Male Reproductive Competition in the Field Crickets *Gryllus veletis* and *G. pennsylvanicus*

by

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For my Parents and Grandparents

ABSTRACT

Sexual behavior in the field crickets, *Gryllus veletis* and *G. pennsylvanicus*, was studied in outdoor arenas (12 m^2) at high and low levels of population density in 1983 and 1984. Crickets were weighed, individually marked, and observed from 2200 until 0800 hrs for at least 9 continuous nights. Calling was measured at 5 min intervals, and movement and matings were recorded hourly. Continuous 24 hr observations were also conducted, and occurrences of aggressive and courtship songs were noted.

The timing of males searching, calling, courting, and fighting for females should coincide with female movement and mating patterns. For most samples female movement and matings occurred at night in the 24 hr observations and were randomly distributed with time for both species in the 10 hr observations. Male movement for *G. veletis* high density only was enhanced at night in the 24 hr observations, however, males called more at night in both species at high and low densities. Male movement was randomly distributed with time in the 10 hr observations, and calling increased at dawn for the *G. pennsylvanicus* 1984 high density sample, but was randomly distributed in other samples. Most courtship and aggression songs in the 24 hr observations were too infrequent for statistical testing and generally did not coincide with matings.

Assuming residual reproductive value, and costs attached to a male trait in terms of future reproductive success decline with age, males should behave in more costly ways with age; by calling and moving more with age. Consequently, mating rates should increase with age. Female behavior may not change with age. *G. veletis*, females moved more with age at both low density samples, however, crickets moved less with age at high density. *G. pennsylvanicus* females moved more with age in the 1984 low density sample, whereas crickets moved less with age in the 1983 high density sample. For both species males in the 1984 high density samples called less with age. For *G. pennsylvanicus* in 1983 calling and mating rates increased with age. Mating rates decreased with age for *G. veletis* males in the high density sample. Aging may not affect cricket behavior.

As population density increases fewer calling sites become available, costs of territoriality increase, and matings resulting from non-calling behavior should increase. For both species the amount of calling and in *G. veletis* the distance travelled per night was not different between densities. *G. pennsylvanicus* males and females moved more at low density. At the same deneity levels there were no differences in calling, mating, and, movement rates in *G. veletis* , however, *G. pennsylvanicus* males moved more at high density in 1983 than 1984. There was a positive relationship between calling and mating for the *G. pennsylvanicus* low density sample only, and selection was acting directly to increase calling. For both species no relationships between movement and mating success was found, however, the selection gradient on movement in the *G. veletis* high density population was significant. The intensity of selection was not significant and was probably due to the inverse relationship between displacement and weight.

Larger males should call more, mate more, and move less than smaller males. There were no correlations between calling and individual weight, and an inverse correlation between movement and size in the *G. veletis* high density population only. In *G. pennsylvanicus* , there was a positive correlation between individual weight and mating, but, some correlate of weight was under counter selection pressure and prevented significance of the intensity of selection. In contrast, there was an inverse correlation in the *G. veletis* low density B sample. Both measures of selection intensities were significant and showed that weight only was under selection pressures. An inverse correlation between calling and movement was found for *G. veletis* at low density only.

Because males are territorial, females are predicted to move more than males, however, if movement is a mode of male-male reproductive competition then males may move more than females. *G. pennsylvanicus* males moved more than females in all samples, however, *G. veletis* males and females moved similar distances at all densities.

The variation in relative mating success explained by calling scores, movement, and weight for both species and all samples were not significant. In addition, for both species and all samples the intensity of selection never equalled the opportunity for selection.

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INTRODUCTION

Sexual selection is differential reproductive success within a sex. Sexual selection is usually stronger on males, especially in species where males do not contribute much parental investment relative to females (Trivers 1972). Most male insects invest only genes in their offspring and compete for females (Thornhill and Alcock 1983). Darwin (1871) proposed that male traits used in obtaining mates become exaggerated and render the male sex more vulnerable to natural enemies. Exaggerated characters result from males competing physically for females, or from females choosing to mate with particular males.

Although there are many studies concerning sexual behavior in insects, there are few data comparing measures of individual male mating success. This is in contrast with excellent studies on individual male mating success in vertebrates (for example see Andersson 1982; Howard 1983; Passmore and Telford 1983; Price 1984a; Borgia 1985). The purpose of this study was to estimate individual male reproductive success in insects and apply a new method of estimating relative selection pressures to insect populations. The field crickets, *Gryllus veletis* and *G. pennsylvanicus* , were used as experimental animals. Male field crickets compete for females by acoustical signalling and physical aggression (Alexander 1961, 1968, 1975; Cade 1979a, 1980; Otte 1977). The relationships between individual size, individual calling duration per night, individual distance travelled per night, and individual male mating success at different levels of population density were studied.

LITERATURE REVIEW

This chapter reviews some of the information regarding sexual behavior in acoustical insects and will focus on male reproductive behavior. The first section concerns the mating sequence in acoustical insects. That is, males stridulating to attract females, song components important in female phonotaxis, courtship of attracted females, and copulation. Male-male competition and mating behavior in insect aggregations is then discussed, followed by a discussion of intrinsic and extrinsic factors affecting male sexual behavior. The next section deals with the effects of population density and other selection pressures acting on male sexual behavior. Also, measures of mating success used in estimating reproductive success are described. The natural history of *Gryllus veletis* and *G. pennsylvanicus*, the animals used in this study, is then described.

SINGING BEHAVIOR AND PHONOTAXIS

Acoustical signals produced by males inform females of their species, sex, and location by way of sound pressure waves transmitted through the surrounding environment. The signals differ in their production, physical properties, and information transmitted. Alexander (1962) described the types of acoustical signals used by insects, and Otte (1974) discussed the evolution of signals in the context of functional and incidental effects. The most common male signal produced is the female attraction song or "calling song". Female crickets of different species are attracted to the calling song of their own species (reviewed by Popov and Shuvalov 1977). Each closure of the wings results in a pulse of song, and the pulse rate is the most important component of the song responsible for species specific phonotaxis (Hoy *et al.* 1982; Doherty and Hoy 1985; Huber and Thorson 1985). For example, in females of the field cricket, *Scapesipedus marginatus*, the pulse rate determined the degree of positive phonotaxis (Zaretsky 1972). In addition, a series of experiments involving hybrid crickets, *Teleogryllus oceanicus* and *T. commodus*, showed that females preferred the hybrid calling song over either parental song (Bentley 1971; Bentley and Hoy 1972; Hoy *et al.* 1977). Similar studies with anurans resulted in the same conclusions (Doherty and Gehardt 1983). These studies suggest the genetic template for song production and reception is identical or similar in males and females (Alexander 1962).

Other song components besides pulse rates influence female phonotaxis. The carrier frequency of the calling song is important for female phonotaxis in *T. oceanicus* (Moiseff *et al*. 1978). Mole cricket females, *Scapteriscus acletus*, are attracted by high intensities of male calling songs (Ulagaraj and Walker 1975). Furthermore, Forrest (1983) showed that high intensity calling songs of *S. acletus* and *S. vicinus* males attracted more females than lower song intensities, and that song intensity was correlated with male size and soil moisture of male burrows. *Gryllus integer* females also are attracted to high song intensities (Cade 1979a). In addition, Cade (1979b) showed that *G. integer* and *G. veletis* females increased their phonotactic response when deprived of males.

Previous research concentrated on the calling song as a species isolating mechanism (Alexander 1957; Alexander and Moore 1958; Hill *et al.*. 1972; Otte 1970; Walker 1957, 1964a, 1973). For example, the pulse rate and carrier frequency were analyzed as to their effects on the phonotactic behavior of conspecific and heterospecific females. More recently, however, attention to the calling song has focused on its importance in male reproductive competition and female choice (Alexander 1975; Boake 1983; Burk 1983; Cade 1979a, 1985; Dodson *et al*. 1983; Ewing 1984; Feaver 1983; Field and Sandlant 1983; Otte 1972, 1977; Walker 1983a, 1983b).

Once an attracted female contacts a calling male, he changes the song to a soft, rhythmical courtship song which precedes copulation. In crickets females are superior in position to males during copulation. Female house crickets, *Acheta domesticus*, require the courtship song prior to mating (Crankshaw 1979). Burk (1983) showed that, in the laboratory, *Teleogryllus oceanicus* females would not mate with non-courting males, and mated only with the most dominant males which attacked courting subordinant males. Barrass (1979) reviewed the adaptive significance of courtship in insects.

INSECT CHORUSES AND MATING BEHAVIOR

The time of day when males call most frequently should coincide with female sexual receptivity (Walker 1983a). Walker reviewed the diel patterns of choruses in relation to the temporal patterns of female receptivity. For example, in the mole crickets, *Scapteriscus acletus* and *S. vicinus*, females are only phonotactic shortly after sunset which corresponds to the peak calling activity by males (Forrest 1983). In addition, female short-tailed crickets, *Anurogryllus arboreus* , are only attracted to male calling songs shortly after sunset (Walker 1980). Consequently, *A. arboreus* males call for about an hour after sunset. In contrast, *A. muticus* females phonorespond throughout the night to male calling songs (Walker and Whitesell 1982).. Accordingly, *A. muticus* males sing continuously through the night. In species where females are always sexually receptive, Walker suggested there should be no apparent peak in the number of calling males. Sexual receptivity in female field crickets is also continuous, however, the number of calling *G. integer* males peaks at dawn (Cade 1979a), coinciding with a peak in the number of matings (Cade unpublished data). The reason for a dawn peak in mating activity is unknown, but Walker and others have suggested that females may judge the relative genetic quality of males by their calling duration.

Field crickets form spatial aggregations which resemble the leks of vertebrates (Boake 1983). Alexander (1975) and Otte (1977) proposed that insect choruses resulted from male reproductive competition, and suggested reasons males join choruses. Males should join choruses when the probability of mating exceeds that of singing alone. Such a difference may occur if sound intensity is enhanced by chorusing and females prefer high song intensities. In the only test of this hypothesis in crickets, Cade (1981a) found no significant difference in the mean number of attracted females to several loudspeakers as opposed to a single loudspeaker. In other acoustical Orthoptera, however, females orient preferentially to dual calling songs over a single calling song (Morris *et al* . 1978; Otte and Loftis-Hills 1979).

Calling crickets may aggregate where recources important to female reproduction are found. Alexander (1975) referred to such aggregations as "resource-based leks", in contrast to most vertebrate leks where there are no resources other than males of importance to females (Bradbury 1981). In field crickets, distribution of suitable ovipositioning sites may cause signalling males to aggregate. In addition, the moisture content of soil may influence ovipositioning sites chosen by females, and consequently male calling sites. In studies of *G. integer* in an outdoor arena Cade (1979a) found a significant difference in the number of individuals occupying a damp portion of the arena versus a dry portion.

Males compete within choruses by calling near others at varying song intensities and duration. Calling behavior also functions to maintain some minimum distance between males. Spacing distributions of calling crickets has been studied for many species (Cade 1979a, 1981a; Campbell and Clarke 1971; Campbell and Shipp 1979; Clark and Evans 1954; French *et al.* 1986; Schatral *et al.* 1984). Bailey and Theile (1983) suggested that the song intensity received by neighboring males reflects a critical distance between calling males to avoid aggressive encounters. Cade (1979a, 1981a) showed that as a loudspeaker, broadcasting the conspecific song, was moved to a distance of about 1m of calling field crickets, *G. veletis*, *G. integer*, and *T. oceanicus*, males either stopped calling or physically attacked a male tethered to the loudspeaker. Greenfield and Shaw (1983) reviewed the adaptive significance of chorusing behavior.

Male field crickets compete for sexually receptive females in ways other than acoustical interactions. Physical contact between males elicits agonistic behavior in the form of aggressive stridulation and fighting. Aggressive songs are short, loud, rythmical songs similar to calling songs in structure. They influence the dominant and subordinant relationships between male field crickets (Alexander 1962). Boake and Capranica (1982) showed that in the gregarious cricket, *Amphiacusta maya*, male aggressive and courtship chirps were indistinguishable and that the primary function of the chirp was in maintenance of a dominance hierarchy. Alexander (1961) discussed other attributes of male-male combat and defined five different "levels" of aggression. These levels range from contacts between males resulting in no apparent aggression to contacts resulting in escalated battles for dominance. Characteristics of intense fighting include rapid antenna lashing, mandibular flaring (and locking), sparring with forelegs, head-butting, and aggressive stridulation.

Patrolling males may remain silent (so-called "satellite" males), thus avoiding physical aggression from territorial males. Under laboratory conditions, Alexander (1961) showed that in *Gryllus*, dominant males attacked subordinant males when the latter began calling. In *G. integer*, patrolling males occasionally attacked calling males and displaced them from their signalling sites (Cade 1979a, 1980). Dixon and Cade (1986) suggested that *G. integer* males assess the fighting ability of conspecific males only after physical contact.

FACTORS AFFECTING SEXUAL BEHAVIOR IN FIELD CRICKETS

Cade and Wyatt (1984) studied several attributes affecting calling behavior in the laboratory and in an outdoor arena of four species of field crickets, *G. integer*, *G. veletis*, *G. pennsylvanicus*, and *T. africanus* (only *G. integer* was studied in the outdoor arena). They found that neither male age nor male weight affected nightly calling durations in the four species. However, mean nightly calling duration was significantly reduced in *G. integer* when the population density was increased from 20 to 37 males (see following section).

Individual crickets may have a genetic tendency to stridulate for varying durations. Cade (1981b) selected for calling duration in *G. integer* , in the laboratory and found a realized heritability of approximately 0.50. High lines and low lines of callers differed significantly after the first episode and subsequent episodes of selection. Thus, in *G. integer* and possibly other field crickets, about 50 % of the variation in calling duration is due to additive effects of genes.

Female tachinid flies, *Euphasiopteryx ochracea* , acoustically orient to the calling song of *G. integer* in Texas and larviposit on stridulating males (Cade 1975, 1979a, 1980, 1981a, 1984a). After 3 or 4 days parasitized males called significantly less than non-parasitized males and died soon thereafter (Cade 1984a). In addition to parasites, predators acoustically orient to cricket calling songs (Bell 1979; Sakaluk and Belwood 1984; Walker 1964b, 1979). Burk (1982) reviewed the effects of acoustically orienting parasites and predators on insect songs.

POPULATION DENSITY AND INTENSITY OF SELECTION

Individual males vary in duration of searching and calling for females. Alexander (1961, 1968, 1975) suggested that the number of matings resulting from calling would decrease with increasing population density. He reasoned that as density increases suitable calling sites become limited and the energetic costs of maintaining territories increases. Searching behavior would lead to increased mating frequencies if the probability of random encounters with receptive females increased. Greenfield and Shelly (1985) studied the effects of density on male behavior in the grasshopper, *Ligurotettix coquilletti* . Males of this species defend territories on creosote bushes, with the number of males per bush varying (Otte and Joern 1975). Greenfield and Shelly found that actively-signalling males had a greater lifetime mating success than inactive-signalling males in both low density and high density. In addition, they found a significantly higher proportion of inactive males in the high density population compared to the low density population. They also showed that sexual behavior did not vary with body size and age.

Frequency distributions typically reflect the type of selection operating on phenotypic characters (Falconer 1981). A normal distribution will usually indicate stabilizing selection acting on a trait. Distributions that are significantly skewed indicate the operation of directional selection, while bimodal distributions indicate the operation of disruptive selection. These facets of phenotypic distributions do not, however, represent the magnitude of selection pressures. Variance in male mating success was suggested to represent the intensity of sexual selection acting on males (Wade 1979; Wade and Arnold 1980). This is not a good indicator of selection pressures on phenotypic variables, since variation in male mating success could arise by chance (Sutherland 1985a). In addition, neither frequency distributions nor variances in mating success accurately account for selection pressures acting on phenotypically correlated characters, since selection pressure may be masked by stronger, counter-selection pressure on some correlated character (s). Sutherland (1985b) reviewed measures of sexual selection and suggested that the intensity of sexual selection could be assessed by the proportion of time spent seeking mates. Sutherland's model, however, does not consider selection pressures acting on phenotypically correlated characters.

Mathematical models have recently been developed for measuring the intensity of selection on phenotypic characters (Arnold 1983a, 1983b; Arnold and Wade 1984a; Arnold and Wade 1984b; Lande and Arnold 1983). Lande and Arnold showed that the intensity of selection operating on a male trait is equivalent to the standardized selection differential (s') -- also called the "coefficient of selection". This value represents the shift in mean phenotypic value due to the direct and indirect effects of selection. In other words, a metric character under intense selection may not respond if it is highly correlated with another metric character under equal and opposite selection intensity. A major advantage of Lande and Arnold's (1983) model over previous models is that it allows one to separate the direct and indirect effects of selection.

The "intensity of selection" acting directly on a behavioral trait can be calculated as the partial regression coefficient (ß'). This value represents the directional selection gradient (Lande and Arnold 1983). Therefore, directional selection gradients, used in combination with intensities of selection, estimate the adaptive features of an organism's behavioral patterns. This exemplifies another advantage of the models in that selection intensities and selection gradients have a direct relation to equations for predicting evolutionary change of heritable phenotypes.

The variance in relative fitness limits the degree to which the mean fitness of the population can evolve resulting from the forces of selection. Arnold and Wade (1984a, 1984b) called the variance in relative fitness the "opportunity for selection" (I). The opportunity for selection places an upper bound on selection intensities. Therefore, by collecting measurements on components of fitness one may determine the factors favored by selection. Price *et al*. (1984a) applied the models to population of Darwin's finches, *Geospiza fortis*. They used longevity over a six year study as the fitness component and estimated the intensity of selection acting on weight and beak characters. They found intense selection pressures favoring large beak and body size during periods of high adult mortality. Similarly, Grant (1985) used the models to estimate the effects of selection on several male and female characteristics in *G. conirostris*. For competition between males to obtain territories, Grant found significant directional selection pressures to increase bill depth and bill length. In addition, female choice was selecting territory position and male plumage.

In field studies, individual reproductive success (RS) is often estimated by the number of offspring reaching sexual maturity. This value, however, is not easily obtained for most animals, especially in polygynous species where the variation in RS may be considerably different between the sexes (Thornhill and Alcock 1983). Thus obtaining estimated values of RS may require different measures of RS, depending on the organism studied. For example, female RS may be estimated by the number of eggs laid. A common estimate of RS for males may be obtained by observing the number of copulations (mating success) received over their lifetime (reviewed by Howard 1979). Studies on vertebrates have provided most of the data for estimating RS in natural populations (Andersson 1982; Borgia 1985; Clutton-Brock *et al*. 1979; Godwin and Roble 1983; Howard 1978; Price 1984; Trail 1985). With few exceptions, sufficient field data on mating success in insects are lacking (Banks and Thompson 1985; Greenfield and Shelly

1985; Walker 1980). Most studies on mating success in crickets have come from laboratory experiments (Burk 1983; Wyatt 1982).

THE SPECIES STUDIED

Gryllus veletis and *G. pennsylvanicus* are closely related species. They occupy virtually the same ecological niche throughout their geographic distribution (Alexander and Bigelow 1960; Alexander 1968). These two species cannot be distinguished on morphology, however, *G. veletis* females appear to have a shorter ovipositor relative to total body length than *G. pennsylvanicus* females (Alexander 1962). In addition, these are the only gryllines known that inhabit the same area and produce identical songs. Males of both species produce 3-5 pulses per chirp with approximately 115-190 chirps per minute (Weissman *et al*. 1980). The population density levels (judged by the number of calling males) attained during the mating season in *G. pennsylvanicus* greatly exceed the density levels for *G. veletis* (Alexander and Bigelow 1960; Alexander and Meral 1967; Alexander 1968). The difference is due, in part, to the overwintering habits of the species. *Gryllus pennsylvanicus* survives the winters as eggs, emerge as nymphs in the Spring, and mature as reproductive adults in late July or early August. Adults breed throughout the Fall, or until the first frost. *Gryllus veletis* overwinters as late instar nymphs, emerge in early Spring, and mature as reproductive adults in mid Spring. Their mating season ends in late July or early August. The development of eggs continues through August with nymphs emerging in September and growing untill the first frost.

Given the simularities (same songs, same morphological characters, and same geographic distributions) and differences (population density levels and life cycles) between *G. veletis* and *G. pennsylvanicus*, Alexander and Bigelow (1960) suggested they evolved by allochronic speciation. That is, reproductive isolation between the two species resulted from seasonal separation in adults. They speculated that the temporal separation occurred in the ancestral species by the elimination of all but two overwintering stages. For allochronic speciation to occur Alexander and Bigelow proposed three characterics of the ancestral species: (1) only one generation each year (univoltine), (2) short mating season, and (3) two overwintering strategies at two distinct stages of the life cycle. Given these factors *G. veletis* and *G. pennsylvanicus* could have evolved from a common ancestor without geographic isolation. In addition, hybridization experiments between *G. veletis* and *G. pennsylvanicus* resulted in no reproductively viable offspring (Alexander and Bigelow 1960). Recently, however, Harrison (1983, 1985) has shown that *G. pennsylvanicus* females will hybridize with male beach crickets, *G. firmus* , in zones of geographic overlap. Consequently, Harrison suggested that *G. firmus* and *G. pennsylvanicus* share the most recent common ancestor. Harrison's results do not deny the Alexander and Bigelow model of allochronic speciation, rather affects the probability of the *G. veletis* and *G. pennsylvanicus* ancestral stock migrating north or south (Alexander 1968).

METHODS OF STUDY

This study was conducted on the campus of Brock University, St. Catharines, Ontario, Canada (43° 12' N; 79° 10' W). Outdoor arenas were used during August in 1983 and June through August in 1984 to study individual nightly calling duration, nightly movement, and individual mating frequency at different densities in the northern spring and fall field crickets, *G. veletis* and *G. pennsylvanicus*.

RESEARCH ANIMALS

Both species were collected as nymphs and adults in the St. Catharines area. *Gryllus veletis* were collected in late May and early June, and *G. pennsylvanicus* in early August. The crickets were brought into the laboratory and kept at 25 - 30° C and 30 - 35 % relative humidity. The light-dark cycle was maintained at 12 : 12. Females were housed together in terraria. Male nymphs were also housed together in terraria. All terraria were checked daily for newly molted adults, and individual males were placed in 500 ml cardboard cups. Food (Purina Cat Chow ®), lettuce, stopped vials of water, and shelter (chicken egg cartons) were provided. Adult crickets were individually numbered on the pronotum using Liquid Paper © and india ink (Walker and Wineriter 1981). Sexually mature crickets were released into the center of the outdoor arena after being weighed to the nearest 0.1 mg with an Oertling R20 electronic balance. For all samples adult age of males at release ranged from 6 - 49 days past the final molt for *G. veletis* and 4 - 14 days for *G. pennsylvanicus*. For all samples adult age of females at release ranged from 4 - 49 days past the final molt for *G. veletis* and 2 - 9 days for *G. pennsylvanicus*.

