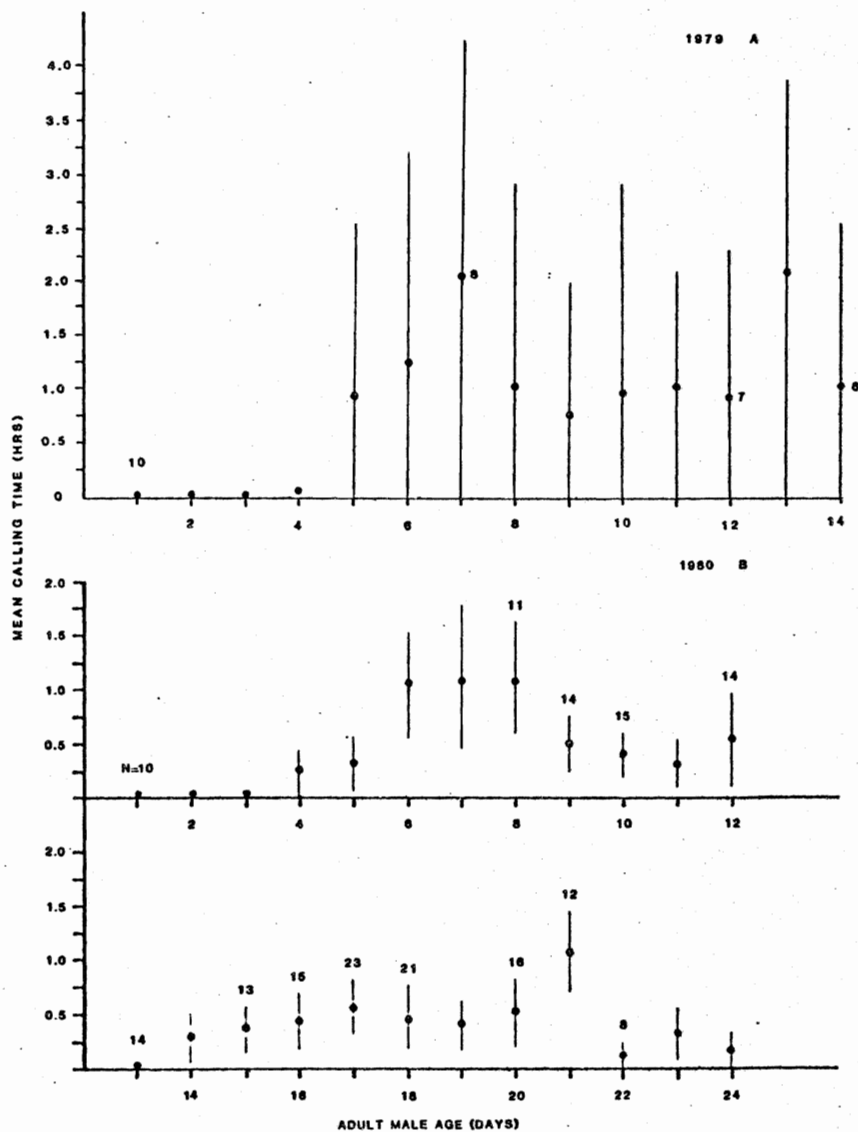


Figure 4. The mean calling time per night of individual G. integer males in the outdoor arena in (a) 1979, (b) 1980 (initial density) and (c) 1980 (high density).

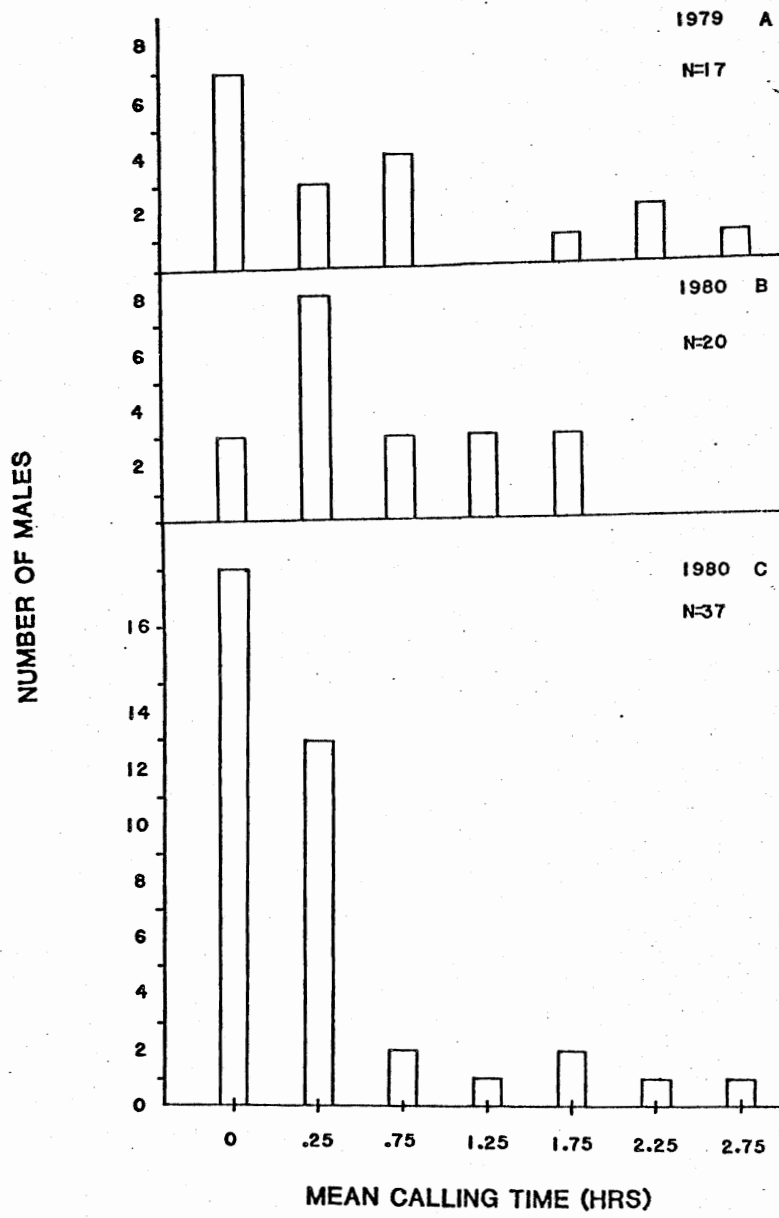


Figure 5 shows the mean time calling of males of known weight for both 1979 and 1980. A large variation in the weights of males occurred, but mean calling times did not differ significantly for the weight intervals shown (Anova; $F = 1.03$; $P > .05$).

Figure 6 shows the mean calling times of males with respect to the temperature for both 1979 and 1980. Crickets called more at higher temperatures than at lower temperatures (Anova; $F = 24.7$; $P < .05$). A linear relationship is the best fit (Slope = 12.56, $r = .5$).

Figure 7a and b show the number of calling G. integer males over 22:00 to 06:00 hrs in 1979 and 1980. In 1979 and 1980 no difference in the calling times of individual males occurred through the hours 22:00 to 06:00 (EDT) (Anova; $F = .92$; $P > .05$; and $F = 4.76$, $P > .05$ respectively). By contrast, Fig. 8 shows the number of G. integer males calling through 12 hours that included the dawn and late morning hours. There was a relatively uniform number of males calling through the night, but there was a sharp increase at 05:00 hrs, a peak at 07:00 hrs, and a subsequent decline towards mid-morning. The difference in the mean number of males calling over 22:00 to 10:00 hrs was significant (Anova; $F = 30.47$; $P < .05$). Table 1 shows the mean calling time during the night (22:00 to 06:00 hrs) compared with mean calling time during dawn (06:00 to 10:00 hrs) for individual males. No significant relationship is observed between the mean calling time at night with that at dawn (Wilcoxin test; $Z = .407$; $P < .05$).

Figure 9 shows the frequency distribution of mean calling time over 22:00 hrs to 10:00 hrs for the 1980 high density population. The mean

Figure 5. The mean calling time per night of individual male G. integer crickets of known weight in the outdoor arena in 1979 and 1980.

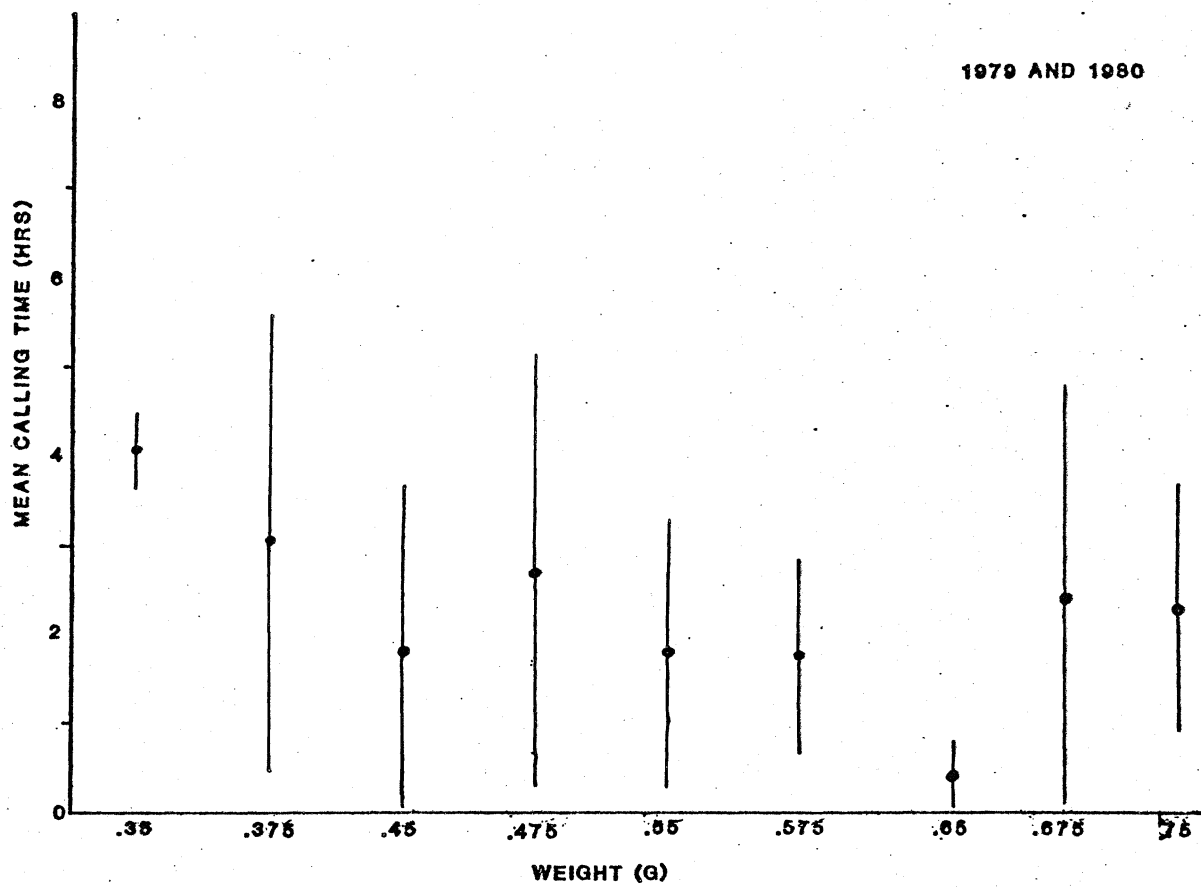


Figure 6. The mean calling times per night of individual male G. integer crickets in the outdoor arena with respect to the nightly temperature in 1979 and 1980.

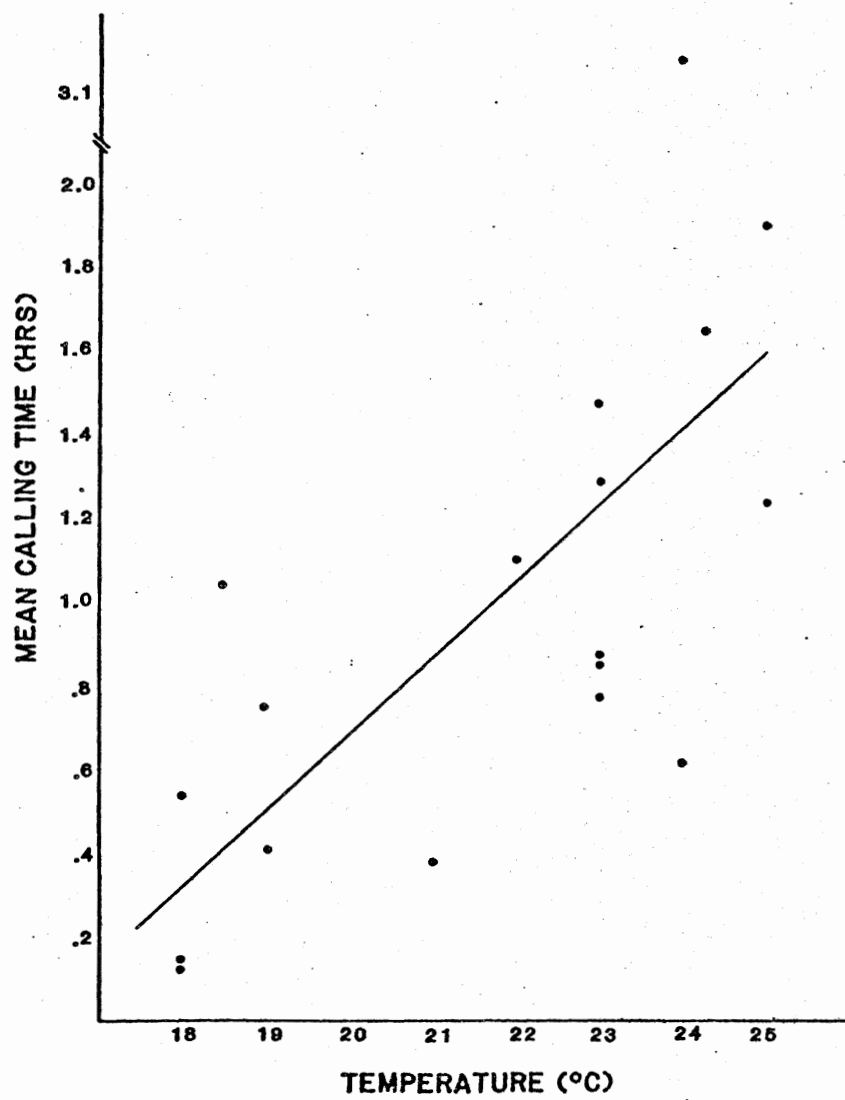


Figure 7. The number of calling G. integer males from 22:00 hrs to 06:00 hrs in the outdoor arena in (a) 1979 and (b) 1980 (sample sizes and standard errors are shown).