OUTDOOR ARENAS

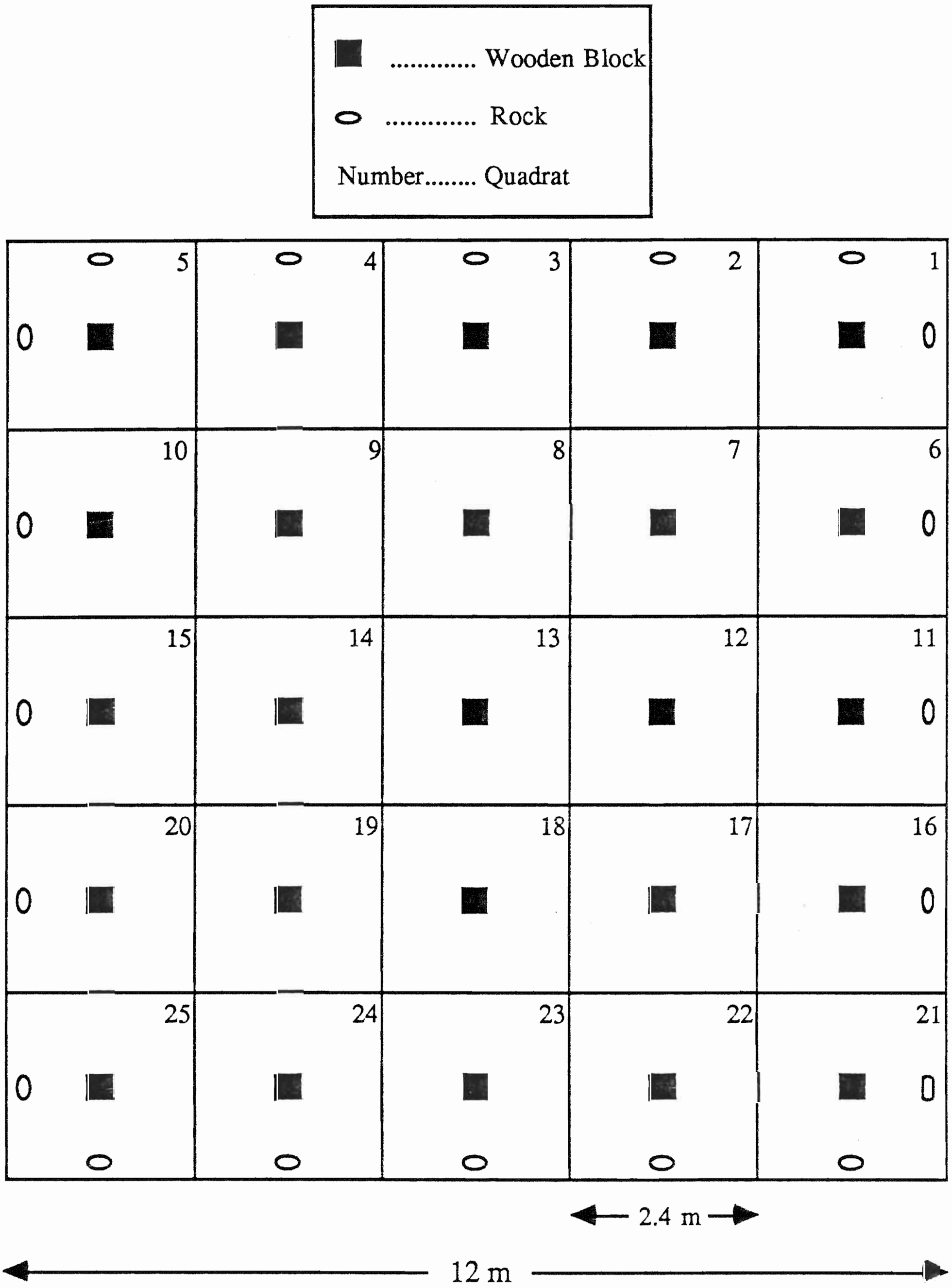
An outdoor arena was constructed in 1984 to simulate a natural environment. The arena was constructed with 1m high aluminum siding (partially buried) to keep crickets from escaping. Orchard bird netting covered the top of the arena and prevented birds from entering. The dimension of the arena measured 12 m x 12 m and was divided into 25, 2.4 m x 2.4 m quadrats. The quadrats were numbered and marked with flags. Artificial burrows covered by wooden blocks were placed in the center of each quadrat and rocks were placed along the aluminum wall of each quadrat to provide refuge for the crickets (Figure 1). For each observation period the grass was initially mowed to a height of about 3 cm and then allowed to grow. The arena was watered every 3 - 4 days or when the ground became too dry for females to oviposit.

In 1983 a very similar arena was used at the Glendridge Campus of Brock University. This arena was abandoned, however, when the Department of Biological Sciences moved to the main campus. The primary difference was in dimension. This arena measured 13 m x 13 m and was divided into 25, 2.6 m x 2.6 m quadrats. A chain-link fence surrounded this arena, in addition to 1 m high galvanized steel sheets. Chicken-wire covered the top of the arena and orchard bird netting surrounded the sides, preventing birds from entering. Cade and Wyatt (1984) used the same arena to study *G. integer*.

ARENA OBSERVATIONS AND DATA COLLECTION

To determine any difference in cricket behavior with changing population density, *G. veletis* was observed in 1984 at a high density (20 males : 20 females) and twice at a low density (5 males : 5 females) (termed low density A and low density B). *G. pennsylvanicus* was observed at high density and at low density in 1984, and once at high density in 1983. The actual number of crickets in the arena varied, however, due to mortality of some individuals. Table I in the appendix shows the means and standard deviations for the number of crickets used in each density. The individually marked crickets were observed for at least 9 continuous nights, with one replicate in 1983 lasting 19 nights. Crickets not found on an observation date were classified as missing and were replaced after 3 nights. Crickets known to be dead were replaced immediately. The observations were from 2200 to 0800 (EDT). In addition, a 24 hour observation was performed once for each species at each density in 1984. At the beginning of each night a complete survey of the arena was conducted using a headlamp to ascertain each cricket's location. The survey involved looking beneath each wooden block and rock for crickets. In addition, each quadrat was scanned for crickets walking about in the arena. Location of

Figure 1. The outdoor arena showing the dimensions, wooden blocks, rocks, and quadrat numbers.


■ .... Wooden Block
⬭ .... Rock
Number......... Quadrat
5
4
3
2
1
10
9
8
7
6
15
14
13
12
11
20
19
18
17
16
25
24
23
22
21
2.4 m
12 m

crickets were marked on scaled maps of the arena, with 1 cm of map distance corresponding to 60 cm arena distance. Complete arena checks were made each hour and provided information on the location of individuals throughout the night.

The presence or absence of calling song from each male location was recorded at 5 min intervals and these intervals were used to determine individual nightly calling duration. For example, if a male was observed calling for 10 checks during an hour, he would be assigned a "score" of 50 min. If, however, a male had been scored as calling from a particular location but later found elsewhere, and another male was found in that location, neither male was scored as calling. Table II in the appendix shows an example of reliability in determining the calling male.

Calling durations were expressed as the time calling/time available for calling, and the term "mean calling score" is used to represent this ratio. Male field crickets stop calling and start courting in the immediate presence of females. The time utilized in courting a female occupies the time that could be used for attracting other females. If a female was in the immediate presence of a male for a given hour, this hour was subtracted from the 10 hour potential calling time. For both species, calling males that had attracted females ceased calling on 22 occasions out of 30.

Female crickets remove and eat spermatophores immediately following copulations (Sakaluk and Cade 1983). This forces males to physically guard females while sperm enters the female reproductive tract. An hour was subtracted when a male was scored a mating, since a male may guard his mate for extended time periods. For example, in the field cricket, *T. commodus*, mate guarding by physical contact prevented the female from removing the spermatophore before sperm had been completely transferred (Loher and Rence 1978). Unguarded females removed the spermatophore after 32 min, which was half the time needed for complete sperm transfer. Average spermatophore attachment time in this species was 105 min while the average guarding time was 83 min. Since male field crickets do not call while mate guarding, the guarding time represents the latency period between mating and the resumption of calling.

Matings were considered to have occurred when a copulation was observed or a female possessed a fresh spermatophore while in the immediate presence of a single male. Spermatophores are white capsules containing mature sperm cells and are attached externally and internally to the female reproductive tract during copulation (Alexander and Otte 1967). A spermatophore remains attached as sperm cells migrate through the female reproductive tract to the sperm storage organ (spermatheca). On 18 occasions, an inseminated female was close to 2 males. In these cases, however, one male "guarded" the female and the mating was assigned to this male. Table II in the appendix shows an example of reliability in determining matings.

STATISTICAL ANALYSES OF DATA

The raw data for each species and each density were placed in a Burroughs TD830 computer file, and analyzed using the program "Statistical Package for the Social Sciences" (SPSS). Most data sets were transformed using natural logarithms for subsequent analyses in order to use parametric tests of significance. Frequency distributions of mean calling times per night, mean displacement per night, and mean number of matings per night were tested with the Kolmogorov-Smirnov goodness of fit test for a normal distribution. Tables III and IV in the appendix contain information on the effects of transformation on normality, skewness, and kurtosis for male and female data sets, respectively. Sample means for each density were tested for significant differences with t-tests. Pearson's product moment correlation coefficients were used to ascertain relationships between variables.

QUANTITATIVE ANALYSIS OF SELECTION

Current models in quantitative genetic studies allow analysis on the intensity of selection (Arnold 1983a, 1983b; Arnold and Wade 1984a, 1984b; Lande and Arnold 1983). The models assess the intensities of selection acting indirectly and directly on phenotypic characters. For these analyses the phenotypic characters were transformed to natural logarithms and standardized to have sample means of 0 and unit variances. The standardization of characters was accomplished by subtracting the sample mean from the individual means and dividing by the sample standard deviation (Zar 1984). In contrast, relative mating success was not transformed to natural logarithms, but only standardized to have means of 1 by dividing individual means by the sample mean (Zar 1984). The fitness component, relative mating success, was not log transformed because transformation would lead to erroneous values for selection intensities (Lande and Arnold 1983). Also, by standardizing only to means of 1, the variation in relative fitness, which is to be explained in the calculations, is unaffected. The squared multiple correlation coefficient (R^2) represents the variation explained in relative fitness by the independent variables and significant levels for R^2 were assessed with ANOVAS. In addition, the variance in relative fitness places an upper bound on the selection intensities. That is, the cumulative selection intensities cannot exceed the variance in relative fitness.

The intensities of sexual selection (s') acting directly and indirectly on phenotypic characters were calculated as the covariances between relative mating success and the standardized variables. This value is also called the "coefficient of selection" (Falconer 1981). Significance was determined using parametric correlation coefficients since the covariance between two variables is directly proportional to the correlation coefficient between the variables (Lande and Arnold 1983; Price 1970). The intensities of sexual selection acting directly on the phenotypic characters were derived as the partial regression coefficients (ß') of relative mating success on the standardized variables. Lande and Arnold called this coefficient the "directional selection gradient". Significance for the selection gradients were determined by t-tests.

RESULTS

CYCLES OF ACTIVITY

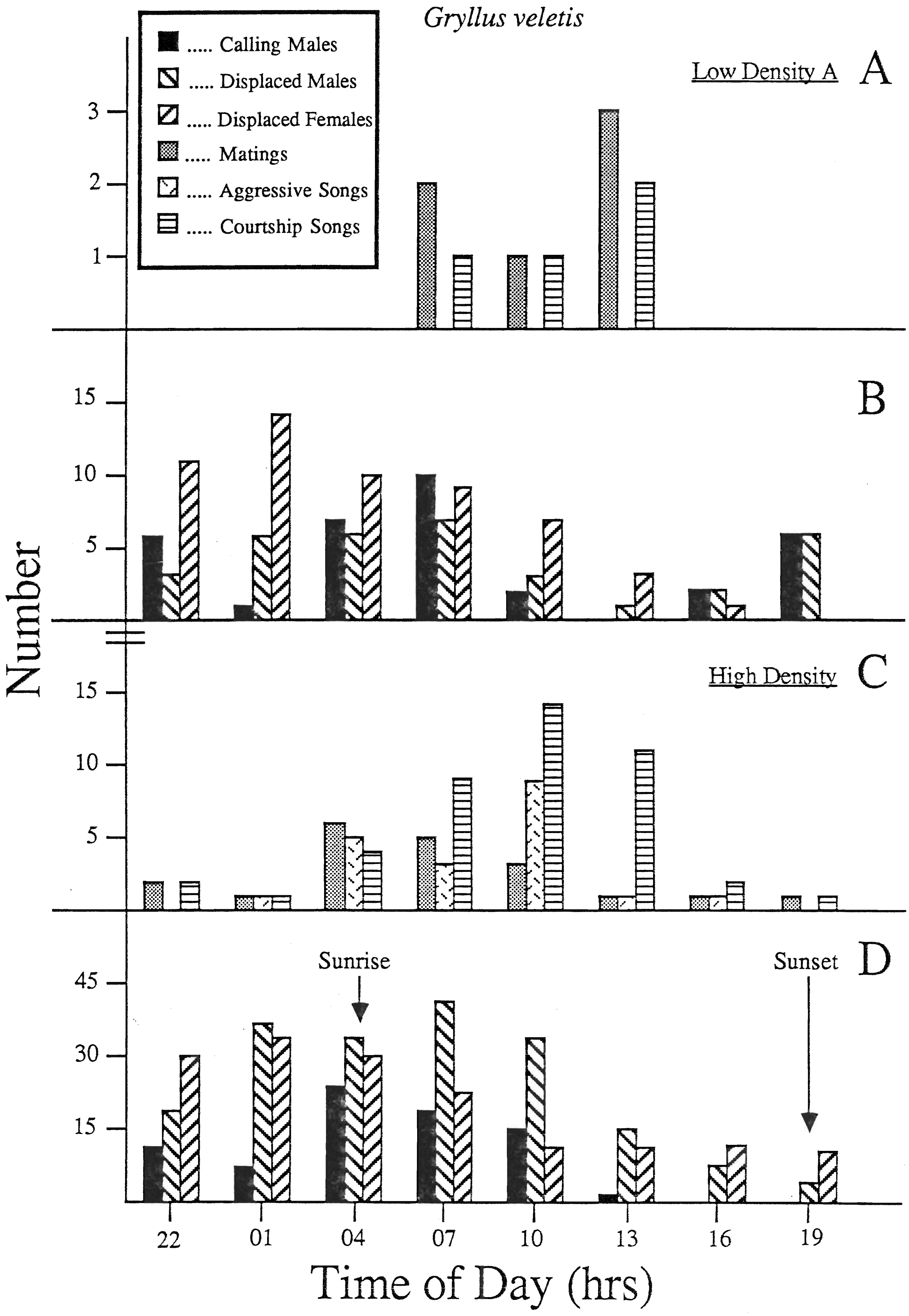
24 Hour Observation Periods

Figure 2a-d shows frequency distributions for the 24 hour activity cycles of *G. veletis* males and females at high density and low density. The 24 hour observation periods were split into 8, 3 hour time blocks for analysis. Chi square (X^2) tests for uniform expected frequencies were used for statistical significance. Males were classified as callers if they called for at least one score within an hour. The number of calling males over the 24 hour period showed a significant difference at high and low densities ($X^2 = 45.6$, df = 7, $P < 0.001$; $X^2 = 13.7$, df = 7, $P < 0.05$), and most males called during the dark hours (Figure 2b and 2d).

The linear distance from a cricket's initial location in the arena to a subsequent location determined its nightly displacement. Points separated by less than 1 cm on the arena maps were considered as no movement for the crickets' nightly totals. This resulted in the crickets having to travel at least 60 cm in the arena before movement was scored. This was the minimum detectable displacement allowed for transferring a cricket's location in the arena to its location on the arena map. There were highly significant differences at high density in the number of females and males moving over the 24 hour period ($X^2 = 37.8$, df = 7, $P < 0.001$; $X^2 = 59.3$, df = 7, $P < 0.001$). At low density the number of displaced males showed no significant variation ($X^2 = 1.9$, df = 5, $P > 0.05$), whereas the number of females was highly significant ($X^2 = 26.0$, df = 7; $P < 0.001$). For both densities individuals were most active during the dark hours of the photoperiod (Figure 2b and 2d).

Behavioral traits other than calling and movement were observed over the 24 hour period including the number of matings, the number of courtship songs, and the number of aggressive songs. For *G. veletis*, only the high density population had sufficient data for statistical testing. The number of matings and the number of aggressive songs were not

Figure 2a-d. The 24 hour activity patterns for *G. veletis* males and females at high density and low density. The data include the number of calling males, number of males and females moving a minimum distance, number of aggressive songs, number of courtship songs, and the number of matings. Also shown are the sunset and sunrise times.


Gryllus veletis
..... Calling Males
..... Displaced Males
..... Displaced Females
..... Matings
..... Aggressive Songs
..... Courtship Songs
Low Density A
A
B
High Density
C
D
Sunrise
Sunset
Number
3
2
1
15
10
5
15
10
5
45
30
15
22
01
04
07
10
13
16
19
Time of Day (hrs)

significantly different from uniform expected frequencies ($X^2 = 2.5$, df = 1, $P > 0.05$; $X^2 = 0.1$, df = 1, $P > 0.05$). The number of courtship songs was significantly different from random ($X^2 = 33.1$, df = 7, $P < 0.001$), and occurred primarily during mid-morning and early afternoon hours of the photoperiod. This was also the time when courtship songs and matings occurred in low density (Figure 2a).

Figure 3a-d shows frequency distributions for the 24 hour activity patterns of *G. pennsylvanicus*. There was a highly significant difference in the number of calling males at high density with time, but no significant difference at low density ($X^2 = 38.1$, df = 7, $P < 0.001$; $X^2 = 4.0$, df = 3, $P > 0.05$). At high density calling occurred mostly at night (Figure 3d). At low density, the number males and females that moved over the 24 hour period was not significantly different from random ($X^2 = 6.0$, df = 7, $P > 0.05$; $X^2 = 3.6$, df = 5, $P > 0.05$). At high density, however, there was a highly significant difference in the number of females moving over the observation period ($X^2 = 31.2$, df = 7, $P < 0.001$), but no significant difference in the number of males ($X^2 = 13.6$, df = 7, $P > 0.05$). Female movement activity occurred mostly during the daylight hours of the photoperiod.

The number of matings and aggressive songs at high density and aggressive songs at low density was too few for statistical testing, but Figure 3c shows that these activities occurred between sunset and sunrise. The number of matings with time at low density was significantly different from random ($X^2 = 4.9$, df = 1, $P < 0.05$). Figure 3a shows that matings at low density occurred mostly at night. The number of courtship songs at both densities were not statistically significant with time ($X^2 = 2.5$, df = 5, $P > 0.05$; $X^2 = 1.1$, df = 1, $P > 0.05$).

10 Hour Observation Periods

The mean number of calling males with time and 95 % confidence intervals is in Figure 4a-c for *G. veletis* at the different density levels in 1984. In all cases the 95 % confidence intervals overlap considerably, indicating no significant variation in the number of callers. Figure 5a-c shows the mean number of calling males with time and 95 %

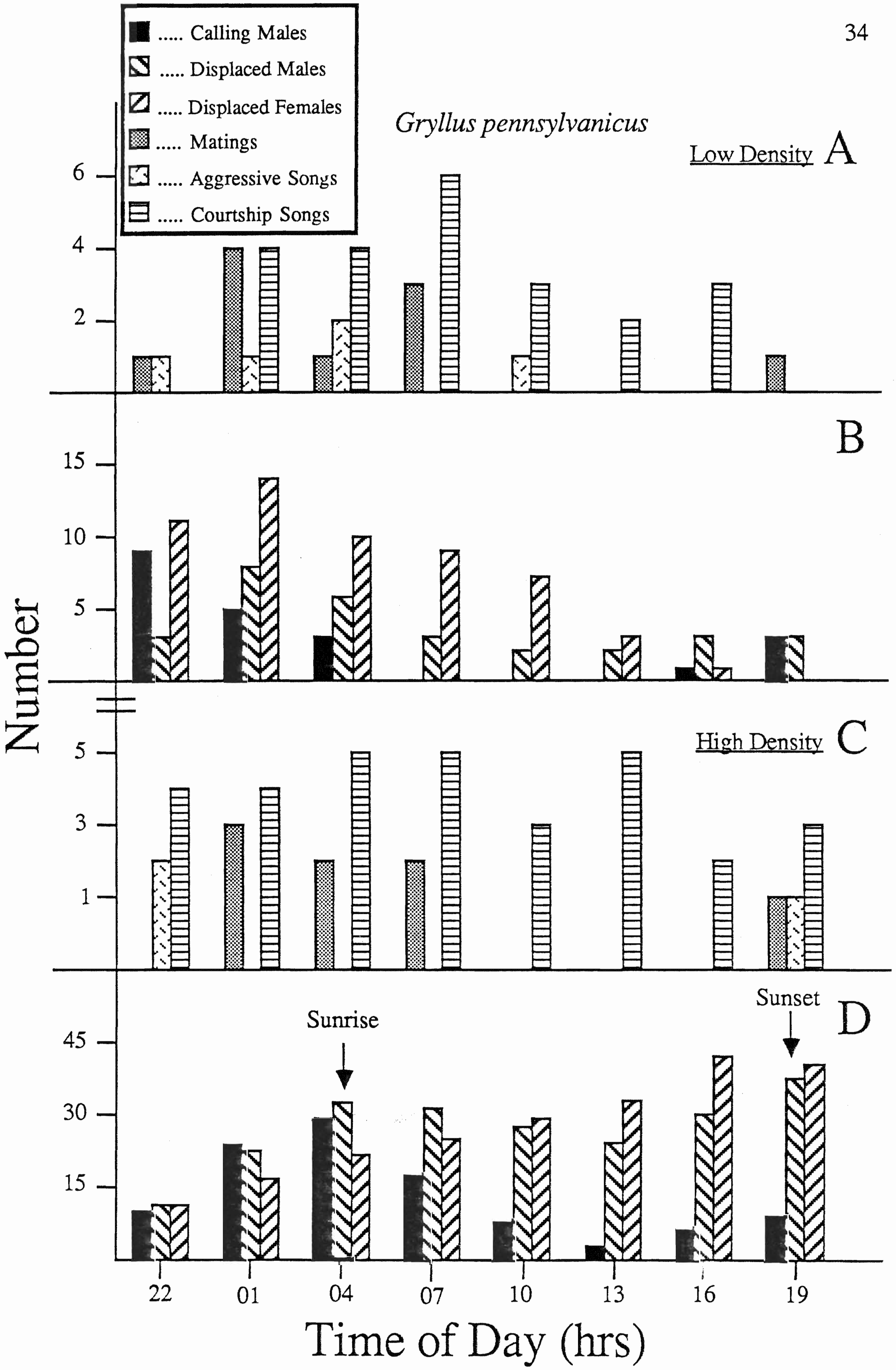

..... Calling Males
..... Displaced Males
..... Displaced Females
..... Matings
..... Aggressive Songs
..... Courtship Songs
Gryllus pennsylvanicus
Low Density
A
B
High Density
C
D
Sunrise
Sunset
Number
6
4
2
15
10
5
5
3
1
45
30
15
22
01
04
07
10
13
16
19
Time of Day (hrs)

Figure 4a-c. Mean number of calling males with time since sunset for *G. veletis* at high and low densities (bars indicate 95 % confidence intervals).