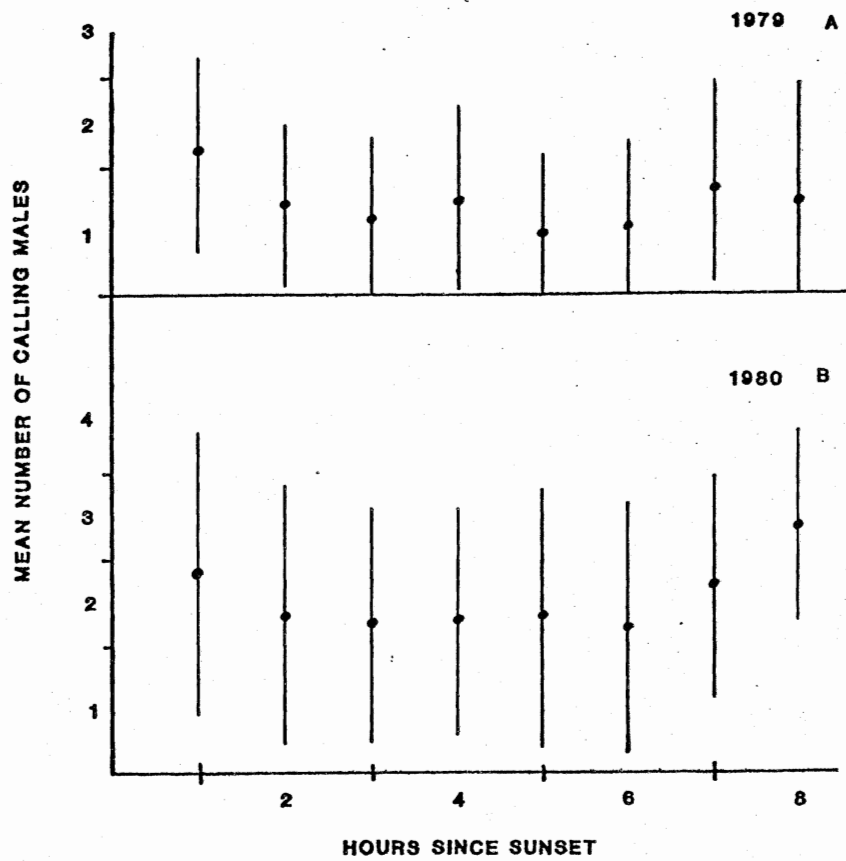


Figure 8. The number of individual G. integer males calling per night from 22:00 hrs to 10:00 hrs in the outdoor arena in 1980 (high density).

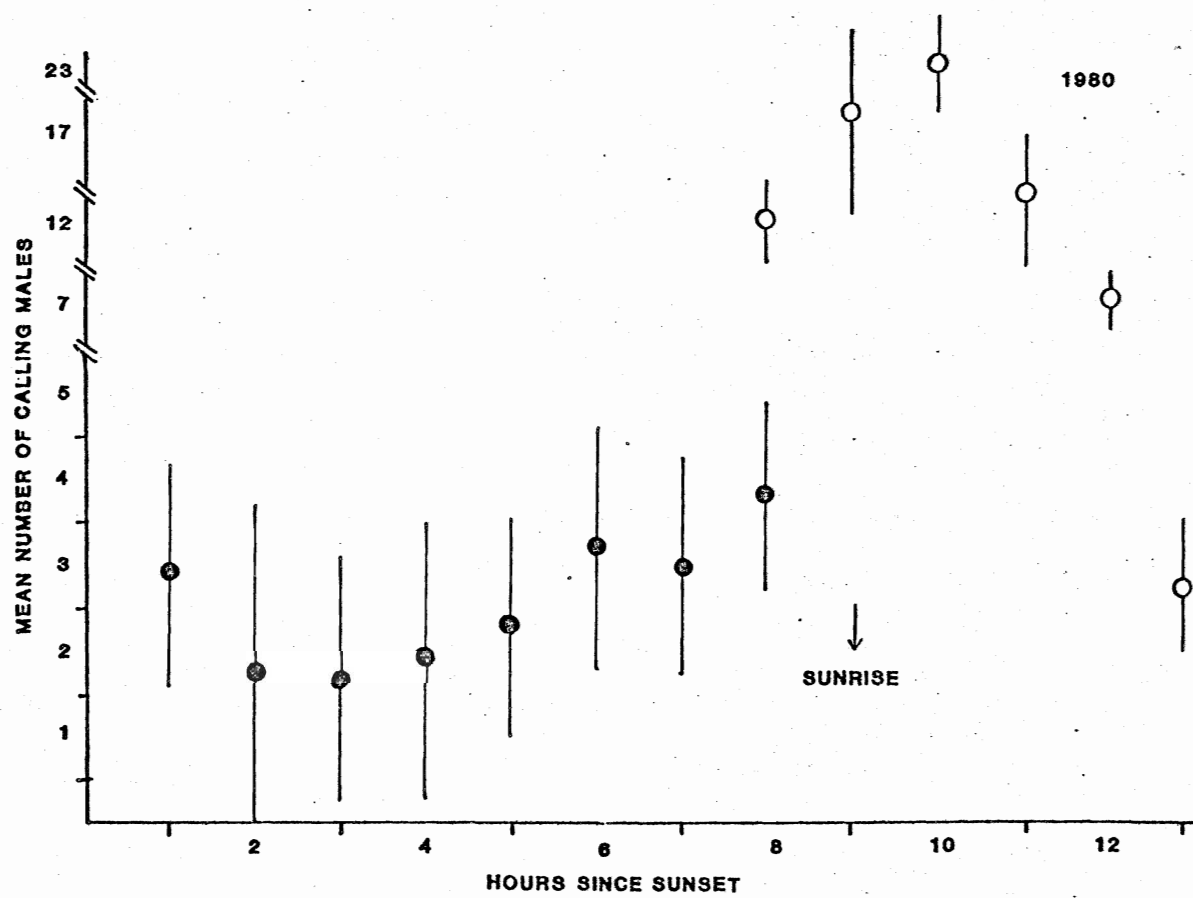


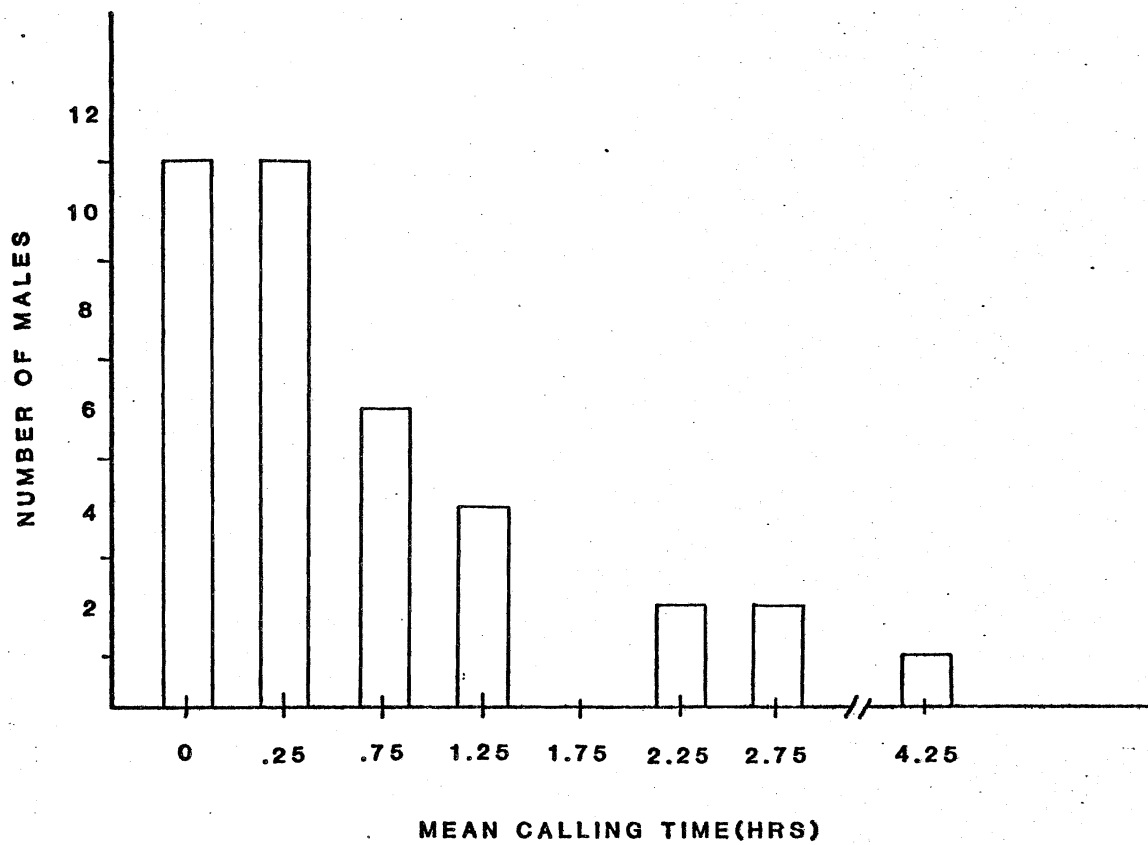
Table 1. Mean calling time during the night 20:00 to 06:00
 compared with mean calling time from 06:00 to 10:00
 hrs for individual G. integer males in the 1980
 (high density) outdoor arena.

Male Number	Mean Calling Time During Night (hrs)	Mean Calling Time During Dawn (hrs)
29	2.9	0
63	0	1.4
65	1.3	.96
71	.375	0
73	.41	0
77	.29	.08
89	.33	.58
87	0	0
95	0	0
12	.25	0
1	0	.54
3	.5	.3
5	0	1.38
7	2.1	0
9	0	.12
11	.29	.35
13	3.5	.86
15	.38	0
17	1.1	.2
19	.7	.29
23	2.9	0
25	0	0
27	0	0
29	0	.46
31	.08	.38
33	0	.86
37	.2	0

Table 1 (cont'd).

Male Number	Mean Calling Time During Night (hrs)	Mean Calling Time During Dawn (hrs)
39	.21	.3
41	0	0
43	0	0
45	0	.19
47	0	0
49	0	0
51	.08	0
53	0	0
55	0	0
57	0	0

Figure 9. The mean calling times per night of individual male G. integer crickets in the outdoor arena over 22:00 hrs to 10:00 hrs in the 1980 high density population.



calling time for this period was .75 hrs/night ($N = 37$; $SD = 1.04$; Range = 0 - 4.4 hrs/night). Data on calling behaviour were gathered from 10:00 to 06:00 unless otherwise indicated in the following data sets.

Figure 10a and b shows the calling time of individual males each night compared with the total calling in 1979 and 1980 (initial) respectively. There is no significant relationship observed in either data set (Anova; $F = .42$; $P > .05$; $F = .23$; $P > .05$, respectively).

The average G. integer song intensity was 78 dB ($N = 7$; $SD = 7.2$; Range = 60 - 83 dB) in 1979, 75dB ($N = 12$; $SD = 8.1$; Range = 50 - 88 dB) in the 1980 initial density and 80 dB ($N = 12$; $SD = 5.2$; Range = 70 - 87 dB) in the 1980 high density population. There was no significant difference between the 1979 and the initial group of 1980 males (U test, $Z = 1.46$; $P > .05$). The 1980 initial and high density populations did, however, differ significantly in the average calling intensity (U test; $Z = 3.49$, $P < .01$). Individual variation in calling intensities are shown in Table 2. Mean calling song intensities for the 1980 high density population over 22:00 to 06:00 hrs are in Fig. 11. There was no significant difference in calling intensities with time in this group of males (Anova; $F = .61$, $P > .05$).

The mean number of times females were observed with a male and the mean calling times of individual males for 1979, 1980 initial density, and 1980 high density, are in Fig. 12a, b and c, respectively. In the 1979 and 1980 (initial) density the mean number of females observed with males varied significantly for 1979, (Anova; $F = 21.82$; $P < .05$, for the 1980 initial density, Anova; $F = 20.86$; $P < .05$). In the 1980 high density no relationship was seen (Anova; $F = .056$; $P > .05$). A logarithmic relationship is the best fit in Fig. 12 a (Slope = .056; $r = -.79$). In Fig. 12b a linear relationship is the best (Slope = $-.2$; $r = .4$).

Figure 10. The total time calling by individual G. integer males each night compared with the total time calling of other individuals per night in the outdoor arena in (A) 1979 and (B) 1980 (initial density).