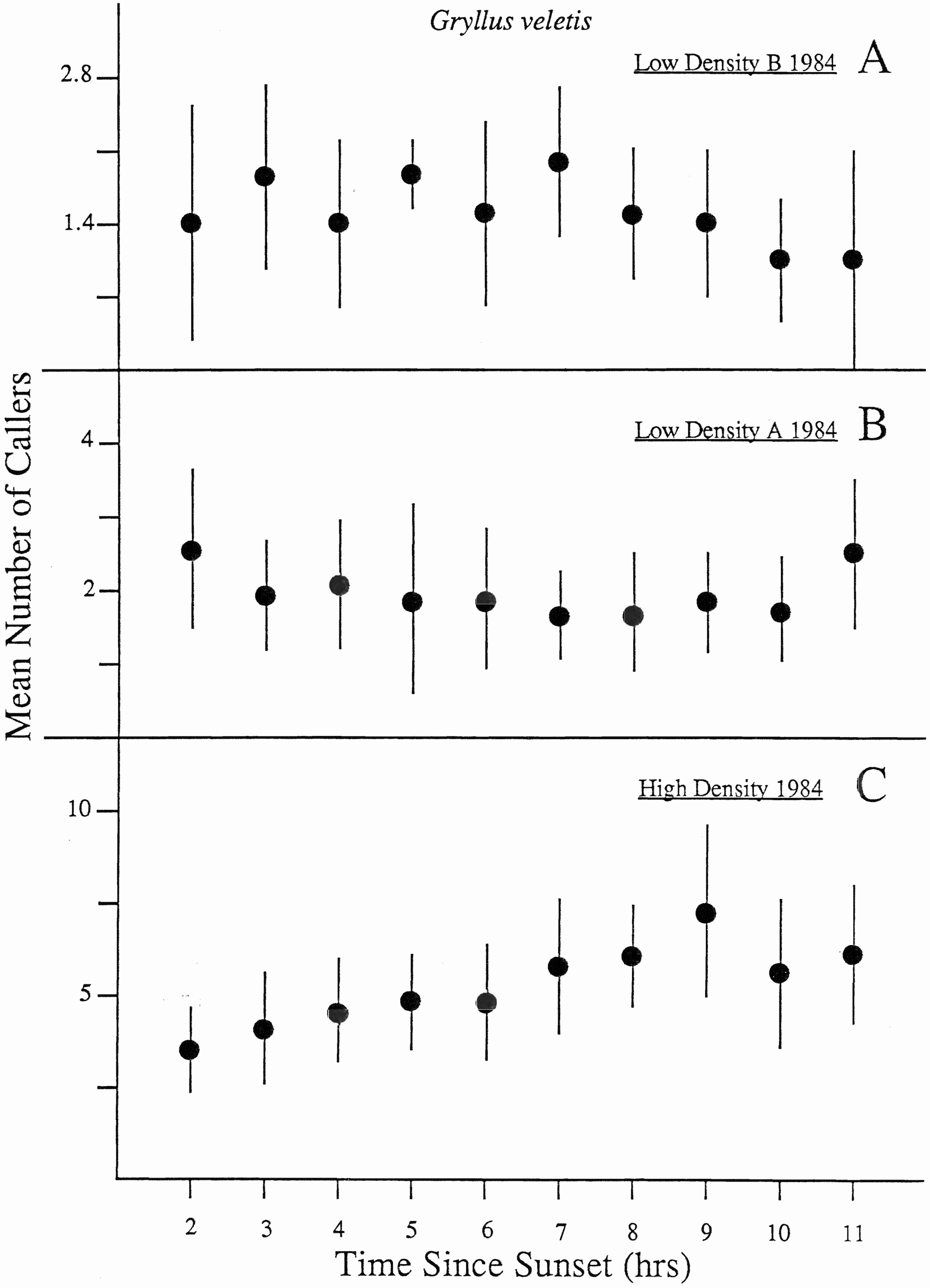
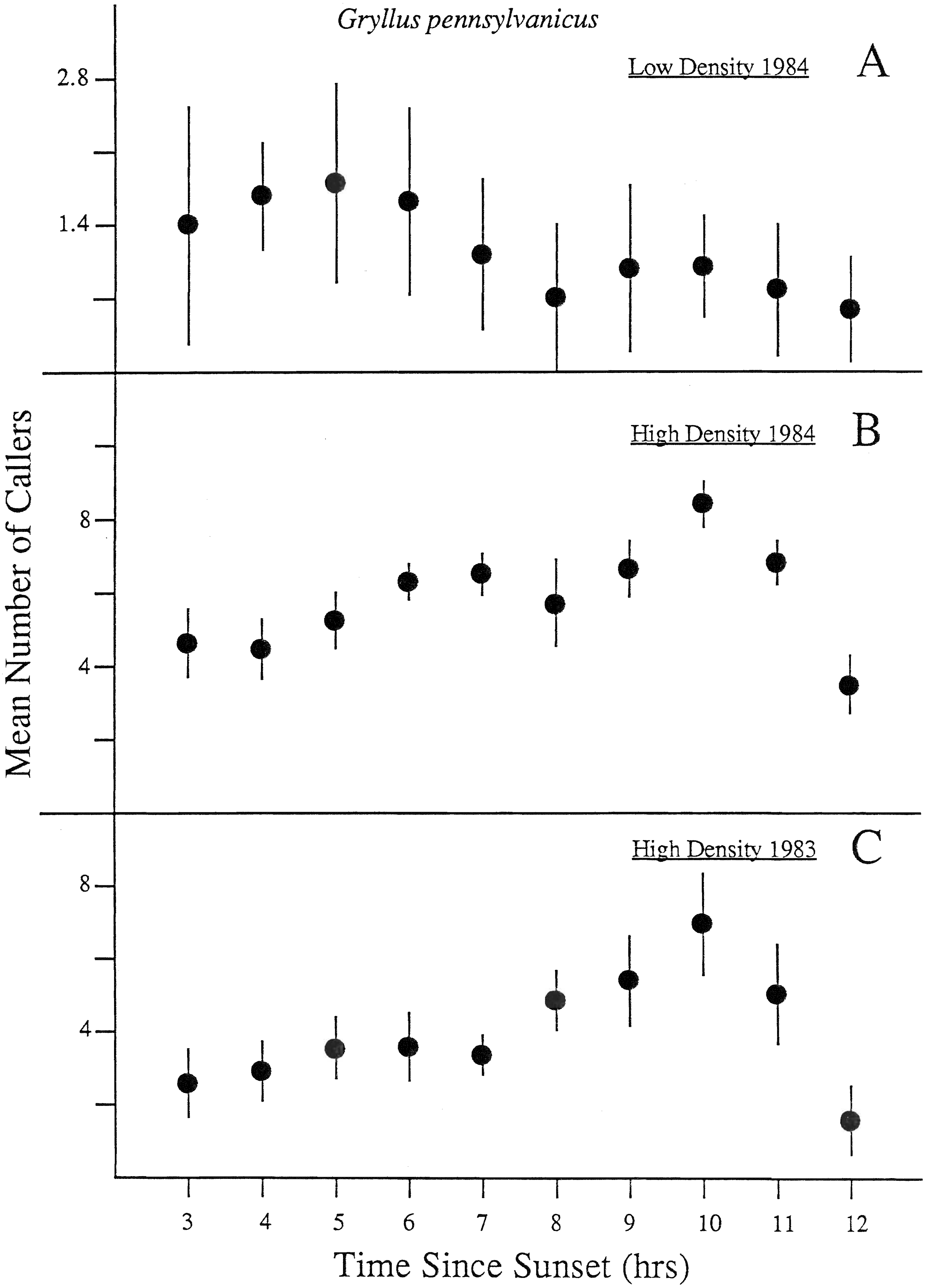

Gryllus veletis
Low Density B 1984
A
2.8
1.4
Low Density A 1984
B
4
2
High Density 1984
C
10
5
Mean Number of Callers
2
3
4
5
6
7
8
9
10
11
Time Since Sunset (hrs)

Figure 5a-c. Mean number of calling males with time since sunset for *G. pennsylvanicus* at high and low densities (bars indicate 95 % confidence intervals).


Gryllus pennsylvanicus
Low Density 1984
A
2.8
1.4
High Density 1984
B
8
4
Mean Number of Callers
High Density 1983
C
8
4
3
4
5
6
7
8
9
10
11
12
Time Since Sunset (hrs)

confidence intervals for *G. pennsylvanicus* . The 95 % confidence intervals for the 1983 high density and 1984 low density samples indicated no significant variation in the number of callers. The 1984 high density sample, however, showed a significant increase in the number of calling males around dawn.

The mean number of crickets that were scored as moving with time and 95 % confidence intervals for *G. veletis* males and females at the different density levels in 1984 are in Figure 6a-c and Figure 7a-c, respectively. There was no significant variation among any of the samples. Figure 8a-c and Figure 9a-c show the mean number of crickets that were scored as moving with time and 95 % confidence intervals for *G. pennsylvanicus* males and females in 1983 and 1984. There was no significant variation in the movement patterns at any density as shown by overlapping confidence intervals.

The mean number of matings with time and 95 % confidence intervals for *G. veletis* in 1984 are in Figure 10a-c. For all densities there were no significant differences in matings with time. Figure 11a-c show the mean number of matings with time and 95 % confidence intervals for *G. pennsylvanicus* in 1983 and 1984. For all densities there were no significant differences in matings with time.

In addition to the 95 % confidence intervals, the mean number of callers, the mean number of matings, and the mean number of males and females that moved a detectable distance were tested for significant departure from randomness with the runs test. The findings are given in Tables V, VI, and VII in the appendix.

BEHAVIORAL VARIATION OF INDIVIDUALS

Tables VIII and IX in the appendix show the transformed sample means and standard deviations for males and females that were used for statistical testing. Tables X and XI in the appendix give the raw data of males and females used to calculate the sample statistics, also the total number of different mating partners for each male and female are given. Differences in phenotypic characters between species at the same density levels are presented on page 115 in the Appendix.

Figure 6a-c. Mean number of males that moved a minimum detectable distance with time since sunset for *G. veletis* at high and low densities (bars indicate 95 % confidence intervals).

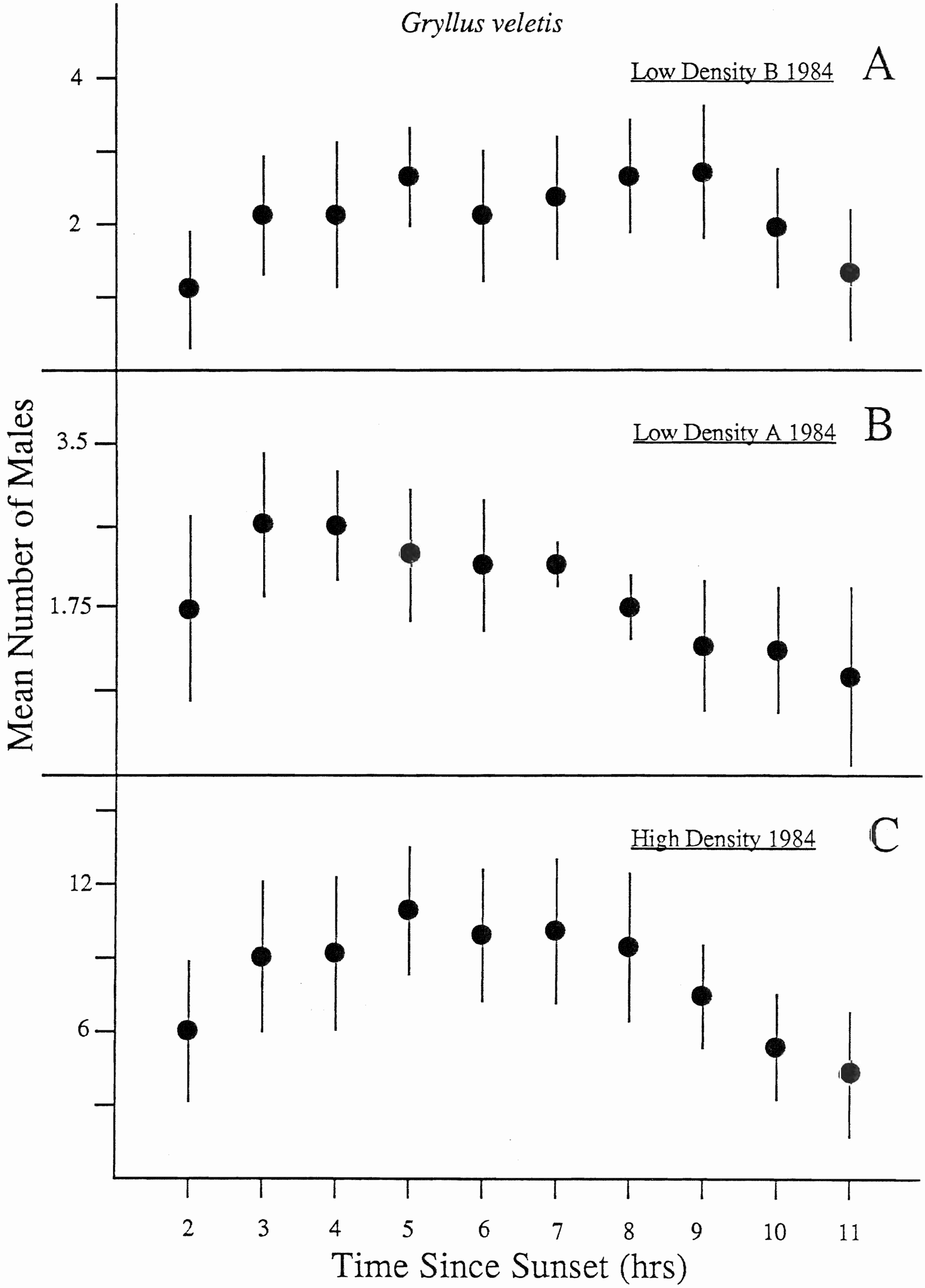

Gryllus veletis
Low Density B 1984
A
4
2
Low Density A 1984
B
3.5
1.75
High Density 1984
C
12
6
Mean Number of Males
2
3
4
5
6
7
8
9
10
11
Time Since Sunset (hrs)

Figure 7a-c. Mean number of females that moved a minimum detectable distance with time since sunset for *G. veletis* at high and low densities (bars indicate 95 % confidence intervals).

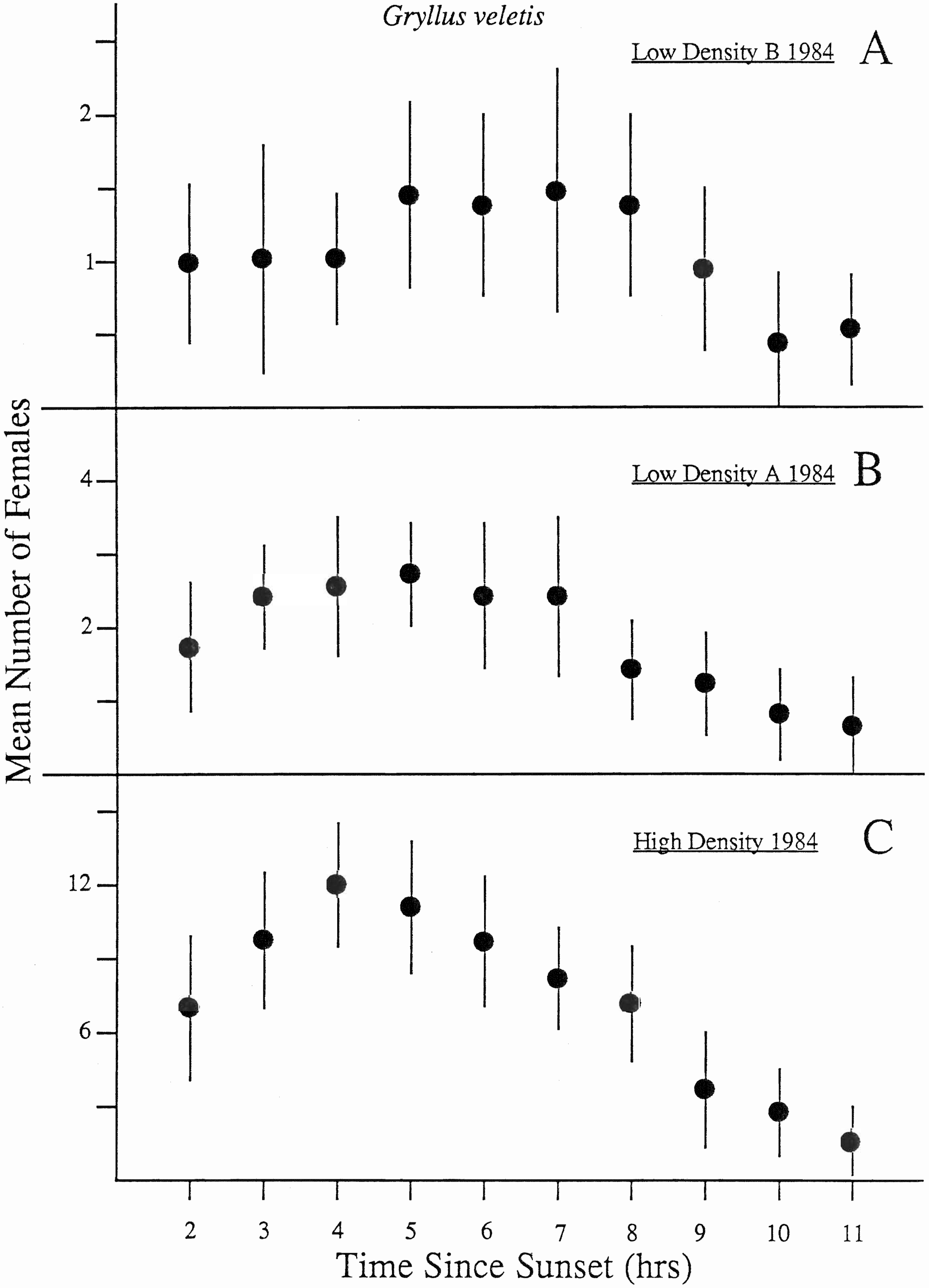

Gryllus veletis
Low Density B 1984
A
Low Density A 1984
B
High Density 1984
C
Mean Number of Females
2
1
4
2
12
6
2
3
4
5
6
7
8
9
10
11
Time Since Sunset (hrs)

Figure 8a-c. Mean number of males that moved a minimum detectable distance with time since sunset for *G. pennsylvanicus* at high and low densities (bars indicate 95 % confidence intervals).

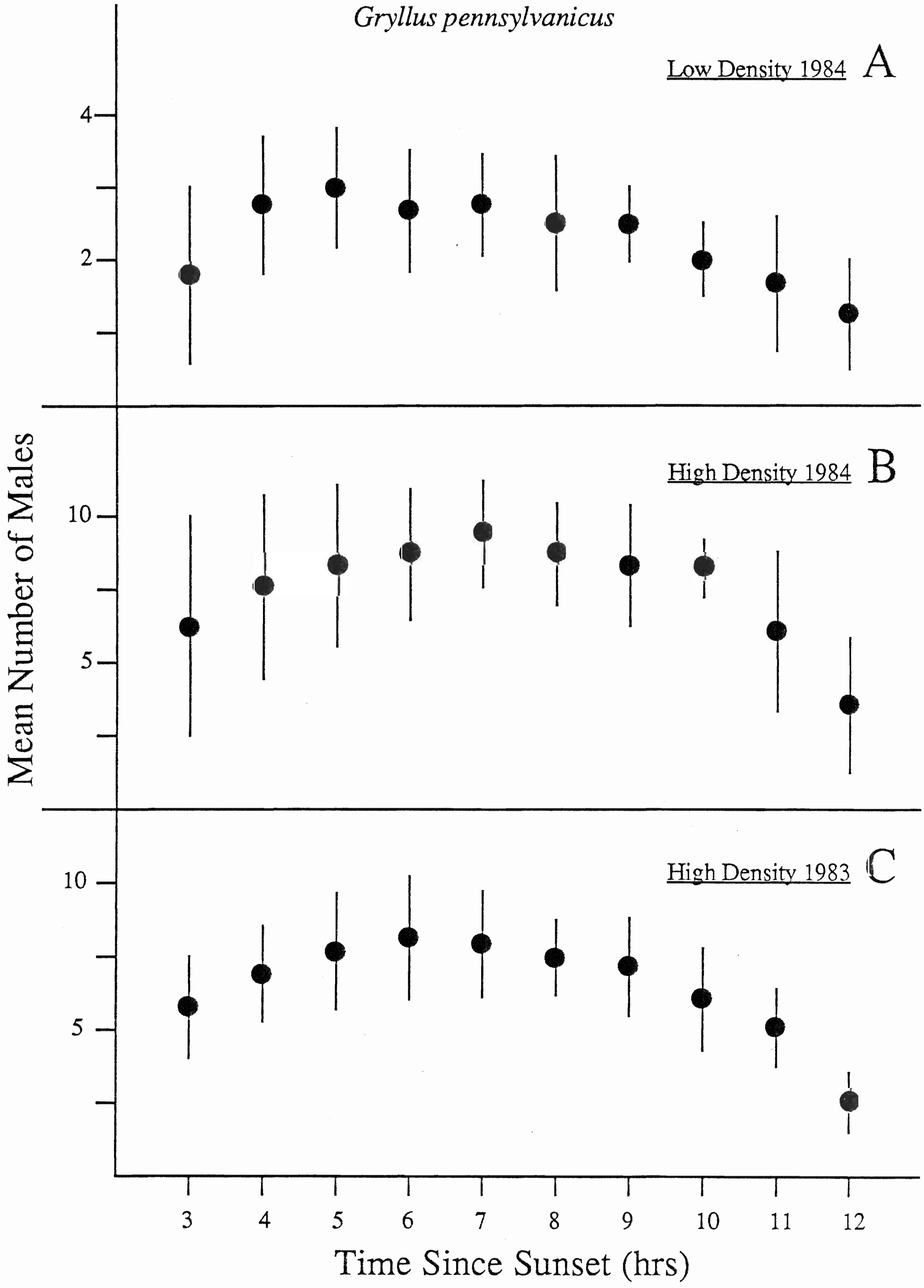

Gryllus pennsylvanicus
Low Density 1984
A
High Density 1984
B
High Density 1983
C
Mean Number of Males
4
2
10
5
10
5
3
4
5
6
7
8
9
10
11
12
Time Since Sunset (hrs)

Figure 9a-c. Mean number of females that moved a minimum detectable distance with time since sunset for *G. pennsylvanicus* at high and low densities (bars indicate 95 % confidence intervals).

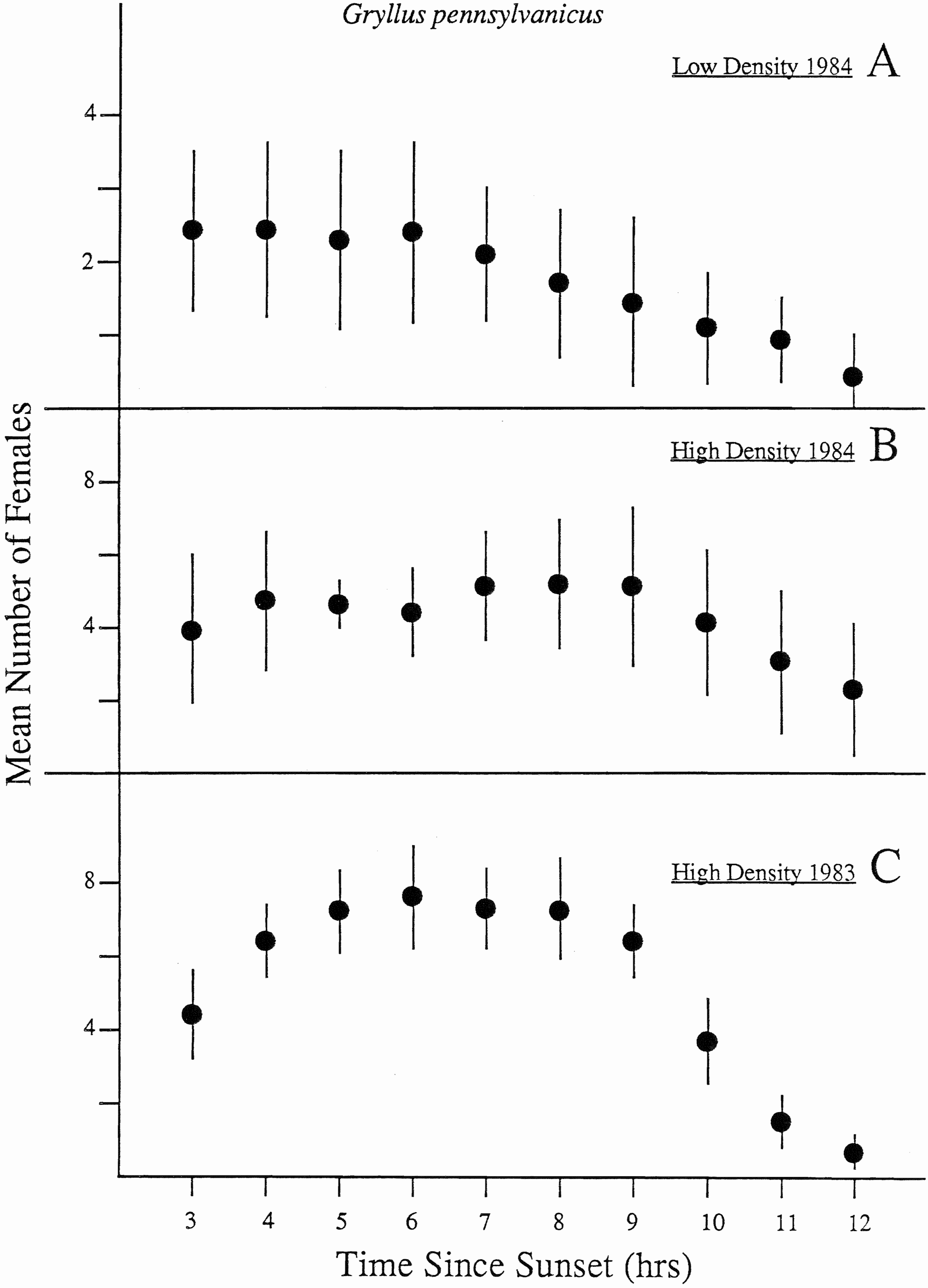

Gryllus pennsylvanicus
Low Density 1984
A
High Density 1984
B
High Density 1983
C
Mean Number of Females
4
2
8
4
8
4
3
4
5
6
7
8
9
10
11
12
Time Since Sunset (hrs)

Figure 10a-c. Mean number of matings with time since sunset for *G. veletis* at high and low densities (bars indicate 95 % confidence intervals).

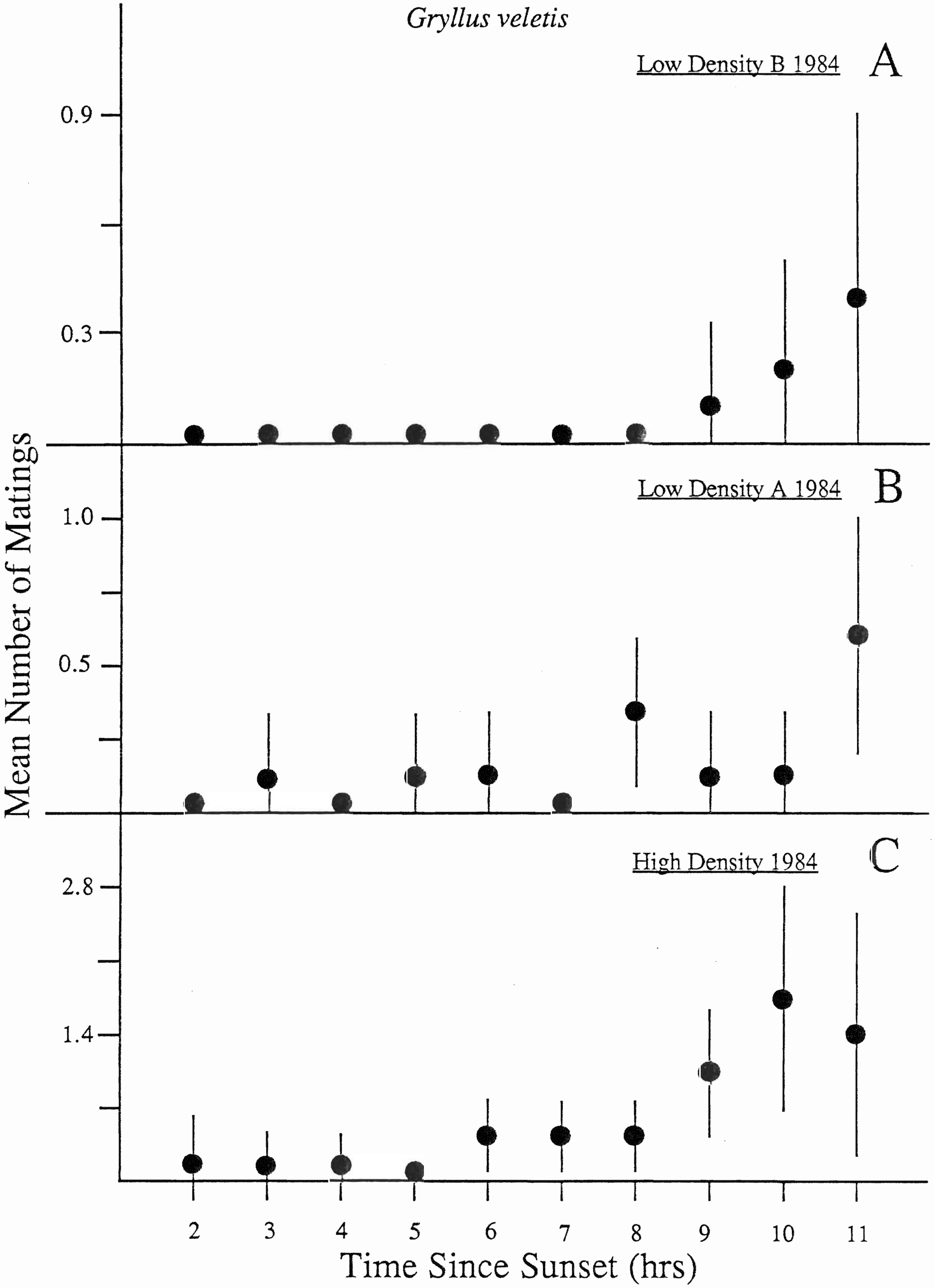
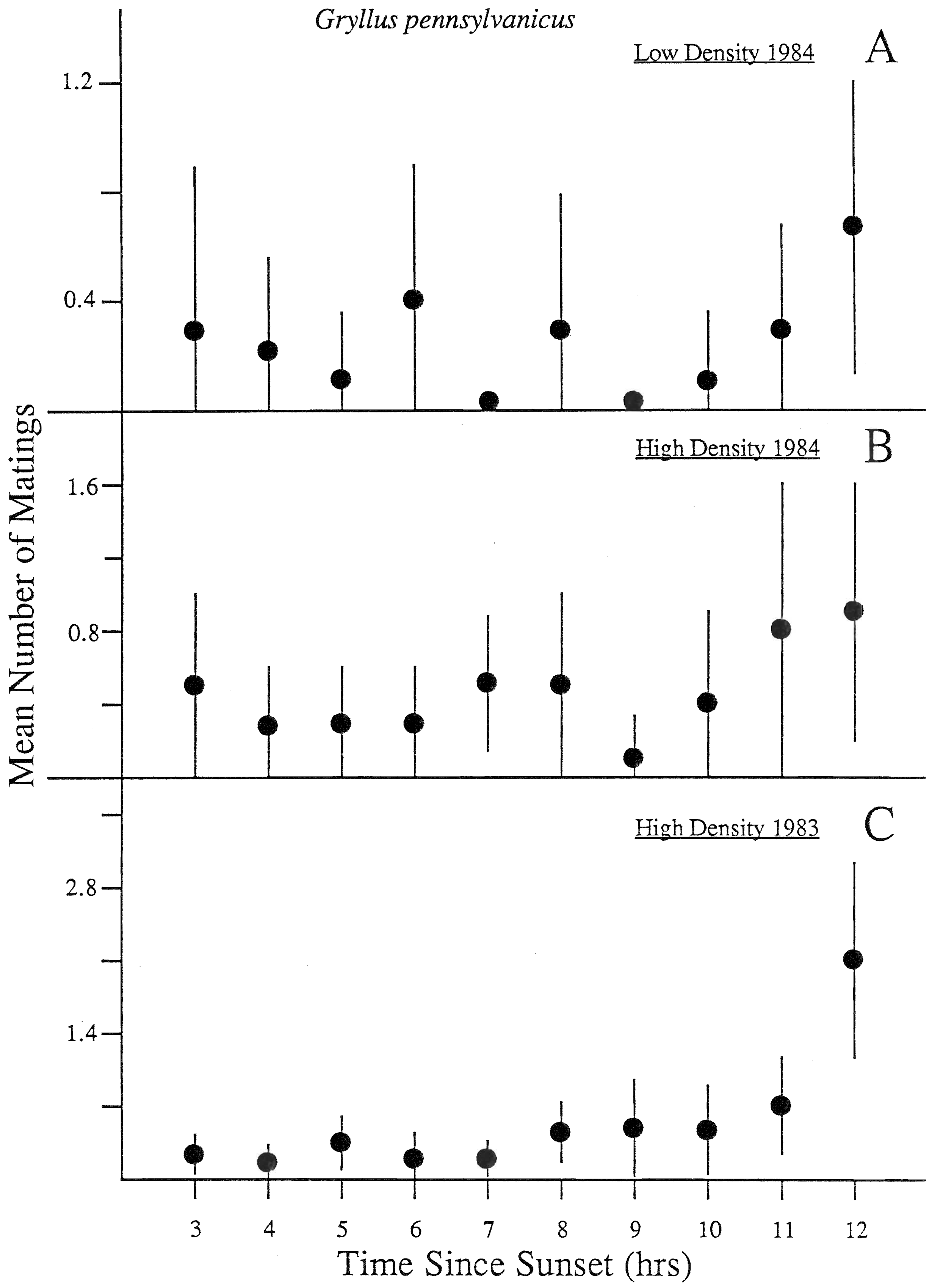

Gryllus veletis
Low Density B 1984
A
Low Density A 1984
B
High Density 1984
C
0.9
0.3
1.0
0.5
2.8
1.4
Mean Number of Matings
2
3
4
5
6
7
8
9
10
11
Time Since Sunset (hrs)

Figure 11a-c. Mean number of matings with time since sunset for *G. pennsylvanicus* at high and low densities (bars indicate 95 % confidence intervals).


Gryllus pennsylvanicus
Low Density 1984
A
1.2
0.4
High Density 1984
B
1.6
0.8
High Density 1983
C
2.8
1.4
Mean Number of Matings
3
4
5
6
7
8
9
10
11
12
Time Since Sunset (hrs)

Calling

Figure 12a-c shows frequency distributions of the ratios of calling duration to time available for calling (termed mean calling score) for *G. veletis* in 1984. The mean calling score for males in the high density was 0.14 (SD = 0.13) per night, whereas the mean calling scores for males in low density A and low density B were 0.22 (SD = 0.15) and 0.17 (SD = 0.12) per night, respectively. There were no significant differences in mean calling score between high density and low density A or between high density and low density B (t = - 1.29, df = 29, P > 0.05; t = - 0.61, df = 30, P > 0.05). Also, there was no significant difference between low density A and low density B in mean calling score (t = 0.60, df = 9, P > 0.05). Figure 13a-c shows frequency distributions of mean calling times for *G. pennsylvanicus* . The mean calling score for males in the 1983 high density sample was 0.10 (SD = 0.11) per night. The mean calling score for males in the 1984 high density sample was 0.15 (SD = 0.12) per night, whereas the mean calling score for males in the low density sample was 0.10 (SD = 0.09) per night. There was no significant difference between 1984 high density and low density sample means (t = 1.12, df = 32, P > 0.05). The sample means for high densities 1983 and 1984 were also non-significant (t = 1.49, df = 49, P > 0.05).

Spatial Displacement

An example of an individual's known movement for one observation night is in Figure 14. This map represents precise measures used in calculating each crickets' nightly displacement. Quadrats 1-5, 10, 15, 20, and 25 were omitted from this representation. The arrows in this Figure are assumed paths of direction, since each cricket could not be followed continuously over the night.

Figure 15a-f shows frequency distributions of the mean distance moved per night for *G. veletis* males and females in 1984. Males in the high density sample moved on average 9.5 (SD = 4.30) m per night, whereas males in low density A and low density B moved on average 10.4 (SD = 5.32) and 10.0 (SD = 8.10) m per night, respectively.

Figure 12a-c. Mean calling score per night for *G. veletis* males at high and low densities.

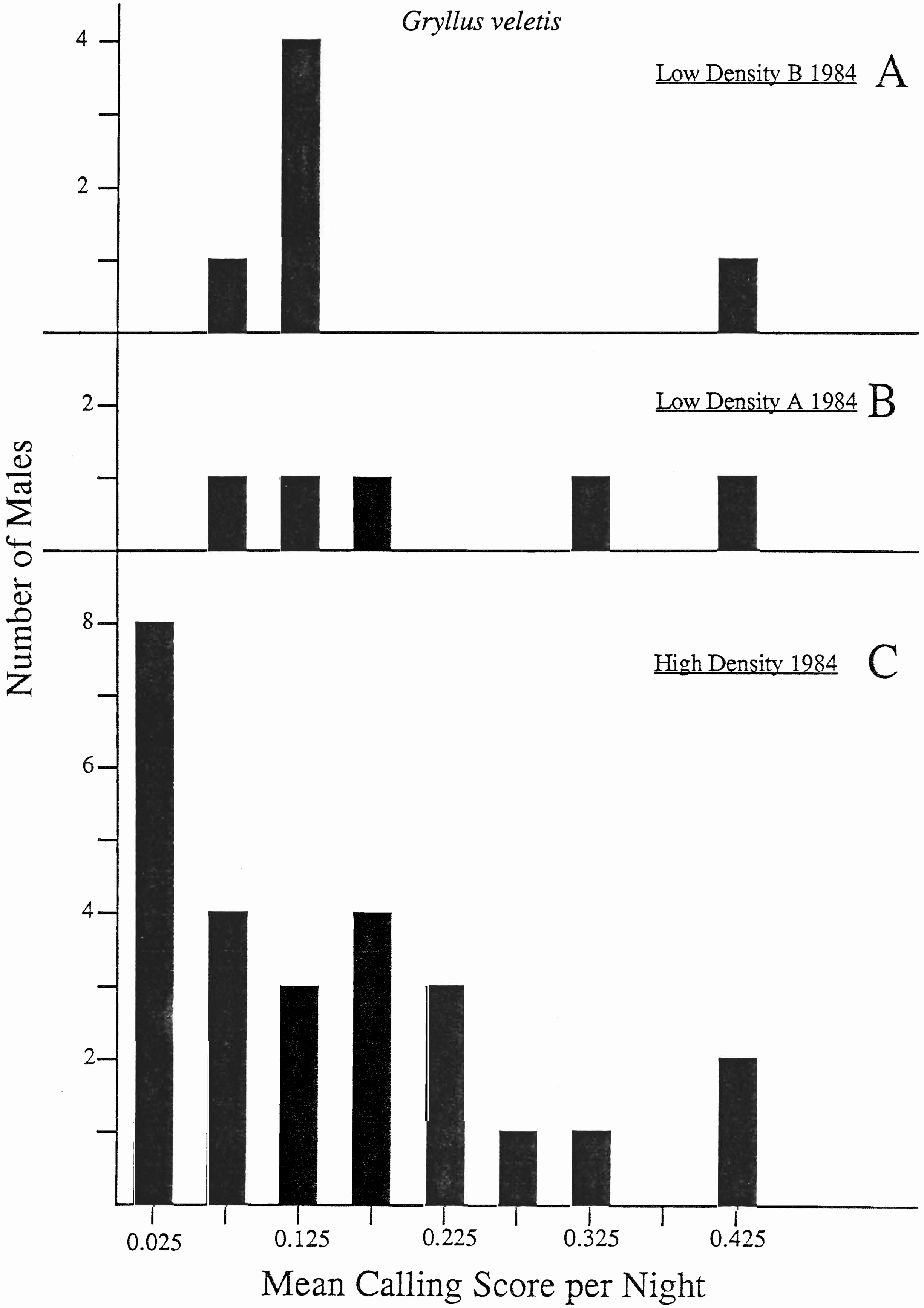

Gryllus veletis
Low Density B 1984
A
Low Density A 1984
B
High Density 1984
C
Number of Males
4
2
2
8
6
4
2
0.025
0.125
0.225
0.325
0.425
Mean Calling Score per Night

Figure 13a-c. Mean calling score per night for *G. pennsylvanicus* males at high and low densities.

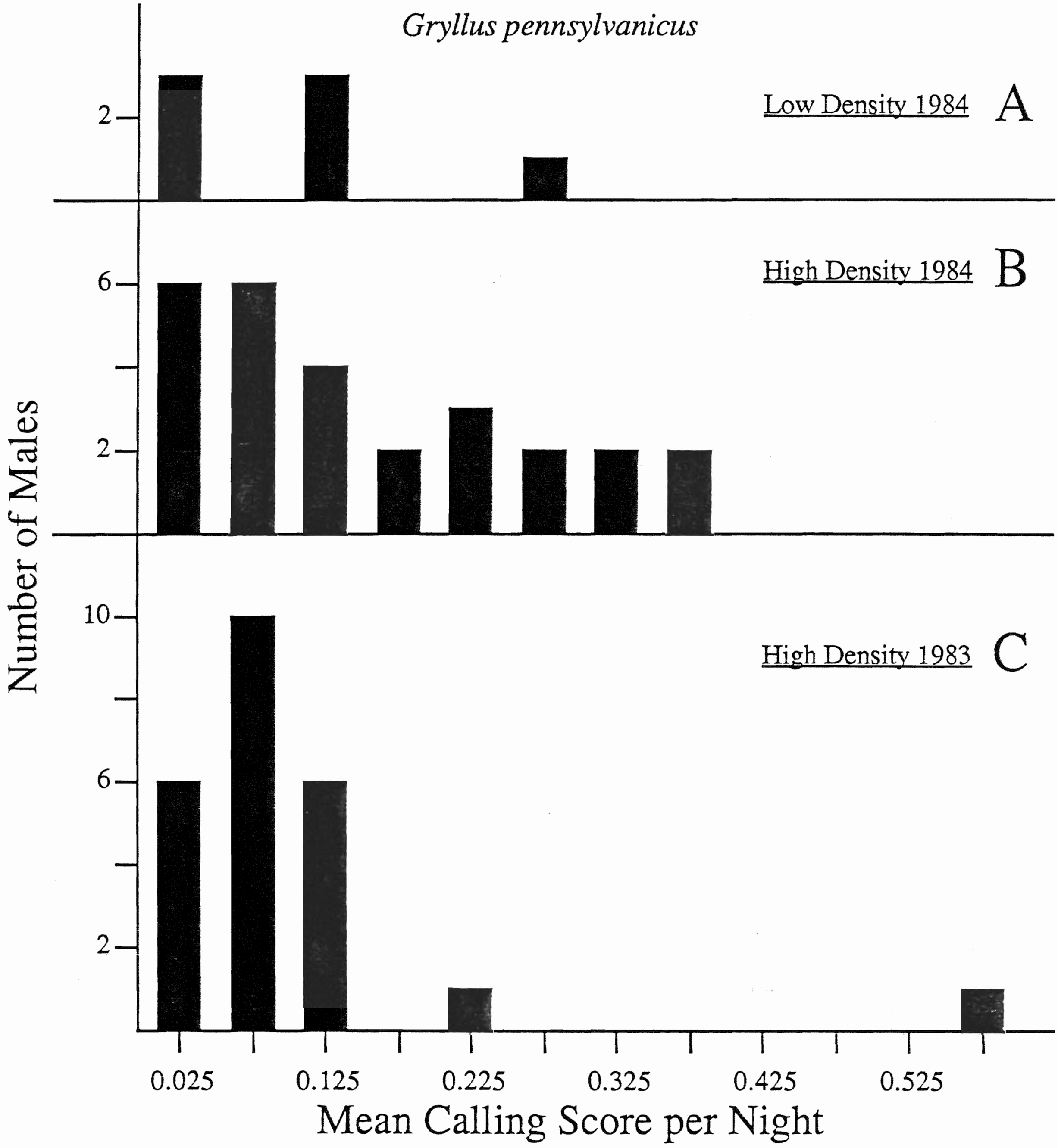

Gryllus pennsylvanicus
Low Density 1984
A
High Density 1984
B
High Density 1983
C
2
6
2
10
6
2
Number of Males
0.025
0.125
0.225
0.325
0.425
0.525
Mean Calling Score per Night

Figure 14. An example of a male's nightly displacement pattern in the outdoor arena. The arrows indicate assumed direction of displacement.