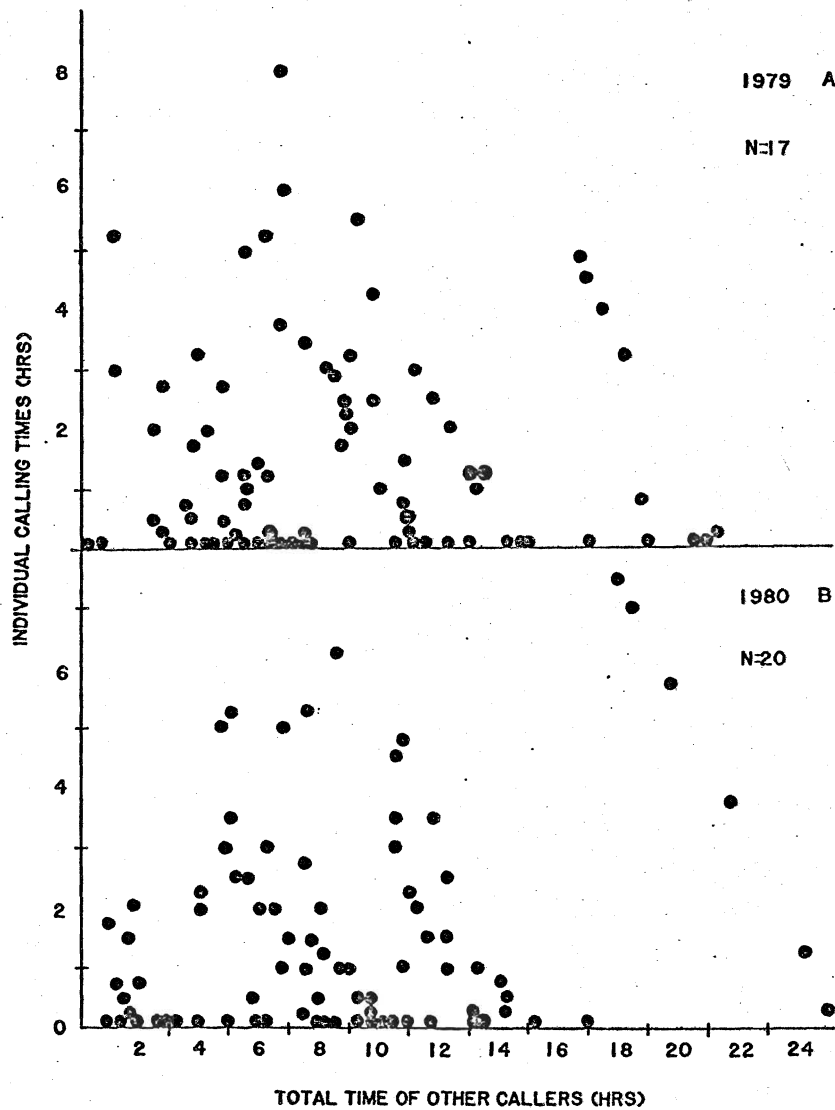


Table 2. Gryllus integer song intensities of individuals measured on different nights in the outdoor arena in 1979 and 1980 (initial).

Number of Individual	Song Intensity (dB)		
	\bar{X}	S.D.	Range
93	75.0	5.6	65 - 82
5	73.6	8.2	62 - 83
85	72.0	5.2	64 - 81
87	65.0	5.1	60 - 72
23	73.0	4.4	66 - 78
29	72.25	4.82	66 - 79
15	72.0	5.7	64 - 77
81	59.5	12.3	50 - 77

Figure 11. The calling song intensities of individual G. integer males
from 2200 hrs. to 0600hrs. in the outdoor arena in 1980 (high density).

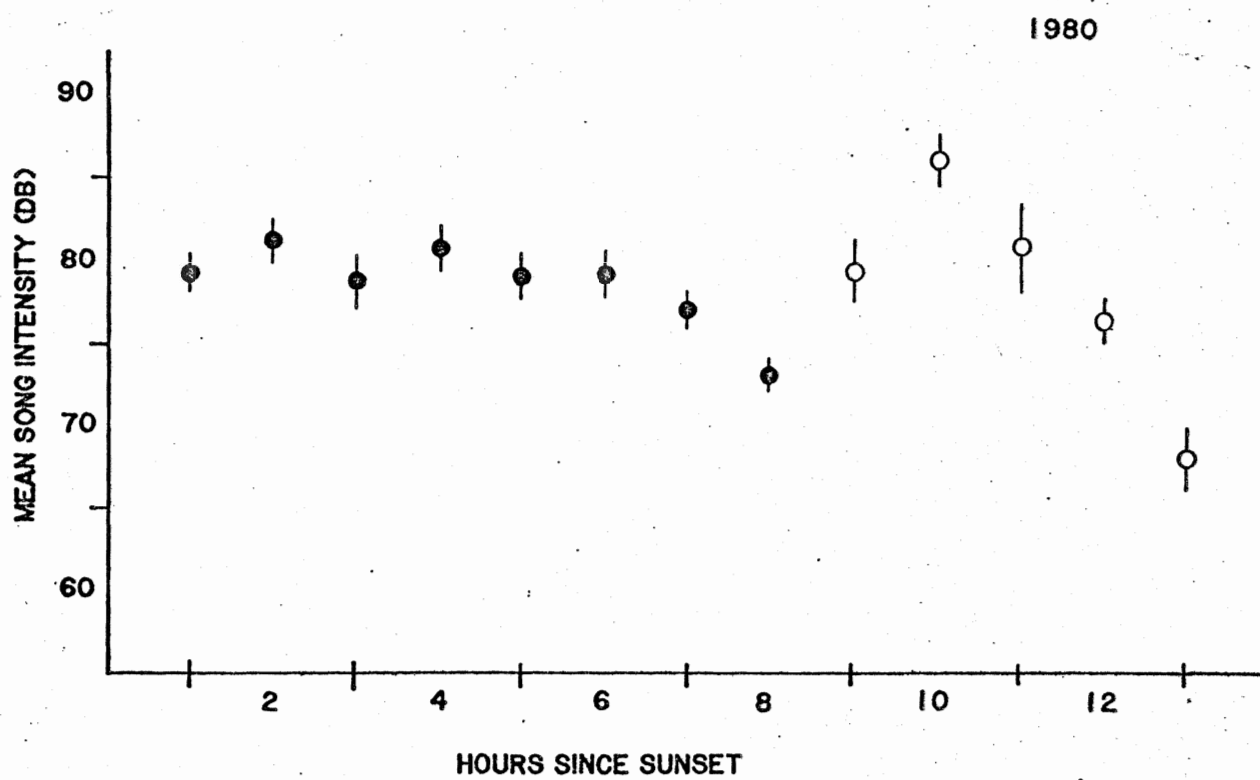
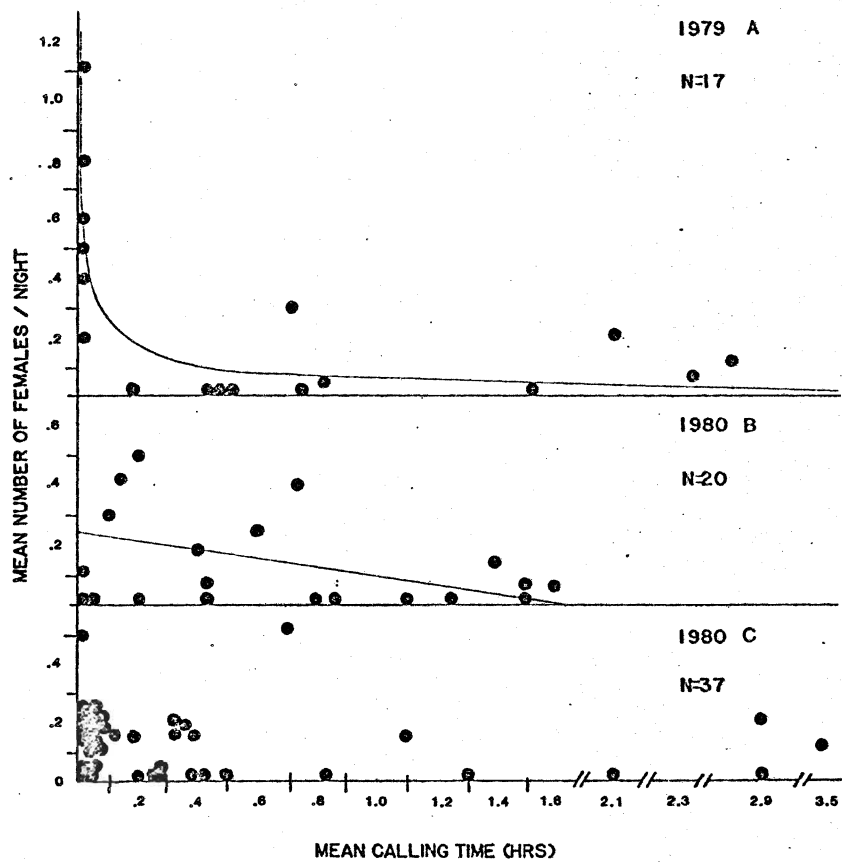


Figure 12. The mean number of times females were observed per night with males and the mean calling times of individual males in the outdoor arena in (A) 1979, (B) 1980 (initial density) and (C) 1980 (high density).



The mean number of females with males who did not call is compared to the ratio of non-callers to callers in Fig. 13a for 1979, Fig. 13b for 1980 (initial density) and Fig. 13c for 1980 (high density). Non-callers are those males who called .5 hrs or less. In 1979 and 1980 (initial) there was a significant difference (Fig. 13a Anova; $F = 19.72$; $P < .05$; Fig. 13b; $F = 20.16$; $P < .05$). A logarithmic relationship is the best fit in Fig. 13a and b. These lines have slopes of $-.197$ and $-.254$ respectively. Correlation coefficients were $-.772$ and $-.756$ respectively. In the 1980 high density Fig. 13c, no difference was seen in the ratio of non-callers to callers ($F = .43$; $P > .05$).

Table 3 shows female acquisition with age in individual G. integer males in the outdoor arena. No difference is seen (Wilcoxin Test; $T = 2$; $P > .05$).

The mean displacement from previous positions compared with the mean calling time per night of individual males is seen in Figs. 14a, b and c for 1979, 1980 (initial density) and 1980 (high density) populations respectively. In all three cases no significant relationship exists (Fig. 14a; Anova; $F = 1.67$, $P > .05$; Fig. 14b, $F = .55$, $P > .05$; Fig. 14c, $F = .49$, $P > .05$).

Fig. 15 shows a case of extreme displacement in a single G. integer male over his period in the outdoor arena.

Fig. 16a, b and c shows the frequency distribution of mean displacement from a previous position over hours 22:00 to 06:00 in 1979, 1980 (initial density) and 1980 (high density) respectively. These males were observed for at least five days and up to 19 days of age. In 1979 individuals had a mean displacement of 1.28 m/night ($N = 17$; $SD = .7$; Range = .09 - 2.66 m/night), while in the initial 1980, individuals moved an average of 5.5 m/night ($N = 20$; $SD = 2.17$; Range = 1.75 - 9.9 m/night). The difference

Figure 13. The mean number of females ~~to~~ non-callers compared to the ratio of non-callers to callers in the outdoor arena in (a) 1979, (b) 1980 (initial) and (c) 1980 (high density).

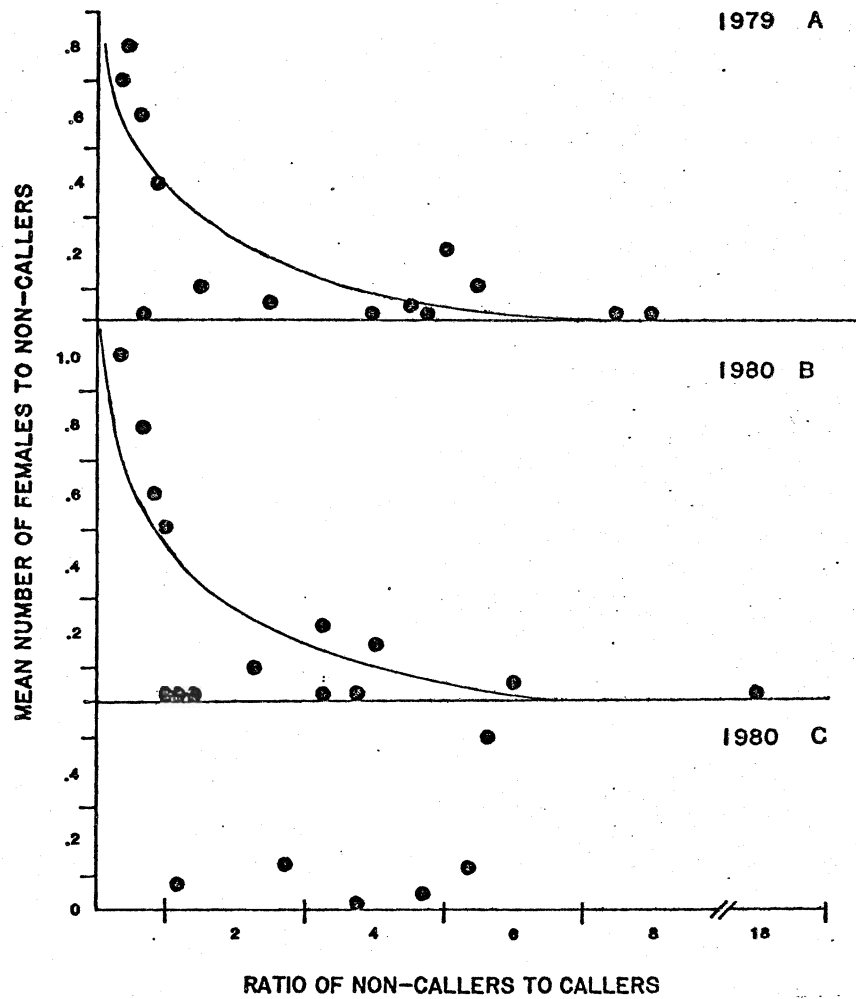
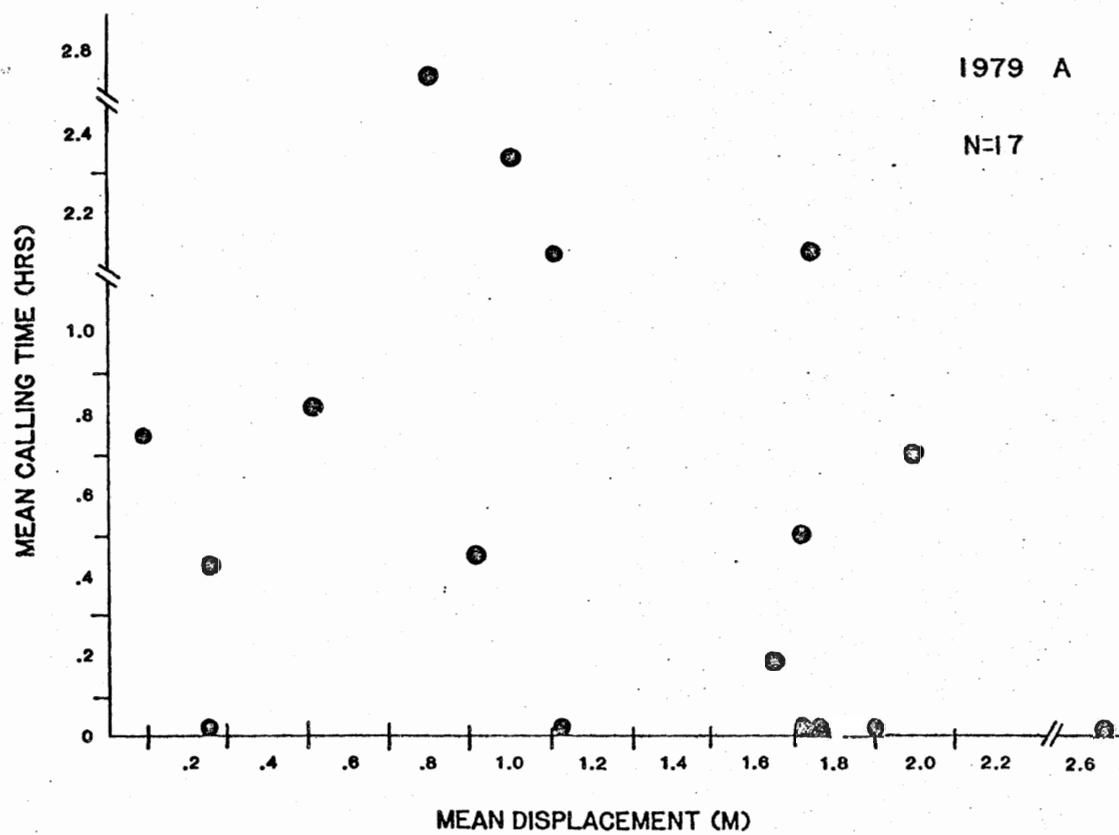
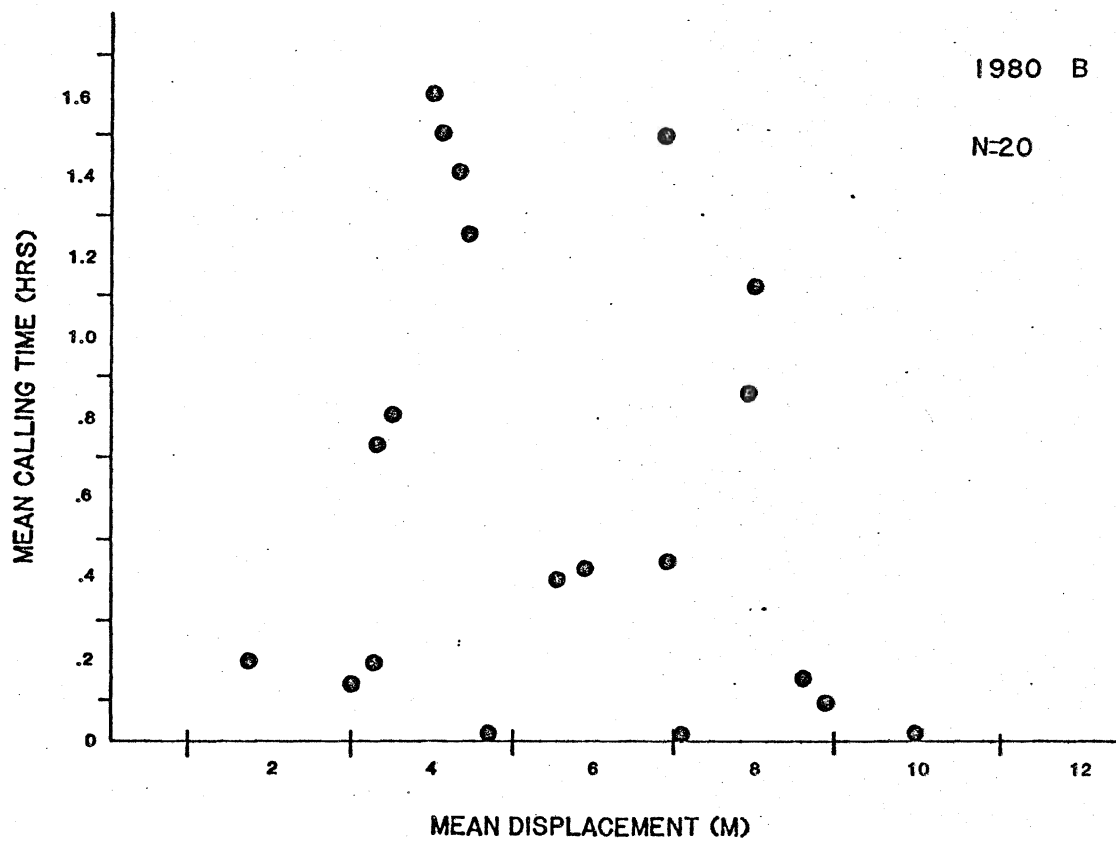


Table 3. The mean number of times individual males of Gryllus integer were seen with females, with respect to male age, in the outdoor arena in 1980.

Number of Individual	Mean Number of Females Acquired Per Night		Total Number of Days Observed
	<u>1st Half of Life</u>	<u>2nd Half of Life</u>	
23	.375	.375	18
15	.833	0	14
29	0	.1	20
39	.1	0	20
41	.11	0	18
75	.14	.14	16
79	.14	.29	14
Total Female Acquisition	<u>13</u>	<u>9</u>	

Figure 14. The mean calling time per night compared to the mean displacement per night from a previous position of individual G. integer males in the outdoor arena in (a) 1979, (b) 1980 (initial) and (c) 1980 (high density).





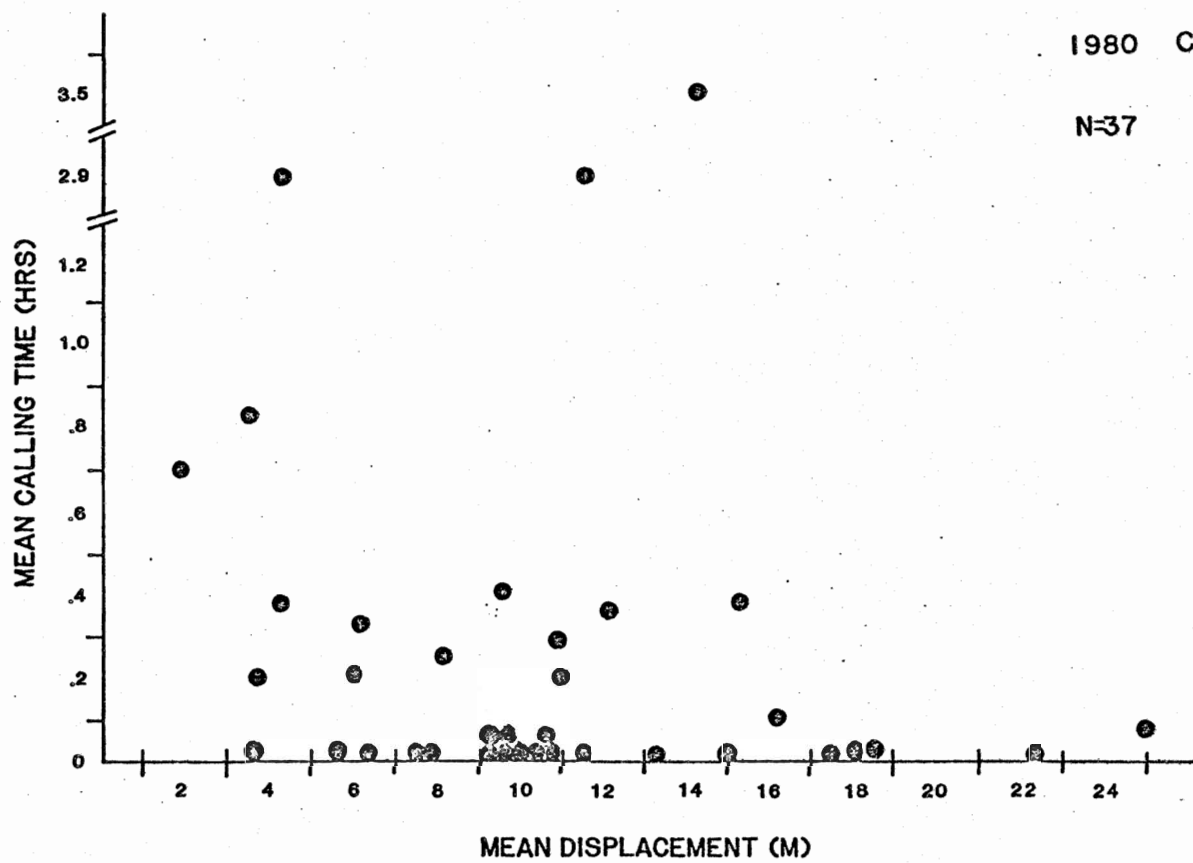
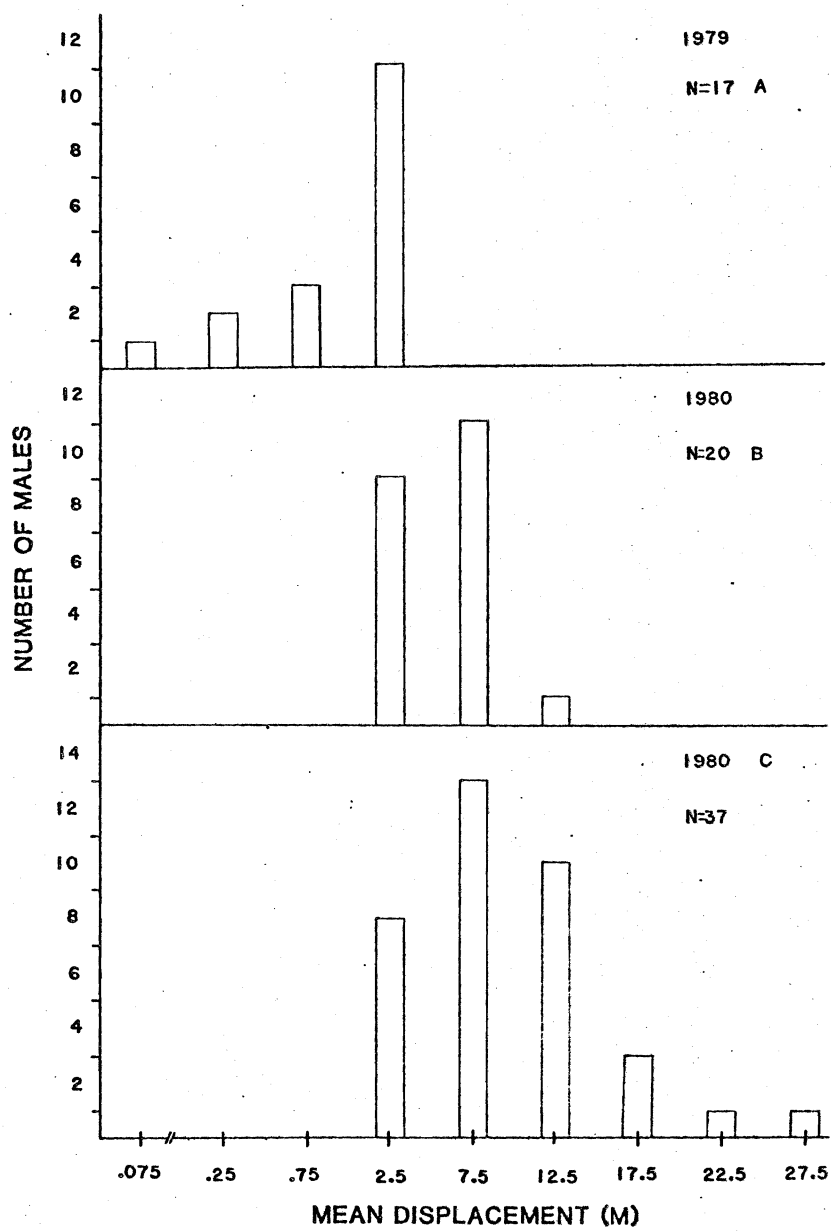


Figure 15. An example of extreme displacement in a single G. integer male during his period in the outdoor arena in 1980.

		13/8 1000	16/8 0100 16/8 1000 16/8 0400 -0600	12/8 0100 12/8 0400 -0600		11/8 1000	5/8 0100
			13/8 0400 -0600	13/8 0100			4/8 0400
							9/8 1000- 0600 10/8 0100-0400
15/8 1000		15/8 0100					11/8 0100 1/8 0400 0600 2/8 1000
5/8 0600	6/8 0100						4/8 0600 5/8 0400
						11/8 0400	
3/8 0400							4/8 1000 2/8 0100
6/8 1000			1/8 1000 -0100				
3/8 0600			11/8 0600		3/8 0100		

Figure 16. The mean displacement per night from a previous position of individual G. integer males in the outdoor arena in (A) 1979, (B) 1980 (initial density) and (C) 1980 (high density).



between these two populations was significant (U test; $U = 7$; $P < .05$). The 1980 high density population moved more than that of the initial 1980 density ($\bar{X} = 9.48$ m/night; $N = 37$; $SD = 4.7$; Range = 1.9 - 25.4 m/night). This is a significant difference (U test; $Z = 2.8$; $P < .01$).