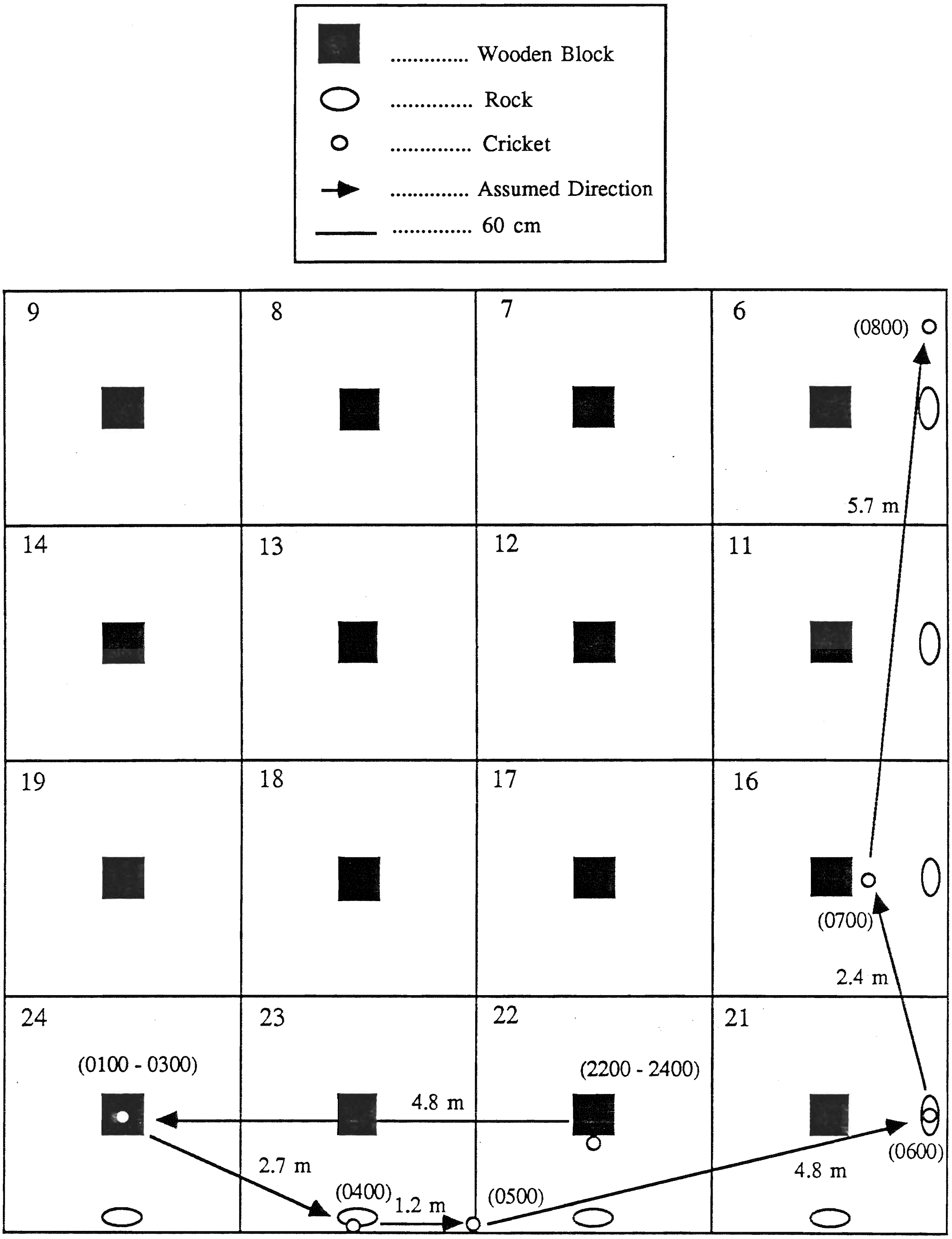
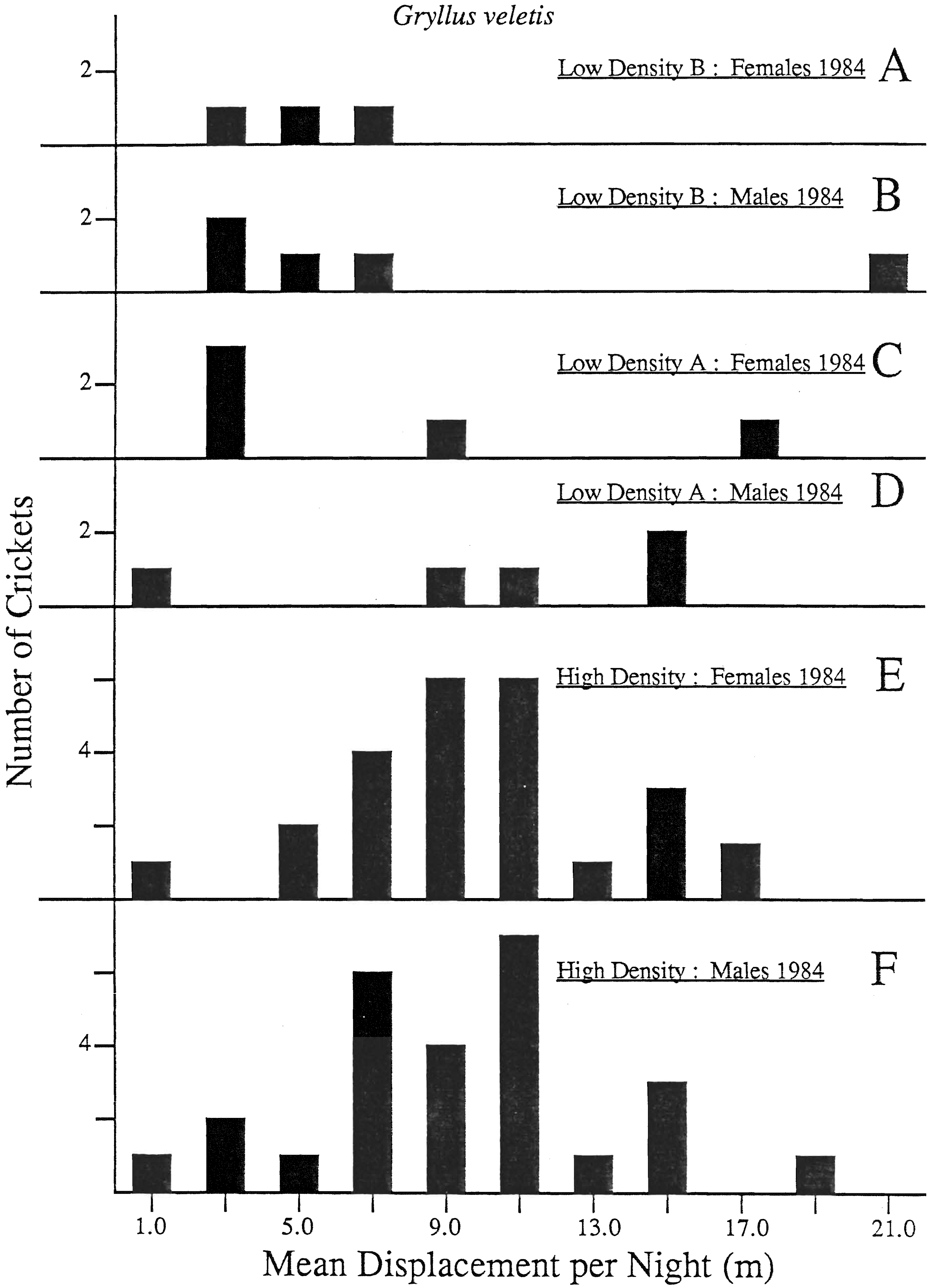

.... Wooden Block
.... Rock
.... Cricket
.... Assumed Direction
.... 60 cm
9
8
7
6
(0800)
5.7 m
14
13
12
11
19
18
17
16
(0700)
2.4 m
24
23
22
21
(0100 - 0300)
(2200 - 2400)
4.8 m
2.7 m
(0400)
1.2 m
(0500)
4.8 m
(0600)

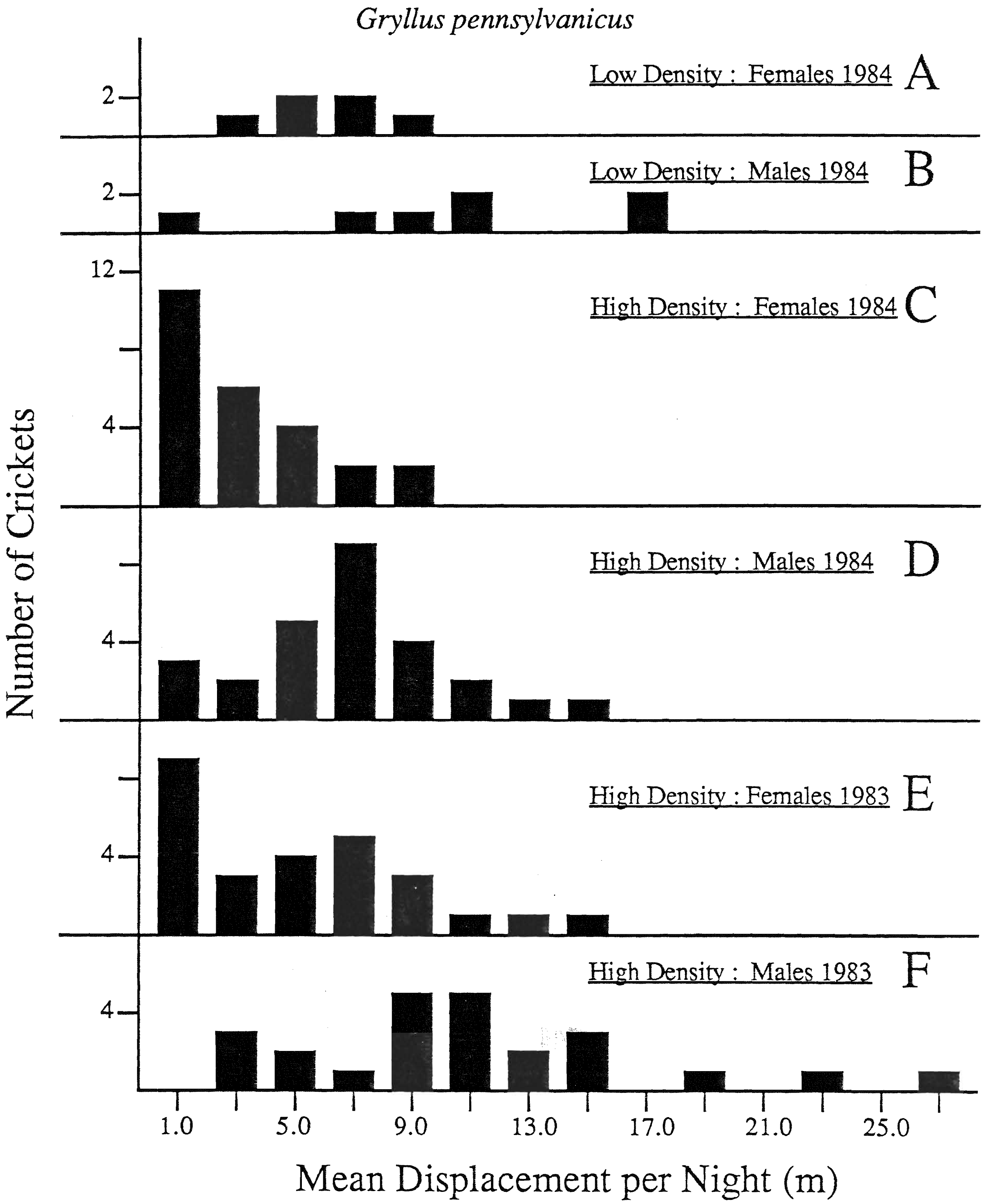
Figure 15a-f. Mean displacement (m) per night for *G. veletis* males and females at high and low densities.


Gryllus veletis
Low Density B : Females 1984
A
Low Density B : Males 1984
B
Low Density A : Females 1984
C
Low Density A : Males 1984
D
High Density : Females 1984
E
High Density : Males 1984
F
2
2
2
2
4
4
Number of Crickets
1.0
5.0
9.0
13.0
17.0
21.0
Mean Displacement per Night (m)

There were no significant differences between mean displacement of males at high density and low density A or low density B (t = - 0.02, df = 29, P > 0.05; t = - 0.46, df = 5.7, P > 0.05), nor a significant difference between low densities (t = - 0.37, df = 9, P > 0.05). Females in the high density sample moved on average 10.0 (SD = 4.04) m per night, whereas females in low density A and low density B moved on average 7.3 (SD = 6.03) and 5.2 (SD = 1.68) m per night, respectively. There were no significant differences between mean displacement of females at high density and low density A or low density B (t = 1.98, df = 26; t = 1.57, df = 24), nor a significant difference between low densities (t = - 0.04, df = 6, P > 0.05). Differences in mean nightly displacement between males and females were not significant for high density, low density A, and low density B populations (t = 0.11, df = 47; t = -1.35, df = 8; t = - 1.06, df = 7, P > 0.05).

The mean displacements for *G. pennsylvanicus* males and females are in Figure 16a-f. Males in the 1983 high density sample moved on average 10.9 (SD = 5.92) m per night. Males in the 1984 high density sample moved on average 6.6 (SD = 3.35) m per night, whereas males in the low density sample moved on average 10.7 (SD = 5.36) m per night. Males at low density moved significantly farther than high density males (t = - 2.34, df = 32, P < 0.05). In addition, the 1983 high density males moved significantly farther than the 1984 high density males (t = - 1.71, df = 49, P < 0.05). Females in the 1983 high density sample moved on average 6.0 (SD = 4.18) m per night. Females in the 1984 high density sample moved on average 3.3 (SD = 2.64) m per night, whereas females in the low density sample moved on average 5.8 (SD = 2.49) m per night. There was a significant difference between the mean displacement of females in 1984 at high density and low density (t = - 3.52, df = 29, P < 0.001), and a significant difference between the 1983 high density and 1984 high density females (t = - 3.88, df = 50, P < 0.0005). Significant differences in mean displacement between males and females were found for the 1983 high density, 1984 high density, and low density populations (t = -3.88, df = 49; t = -5.62, df = 50, P < 0.0005; t = - 2.32, df = 11, P < 0.05).

Figure 16a-f. Mean displacement (m) per night for *G. pennsylvanicus* males and females at high and low densities.


Gryllus pennsylvanicus
Low Density : Females 1984 A
Low Density : Males 1984 B
High Density : Females 1984 C
High Density : Males 1984 D
High Density : Females 1983 E
High Density : Males 1983 F
Number of Crickets
2
2
12
4
4
4
4
1.0
5.0
9.0
13.0
17.0
21.0
25.0
Mean Displacement per Night (m)

Matings

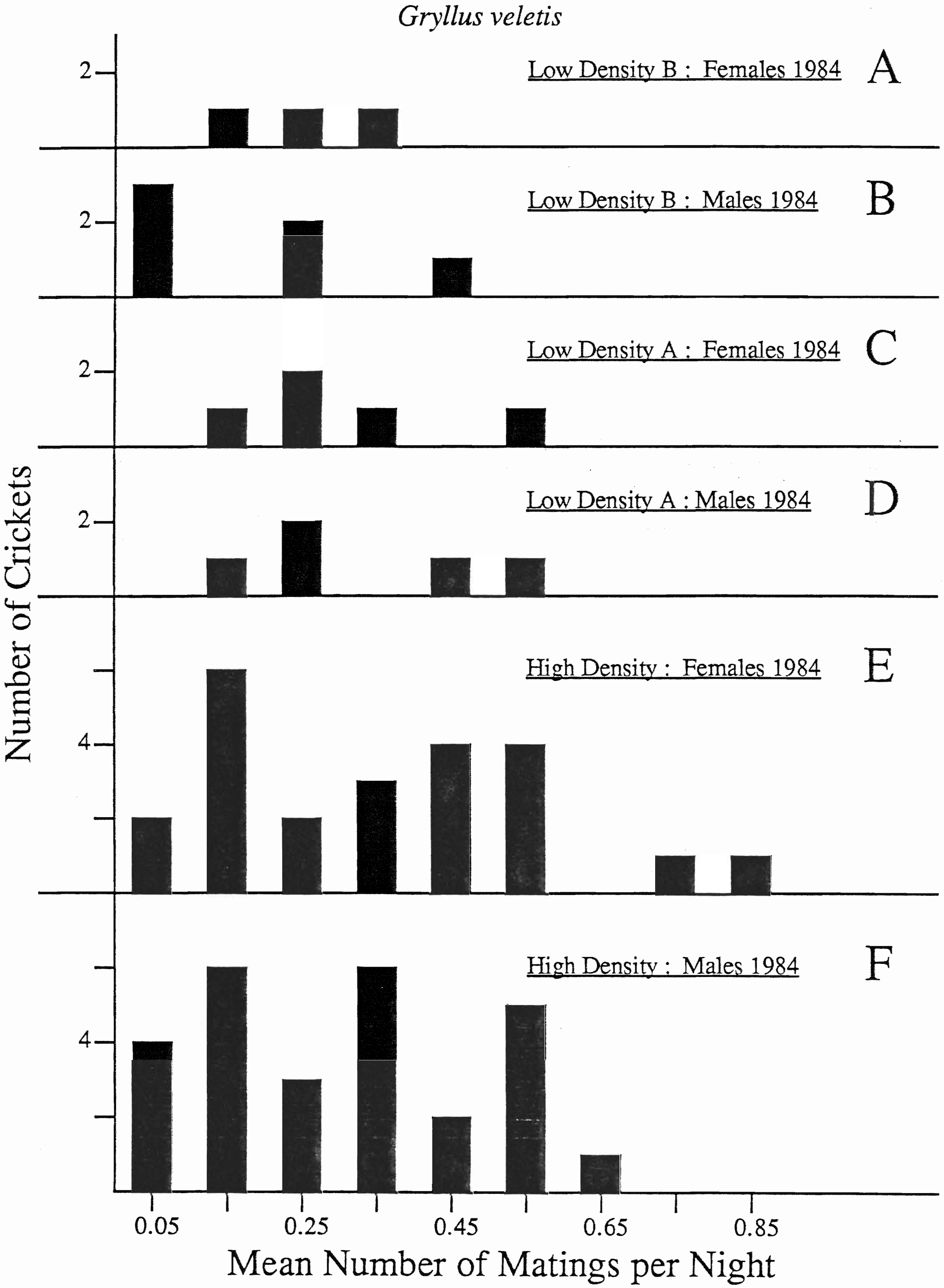
The mean number of matings per night for *G. veletis* males and females in 1984 are in Figure 17a-f. Males in the high density sample mated on average 0.26 (SD = 0.18) times per night, whereas males in low density A and low density B mated on average 0.28 (SD = 0.16) and 0.15 (SD = 0.18) times per night, respectively. Females in the high density mated on average 0.31 (SD = 0.22) times per night, whereas females in low density A and low density B mated on average 0.29 (SD = 0.22) and 0.20 (SD = 0.10) times per night, respectively. The mean number of matings did not vary significantly between densities for males (t = 0.31, df = 29; t = - 1.52, df = 30; t = 1.49, df = 9, P > 0.05) or females (t = 0.14, df = 26; t = 0.69, df = 24; t = 0.52, df = 6, P > 0.05).

Figure 18a-f shows the mean number of matings per night for *G. pennsylvanicus* males and females. Males in the 1983 high density sample mated on average 0.25 (SD = 0.21) times per night. Males in the 1984 high density sample mated on average 0.24 (SD = 0.26) times per night, whereas males in the low density sample mated on average 0.40 (SD = 0.43) times per night. Females in the 1983 high density sample mated on average 0.34 (SD = 0.22) times per night. Females in the 1984 high density sample mated on average 0.23 (SD = 0.21) times per night, whereas females in the low density sample mated on average 0.47 (SD = 0.40) times per night. No significant differences were found between mean number of matings for males in the1983 and 1984 high density or between the 1984 high density and low density males (t = - 0.20, df = 49; t = 1.25, df = 32, P > 0.05). No significant differences were found between mean number of matings for females in the 1983 and 1984 high densities or between the 1984 high density and low density females (t = 1.31, df = 50; t = - 1.46, df = 5.7, P > 0.05).

Age and Calling

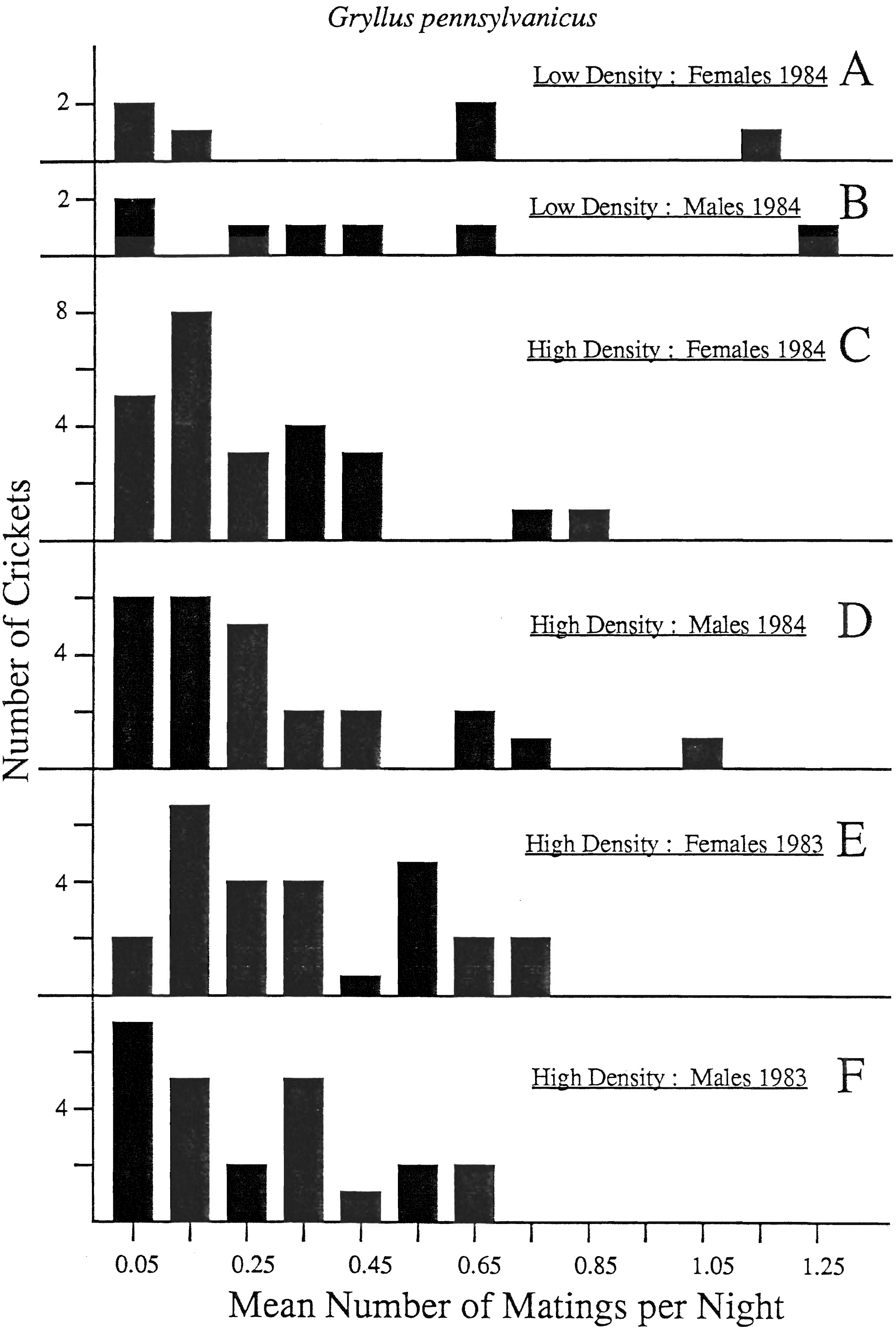
Behavioral variation was also analyzed with respect to different times of adult life. To determine the effects of relative age on the variables each sample was split equally and the resulting values were assessed for significant differences with paired t-tests. Relatively

Figure 17a-f. Mean number of matings per night for *G. veletis* males and females at high and low densities.



Gryllus veletis
Low Density B : Females 1984
A
Low Density B : Males 1984
B
Low Density A : Females 1984
C
Low Density A : Males 1984
D
High Density : Females 1984
E
High Density : Males 1984
F
2
2
2
2
4
4
Number of Crickets
0.05
0.25
0.45
0.65
0.85
Mean Number of Matings per Night

Figure 18a-f. Mean number of matings per night for *G. pennsylvanicus* males and females at high and low densities.


Gryllus pennsylvanicus
Low Density : Females 1984 A
Low Density : Males 1984 B
High Density : Females 1984 C
High Density : Males 1984 D
High Density : Females 1983 E
High Density : Males 1983 F
2
2
8
4
4
4
4
Number of Crickets
0.05
0.25
0.45
0.65
0.85
1.05
1.25
Mean Number of Matings per Night

young crickets represent the first half of arena observations, whereas relatively old crickets represent the second half of arena observations. Individual crickets whose means could not be calculated for both catagories were omitted from the analysis. The average ages for males and females entering the arena are in Table XII in the appendix. The effects of relative age on mean calling scores for *G. veletis* and *G. pennsylvanicus* males are in Table 1. For *G. veletis*, the mean calling scores for relatively young and old males in the high density population were 0.15 (SD = 0.13) and 0.10 (SD = 0.13) per night, respectively. The mean calling scores for relatively young and old males in the low density A population were 0.20 (SD = 0.18) and 0.24 (SD = 0.24) per night, whereas the mean calling scores for relatively young and old males in low density B population were 0.19 (SD = 0.19) and 0.21 (SD = 0.12) per night. Males called significantly less with age in the high density population ($t = 1.93$, $df = 15$, $P < 0.05$). The mean calling scores for males in low density A and low density B did not change significantly with age ($t = 1.02$, $df = 4$; $t = -0.36$, $df = 3$, $P > 0.05$).

For *G. pennsylvanicus*, the mean calling scores for relatively young and old males in the 1983 high density population were 0.08 (SD = 0.10) and 0.14 (SD = 0.16) per night, whereas the mean calling scores for relatively young and old males in the 1984 high density population were 0.19 (SD = 0.14) and 0.15 (SD = 0.12) per night. The mean calling scores for relatively young and old males in the low density population were 0.22 (SD = 0.18) and 0.07 (SD = 0.05) per night, respectively. Males in the 1983 high density populations called significantly more with age ($t = -2.83$, $df = 17$, $P < 0.01$), whereas males in the 1984 high density population called significantly less with age ($t = 2.59$, $df = 17$, $P < 0.01$). Male calling scores did not change significantly with age in the 1984 low density population ($t = 1.92$, $df = 3$, $P > 0.05$).