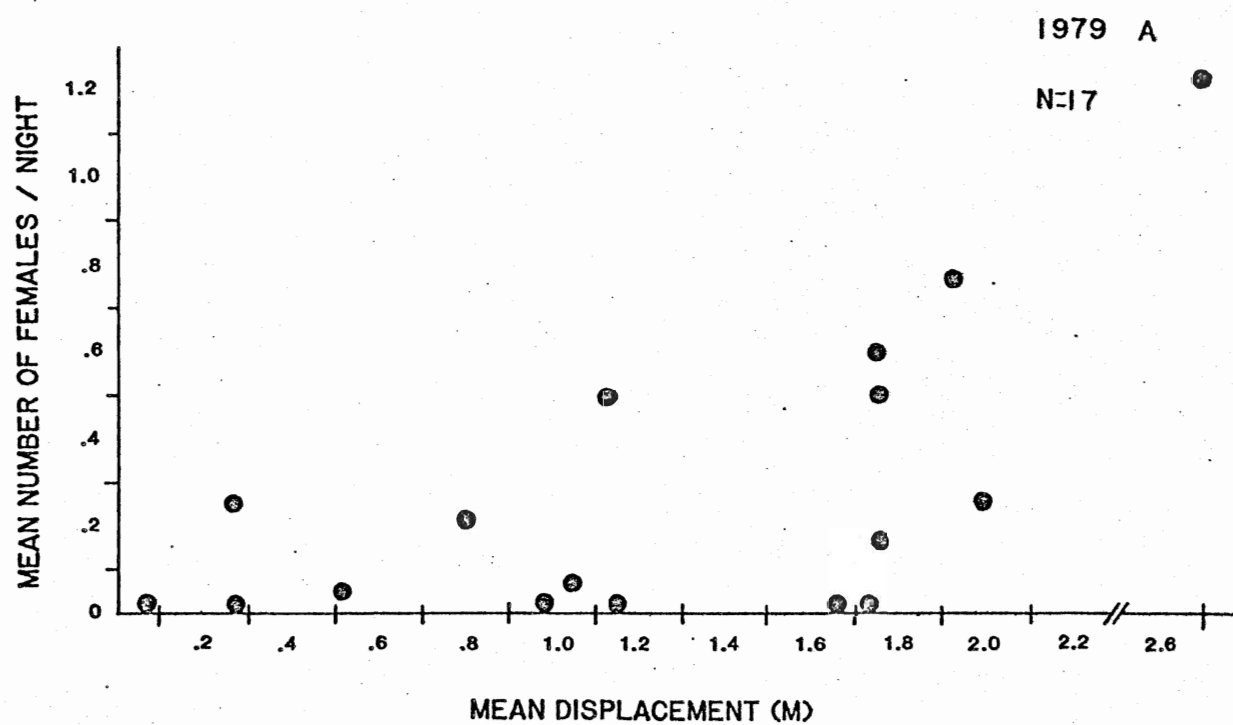
Figure 17a, b and c show the mean number of times males were observed with females and the mean displacement from a previous position for 1979, 1980 (initial density), and 1980 (high density) populations, respectively. In each case, no significant relationship was observed (Fig. 17 a; Anova; $F = 0.23$, $P > .05$; Fig. 17b; $F = 0.47$, $P > .05$; and Fig. 17c; $F = 0.33$; $P > .05$, respectively).

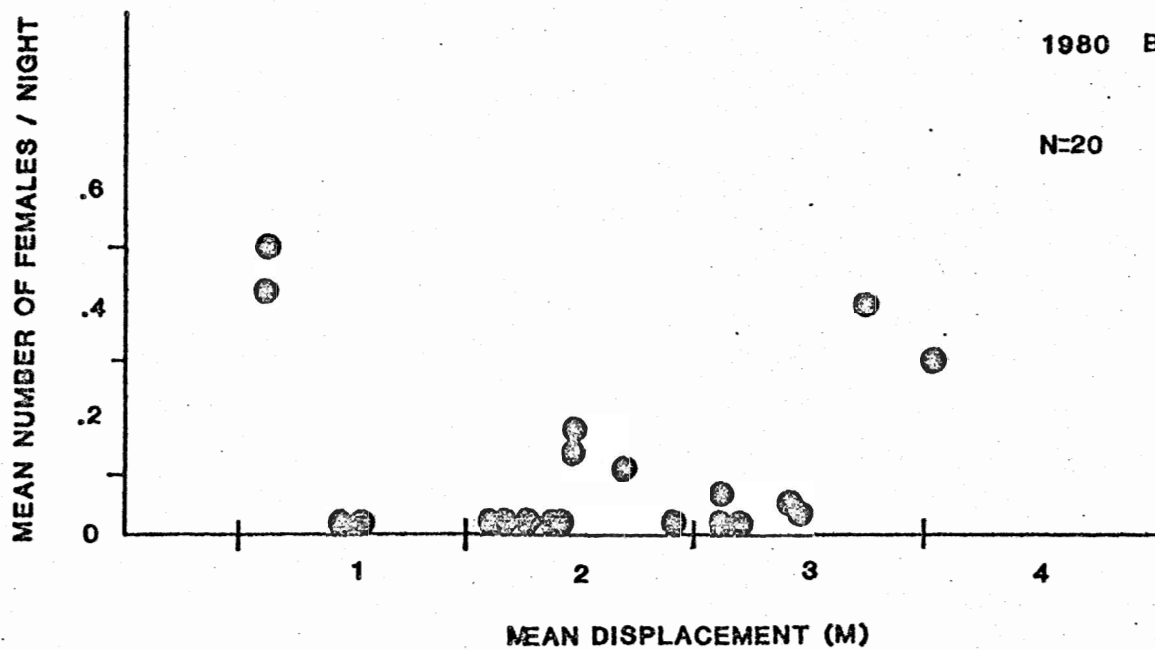
Indoor Arena - *G. integer*

In this section three sets of comparisons are made. In the first comparison, the mean for a particular behaviour for the initial six males is compared with the mean from observations on 12 males. These 12 were made up of the initial six males plus a second group of six males. This comparison made it possible to examine the effects that a change in density had on male behaviour. In the second comparison, the means for the initial six males are compared with the means for the same six males, but after the 12 density population had been observed and the second group of six males removed. Thus it was possible to examine individual male behaviour before and after a change in density. The third comparison is made on the means for the initial six males before the 12 male observations with the means for these same males (only) during the 12 male observations. This comparison permits examination of the behaviour of individual males in a high density.

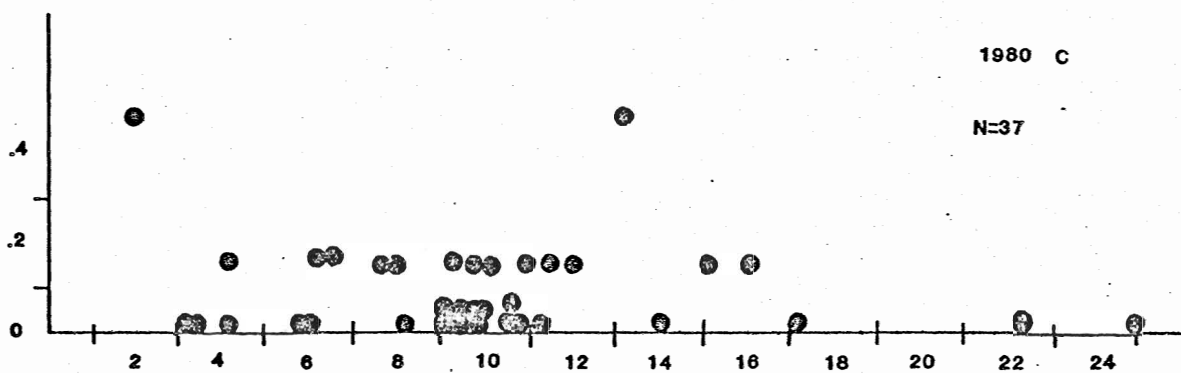
Table 4 shows the mean time in hours per day for calling, walking, aggressive calling, fighting, aggressive calling to fighting, and non-calling to aggressive calling. Table 5 shows the calculated Mann-Whitney

Figure 17. The mean number of times males were observed with females and the mean displacement of individual males of G. integer in the outdoor arena in (a) 1979, (b) 1980 (initial) and (c) 1980 (high density).





MEAN NUMBER OF FEMALES / NIGHT



1980 C

N=37

MEAN DISPLACEMENT (M)

Table 4. The mean time in hours per observation day for calling, walking, aggressive calling, fighting, aggressive calling to fighting ratio and non-calling to aggressive calling ratio for G. integer at different densities in the indoor arena.

Behaviour	MALE DENSITY											
	Initial Six			Overall Twelve			Initial Six After Observations on 12			Initial Six During Observations on 12		
	\bar{X}	SD	Range	\bar{X}	SD	Range	\bar{X}	SD	Range	\bar{X}	SD	Range
Calling	.53	.27	.19 - 1.0	.13	1.35	0 - .65	.51	3.34	0 - 1.7	.21	4.3	.28 - 6.5
Walking	.24	.14	.13 - .49	.267	.289	0 - .56	.027	.018	.005 - .073	.288	.45	.1 - .56
Aggressive Calling	.009	.003	.005 - .014	.005	.0004	0 - .073	.001	.003	0 - .0035	.006	.005	0 - .017
Fighting	.0006	.0003	.0005 - .01	.003	.0002	0 - .01	.0007	.0009	0 - .002	.004	.0003	.002 - .01
Aggressive Calling To Fighting	2.98	1.42	1 - 4	5.26	5.5	0 - 16.3	1	.58	0 - 1.5	6.81	6.5	.83 - 16.3
Non-Calling to Aggressive Calling	.031	.015	.02 - .0625	.187	.23	0 - 8.66	.297	.26	0 - .66	.23	.29	.028 - .866

Table 5. The calculated Mann-Whitney U values and Wilcoxon T values for mean time in hours, per observation spent, calling, walking, aggressive calling, fighting, in aggressive calling as opposed to fighting, and in non-calling as opposed to aggressive calling for given comparisons in G. integer in the indoor arena.

Behaviour	Comparison		
	initial six vs overall twelve	initial six vs initial six after twelve	initial six vs initial six within twelve
Calling	U = 6**	T = 7	T = 0*
Walking	U = 34	T = 0*	T = 0*
Aggressive Calling	U = 17*	T = 0*	T = 3
Fighting	U = 13*	T = 0*	T = 7
Aggressive Calling to Fighting	U = 27	T = 0	T = 6
Non-Calling to Aggressive Calling	U = 6**	T = 2	T = 0*

* = p .05

** = p .01

and Wilcoxon values comparing the means for each behaviour in terms of the initial six males vs. 12 males, the initial six before and after the 12 male observations, and the initial six before and during the 12 male observations. There was more calling in the initial observations on six males than in the overall 12 and more than the initial six while being observed in the 12 density. The same six males showed no significant difference before and after the 12 male observations. The initial six males walked more after being observed in the 12 density and while in the 12 density. In the initial observations on six males there was more aggressive calling than in the overall 12 and more than the initial six after being in the 12 density. The initial six males fought more than did males in the overall 12, and more than the initial six males after being in the 12 density.

The ratios of aggressive calling to fighting and non-calling to aggressive calling were observed to determine whether individual males would perform the least costly behaviour in each comparison when in a higher density. The ratio of aggressive calling to fighting was higher in the 12 density than in the initial six density of males. The ratio non-calling to aggressive calling is higher in the overall 12 density and in the initial six while in the 12 density than in the initial six density.

Indoor Arena - *G. veletis*

In this study of *G. veletis*, densities of three, six and 12 males were used. Five separate comparisons were made with respect to the behaviours observed. Mean times spent in a particular behaviour for the initial three males were compared with the overall means for the group of 6 males, and with the overall means for the group of 12 males. In addition, the initial three males before the six male observations were compared with themselves during six male observations, and after the six

male observations were completed. The final comparison involves the overall means for the six male observations and for the observations involving 12 males.

Table 6 shows the mean time in hours per observation day for calling, walking, aggressive calling, fighting, aggressive calling to fighting ratio and non-calling to aggressive calling. Table 7 shows the calculated Mann-Whitney U and Wilcoxon T values for mean time in hours per observation spent calling, walking, aggressive calling, fighting. Also, the ratios of aggressive calling to fighting, and non-calling to aggressive calling were compared. Males in the initial three and the overall six densities called more than the overall 12 density. The initial three moved more than the initial three after being in the overall six, and more than the overall 12. Individuals in the overall six density moved more than in the overall 12 density. Individuals in the overall 12 density called aggressively more, than those in the six density. The initial three and the overall six spent more time fighting than the 12 density. The ratio of aggressive calling to fighting was higher in the 12 density than in the initial three males. The ratio of non-calling to aggressive calling was higher in the initial three and the overall six than in the 12 density population. Other comparisons were not significantly different.

Table 8 shows the mean calling time of a separate group of male G. veletis in the indoor arena when females were absent and when females were present. Males called significantly more when females were absent than when they were present ($U = 0$; $P < .05$).

Table 6. The mean time in hours per observation for calling, ~~walking~~, aggressive calling, fighting, aggressive calling to fighting, and non-calling to aggressive calling for G. veletis at different densities in the indoor arena.

Behaviour	Male Density														
	Initial Three			Overall Six			Initial Three After Observations on 6			Initial Three During Observations on 6			Overall 12		
	\bar{X}	SD	Range	\bar{X}	SD	Range	\bar{X}	SD	Range	\bar{X}	SD	Range	\bar{X}	SD	Range
Calling	1.4	.35	.68-2.14	1.09	1.03	.074-3.19	1.59	1.28	.72-3.18	.78	.14	.34-1.28	.16	.6	.03-2.4
Walking	1.12	.17	.7-1.68	1.09	.26	.076-1.74	.36	.02	.22-.56	1.19	.019	1.02-1.38	.68	1.24	10-4.73
Aggressive Calling	.039	.0007	.004-.072	.04	.0006	.01-.07	.015	.0001	.006-.032	.048	.007	.01-.07	.05	.0008	0-.098
Fighting	.048	.002	0-.098	.013	.00003	.0001-.0004	0	0	0	.01	.0006	.0005-.002	.007	.00008	0-.0004
Aggressive Calling to Fighting	9.6	8.6	2.1-21.7	42.8	44.7	6.2-138	10.7	9.5	3.2-24	60.25	56.4	6.2-138	42.9	30.3	7-116.8
Non-calling to Aggressive Calling	.08	.08	.008-.19	.07	.05	.01-.16	.03	.005	.02-.02	.09	.003	.03-.16	.013	.0008	0-.02

Table 7. The calculated Mann-Whitney and Wilcoxon values for mean time in hours, per observation spent, calling, walking, aggressive calling, fighting, in aggressive calling as opposed to fighting, and in non-calling as opposed to aggressive calling for given comparisons in G. veletis in the indoor arena.

Behaviour	Initial Three vs Overall Six	Initial Three vs Initial Three After Observations on Six	Initial Three vs Initial Three During Observations on 12	Initial Three vs Overall 12	Overall Six vs Overall 12
Calling Time	U = 6	T = 2	T = 1	U = 1**	U = 12**
Walking Time	U = 6	T = 0*	T = 2	U = 2**	U = 11**
Aggressive Calling Time	U = 7	T = 1	T = 2	U = 8	U = 8**
Fighting Time	U = 4	T = 1	T = 1	U = 3*	U = 5**
Aggressive Calling to Fighting	U = 3	T = 1	T = 1	U = 1*	U = 16
Non-calling to Aggressive Calling	U = 9	T = 2	T = 1	U = 4*	U = 4**

* = P .05

** = P .01

Table 8. The mean time spent calling for males when females were absent and the mean time spent calling for males when females were present in the indoor arena for G. veletis.

Females Absent			Females Present		
\bar{X}	SD	Range	\bar{X}	SD	Range
1.56	.72	.6 - 2.3	.17	.17	0 - .4

DISCUSSION

The results obtained from this study of G. integer and G. veletis are discussed with regards to quantification of calling, movement, and aggressive behaviours in males. The factors affecting male behaviour, and the mating success derived from acoustical behaviour and movement are also considered.

Calling Behaviour

Sexual signalling is often proposed to be age dependent, with older males displaying more. Older males may also have better opportunities to control high quality resources due to an imbalance in size and/or experience. Age might also be a good indicator of a male's genetic quality in that it indicates that his phenotype can survive for extended periods (Howard, 1978).

In this study size and age did not influence calling behaviour in G. integer, in the outdoor arena. An increase in calling does occur between three and six days of adult age, but this is due to the spermatophore being first produced at this time (Cade, personal communication). The spermatophore is required for male calling in field crickets (Huber, 1962). Laboratory measurements of total calling time of isolated G. integer, G. pennsylvanicus, G. veletis, Teleogryllus oceanicus and T. posticus also show no correlation between calling duration and male age or size after six days of age (Cade, unpublished data).

These field crickets are relatively short-lived. In longer-lived species such as the bullfrog studied by Howard (1978) the effects of experience makes possible preference by females more likely. Also, Pugesek (1981) demonstrated that in the California gull, Larus californicus, selection for increased reproductive effort can occur in a long-lived species. Further, R. catesbeiana is a resourced based lek species where

control of limiting resources by older, larger males is advantageous to the females (Howard, 1978). Although there is no distinct line between resource and non-resource based leks, G. integer is probably closer to the non-resource based lek (Cade, 1981b). In this case no limiting resource is controlled by males, and age or size of the individual should be less important in intrasexual or intersexual selection. In addition, G. integer is at the r end of the r-k selection continuum (Walker, 1980). Species that are r-selected are iteroparus and have a high juvenile mortality rate (Pianka, 1970). Thus any adult male regardless of age has demonstrated the capability to survive critical developmental stages. All adult males might therefore be judged as genetically fit by females capable of this type of discrimination.

Temperature affected the amount of male calling in G. integer in the outdoor arena. Males called significantly more at higher temperatures. Crickets are ectothermic as body temperature and hence activity are controlled largely by outside heat. Nielsen and Dreisig (1971) had similar findings in the bush cricket, Tettigonia viridissima. Bush crickets called sporadically between 12 and 20° C, and not at all below 12° C. Normal calling occurred above 20° C. In this study, the relationship between calling and temperature had a linear relationship. This is different from the Q_{10} exponential relationships used by physiologists to describe the relationship between temperature and biological activity (Walker, 1975). More measurements at extreme temperatures might result in an exponential curve, but it is also possible that calling is simply not expressed at low temperature, although the underlying physiological mechanisms may be slightly active. This study did not address physiological aspects of

male behaviour, but G. integer naturally occurs in warmer areas such that the low calling times here may have resulted from unusually cold nights for this species.

Another factor that may affect the amount a male calls during the night is the presence of females (Alexander and Meral, 1967). In this study, G. integer and G. veletis males called more in the indoor arena when females were absent than when they were present. Huber (1965) and Nielsen and Dreisig (1971) found a reduction in calling by males when females were present. Huber demonstrated that after mating male G. campestris do not resume calling until the next night. In G. campestris it takes 24 hours to produce a new spermatophore. Huber has also showed that the spermatophore is needed to stimulate calling. The speed of replacement of the spermatophore in G. integer is, however, approximately 15 min. (Alexander, 1962), and sperm limitation should not be a factor limiting calling behaviour. Instead, calling attracts parasitoid flies and conspecific males in G. integer, and is also very expensive energetically in both species (Prestwich and Walker, in press), such that males who have attracted females should not continue calling.

Calling should decrease with increasing density (Alexander, 1961). Alexander explained that non-calling becomes more common at high densities due to the increased cost of territorial defense and signalling in this situation. Calling may also decrease at higher densities if random collisions between males and females result in increased matings that don't involve calling. Another factor is that of territory availability. Alexander argued that males may not find a suitable territory to signal from. These factors should be effective in promoting a maximum of success-

ful copulations for non-calling individuals in high densities.

In 1980, two densities of G. integer were studied in the outdoor arena. Males in the higher density called less per night than those in the lower density. In the indoor arena G. integer and G. veletis males also called less at higher densities than at lower densities. These findings support Alexander's proposals for acoustical insects and his first two mechanisms agree with what occurred in this study: males were less aggressive and more movement was observed at higher densities (these findings are discussed later). The lack of suitable signalling sites is not as strong an assumption as the first two. In the outdoor arena, non-calling males occupied the same type of shelter as callers. Cade (1979a) also argued that limited territories at high densities were not important in controlling the amount of calling. He found that at times of high population density many crickets did not call even though suitable signalling sites were available.

Song intensity is a measure of the amount of energy a male puts into his song and consequently into competition for females (Prestwich and Walker, in press). In this study, G. integer males outdoors called at similar intensities in 1979 and in the 1980 initial density population. Males called more loudly in the higher density than in the initial density, an indication that some males may invest more heavily in signal transmission when potential competitors are more numerous. Density may affect individual males differently in that calling is reduced on average at higher density, but for those males who call, the signal is more intense. In all populations observed, however, males called at highly variable intensities ranging from the high 40 dB level to 80 dB. It is clear that individuals are able to

vary their calling song intensities. Cade (1979a) also demonstrated changes in individual song intensity in G. integer. Males of G. integer who called loudly should attract more females, but at the same time incur greater costs by attracting parasitic flies more readily. In field studies using amplified tape recordings of G. integer song, Cade (1979b) showed that female crickets and flies were attracted more often to loud signals. Forrest (1980) also showed that more females of Scapteriscus acletus, a Florida mole cricket, responded to louder signals. In this study, however, the pattern of female attraction to calling males of varying song intensities was not examined since song intensities were measured irregularly.

Conspecific song may inhibit calling in some males possibly due to a threat of attack (Alexander, 1961). Calling times outdoors of G. integer males were compared with the total calling of individuals for each night. No pattern was seen in this comparison. Individual differences in calling behaviour are not greatly affected by the calling behaviour of other individuals at least in a large arena. By contrast Cade (1979a, 1981b) showed that taped conspecific song played to calling G. integer (and other species) often inhibited song production in the previously calling male. Cade's experiments simulated direct confrontations between males, whereas my observations measured overall calling behaviour and may be more representative of behaviour under field conditions.

In some acoustical insects the number of males calling and their song intensities may vary with time. In this study, the song intensity of calling males showed no change with time of observation. By contrast, the number of males calling increased sharply just before sunrise in observations which were continued until 10:00 hrs. Cade (1979a) also observed "dawn calling" in field populations of G. integer. At

dawn, however, he was unable to attract females to taped songs in the field. It might be expected that the greatest amount of calling should occur when most females are responsive. Cade speculated that an explanation for this increase in calling may be that dawn calling males no longer orient to calling song. Also, flies were less likely to be attracted at dawn. If females are still sexually receptive, then this decreased probability of attracting conspecific males and flies may result in an increase in calling. There was no significant difference in individual male tendency to call at particular times. During the twelve hour observations, however, very few females were observed with males and it is thus impossible to evaluate the effects of female receptivity on dawn calling.

Calling and Mating Success

Since field crickets are nocturnal animals and since copulation requires only a few seconds in G. integer, actual matings could not be observed under the semi-natural conditions in the field arena. The number of observations of males with females in 1979 and the number of observations of males with females bearing spermatophores in 1980 were therefore used as measures of male mating success. Females were considered as "being observed with a male" only when they were under the same shelter or otherwise immediately adjacent to a male. In laboratory observations, male G. integer guarded their recent mates by driving other males away from the immediate vicinity. The guarding period lasts approximately one hour during which time the spermatophore remains attached. After an hour, the female usually removes the spermatophore (Graham, 1981). If a spermatophore is attached for longer than one hour, it turns brown and can be readily distinguished from a recently deposited spermatophore

(Sakaluk and Cade, 1980). In this study, all spermatophores were checked for ageing, but all were milk-white indicating a recent mating. Also, there was never more than one male observed with a female in 1979, and never more than a single male with a recently mated female in 1980. For these reasons, the number of observations of a male with a female is probably a good approximation of mating frequency.

In many insects the last male to mate with the female fertilizes her eggs. A definite statement on the actual mating success and hence fitness cannot be made with respect to the satellites, here. Although many females were seen to have a spermatophore attached, (presumably by an adjacent male), sperm transfer may not have been completed if the spermatophore dropped off, was consumed prematurely by the female (as is often the case in G. integer; Sakaluk and Cade, 1980), or if sperm displacement occurred due to a later mating with other males. With these factors in mind, data on female acquisition represent an approximation of reproductive success for males behaving differently.

Individuals pursuing satellite-like behaviour in various species are often thought to have a lower mating success than signaling individuals in the same population (Cade, 1979a; Waltz, unpublished manuscript). Data presented in this study demonstrate, however, that satellite-like behaviour or non-calling can be a successful alternative. It was demonstrated that in the 1979 and in the 1980 initial observations, non-calling males and males calling under 0.5 hours per night were observed with females on average more often than males who were very frequent callers. Indeed, in the 1979 arena, the negative log relationship between observations with females and mean calling times suggests that mating success drops off sharply with increased calling. In 1980, the decline is less sharp in the initial density,

but there was no significant difference in the high density population. These data over both years are the opposite of what was expected in that male mating success should increase with calling time, but this increase should be less pronounced at high density (Alexander, 1961).

If my measure of mating success is reliable, the departure of the data from the expected results may have several explanations. One possibility is that additional observations at varying frequencies of callers to non-callers would demonstrate different trends. Mating success in other species is known to fluctuate greatly between years (see Howard, 1978 for example). In this connection, the theoretical prediction of increased mating success with increased signal transmission is based on average values over several generations. Observations over two field seasons are not sufficient to determine average mating rates. A second possibility is that data on G. integer mating success in St. Catharines are not reliable for this Texas species. In central Texas where G. integer occurs, flying female G. integer routinely orient to and mate with calling males (Cade 1979 a and b). Acoustically orienting, flying females were absent in this study. Additional studies in Texas must be conducted to evaluate the importance of flying female G. integer on mating success and calling in this species. A third possibility is that non-calling males do have a much greater mating success than callers and that this species simply does not conform to theoretical expectations. If so, then calling and non-calling may represent an unstable polymorphism in G. integer, and this species may be in a transitional stage to muteness (Cade, 1980). This possibility is considered again later, but high satellite mating success has been reported in at least one other case. Perill et al. (1978) found that in 40% of the trials in which female green tree frogs, Hyla cinerea, were released next to a calling male and his satellite, the satellite achieved amplexus.

In species where males display alternative modes of reproductive behaviour, mating success should be frequency dependent in the population. That is, mating success for a given type of male should be inversely proportional to that type's frequency in the population (Dawkins, 1979; Gadgil, 1972; Waltz, unpublished manuscript). For example, satellite males should be most successful when there are many callers and few satellites, and therefore many opportunities for satellites to intercept attracted females. In cases where non-callers are much more numerous, few opportunities for female attraction should exist such that the mating success of satellites should be lower (Cade, 1980). This study demonstrated that on a given night the number of females with males who did not call varied with the ratios of non-callers to callers in 1979 and the 1980 initial density populations. In both cases, negative log plots suggest that frequency dependence between mating success and the ratio of male types is very pronounced.