Age and Spatial Displacement

The effects of relative age on mean nightly displacement for *G. veletis* males and females are in Table 2. In the high density population relatively young and old males

Table 1. Effects of relative age on calling behavior of *G. veletis* and *G. pennsylvanicus* males for each sample. The differences between mean calling scores ($\bar{x}$ ± SD) for relative young and old males were assessed with paired t-tests. Data for young individuals are from the first half of arena observations and data for old individuals are from the last half of arena observations. Degrees of freedom (df) and significance levels (P) are given.

Species	Density	Young $\bar{x}$ ± SD	Old $\bar{x}$ ± SD	Paired t	df	P
G. v.	High	0.15 ± 0.13	0.10 ± 0.13	1.93	15	< 0.05
	Low A	0.20 ± 0.18	0.24 ± 0.13	1.02	4	> 0.05
	Low B	0.19 ± 0.19	0.21 ± 0.12	- 0.36	3	> 0.05
G. p.	High 83	0.08 ± 0.10	0.14 ± 0.16	- 2.83	17	< 0.01
	High 84	0.19 ± 0.14	0.15 ± 0.12	2.59	17	< 0.01
	Low 84	0.22 ± 0.18	0.07 ± 0.05	1.92	3	> 0.05

Table 2. Effects of relative age on displacement behavior of *G. veletis* and *G. pennsylvanicus* males (M) and females (F) for each sample. The differences between mean displacements ($\bar{x}$ ± SD) for relative young and old males and females were assessed with paired t-tests. Data for young individuals are from the first half of arena observations and data for old individuals are from the last half of arena observations. Degrees of freedom (df) and significance levels (P) are given.

Species	Density	Sex	Young $\bar{x}$ ± SD	Old $\bar{x}$ ± SD	Paired t	df	P
G. v.	High	M	9.83 ± 4.53	7.04 ± 4.12	1.79	15	< 0.05
		F	12.49 ± 6.14	8.47 ± 4.85	2.03	14	< 0.05
	Low A	M	11.21 ± 7.17	9.61 ± 6.73	0.19	4	> 0.05
		F	3.35 ± 3.07	10.77 ± 10.32	- 5.83	4	< 0.01
	Low B	M	9.70 ± 5.08	8.09 ± 9.98	1.23	3	> 0.05
		F	2.55 ± 1.65	7.74 ± 1.86	- 6.82	2	< 0.05
G. p.	High 83	M	18.59 ± 8.78	5.60 ± 4.40	6.54	17	< 0.01
		F	9.02 ± 5.76	5.15 ± 4.03	1.38	18	< 0.01
	High 84	M	7.57 ± 4.68	7.07 ± 3.89	- 0.24	17	> 0.05
		F	2.15 ± 1.98	2.31 ± 2.84	- 0.22	15	> 0.05
	Low 84	M	15.33 ± 3.54	12.87 ± 3.06	- 1.70	3	> 0.05
		F	2.63 ± 1.46	7.07 ± 3.55	2.97	4	< 0.05

moved on average 9.7 (SD = 4.53) and 7.0 (SD = 4.12) m per night, whereas relatively young and old males in low density A and low density B moved on average 11.2 (SD = 7.17), 9.6 (SD = 6.73), 9.7 (SD = 5.08), and 8.1 (SD = 9.99) m per night, respectively. Males moved significantly less with age in the high density population ($t = 1.79$, $df = 15$, $P < 0.05$), but no significant differences in mean displacements with age for males in low density A or low density B populations ($t = 0.19$, $df = 4$; $t = 1.23$, $df = 3$, $P > 0.05$).

In the high density population relatively young and old females moved on average 12.5 (SD = 6.14) and 8.5 (SD = 4.85) m per night, whereas relatively young and old females in low density A and low density B moved on average 3.4 (SD = 3.07), 10.8 (SD = 10.32), 2.6 (SD = 1.65), and 7.7 (SD = 1.86) m per night, respectively. Females in the high density population moved significantly less with age ($t = 2.03$, $df = 14$, $P < 0.01$), whereas females moved significanltly more with age in tlow density A and low density B populations ($t = - 5.83$, $df = 4$; $t = - 6.82$, $df = 2$, $P < 0.05$).

The effects of relative age on mean nightly displacement for *G. pennsylvanicus* males and females are in Table 2. In the 1983 high density population relatively young and old males moved on average 18.6 (SD = 8.79) and 5.6 (SD = 4.40) m per night, whereas relatively young and old males in the 1984 high density and low density moved on average 7.6 (SD = 4.68), 7.6 (SD = 3.62), 15.3 (SD = 3.54), and 12.9 (SD = 3.06) m per night, respectively. Males in the 1983 high density population moved significantly less with age ($t = 6.54$, $df = 17$, $P < 0.01$), but movement for males in the 1984 high density and low density populations did not change significantly with age ($t = - 0.24$, $df = 17$; $t = 1.70$, $df = 3$, $P > 0.05$). In the 1983 high density population relatively young and old females moved on average 9.0 (SD = 5.76) and 5.2 (SD = 4.03) m per night, whereas relatively young and old females in the 1984 high density and low density moved on average 1.2 (SD = 1.05), 1.3 (SD = 1.34), 1.3 (SD = 0.64), and 3.8 (SD = 1.76) m per night, respectively. Females in the 1983 high density population moved significantly less with age ($t = 1.38$, $df = 18$, $P < 0.01$), whereas females in the 1984 low density population moved significantly more with age (t = 2.97, df = 4, P < 0.05). Movement for females in the 1984 high density population did not change significantly with age (t = - 0.22, df = 15, P > 0.05).

Age and Mating

The effects of relative age on mean number of matings for *G. veletis* males and females are in Table 3. In the high density population relatively young and old males mated on average 0.34 (SD = 0.20) and 0.24 (SD = 0.20) times per night. Relatively young and old males in low density A mated on average 0.36 (SD = 0.39) and 0.20 (SD = 0.14) times per night, whereas relatively young and old males in low density B mated on average 0.19 (SD = 0.24) and 0.10 (SD = 0.12) times per night, respectively. Males in the high density population mated significantly less with age (t = 1.90, df = 15, P < 0.05), but the frequency of mating did not change significantly with age for males in low density A or low density B populations (t = 0.45, df = 4; t = 1.22, df = 3, P > 0.05). In the high density population relatively young and old females mated on average 0.33 (SD = 0.28) and 0.27 (SD = 0.25) times per night. Relatively young and old females in low density A mated on average 0.41 (SD = 0.51) and 0.20 (SD = 0.14) times per night, whereas relatively young and old females in low density B mated on average 0.13 (SD = 0.12) and 0.27 (SD = 0.31) times per night, respectively. The frequency of mating did not change significantly with age for females in the high density, low density A, and low density B populations (t = 0.66, df = 14; t = 0.83, df = 4; t = - 0.26, df = 2, P > 0.05).

The effects of relative age on the mean number of matings for *G. pennsylvanicus* males and females are in Table 3. In the 1983 high density population relatively young and old males mated on average 0.17 (SD = 0.18) and 0.42 (SD = 0.34) times per night, whereas relatively young and old males in the 1984 high density population mated on average 0.20 (SD = 0.25) and 0.30 (SD = 0.29) times per night, respectively. Relatively young and old males in the low density population mated on average 0.73 (SD = 0.22) and 0.63 (SD = 0.75) times per night. Males in the 1983 high density population mated significantly more with age (t = - 2.79, df = 17, P < 0.05), but the frequency of mating did

Table 3. Effects of relative age on mean number of matings for *G. veletis* and *G. pennsylvanicus* males (M) and females (F) for each sample. The differences between mean number of matings ($\bar{x}$ ± SD) for relative young and old males and females were assessed with paired t-tests. Data for young individuals are from the first half of arena observations and data for old individuals are from the last half of arena observations. Degrees of freedom (df) and significance levels (P) are given.

Species	Density	Sex	Young $\bar{x} \pm$ SD	Old $\bar{x} \pm$ SD	Paired t	df	P
G. v.	High	M	0.34 ± 0.21	0.24 ± 0.20	1.90	15	< 0.05
		F	0.33 ± 0.28	0.27 ± 0.25	0.66	14	> 0.05
	Low A	M	0.36 ± 0.38	0.20 ± 0.14	0.45	4	> 0.05
		F	0.41 ± 0.51	0.20 ± 0.14	0.83	4	> 0.05
	Low B	M	0.19 ± 0.24	0.10 ± 0.12	1.22	3	> 0.05
		F	0.13 ± 0.12	0.27 ± 0.31	- 0.26	2	> 0.05
G. p.	High 83	M	0.17 ± 0.18	0.42 ± 0.34	- 2.79	17	< 0.01
		F	0.22 ± 0.22	0.38 ± 0.22	- 1.96	18	< 0.05
	High 84	M	0.20 ± 0.25	0.30 ± 0.29	- 1.27	17	> 0.05
		F	0.25 ± 0.30	0.28 ± 0.32	- 0.33	15	> 0.05
	Low 84	M	0.73 ± 0.22	0.63 ± 0.75	- 0.21	3	> 0.05
		F	0.40 ± 0.24	0.50 ± 0.87	- 0.27	4	> 0.05

not change significantly with age for males in the 1984 high density or low density populations ($t = -0.33$, $df = 15$; $t = -0.27$, $df = 4$, $P > 0.05$). In the 1983 high density population relatively young and old females mated on average 0.22 (SD = 0.22) and 0.38 (SD = 0.22) times per night, whereas relatively young and old females in the 1984 high density mated on average 0.25 (SD = 0.30) and 0.28 (SD = 0.32) times per night, respectively. Relatively young and old females in the low density population mated on average 0.40 (SD = 0.24) and 0.50 (SD = 0.87) times per night. Females in the 1983 high density population mated significantly more with age ($t = -1.96$, $df = 18$, $P < 0.05$), but the frequency of mating did not change significantly with age for females in the 1984 high density and low density populations ($t = -0.33$, $df = 15$; $t = -0.27$, $df = 4$, $P > 0.05$).

RELATIONSHIPS BETWEEN VARIABLES

The parametric correlation coefficients between phenotypic characters for *G. veletis* and *G. pennsylvanicus* males at each density are in Table 4. There was a significant negative correlation between mean nightly displacement and individual weight for *G. veletis* males in the high density population ($r = -0.41$, $P < 0.05$; $y = -4.10x + 28.74$). In addition, a significant negative correlation was found between mean calling score and mean nightly displacement for *G. veletis* males in the low density A population ($r = -0.94$, $P < 0.05$; $y = -0.52x + 3.60$). There were no significant correlations found between any characters at any density for *G. pennsylvanicus* males.

Correlation analyses were used to assess the relationships between phenotypic characters and mating success. Figure 19a-c shows the mean number of matings compared with mean calling score for *G. veletis* males in 1984. The mean number matings did not change significantly with increase calling in the high density, low density A, or low density B populations ($r = 0.27$; $r = -0.07$; $r = -0.52$, $P > 0.05$). The mean number of matings compared with mean calling scores for *G. pennsylvanicus* are in Figure 20a-c. There were no significant correlations at high density for 1983 and 1984 ($r = 0.19$; $r = 0.05$, $P >$

Table 4. Parametric correlation coefficients between mean calling score, mean displacement (Displ.), and individual weight for *G. veletis* and *G. pennsylvanicus* for each sample.

	Gryllus veletis			*Gryllus pennsylvanicus*		
Variables	High	Low A	Low B	High 83	High	Low
Calling - Displ.	0.01	- 0.94*	- 0.32	- 0.06	0.30	0.72
Calling - Weight	0.03	0.49	0.72	0.34	0.23	0.03
Displ. - Weight	- 0.41*	- 0.49	- 0.06	0.12	0.09	0.19

*P < 0.05

Figure 19a-c. The relationships between mean number of matings and mean calling scores for *G. veletis* males at high and low densities.

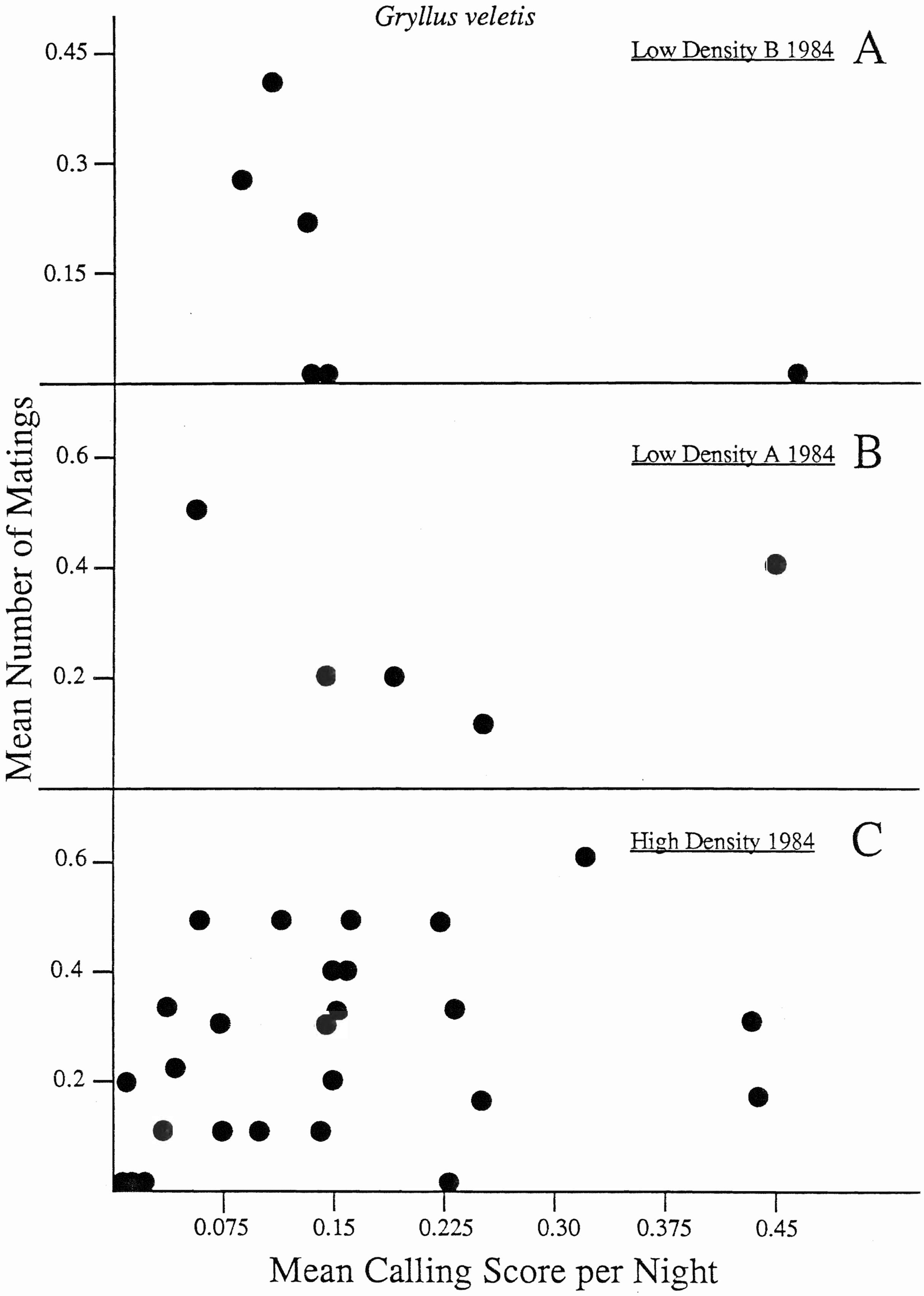
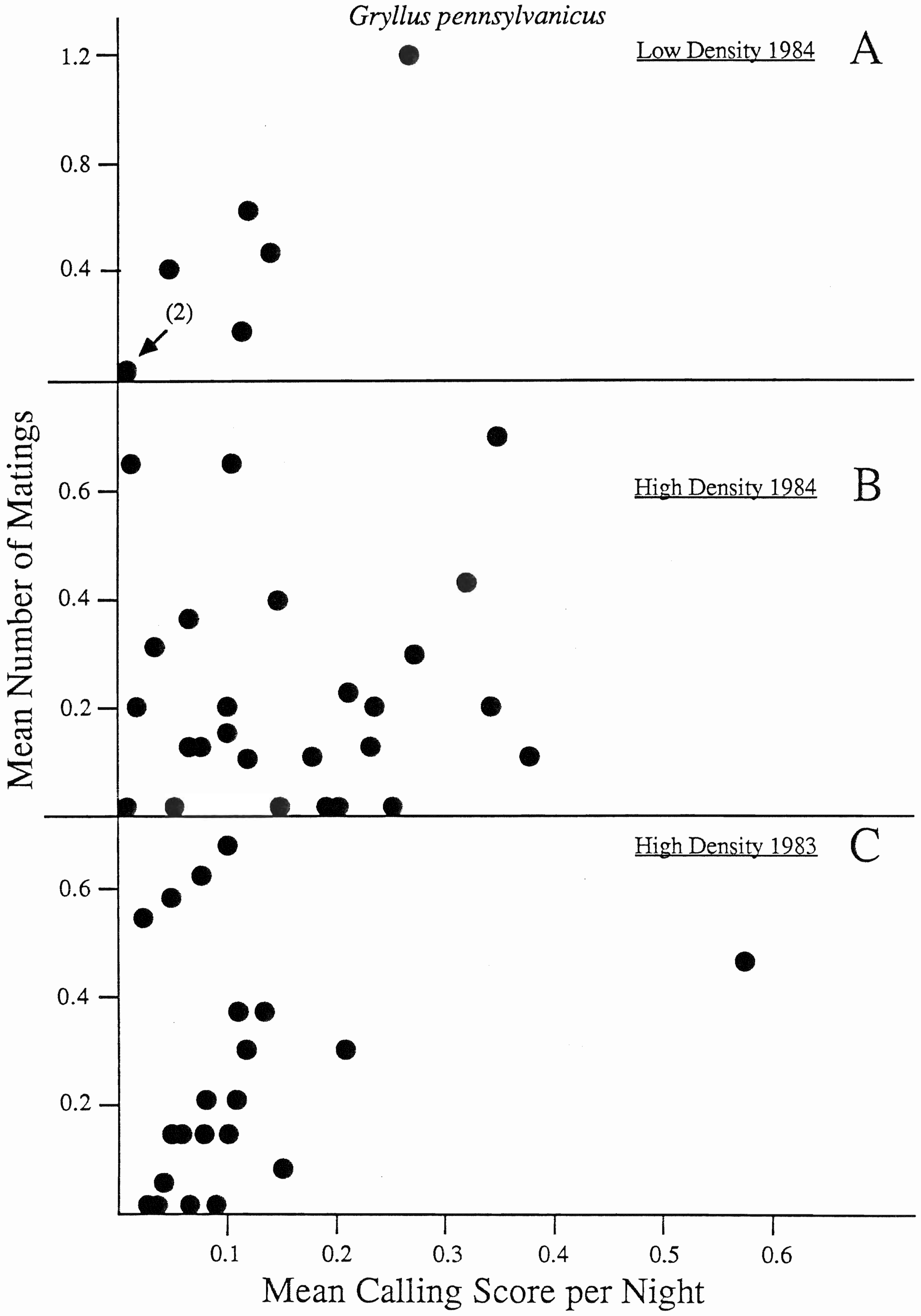

Gryllus veletis
Low Density B 1984
A
0.45
0.3
0.15
Low Density A 1984
B
0.6
0.4
0.2
High Density 1984
C
0.6
0.4
0.2
0.075
0.15
0.225
0.30
0.375
0.45
Mean Number of Matings
Mean Calling Score per Night

Figure 20a-c. The relationships between mean number of matings and mean calling scores for *G. pennsylvanicus* males at high and low densities.


Gryllus pennsylvanicus
Low Density 1984
A
High Density 1984
B
High Density 1983
C
(2)
1.2
0.8
0.4
0.6
0.4
0.2
0.6
0.4
0.2
Mean Number of Matings
0.1
0.2
0.3
0.4
0.5
0.6
Mean Calling Score per Night

0.05). However, a significant positive correlation was found at low density ($r = 0.92$, $P < 0.01$; $y = 0.45x - 0.02$).

Figure 21a-c shows the mean number of matings compared with mean displacement for *G. veletis* males in 1984. No significant correlations were found at high density, low density A, or low density B ($r = 0.35$; $r = - 0.18$; $r = - 0.12$, $P > 0.05$). Similarily, no significant correlations were found for *G. pennsylvanicus* at high densities 1983, 1984, and low density ($r = 0.04$; $r = 0.14$; $r = 0.73$, $P > 0.05$) as shown in Figure 22a-c.

Individual weights for crickets are in Tables VII and VIII in the appendix. These values were transformed and used in the analysis. The relationships between individual male weight and mean number of matings for *G. veletis* in 1984 are in Figure 23a-c. There were no correlations found for high density and low density A ($r = 0.10$; $r = 0.04$, $P > 0.05$). At low density B, however, an inverse relationship between mean number of matings and individual weight was found ($r = - 0.87$, $P < 0.05$). Figure 24a-c shows the relationships for *G. pennsylvanicus* males. No correlations between mean number of matings and individual weight were found for the 1983 high density and 1984 low density populations ($r = - 0.37$; $r = - 0.20$, $P > 0.05$). At high density 1984, however, a positive correlation betweeen the variables was obtained ($r = 0.40$, $P < 0.05$; $y = 0.31x - 1.75$).

INTENSITY OF SELECTION

The intensities of selection (s') and directional selection gradients (ß') were calculated to identify the male phenotypic characters under significant selection pressures. Significant levels for the selection intensities were assessed by the parametric correlation coefficient (r), while significant levels for the selection gradients were assessed with t-tests (see Methods).

The selection intensities and directional selection gradients operating on calling duration, movement, and individual weight are given in Table 5 for *G. veletis*. At high density the intensity of selection acting directly on movement was positive and significant ($t = 2.29$, $P < 0.05$). In the low density A population, no significant force of selection was

Figure 21a-c. The relationships between mean number of matings and mean displacement (m) for *G. veletis* males at high and low densities.