Movement or Displacement From a Previous Position

Actual movement patterns are not available for male G. integer outside since gathering such data would have disturbed males and probably reduced calling behaviour. The mean distance a male was displaced from a previous position during the course of a night was used to approximate rates of movement in the arena. For males who moved greatly as in the case of extreme displacement shown previously, mean displacement is an underestimate of actual movement.

Movement patterns are of interest since males should partition their time into searching or signalling for mates. The optimal ratio of searching to signalling is that which results in maximum reproductive success (Alexander, 1975; Otte, 1977). In this study, however, there was no relationship between calling and movement or between movement and number of observations with females in any of the three groups studied. Failure of

the data to comply with theoretical expectations might result from inaccuracies in measures used to approximate mating success and movement. In addition, Alexander's theoretical arguments do not take into consideration the possibility that signalling males might change their position in response to previous mating success or other variables. For example, Walker (1980) demonstrated that male short tailed crickets, Anurogryllus muticus, rarely called from the same burrow on successive nights. Any effect of previous experience on movement in male A. muticus or, in this study, on male G. integer is unknown.

One factor postulated to influence male movement is density. As density increases, searching for females should be more profitable than at low density. Increased movement should be permitted if territoriality decreases and males become more tolerant of each other (Alexander, 1961). Although there was no relationship between movement and observations with females, data from the 1980 initial and high density comparisons in G. integer outside show that males moved more at higher density. Regarding indoor arena data, there was no difference between overall means for the six and 12 males. If only the same six males are considered, they moved significantly more during and after the observation on 12 males. Data on G. veletis are also contradictory in that there was no difference in movement between three and six males, the same three decreased their movement after exposure to other males, and the 12 male density showed the lowest average walking time. Interpretations of data from the indoor arenas are confounded generally by a lack of control of male histories (age, experience, etc.) as well as a lack of replicates.

Aggressive Behaviour

Aggressive behaviour in this study involved actual fighting as well as the production of the aggressive song both in fights and in conflict

between males which does not involve physical combat. This behaviour was only studied in the indoor arenas.

A factor influencing aggression is density. Alexander (1961) stated that as the density of individuals increase levels of aggression should decrease. The proposed lack of aggression at higher densities may result from a high effort needed for territorial defense when competitors are common. Otte and Joern (1975) proposed a similar model.

In G. veletis mean aggressive calling was significantly more in the 12 male arena, a trend opposite that expected. Other comparisons within this species for aggressive calling are not significant. In G. integer, aggressive calling decline from six to 12 males as predicted, but the reduction is due to newly added males. The same six males continued to call aggressively at the same rate in a higher density, but their aggressive calling dropped off sharply after the high density observation.

With respect to actual fights, G. integer males spent more time fighting in the high density as opposed to the 12 male arena. There was no difference when the same males are considered in the six and 12 observations, but these same males increased their fighting time after being returned to a six male density. In G. veletis, the only two statistically significant comparisons showed an increase in mean fighting time when density was increased.

Aggressive calling is probably less costly in terms of energy and risk than fighting behaviour. It is therefore possible that reduction in aggression with increased density will be reflected in an increased ratio of aggressive calling to fighting. That is males should spend relatively more time calling at opponents than fighting with them. In G. veletis, there was only one significant comparison of this ratio, and it indicated relatively more aggressive calling than fighting in the 12

as opposed to the three male density. In G. integer there were no significant differences with density, but the same six males showed relatively more fighting to aggressive calling after 12 male observations.

The ratio of non-calling to aggressive calling in actual fights might also reflect density effects. The ratio of non-calling to aggressive calling should increase with density since males are expected to retreat from fights without signalling in cases when competitors are numerous. In G. integer, this ratio did increase significantly in comparing the six males with the overall ratio for 12 males and for those same six when in the 12 male observation. In G. veletis, however, the ratio of non-calling to aggressive calling decreased in two of the comparisons. When taken together, the indoor arena observations provide little or no support for the predicted decline in aggression with increasing density. Indeed, the data are inconsistent, and do not appear to represent any recognizable trends. As discussed in a previous section, data for the indoor arena are confounded by various factors.

Conclusion: Evolutionarily Stable Strategies

Alternative male behaviour is best analyzed in terms of evolutionarily stable strategies, commonly called ESS. An ESS is a genetically determined (in large part) set of behavioural and/or morphological features which when a certain frequency of the population adopts it is unbeatable reproductively compared with given alternatives. There may also exist 2 or more strategies whose fitness gains are approximately equal. Three types of situations may characterize the occurrence of alternative male behaviour in a species. There may exist 2 pure strategies in a genetic polymorphism with each male performing only one of the alternative behaviours. Also, all males may have the same genetic composition, but display one or more behaviours in response to individual or environmental factors. In this case the alternatives are said to represent a single conditional strategy. In addition, males may

also have the same genetic composition but change their behaviour without environmental factors being important. Such a strategy is termed "mixed". These categories are somewhat overlapping. For example, it is possible for two separate genetic strategies to occur in a population, and for each strategy to respond to different conditional events in the environment.

This study concentrated largely on differences in calling and associated behaviour in male G. integer and G. veletis. Field observations on G. integer indicated a high degree of variation in calling behaviour in this study and in previous studies (Cade, 1979a, 1980). This study also indicated that these differences in calling are independent of age and size, but that density, presence of females, and time of day influence calling behaviour. It is clear, therefore that calling represents at least one conditional strategy in the population. Cade (1981a) has recently presented data, however, which demonstrate that the duration of calling in G. integer has an important genetic component. Cade discussed the selective forces operating to maintain genetic variation and concluded that calling and non-calling or satellite behaviour in G. integer probably represent two separate genetic strategies. In Cade's study most males were capable of calling, but in a line selected for absence of calling the signalling time was low. In my study some males did not call. This observation adds support to Cade's contention that separate genetic strategies occur in G. integer, and that one reason his low line males called was isolation in the laboratory. Furthermore, my data show that environmental conditions can have a varied effect on male behaviour. In this connection, Cade proposed that if two genetic strategies occur in G. integer then these strategies should have different switch points at which a response to environmental conditions occurs. Further research is necessary to study this possibility, but the variability of male response to environmental conditions suggests that different switch points may occur.

It seems likely that there does exist at least two separate genetic strategies underlying G. integer acoustical behaviour. If so, then these strategies may coexist if on the average their fitness returns are approximately equal (Gadgil, 1972). Cade (1979b) speculated that this might be so since calling males attracted parasitoid flies, and, based on circumstantial evidence, also appeared to attract more females. Satellite males were not very successful with females in Cade's experiments, a cost that may be offset by the avoidance of acoustically orienting flies (Cade, 1975). In Cade's experiments, however, results were obtained by broadcasting G. integer calling song and comparing the number of females attracted to the song with the number of successful matings with males who were satellites of the loudspeaker. The results presented here regarding reproductive success are more complete than those provided previously for this species. In contrast with Cade's findings, my data indicate that non-calling males are more successful reproductively than males who called often. Although these data may be biased since acoustically orienting and flying females were not present, they suggest that calling and non-calling in G. integer represent a transient polymorphism in which non-calling is becoming the primary mode of behaviour. Many cricket species are known to have lost the ability to call, and the situation in G. integer may represent a stage in the progressive loss of signalling ability (Otte, 1977). Data on reproductive success in G. integer in its natural habitat are necessary to test this possibility.

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Appendix

Table 1. The length of time observed, average calling times at night (with standard deviations), average displacement (with standard deviations), weight and mean number of females required with regards to individual G. integer for 1979 (a), 1980 (initial) (b) and 1980 (high density) (c).

1979 (a)

Male Number	Number of Nights Observed	Average Calling Time Per Night (hrs)	S.D.	Average Displacement Per Night (hrs)	S.D.	Weight (grms)	\bar{X} # ♀♀ Per Night
5	16	2.37	1.96	1.04	5.46	.565	.07
3	9	.75	1.33	.09	1.05	.412	0
13	19	0	0	1.74	3.1	.473	.58
59	19	0	0	1.12	2.46	.453	.53
87	18	.82	1.22	.51	2.1	.482	.06
93	18	2.77	2.07	.80	1.89	.361	.27
85	18	1.5	1.34	1.14	3.83	.394	0
71	9	0	0	1.76	5.27		.4
51	7	0	0	.26	3.47		.2
99	6	.45	.62	.99	3.48		0
97	5	.19	.4	1.66	3.9		0
95	8	.5	.22	1.72	2.84		0
19	9	2.15	2.0	1.75	3.89	.702	.2
63	10	.7	1.27	2.05	4.55	.483	.27
69	8	0	0	1.9	4.0		.8
77	8	0	0	2.66	4.22	.577	1.1
31	7	.43	.51	.26	1.01	.337	0

1980 (initial) (b)

Male Number	Number of Nights Observed	Average Calling Time Per Night (hrs)	S.D.	Average Displacement Per Night (hrs)	S.D.	Weight (grms)	\bar{X} # ♀♀ Per Night
5	5	.2	.46	1.75	1.67	.673	.5
15	11	.14	.39	3.0	4.27	.500	.42
17	5	1.25	1.2	4.4	6.46	.546	0
41	13	.42	1.45	6.9	6.25	.440	.077
29	17	1.5	1.45	6.4	6.32	.398	.12
39	13	1.6	1.48	3.5	3.70	.688	.077
23	13	.73	2.5	9.9	8.9	.504	.46
63	12	0	0	4.7	5.17	.514	0
65	12	1.4	1.6	4.3	5.24	.731	.17
71	10	.43	1.2	5.9	3.86	.526	0
73	10	.2	.89	3.3	5.3	.42	0
75	10	.4	.72	5.3	8.37	.598	.2
77	10	0	0	7.0	6.18	.398	0
79	10	.1	.22	8.9	8.99	.398	.3
81	10	.86	1.2	7.7	4.4	.609	0
87	10	.8	2.34	3.5	4.1	.482	0
91	10	1.5	2.2	5.3	5.88	.494	0
97	5	0	0	4.2	.8	.486	0
99	5	.15	.2	8.6	5.76	.615	0
R	5	1.1	1.3	8.0	9.73	.495	0

1980 (high density) (c)

Male Number	Number of Nights Observed	Average Calling Time Per Night (hrs)	S.D.	Average Displacement Per Night (hrs)	S.D.	Weight (grms)	\bar{X} # ♀♀ Per Night
29	5	2.9	3.24	4.29	3.56		.2
63	6	0	0	9.7	7.94		.16
65	6	.83	1.5	3.5	5.94		0
71	6	.375	.45	12.1	12.6		.16
73	6	.41	.51	9.6	6.75		0
77	6	.29	.36	9.9	4.98		0
89	6	.33	.71	6.2	4.1		.16
87	6	0	0	5.8	4.26		.16
95	6	0	0	10.2	7.0		.16
R	6	.25	.35	8.2	4.04		0
1	6	0	0	22.3	11.87		0
3	6	.5	1.67	10.5	4.9		0
5	6	0	0	17.4	8.73		0
7	6	2.1	1.6	6.0	3.77		0
9	6	0	0	7.7	5.38		.16
11	6	.29	.44	10.9	16.6		0
13	6	2.5	2.5	14.2	12.28		.16
15	6	.38	.84	4.3	4.69		0
17	6	1.1	1.5	16.2	14.01		.16
19	6	.7	.97	1.9	5.3		.5

1980 (high density) (c) cont'd

Male Number	Number of Nights Observed	Average Calling Time Per Night (hrs)	S.D.	Average Displacement Per Night (hrs)	S.D.	Weight (grms)	\bar{X} # ♀♀ Per Night
23	5	2.9	2.1	11.5	14.69		0
25	6	0	0	13.2	14.66		.5
27	6	0	0	7.6	5.61		.16
29	6	0	0	11.5	10.15		.16
31	6	.08	.17	18.75	4.02		0
33	6	0	0	6.3	7.64		.16
37	6	.2	.64	10.9	12.07		.16
39	6	.21	.22	3.7	3.44		0
41	6	0	0	9.2	9.4		.16
43	6	0	0	9.5	14.45		0
45	6	.38	.4	15.25	7.35		.16
47	6	0	0	10.1	5.69		.16
49	6	0	0	9.36	10.12		.16
51	6	.08	.2	25.4	9.2		0
53	5	0	0	3.7	3.9		.16
55	5	0	0	18.0	7.5		.16
57	5	0	0	15.0	6.23		0

Table 2. The distribution of calling with age for individual G. integer males in 1979(a), 1980 (initial) (b) and 1980 (high density) (c).

Male	Age (Days)																		
Number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
5	0	0	0	0	0	0	2.75	3.75	4.5	2.75	3.0	2.75	4.5	4.5	3.75	5.5			
3	0	0	0	0	0	0	2.0	4.0	0										
13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
59	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
87	0	0	0	0	0	0	0	0	0	0	2.5	4.5	2.75	.75	1.75	.5	1.25	.75	
93	0	0	0	0	2.5	5.75	6.0	7.5	5.5	0	3.25	2.75	3.25	3.25	3.75	3.5	0	3.25	
85	0	0	0	0	0	2.75	2.5	2.0	2.75	2.0	4.75	2.25	1.0	2.75	.25	1.25	1.25	3.25	
71	0	0	0	0	0	0	0	0	0										
51	0	0	0	0	0	0	0												
99	0	0	0	0	1.5	0	1.25												
97	0	0	0	0	1.0														
95	0	0	0	.25	.5	.5	.25	.5											
19	0	0	0	.5	2.5	2.25	4.25	5.0	4.75										
63	0	0	0	0	0	0	0	4.0	1.0	2.0									
69	0	0	0	0	0	0	0	0											
77	0	0	0	0	0	0	0	0											
31	0	0	0	0	1.0	.75	1.25												

Table 2 (cont'd)

Male Number	Age (Days)																	1980 (initial) (b)																
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
5																		1.25	0	0	0	0	0											
15																		0	0	1.25	0	0	0	0	0	0								
17																		3.0	1.0	2.25	0	0												
41																		1.0	0	.25	0	0	.25	.5	0	0	.5	1.0	.25	2.0				
29																		2.5	0	5.0	7.0	1.5	0	.75	0	.5	1.0	6.25	0	0	0	2.0	.5	0
23																		1.0	0	5.25	7.5	5.25	0	2.0	0	0	0	1.5	0	0				
63	0	0	0	0	0	0	0	0	0	0	0	0																						
65	0	0	1.75	0	3.0	5.25	2.0	2.5	0	0	0	0	0	2.0																				
71	0	0	0	2.75	1.5	0	0	0	0	0																								
73	0	0	0	0	0	0	0	0	.5	1.5																								
75	0	0	2.0	0	.5	1.5	0	0	0	0																								
77								0	0	0	0	0	0	0	0	0	0	0																
79								0	0	0	.25	.75	0	0	0	0	0	0																
81	0	0	2.5	0	3.5	.5	1.0	1.25	0	0																								
87	0	0	0	0	.75	0	5.0	0	6.75	0																								
91	0	0	0	0	3.0	7.5	2.75	1.0	.75	0																								
97									0	0	0	0	0																					
99									0	0	0	.25	.5																					
12																		0	0	3.5	0	2.0												
39																		3.0	5.0	1.0	0	0		0	0	0	0	.5	0	0				

Table 2 (cont'd)

1980 (high density) (for males from initial density)

Male Number	Day Number in High Density					
	1	2	3	4	5	6
29	2.75	7.5	7.0	0	0	0
63	0	0	0	0	0	0
65	3.0	0	0	0	1.25	3.75
71	0	0	1.0	1.0	.25	0
73	.25	1.0	0	0	0	1.25
77	.25	0	1.0	0	.5	0
89	2.0	0	0	0	0	0
95	0	0	0	0	0	0
12	0	0	.75	0	0	.75
87	0	0	0	0	0	0

Table 2 (cont'd)

Male Number	Age (Days)																			1980 (high Density (c))	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19		
1														0	0	0	0	0	0		
3														3.0	0	0	0	0	0		
5														0	0	0	0	0	0		
7														4.5	3.0	2.5	2.75	0	0		
9														0	0	0	0	0	0		
11														1.0	0	0	0	.75	0		
13												2.5	2.0	2.75	6.5	7.25	0				
15												0	2.25	0	0	0	0				
17												3.75	0	0	0	2.75	0				
19												.75	.75	0	0	0	2.75				
23												2.5	6.0	3.0	1.0	5.0	0				
25												0	0	0	0	0	0				
27												0	0	0	0	0	0				
29										0	0	0	0	0	0						
31										0	0	0	0	.5	0						
33										0	0	0	0	0	0						
37										1.75	0	0	0	0	0						
39								.5	.25	0	0	0	.5								
41							0	0	0	0	0	0									
43								0	0	0	0	0	0								
45				0	.5	.75	1.0	0	0												

Table 2 - 1980 (High Density) (c) cont'd

Male
Number

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
47				0	.75	0	0	0	0										
49				0	0	0	0	0	0										
51				0	0	0	.5	0	0										
53				0	0	0	0	0	0										
55				0	0	0	0	0	0										
57				0	0	0	0	0	0										

Table 3. The intensities of calling for individual G. integer males in 1979 (a), 1980 (initial density) (b) and 1980 (high density) (c).

Individual	dB	1979(a)
93	74, 72, 80, 77, 82, 65	
5	62, 81, 83, 78, 63, 75	
85	70, 74, 80, 72, 64, 81	
3	64, 75, 75	
87	72, 63, 60	
63	62	
31	60, 77	

Individual	dB	1980 (Initial) (b)
65	86, 84, 86, 86	
67	88, 82	
10	73, 78, 75	
23	73, 75, 66, 78	
15	64, 75, 77	
59	65, 69, 62	
53	73, 74, 74, 76	
29	70, 66, 74, 79	
39	78, 77, 78, 73	
81	77, 50	
12	77, 66, 68	
5	72, 75, 67	

Table 3 (cont'd)

Individual	dB 1980 (High Density) (c)
13	85, 78, 80, 70
17	87, 85
7	82, 74
23	86, 82, 73
31	70, 73
65	80, 80
11	80, 83, 74
73	85
19	82
12	86

Table 4. The mean number of females to non-callers as well as the ratio of non-callers to callers for 1979 (a), 1980 (initial) (b) and 1980 (high density) (c).

1979 (a)		
Date	Mean Number of Females to Non-callers	Ratio of Non-callers to Callers
26/7	.8	.45
28/7	.7	.3
29/7	.6	.55
30/7	.4	.9
3/17	.0	.65
1/8	.0	1.5
2/8	.05	2.5
3/8	0	4.0
4/8	.04	4.5
5/8	0	4.75
6/8	.2	5.0
7/8	0	8.0
8/8	.02	7.5
9/8	.1	5.5

Table 4 (cont'd)

1980 (initial) (b)

Date	Mean Number of Females to Non-callers	Ratio of Non-callers to Callers
30/7	.6	.8
1/8	.8	.71
3/8	.5	1.0
4/8	1.0	.33
6/8	.33	1.5
9/8	.11	2.25
10/8	0	1.16
11/8	0	1.4
13/8	.16	4.0
15/8	.06	5.0
16/8	0	18.0
17/8	0	3.75
18/8	0	3.25
19/8	.23	3.25

1980 (high density) (c)

20/8	.08	1.3
21/8	.13	2.7
22/8	0	3.75
23/8	.15	5.6
24/18	.05	4.7
25/8	.125	5.3

Table 5. The length of time observed and the average calling times (with standard deviations) of individual G. integer from 22:00 to 10:00 hrs and from 06:00 to 10:00 hrs in the 1980 (high density).

Male Number	Mornings Observed	Mean Calling Time Per Night From		Mean Calling Time Per Morning From	
		22:00 - 06:00 hrs	S.D.	06:00 - 10:00 hrs	S.D.
65	6	2.4	2.3	.96	.01
11	5	.58	.51	.35	.19
19	6	1.0	.9	.29	.08
33	6	.86	.74	.86	.74
13	6	4.4	6.4	.86	.8
89	6	.91	1.0	.58	.06
63	6	1.4	.036	1.4	.036
9	4	.12	.046	.12	.046
77	3	.33	.14	.08	.014
31	4	.33	.31	.38	.42
39	5	.46	.38	.3	.36
17	6	1.3	2.2	.2	.2
29	6	.46	.16	.46	.16
3	5	.9	1.2	.3	.135
5	6	1.38	1.47	1.38	1.47
45	4	.5	.27	.19	.11
1	6	.54	.3	.54	.3
29	5	2.9	2.7	.01	0
71	6	.515	.2	0	0
73	6	.41	.26	0	0
87	6	0	0	0	0
95	6	0	0	0	0
12	6	.25	.12	0	0
7	6	2.1	2.6	0	0
15	6	.38	.7	0	0
23	5	2.9	4.4	0	0
25	6	0	0	0	0
27	6	0	0	0	0
37	6	.2	.42	0	0

Table 5 (cont'd)

Male Number	Mornings Observed	Mean Calling Time Per Night From		Mean Calling Time Per Morning From	
		22:00 - 06:00 hrs	S.D.	06:00 - 10:00 hrs	S.D.
41	6	0	0	0	0
43	6	0	0	0	0
47	6	0	0	0	0
49	6	0	0	0	0
51	6	.08	.04	0	0
53	5	0	0	0	0
55	5	0	0	0	0
57	5	0	0	0	0

Table 6: The dates that individual females were acquired by individual G. integer males in 1979 (a), 1980 (initial) (b) and 1980 (high density) (c).

1979 (a)																					
Male Number	Date																				
	July										August										
	22	23	24	25	26	27	28	29	30	31		1	2	3	4	5	6	7	8	9	10
5																		24			
13							92*	92							26	26		54	24	24	
							92	92													
							92	92													
59						18				6		6	6			2					
													6			2					
													6			2					
87						76															
93									42	2						12		14			
									42												
51	46																				
	46																				
19									42	6											
63									14									14			
									54												

Table 6 (cont'd)

1979 (a) (cont'd)																					
Male Number	Date																				
	22	23	24	25	July							August									
					26	27	28	29	30	31		1	2	3	4	5	6	7	8	9	10
69				76	92	92	18	22													
					76	92	18														
							18														
							18														
77			46																		

* Female Identity

Table 6 (cont'd)

1980 (initial) (b)																			
Number	Date																		
	July	July	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
	30	31																	18
																			19
5			6 *	8	12														
15	10		22	12	8														
			12																
41			36																
29															36				
39							26												
23				14		14		28		18				38	6				
65								28						38					
75														38			38		
79														32			36		
																	32		

* Female Identity

Table 6 (cont'd)

1980 (high density) (c)						
Male Number	Date August					
	20	21	22	23	24	25
29	30*					
63				32		
89						68
71						68
95	20					
9		32				
13		72				
17	72					
19		70		70		
				70		
25		62	68			70
29		28				
33		72				
37		36				
47					54	
45						28
55	18					

* Female Identity

Table 7. The amount of calling, aggressive signalling, displacement, fighting times, number of fights (showing wins and losses) and meetings (showing those with calling as well as those without calling) for individual G. integer males at densities of six and 12 in the indoor arena.

<u>Density 6</u>							
Male	Non-Aggressive min	Aggressive min:sec	Movement min	Fighting min	Fights W L	Meetings C N/C	
Lf	608	6:35	166	.514	5-4	10M 21M	3
rf	115	7:09	108	.618	6-2	2M 91M	5
ld	245	4:07	91	.224	1-1	5M 611M	3
ldhf	445	3:02	77	.034	1	3M 211M	2
ldrf	198	8:36	292	.555	5-3	23M 61M	7
2dhf	309	4:31	131	.318	3-2	16M 211M	11
Total	1920	33:51	865	2.263	33	59M 271M	31

<u>Density 12</u>							
Lf	390	10:03	337	.147	1-2	44M 221M	22
rf	120	7:11	143	.647	1-4	2M 31M	11
ld	31	0	0	.338	1-1	0	0
ldhf	126	2:14	63	.103	0-1	3M 111M	4
ldrf	17	1:06	336	.157	0-2	3M 11M	17
2dhf	80	2:28	159	.212	0-3	2M 61M	6
2dbf	7	3:10	67	.118	1-1	2M 61M	3
10bf	0	0	27	0	0	0	3

Table 7 (cont'd)

<u>Density 12 (cont'd)</u>							
Male	Non-Aggressive min	Aggressive min:sec	Movement min	Fighting min	Fights W L	Meetings C N/C	
2d	71	5:34	202	.253	7-0	18M 8iM	26
2drf	14	1:16	157	0	0	4M 7iM	6
Bf	90	2:03	158	.02	0-1	2M 2iM	7
BL	5	2:06	172	.03	0-1	2M 10iM	16
Total	944	34:01	1754	2.02	25	80M 70iM	106

<u>Density 6</u>							
Lf	1033	2:10	27	.120	1-0	2M	0
r0	0	0	2	0	0	0	0
ld	257	:05	32	.04	1-0	2M 1iM	2
ldhf	274	:07	20	0	0-1	1M	0
ldbf		0	3	0	0	0	0
2dhf	268	1:30	13	.120	1-0	1M	0
Total	1832	3:52	95	0	2-0	3M 3iM	2

Table 8. The amount of calling, aggressive signalling, displacement, fighting times, number of fights (showing wins and losses), and meetings (showing those with calling as well as those without calling) for individual G. veletis males at densities of three, six, and 12 crickets in the indoor arena.

<u>Density 3</u>								
No.	Calling	Aggressive Signalling	Movement	Fighting Time	Fights		Meetings	
	min	min:sec	min		W	L	C	N/C
ld	641	21:49	208	.23	2	4	122	7
ldhf	410	12:66	296	.49	4	2	94	5
ldrf	205	1:03	502	0	-	-	47	9

<u>Density 6</u>								
ld	382	20.1	408	.11	2	0	186	5
ldhf	102	20.7	305	.03	1	0	29	4
ldrf	226	3.1	258	0.3	0	1	104	7
Bf	957	15.9	23	.07	1	0	116	4
Lf	22	6.5	522	.07	0	1	117	13
rf	267	5.9	349	.08	0	2	99	1

<u>Density 3</u>								
ld	956	9.6	66	0	-	-	47	-
ldhf	260	1.6	169	0	-	-	38	-
ldrf	215	2.4	94	0	-	-	38	-

<u>Density 12</u>								
ld	45	16.5	284	.001	-	1	130	
ldhf	142	11.8	120	0	-	-	48	
ldrf	10	15.2	94	.1	1	-	60	
Bf	38	29.2	118	.05	1	2	130	
Lf	2	4.01	92	0	-	-	48	
pf	3	-	10	0	-	-	-	
0	105	23.5	138				286	
0 ⁷	16	18.4	-	1	1	-	60	

Table 9. The amount of calling, aggressive signalling, displacement, number of fights and meetings (showing those with calling as well as those without calling) for individual G. veletis males when females were absent (a) and when females were present (b).

<u>Density 3 (without females) (a)</u>							
Male	Calling Time	Aggressive Signalling	Displacement	Fights		Meetings	
	min	min:sec	min	W	L	C	N/C
ld	140	1.05	15	1		5	-
ldhf	105	.8	22	1		5	-
ldrf	36	.75	2		2	6	-

<u>Density 3 (with females) (b)</u>							
ld	24	1.98	-	-	-	8	-
ldhf	7	-	9	-	-	5	-
ldrf	0	-	-	-	-	3	-