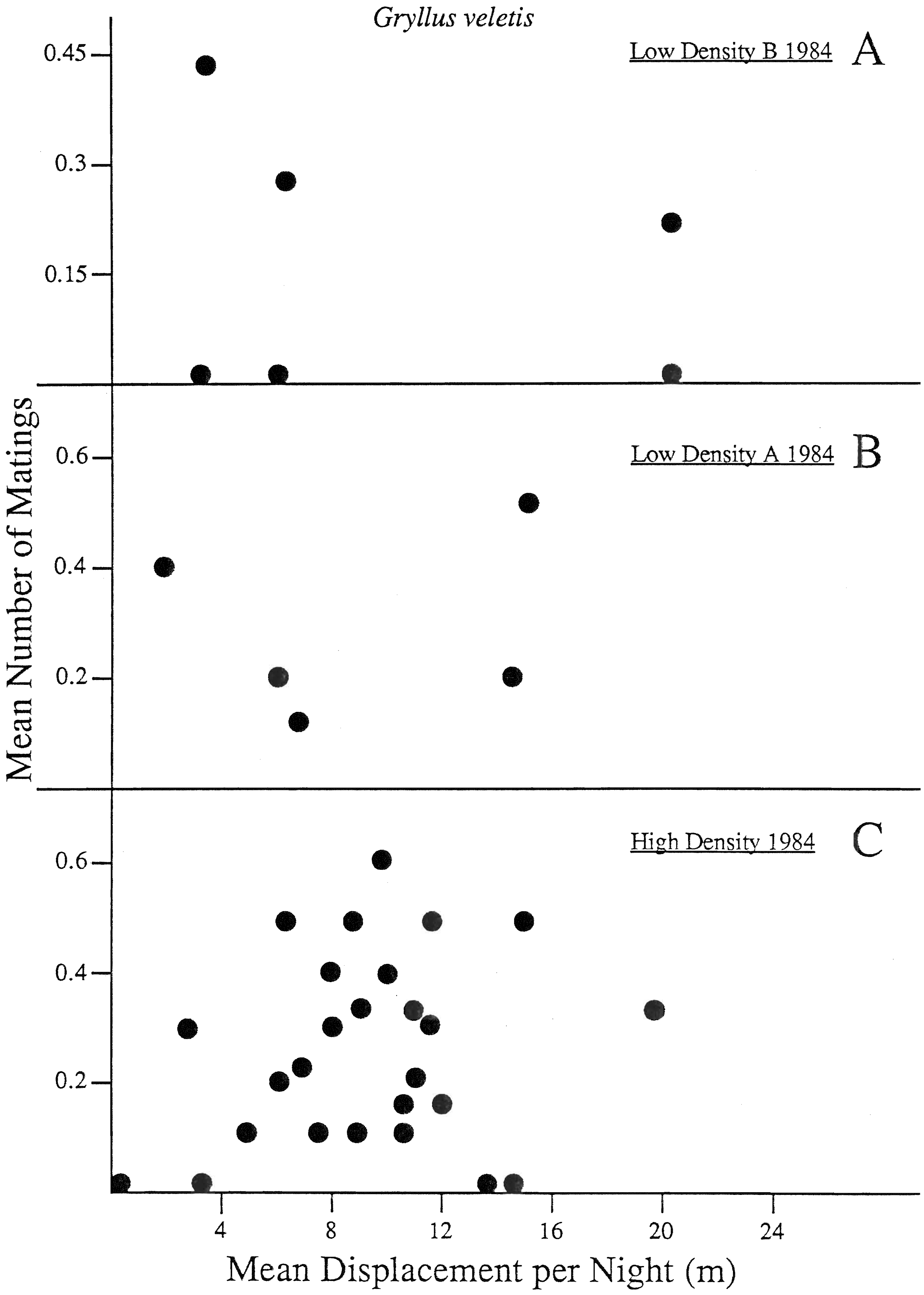

Gryllus veletis
Low Density B 1984
A
0.45
0.3
0.15
Low Density A 1984
B
0.6
0.4
0.2
High Density 1984
C
0.6
0.4
0.2
Mean Number of Matings
4
8
12
16
20
24
Mean Displacement per Night (m)

Figure 22a-c. The relationships between mean number of matings and mean displacement (m) for *G. pennsylvanicus* males at high and low densities.

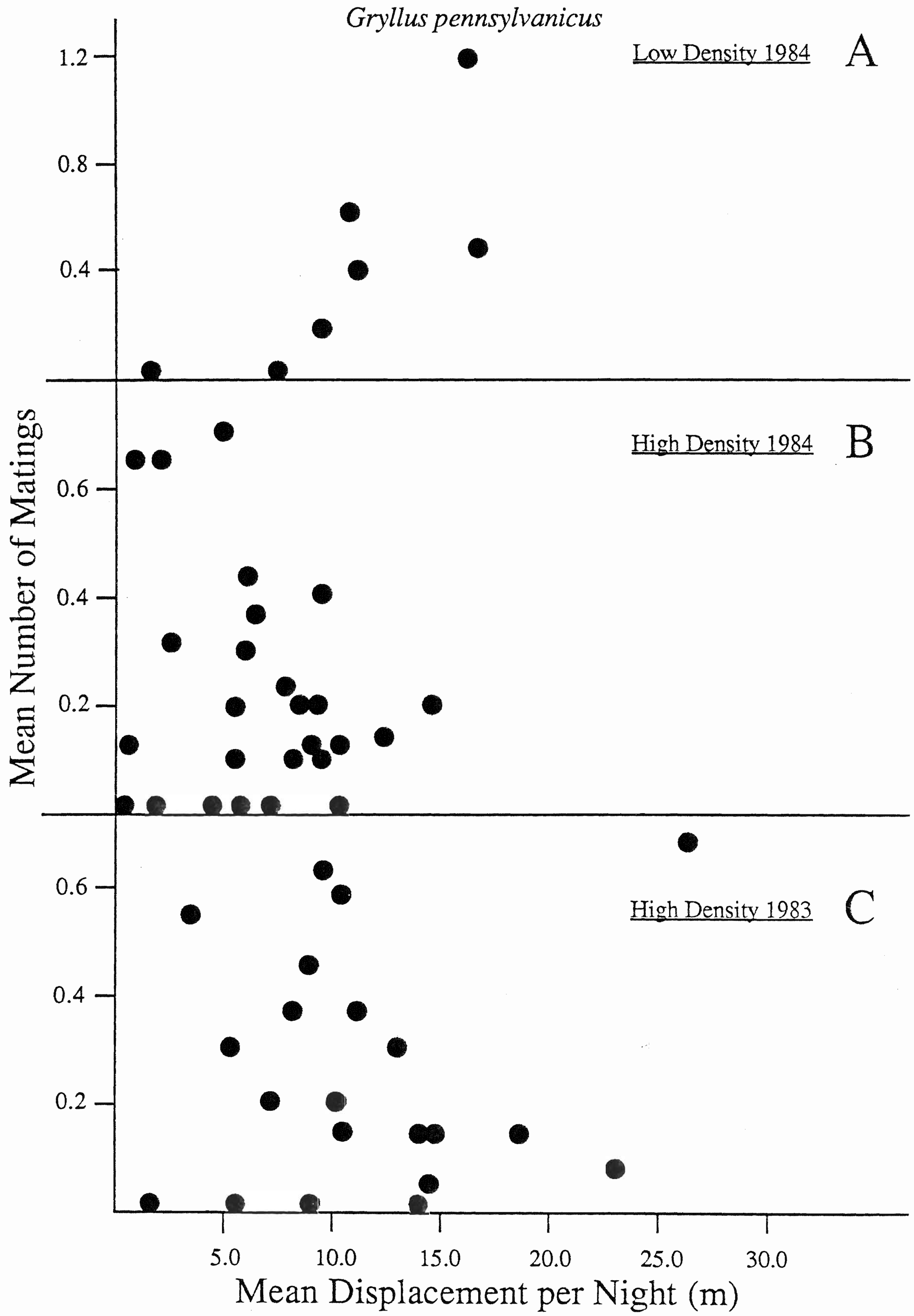

Gryllus pennsylvanicus
Low Density 1984
A
High Density 1984
B
High Density 1983
C
Mean Number of Matings
1.2
0.8
0.4
0.6
0.4
0.2
0.6
0.4
0.2
5.0
10.0
15.0
20.0
25.0
30.0
Mean Displacement per Night (m)

Figure 23a-c. The relationships between mean number of matings and individual weight (mg) for *G. veletis* males at high and low densities.

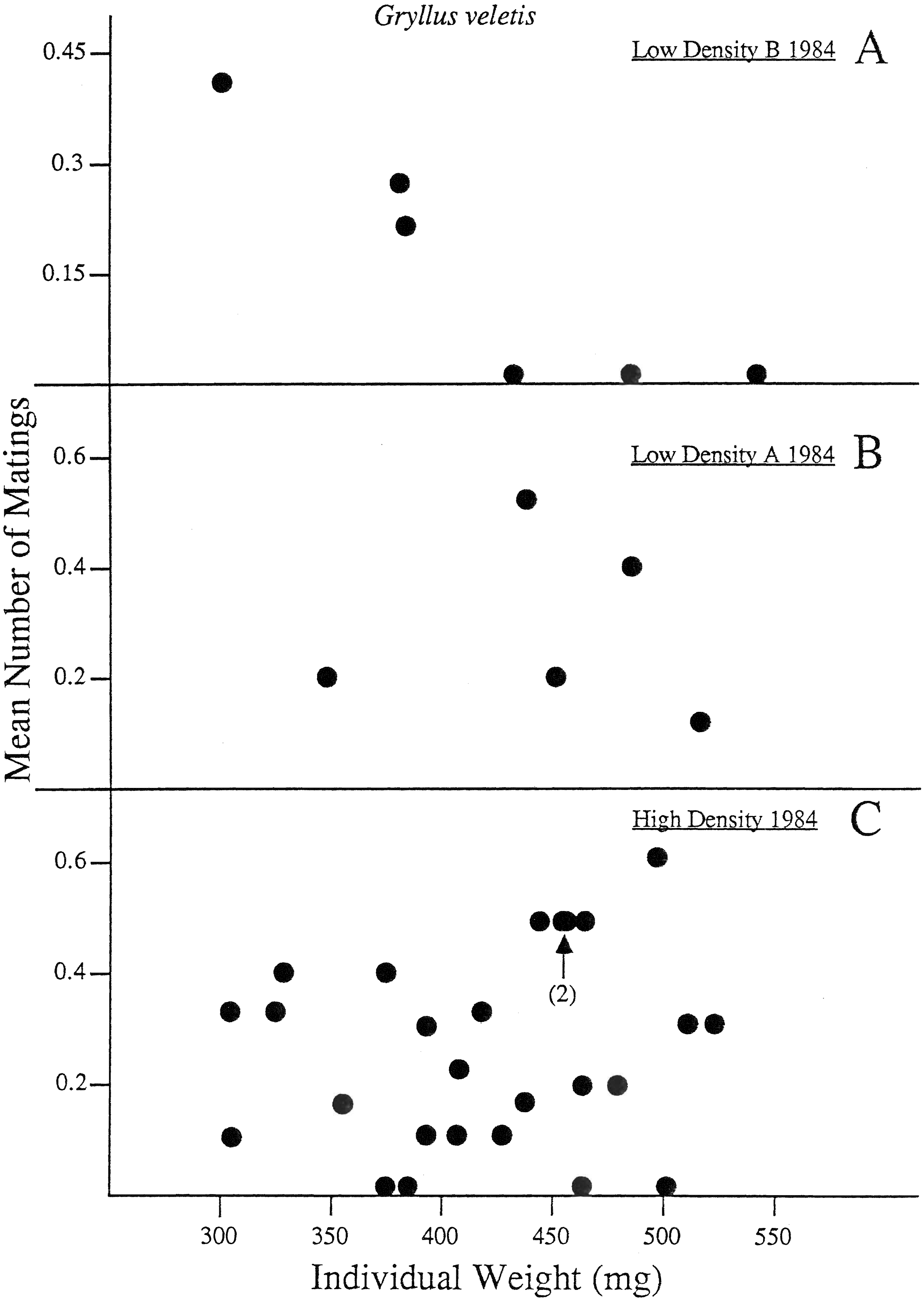

Gryllus veletis
Low Density B 1984
A
Low Density A 1984
B
High Density 1984
C
0.45
0.3
0.15
0.6
0.4
0.2
0.6
0.4
0.2
(2)
Mean Number of Matings
300
350
400
450
500
550
Individual Weight (mg)

Figure 24a-c. The relationships between mean number of matings and individual weight (mg) for*G. pennsylvanicus* males at high and low densities.

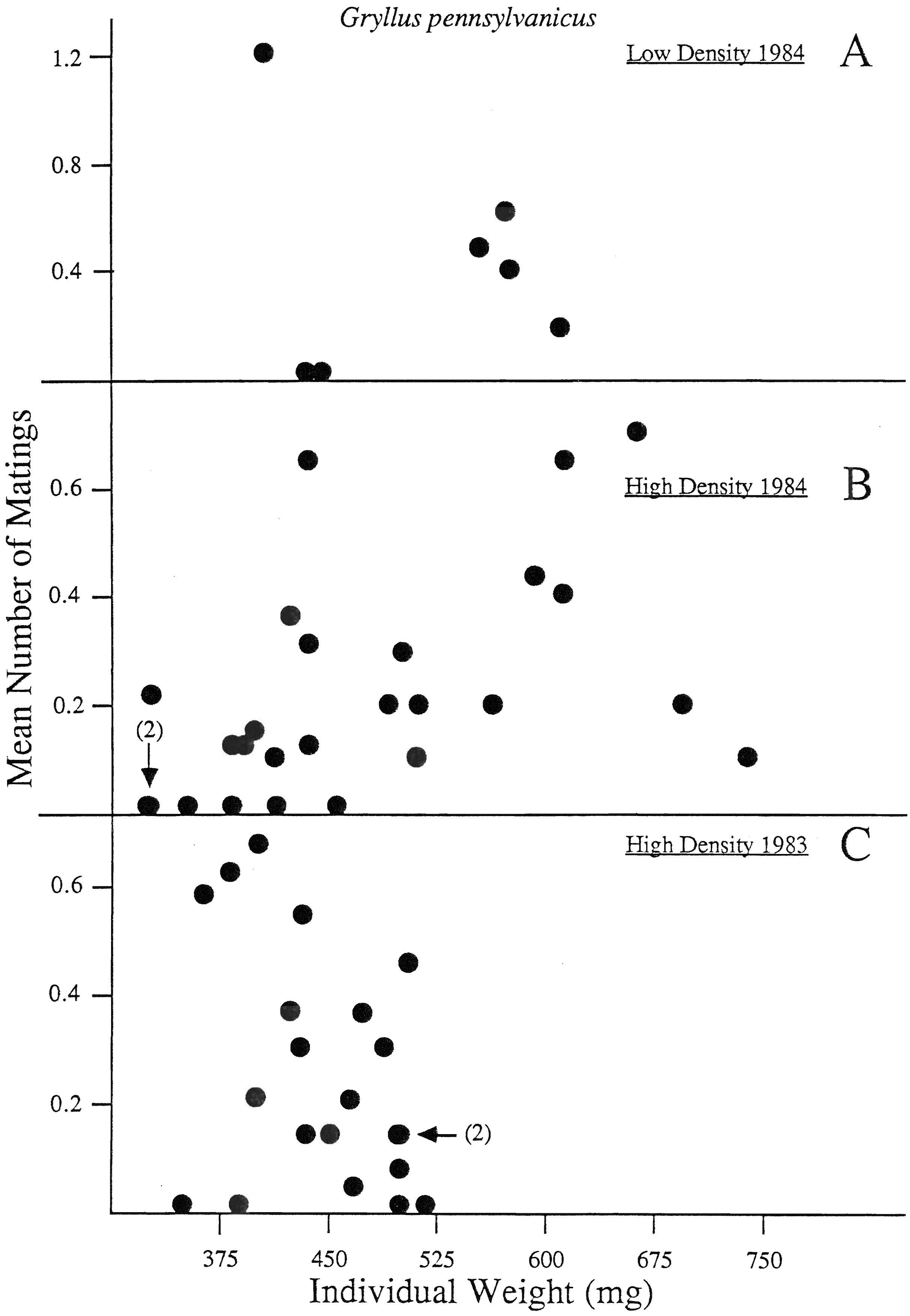

Gryllus pennsylvanicus
Low Density 1984
A
High Density 1984
B
High Density 1983
C
(2)
(2)
Mean Number of Matings
1.2
0.8
0.4
0.6
0.4
0.2
0.6
0.4
0.2
375
450
525
600
675
750
Individual Weight (mg)

Table 5. The standardized intensities of selection (s') and selection gradients (ß') (± standard error) on calling score, movement (m), and individual weight (mg) for *Gryllus veletis* males at high and low population densities. Upper limits for selection intensities are the opportunities of selection (I). The variation explained in relative mating success by the variables is the squared multiple correlation coefficient (R^2), and the number of males (N) used in each density are given.

Density	N	Variable	s'	ß' ± SE	I	R^2
High	26	Calling	0.19	0.18 ± 0.12	0.45	0.26
		Movement	0.23	0.31 ± 0.14*		
		Weight	0.07	0.18 ± 0.14		
Low A	5	Calling	-0.06	-1.29 ± 1.06	0.34	0.61
		Movement	-0.11	-1.31 ± 1.07		
		Weight	0.03	0.01 ± 0.42		
Low B	6	Calling	-0.63	-0.10 ± 0.43	1.35	0.89
		Movement	-0.22	0.26 ± 0.30		
		Weight	-1.05*	-1.17 ± 0.41		

*$P < 0.05$

detected. However, selection was acting against heavier males in low density B. In this case, however, the selection intensity only was significant (r = - 0.91, P < 0.05), indicating that some unknown correlate of weight was also under intense, negative selection pressures. For all samples the intensity of selection on the phenotypic characters never equalled the opportunity for selection. In addition, the variation explained in relative mating success by calling, movement, and weight was not significant at high density, low density A, and low density B (ANOVAS, F = 2.6, df = 3, 22; F = 0.6, df = 3, 1; F = 5.4, df = 3, 2; P > 0.05).

Table 6 shows the selection intensities and the directional selection gradients calculated for *G. pennsylvanicus* . In the 1983 high density sample, significant directional selection pressure was against male weight (t = - 2.21, P < 0.05). There was, however, selection on some correlated character (s) that prevented statistical significance for the selection intensity. In contrast, larger males were favored by selection in the 1984 high density sample as shown by the significant selection intensity and directional selection gradient (r = 0.40, P < 0.05; t = 2.16, P < 0.05). The force of selection was acting only on male weight since s' and ß' were the same. In the low density sample, there was significant directional selection pressure to increase calling duration (t = 2.77, P < 0.05). Also, some correlate of calling duration was apparently favored significantly by selection as indicated by the higher selection intensity value (r = 0.91, P < 0.05). For all samples the intensity of selection on the phenotypic characters never equalled the opportunity for selection. In addition, the variation explained in relative mating success by calling, movement, and weight was not significant at the 1983 high density, 1984 high density, and 1984 low density populations (ANOVAS, F = 1.9, df = 3, 17; F = 1.8, df = 3, 23; F = 8.9, df = 3, 3; P > 0.05).

Table 6. The standardized intensities of selection (s') and selection gradients (ß') (± standard error) on calling score, movement (m), and individual weight (mg) for *Gryllus pennsylvanicus* males at high and low population densities. Upper limits for selection intensities are the opportunities of selection (I). The variation explained in relative mating succes by the variables is the squared multiple correlation coefficient (R^2) and the number of males (N) used in each density are given.

Density	N	Variable	s'	ß' ± SE	I	R^2
High 83	21	Calling	0.16	0.30 ± 0.19	0.70	0.25
		Movement	-0.03	0.03 ± 0.18		
		Weight	-0.31	-0.41 ± 0.19*		
High	27	Calling	0.04	0.02 ± 0.22	1.20	0.19
		Movement	-0.15	-0.18 ± 0.22		
		Weight	0.44*	0.46 ± 0.21*		
Low	7	Calling	0.97**	0.76 ± 0.28*	1.12	0.90
		Movement	0.77	0.26 ± 0.29		
		Weight	-0.20	-0.27 ± 0.20		

*P < 0.05; **P < 0.01

DISCUSSION

The general activity patterns over 24 hours, nightly activity patterns, effects of density and other factors which may influence male phenotypic characters in the context of sexual selection theory, and the adaptive significance of male phenotypic characters are discussed in this section.

SCHEDULES OF SEXUAL ACTIVITY

Acoustical and Mating Behavior

Walker (1983a) suggested that continuously receptive females postpone matings until night to avoid diurnal predators thus resulting in the generally observed nocturnal activity of crickets. Cade (1979a) reported grackles feeding on crickets in central Texas, and I observed starlings that entered the arena in 1983 looking beneath wooden blocks apparently in search of crickets during the day. Under laboratory conditions most *G. campestris* males called during the dark phase of a 12 : 12 h light : dark cycle (Honegger 1981). In addition, movement and matings of *T. commodus* males and females occurred primarily during the dark phase of a 12 : 12 h light : dark cycle (Loher 1979, 1981). With some exceptions, the 24 hour activity patterns in *G. veletis* and *G. pennsylvanicus* generally showed that matings, aggressive songs, courtship songs, and calling songs occurred at night between 2100 and 0800. Courtship songs entice females to copulate and should coincide with female sexual receptivity. In *G. veletis* courtship songs at both densities occurred mostly during midmorning and midafternoon hours, whereas matings in the 24 hour observation periods for *G. veletis* occurred randomly in the high density population and during early morning hours through early afternoon hours in the low density population. In *G. pennsylvanicus* courtship songs at both densities occurred randomly with respect to time, however, matings in the 24 hour observation periods for *G. pennsylvanicus* occurred almost entirely between sunset and sunrise in both samples. Possibly, the frequency of courtship songs during these time periods resulted from reduced male-male aggression, since dominant males of some crickets respond aggressively toward subordinant, courting males (Burk 1983).

Aggressive songs are used in dominance disputes between conspecific males, and the relative frequency of aggressive songs should be highest when males are actively seeking sexually mature females. The data on aggressive songs for *G. veletis* and *G. pennsylvanicus* were inconclusive to support this prediction, however, of the aggressive songs detected, most occurred at night. These data on courthip songs and aggressive songs may not, however, indicate the true relationship with daily cycles. Aggressive songs are usually loud but occur in short bursts (Alexander 1962), thus making detection difficult when other acoustical activity is high. This may have led to an underestimation of the number of aggressive songs. The courtship song is generally difficult for humans to hear during periods of enhanced acoustical activity and may go unnoticed. This probably accounted for the occurrance of matings in *G. pennsylvanicu*s at low density even though courtship songs were not observed, and since some female field crickets require the courtship song before copulating (Loher and Rence 1978; Burk 1983). In addition, the sound produced by male crickets at the beginning of courtship is similar to that produced during aggression. Therefore, it is possible that the function of some songs could have been misinterpreted.

Walker (1983a) suggested that the number of calling males reflects the temporal availability of sexually receptive females. Thus in species where females mate mostly at night, males should call mostly at night. In addition to the number of matings, the 24 hour calling schedule for *G. pennsylvanicus* males showed an increase in the number of callers at night at high density and low density. The 24 hour calling patterns at high density and low density for *G. vletis* males were similar to those reported by Alexander and Meral (1967) for *G. veletis* males in Michigan. That is, most males called during the dark phase of the photoperiod. However, in both high and low densities for *G. veletis* , the number of calling males did not coincide with the number of matings in the 24 hour observations.

Alexander and Meral reported that when nightly temperatures dropped below 10° C, however, the males switched to midafternoon calling. But in my study temperatures were rarely below 10° C.

Walker (1983a) suggested that most females become sexually mature during the warmest time of day and thus concentrate their mating activity immediately following sunset. However, matings occurring in the 10 hour observation periods for *G. veletis* and *G. pennsylvanicus* were randomly distributed in all samples. Walker referred to such mating patterns as extended mating "sprees" and suggested that females in such species may judge male genetic quality by their calling duration. Extended mating sprees would result from variability in females choosing males. That is, some females would require less time in choosing mates than other females. In addition, females may spend a portion of the night ovipositing or feeding before mating, which would also cause variation in nightly mating patterns. Females ovipositing before mating was observed several times in both species. Calling duration is heritable in *G. integer* , but that females choose males based on these genotypic differences has not been shown. These data for *G. veletis* and *G. pennsylvanicus* in the 24 hour and 10 hour observations suggest that selection is favoring females that postpone mating until the dark phase of the photoperiod (possibly due to predation pressures), at which time matings are equally likely to occur.

In species where females are continuously sexually receptive at night, Walker (1983a) predicted that the number of calling males would not vary significantly over the night. That is, there would be no significant nightly peak in acoustical activity. In agreement with Walker's prediction, there were no peaks in the mean number of calling *G. veletis* or *G. pennsylvanicus* males for most samples. The 1984 *G. pennsylvanicus* high density population, however, showed a significant increase in the mean number of calling males at dawn. A similar situation was found by Cade (1979a) for high density populations of *G. integer* in Texas, but not at low density. Cade identified differences in male calling behavior and attributed the increase in calling males at sunrise to a decrease in male-male aggression and avoidance of acoustically orienting parasitoids which are active primarily at night. In contrast, Walker (1983a) suggested that the calling song of males at dawn no longer functioned in attracting females since the song intensity is relatively lower at this time of day. He speculated that sunrise calling resulted from pheromones emitted by nearby females. Cade (unpublished data) found a significant increase in the number of matings at dawn, the time when most males were observed calling. The song may function to stimulate mating in females at dawn. There have been no reported incidents of parasitism on calling *G. pennsylvanicus* males, however, and the increase in activity at dawn in the 1984 high density population was not as steep as that reported by Cade for *G. integer*. A rise in temperature cannot account for this peak since the difference in mean temperature at sunrise was less than 1° C for most other means throughout the night. Possibly, the 1984 peak in callers resulted from reduced male-male aggression since according to Walker, the number of matings should have also shown a peak but did not.

Spatial Displacement

The spatial displacement of individuals over 24 hours should occur mostly at night since females orient to calling males at night, perhaps avoiding diurnal predators. If male movement functions in mate acquisition, male movement should coincide with female movement and mating patterns. Displacement patterns of *G. veletis* males at high density did coincide with female movement but not with mating patterns. Male and female movement were concentrated in the dark hours of the photoperiod, whereas matings occurred randomly over the 24 hour observation period. At low density, however, male movement did not coincide with female movement or mating. In this sample only females showed increased locomotion in the dark. Matings were too few for statistical testing and male movement was randomly distributed over the 24 hours. The 24 hour movement patterns for *G. pennsylvanicus* males at high density did not coincide with female movement or matings. Male movement was randomly distributed and female movement occurred during the day. Matings occurred mostly at night but were too few for statistical testing. Cold temperatures cannot account for the displacement pattern of *G. pennsylvanicus* females in the high density population since temperatures were well within their activity range. Because this species overwinters as eggs and emerge in high numbers, selection may have favored crickets that were more inclined to disperse into new localities regardless of time of day. The 24 hour movement patterns for *G. pennsylvanicus* males at low density did coincide with female movement in that both occurred randomly over the 24 hours. Male movement did not coincide with mating since matings were observed mostly at night.

The nightly movement patterns over the regular observations for *G. veletis* and *G. pennsylvanicus* males in all samples were evenly distributed and coincided with female movement and mating patterns . There were, however, trends for decreased activity towards dawn for both sexes. These behavioral patterns were similar to those found by Sakaluk (in press a) for the decorated cricket, *Gryllodes supplicans* , where female phonotaxis, male calling, and matings occurred throughout the night with a decline in activity toward sunrise. Furthermore, the regular observation periods in this study from 2200 to 0800 on *G. veletis* and *G. pennsylvanicus* were conducted at the appropriate time to observe most behavior.

Alexander (1968) suggested that females were more mobile than males since males are territorial. Therefore, females should move more on average than males. This difference should be greatest in low density populations where territories are assumed to be abundant (Alexander 1961, 1968, 1975). In some field crickets female dispersal, determined as the number of flying *G. integer* to streetlights (Cade 1979c), and the number of *G. rubens* and *G. firmus* falling into pitfall traps (Veazey *et al*. 1976) was significantly greater than males. In my study, however, *G. pennsylvanicus* males moved more than females in all samples, but there were no differences in movement between males and females in any sample for *G. veletis* . However, when male mating effort is high relative to females then males should behave in more costly ways in acquiring mates (Alexander and Borgia 1979). If movement is a form of mating competition by searching for females, then the distance displaced each night may be greater in males than in females. These findings suggest movement is a form of mate competition in *G. pennsylvanicus* but possibly not in *G. veletis*. That movement is a function of male-male competition in *G. pennsylvanicus* and not in *G. veletis* may be due to the natural population densities of the two species. That is, *G. pennsylvanicus* males usually occur in high population densities, thus males may be forced to move in search of females since few calling sites are available. Population density levels are much lower in *G. veletis* and males may rely less on movement as a form of mate acquisition. The relationships between mating and movement for males are discussed later. Similar to the *G. pennsylvanicus* results, Evans (1983) found that *T. commodus* females were less mobile than males. Sakaluk (in press a), however, showed that *G. supplicans* females moved farther on average than males. Sakaluk suggested that female movement functioned to increase the consumption of additional spermatophores. In *G. supplicans* males produce bipartite spermatophores consisting of a large gelatinous portion (spermatophylax) and a sperm containing ampulla (Alexander and Otte 1967). Immediately following a copulation the female removes and consumes the spermatophylax in about one hour while sperm empties from the ampulla into the female's reproductive tract (Sakaluk 1984). Sakaluk (1985) reported that it takes males three hours to produce another spermatophore. Male *G. veletis* and *G. pennsylvanicus* do not produce spermatophylaxes, however, and unnecessary movement by females may result in increased predation and/or parasitism as reported for *G. supplicans* females (Sakaluk and Belwood 1984). Therefore, in field crickets, female movement probably serves primarily as a means of finding mates rather than acquiring nutrients from males.

FACTORS AFFECTING INDIVIDUAL BEHAVIOR IN FIELD CRICKETS

Age

Females should choose males on the qualities they possess and how they present these qualities to females. One quality in males that females should choose is a superior genotype, especially in species where males do not invest parentally. By virtue of being relatively older, males demonstrate their ability to survive and may be preferred by females (Trivers 1972). How females detect age variation is unknown for most species. Another age-related phenomenon is that residual reproductive value should decline with age, such that the costs attached to a behavior in terms of future mating success will also decline. Older individuals should therefore behave in a way which increases costs (Williams 1966a, 1966b).

Age and Calling

Age may influence calling behavior in field crickets. If residual reproductive value declines with cricket age, then males may behave in more costly ways by calling more as they age. In *L. coquilletti* , for example, male grasshoppers increased their activity of signalling with age (Greenfield and Shelly 1985). In field crickets, however, Cade and Wyatt (1984) found no significant variation in calling duration for *G. veletis* , *G. pennsylvanicus* , *G. integer* , and *T. africanus* with respect to age once males were sexually mature. Zuk (pers. com.), however, has shown that older *G. veletis* and *G. pennsylvanicus* males calling over pitfall traps attract more females than younger males, but that calling duration did not increase with age. In this study, the effects of relative age on calling duration in *G. veletis* and *G. pennsylvanicus* were prominent only at high densities. Supporting the hypothesis, males called more with age in the 1983 *G. pennsylvanicus* population. In contrast, males called less with age for both species in 1984. These data are not consistent and suggest that females do not use calling song to detect male age since such a trait would be an unreliable prediction of male longevity. Also, calling may incur energetic costs in these species, but no acoustically orienting parasite or predator are known for *G. veletis* and *G. pennsylvanicus* . Therefore, the prediction regarding declining reproductive value and associated costs may not apply.

Age and Mating

Male mating frequency should increase with age if females prefer older males. In *G. pennsylvanicus* , males at high density in 1983 mated more frequently as they aged. But in *G. veletis* , males at high density mated less frequently as they aged. There were no differences in male mating rates for the other four samples. In general, therefore, age does not appear to contribute greatly to variation in male mating frequency in field crickets.

Females in the *G. pennsylvanicus* 1983 high density sample mated more frequently as they aged, but this may have been due to the very young age of females entering the arena in this sample. There were no differences in the frequency of matings by females as they aged in any other sample. Multiple matings by females are discussed later.

Age and Spatial Displacement

The nightly movement of males should increase with age if reproductive value declines with age and costs are attached to male movement. However, results on mean displacement for the 1983 *G. pennsylvanicus* high density and the 1984 *G. veletis* high density samples showed that displacement of males decreased with age. There was no relationship between age and movement in the other samples and there are no known costs attached to cricket locomotion.

In *G. veletis* , females in both low density populations moved more as they aged, whereas females at high density moved less with age. In *G. pennsylvanicus* , females in the 1984 low density population moved more as they aged, whereas females in the 1983 high density sample moved less as they aged. There were no differences in female movement with age in the 1984 high density population. The consistency of females moving farther distances with age in all low density samples and moving less with age in 2 of 3 high density samples suggests that population density may affect locomotion behavior of females differently as they age. The effects of density on movement are discussed later.

The variation of the effects of age on male characters for both species and all samples suggests, for the most part, age-related theories may not generally apply to these insects, but are suitable for vertebrates, which live several years as breeding adults. For example, Howard (1978) demonstrated that older male bullfrogs, *R. catesbeiana* , are more territorial and call more than younger males. But older males are larger than younger males, and size may not change greatly in mature aging insects.

Size and Calling

The calling song of male field crickets is used for territorial advertisment (Alexander 1975; Cade 1979a; Otte 1977). It is possible that larger males control available territories and consequently call for longer durations. In bullfrogs, for example, *R. catesbeiana* , larger males called more than smaller males and larger males physically repelled them from available territories (Howard 1978). In the laboratory larger male field crickets usually win aggressive encounters and there is a positive correlation between individual weight and figthting success (Alexander 1961; Burk 1983; Dixon and Cade 1986). Because calling behavior in field crickets is indicative of owning territories, individual calling duration should be positively correlated with male size. Using individual weight as an indicator of male size, no correlations were found between size and calling scores in *G. veletis* or *G. pennsylvanicus* for any sample. Cade and Wyatt (1984) also found no correlations between weight and calling duration for *G. veletis* , *G. pennsylvanicus* , *G. integer* , and *T. africanus* in the laboratory and for *G. integer* in an outdoor arena. Calling behavior may not be correlated with fighting ability in field populations, however, and Cade (1979a) showed that some calling males adopt non-calling behavior in aggressive encounters.

Size and Spatial Displacement

Among highly territorial species, smaller males may be forced into searching or employing other mating strategies by larger, more aggressive males. In this context smaller male field crickets are predicted to travel farther distances per night than larger males. There were no correlations, however, between male weight and nightly movement for either species at low density. This may have resulted from fewer male-male interactions at low density, since territories may not be limiting at low density.

The difference between large and small males in nightly movement should be more pronounced at high density than at low density since the probability of male-male confrontations increases with density. Supporting this prediction is the result obtained for *G. veletis* males at high density, where an inverse correlation between mean nightly movement and male weight was found. Male size was not correlated with movement in the 1983 and 1984 *G. pennsylvanicus* high density populations. Because this species occurs naturally in high numbers, the males may not express the same frequency of levels of aggression as do *G. veletis* males. That is, *G. pennsylvanicus* males may be more "tolerant" of conspecific males.

Calling and Spatial Displacement

The amount of time calling should be inversely proportional to the distance travelled. That is, non-calling males should move greater distances than calling males, since calling males are territorial and more sedentary. Supporting the hypothesis, an inverse relationship was found for *G. veletis* males in the low density A population. However, there were no other relationships between calling and displacement for males of both species at any density. The mean number of calling males in the high density populations were probably low since available calling sites were presumably limited (Alexander 1961, 1968, 1975), and resulted in what Cade (1979a) called irregular calling. That is, males may have switched between calling and searching at varying intervals so that no correlations existed between the variables. Why no relationships were found in two of the low density populations is puzzling since calling sites were (presumably) readily available, and calling should be most adaptive at low density.

Population Density and Calling

Male calling behavior should change with fluctuating population densities, as calling sites become limited and the costs of defending territories increases (Alexander 1961, 1968, 1975). In the only report of the effects of density on calling duration for field crickets in a seminatural environment, Cade and Wyatt (1984) found that *G. integer* males called less at high density than at low density. In this study, population density had no effect on individual calling scores for *G. veletis* or *G. pennsylvanicus* males. That is, within a species, the mean calling scores were not different between high densities and low densities. For *G. veletis* it is possible that the low density samples were too high to reflect any behavioral changes with densities. In other words, the males in the low density population were under similar selective pressures as males in the high density population with respect to calling. Alexander and Meral (1967) reported that the number of calling *G. pennsylvanicus* males greatly exceeded the number of calling *G. veletis* males. Using the area of their study site, I calculated their data to show that during the seasonal peak in activity calling *G. veletis* males reached a population density of 0.0056 crickets per meter squared, whereas calling *G. pennsylvanicus* males reached a population density of 0.0075 crickets per meter squared. In the only other published account of population density of calling males in *G. veletis*, Cade (1981a) reported a range of 0.0009 to 0.009 crickets per meter squared during the seasonal peak in population of adults. It is also possible that holding territories is not as costly as Alexander predicted, that density effects become obvious at some other density, or that the effects of density on calling duration were masked by selection operating on some correlated character such as size and/or age. For example, aging males and relatively large males may call more regardless of density. However, data on these field crickets do not support this last hypothesis.

The amount of calling should not differ at the same population density levels. The calling scores for *G. veletis* males did not differ between the low density samples. Interestingly enough, males in the low density B sample were on average 36 days older than males in low density A. In addition, calling scores for *G. pennsylvanicus* males in the 1983 and 1984 high population densities did not differ.

Population Density and Mating

Females mated repeatedly in both species at high and low population densities. In most *G. veletis* and *G. pennsylvanicus* samples, the variation in the number of matings for females was similar to the variation in the number of matings for males. Several advantages have been proposed to account for multiple matings by females. Because female crickets attempt to remove and consume spermatophores after copulating, continuously receptive females may gain nutritional benefits from repeated matings that are used for growth, physiological maintenance, and/or in the production of eggs (Sakaluk and Cade 1980, 1983). For example, in the katydid, *Requena verticalis* , protein contained in the spermatophylax is used by females to produce more and larger eggs (Bowen *et al* . 1984; Gwynne 1984). In this study, removal and consumption of spermatophores was observed only once in 680 hours of observation. Removal of spermatophores probably occurred more frequently but went unnoticed. Possible other advantages for females resulting from repeated matings include sperm replenishment, avoidance of male sexual harassment, and increased genetic diversity of offspring (Walker, W.F. 1980). Male crickets may gain reproductively by transferring more sperm to females relative to conspecific males, or by mating last with a female. This should result in males fertilizing most or all of the female's eggs, since sperm mixing and last male sperm precedence is prominent is some crickets (Sakaluk in press b; Backus and Cade submitted).

Females may mate more frequently at high densities when more males are available from which to choose (Alexander 1975; Bradbury 1981). The mating rates of males and females for *G. veletis* and *G. pennsylvanicus* , however, were not affected by changing population density. That is, females mated as frequently in low density populations as in high density populations. If females were mating solely to avoid male sexual harassment, then the frequency of matings should increase with increasing population density, since random collisions between males and females should increase. Sperm replenishment cannot explain the frequency of matings for females, since females can store viable sperm for long periods of time (Walker, W.F. 1980), and a few matings seem to supply enough sperm to fertilize all of the eggs a female produces. If females were feeding on spermatophores mating rates should have been greater in the high density population, since more males were available to produce spermatophores. Perhaps there are no costs attached to mating for females.

Mating rates should not differ between the same density levels. In *G. veletis* mating rates were not different between the low density samples. Also, the mating rates in *G. pennsylvanicus* were not different between the 1983 and 1984 high density populations.

Population Density and Spatial Displacement

Displacement of males should increase with increasing density, since available calling sites become limited and the costs attached to defending territories increases (Alexander 1975). Otte and Joern (1975) showed increased movement behavior of *L. coquilletti* males initiated by aggressive interactions after artificially increasing the density. The mean displacement for *G. veletis* males at high density was not different, however, from the mean displacement for males in either low density sample. In addition, males and females in both low density samples moved similar distances. Paradoxically, the mean displacements for *G. pennsylvanicus* males were the opposite from Alexander's prediction. That is, males in the 1984 high density population moved less than males in the 1984 low density population. Also, males in the 1983 high density sample moved more than males in the 1984 high density sample. These results differ from those found by Wyatt (1982) where *G. integer* males moved more at high density than at low density. The data for *G. veletis* and *G. pennsylvanicus* males suggest that the distance travelled per night is independent of density, or that density effects on movement are evident at some other density level.

The effects of population density on female movement in crickets are unknown, and no theoretical prediction exists to account for density effects on female movement. In *G. veletis*, there were no differences in the distances females moved in the high density and the low density populations. In *G. pennsylvanicus*, however, females in the 1984 low density and 1983 high density populations moved greater distances than females in the 1984 high density population.

INTENSITY OF SELECTION ON FACTORS AFFECTING MALE MATING SUCCESS IN FIELD CRICKETS

The intensity of selection acting on male phenotypic characters was measured with bivariate correlation analyses and multivariate correlation analyses. Bivariate analysis detects the presence or absence of selection while multivariate analysis measures the magnitude of selection pressures. The latter can also separate the direct and indirect effects of selection acting on phenotypically correlated traits.

Mating and Calling

Because calling entails substantial energetic costs on males (Prestwich and Walker 1981), sexual selection theory predicts that males calling for long periods of time receive more matings than conspecific males calling a shorter duration. Furthermore, Alexander (1961, 1968, 1975) suggested that male calling duration would be most adaptive in low density populations. In this study, calling score was positively correlated with mating success only for *G. pennsylvanicus* males at low density. The multivariate analysis also showed significant directional selection on calling in the low density sample. This is evident by the magnitude of both the selection intensity and the selection gradient. Even though the selection intensity was greater than the selection gradient, the selection intensity was still within range of the selection gradient. That is, the variation in the selection gradient was large enough to account for the higher intensity of selection value, making the direct and indirect effects of selection indistinguishable. In contrast, calling scores for *G. veletis* males were not associated with mating frequency in either low density population. The actual density of males in these low density observations were 0.03 per meter squared, which exceeds other reported density levels for *G. veletis* . As predicted, there were no correlations between mean calling scores and mating success for both species at high densities. Therefore, selection on calling was generally relaxed, but favored calling in one low density sample.

Matings and Spatial Displacement

Relationships between the number of matings and displacement should be most noticable at high densities, since random collisions between males and females should increase and ultimately result in more matings (Alexander 1961, 1968, 1975). In this study, however, bivariate statistical analysis showed that the mean nightly displacements of *G. veletis* and *G. pennsylvanicus* males were not correlated with mating success at any density. From the bivariate analysis, therefore, individual male mating success was independent of nightly movement and density. However, the directional selection gradient showed that the direct force of selection favored increased movement for *G. veletis* males at high density in 1984. In addition, there was enough counter selection on weight to prevent the intensity of selection on movement to be significant, since there was an inverse correlation between weight and movement. The difference in conclusions between the bivariate and multivariate correlation analysis shows one advantage of the multivariate model (Lande and Arnold 1983) in that the direct force of selection on movement was significant, whereas the bivariate correlation analysis between mating success and mean movement showed no significance. Therefore, employing only bivariate statistical analysis would have resulted in a possibly erroneous conclusion of the relationship between movement and mating success for the *G. veletis* high density population. Thus males moving relatively more than conspecific males at high density received a disproportional number of matings in one sample, and supports the notion that movement or searching behavior is a mode of male-male reproductive competition in field crickets. Selection on displacement was relaxed at other times.

Mating and Size

Individual male size may be a determining factor in mate acquisition. In polygynous mating systems male-male competition for mates is expected to be intense

(Borgia 1979). Individual size influences many of the reproductive tactics employed by competing males over access to sexually mature females (Alcock 1979; Alcock *et al*. 1977; Cade 1980, 1985; Dawkins 1980; O'Neill and Evans 1983; Thornhill 1976, 1979, 1980a). Positive correlations between males size and mating success have been demonstrated for many species of animals (Anderson and Fedak 1985; Andersson 1982; Gross 1985; Howard 1978, 1984; Howard and Kluge 1985; Price 1984a, 1984b; Wells 1979; Wickman 1985). The bivariate analysis for *G. pennsylvanicus* showed a significant, postitive correlation between weight and mating success for the 1984 high density sample. In addition, there was significant directional selection to increase body weight for high density males. The magnitude of selection was directly on weight since no indirect force countered or enhanced the intensity of selection. In contrast, there was significant directional selection to decrease male weight in the *G. pennsylvanicus* 1983 high density sample. Again, this force of selection was not obtained through the bivariate statistical analysis. Although there was significant selection pressures operating on male weight, there was selection operating on some correlated character not included in this study which acted to increase weight. This is evident since the selection gradient (direct force) was significant, whereas the intensity of selection (direct and indirect force) was not significant. The bivariate analyses for *G. veletis* showed an inverse correlation between weight and mating success for males in low density B only. In addition, for the low density B males there was significant pressure to decrease body weight with respect to mating success, but the selection pressure was acting indirectly on weight as evident by the significant selection intensity and the non-significant selection gradient. This result may have been spurious, however, since a very small male received most of the matings and three larger males received no matings. In addition, there were only 6 matings in this sample. Selection therefore fluctuated greatly on male size, sometimes due to apparent selection on correlated traits.

Note that for all of the samples the opportunities for selection were greater than the selection gradients and the selection intensities. That is, selection pressures cannot produce a change in mean fitness larger than the variation in fitness (Arnold and Wade 1984a, 1984b). Also, the variation in male mating success explained by calling score, movement, and individual weight were not significant for any density. That is, the squared multiple correlation coefficients, which considers the effects of all independent variables on the dependent variable in its calculation, for both years and densities were not significant.

OBSERVATIONAL AND ARENA EFFECTS ON CRICKET BEHAVIOR

Some of the variation in behavior was probably due to observer and arena effects. For example, the hourly walks through the arena may have briefly disrupted calling, but most males resumed calling immediately. Windy nights occasionally caused arena walls to bend and produce loud noises that momentarily quieted calling males. Movement behavior of crickets may have been disturbed by my walking through the arena such that some crickets turned 180° and walk the other way, but this rarely occurred. The arena may have inhibited some movement behavior of males and females since many travelled along arena walls. Matings were apparently unaffected by my presence or the arena. Many matings were actually observed with light shining directly on the copulating pair. To my knowledge, not once did I prevent a successful copulation by observing. For the most part, crickets were seemingly unaffected by my presence or the arena.

CONCLUSIONS

Many population genetic models employ constant measures of selection intensities in predicting changes in gene frequencies (Falconer 1981; Futuyma 1979). Assuming intense and constant sexual selection intensities Williams (1975), Howard (1978), Maynard-Smith (1978), West-Eberhard (1979, 1984), and Thornhill (1980b) suggested that male fitness traits would be depleted of additive genetic variation and consequently show negligible heritability. This is conceivable for traits affected by a few loci, however, many fitness traits are affected by many loci (Cade 1984b; Falconer 1981). Lande (1976, 1977, 1980) showed mathematically that mutation rates and pleitropic effects were sufficient to maintain additive genetic variation regardless of mating system. My data show another flaw in predictions regarding reduced heritabilities under sexual selection. Calling duration (Cade 1981) and body size (McGowan 1986) are factors which have significant heritabilities in the field cricket, *G. integer* , and my study shows changing selection intensities on these factors in *G. veletis* and *G. pennsylvanicus* . For example, selection pressures on calling fluctuated with changing population density levels as shown by the selection intensities on the 1984 calling scores in *G. pennsylvanicus* . In the low density population selection intensities were favoring increased calling while there was negligible selection pressure at high density. In addition, selection fluctuated annually. In the *G. pennsylvanicus* high density populations selection pressures were acting to "decrease" male size in 1983 and to "increase" males size in 1984. Also, selection favored smaller males in the *G. veletis* low density B population and was relaxed in the other *G. veletis* samples. Price (1984) used the multivariate analysis and showed that the intensity of sexual selection fluctuated annually on beak characters in Darwin's finches, *Geospiza fortis* . One of the major advantages of the multivariate model (Lande and Arnold 1983) is that phenotypically and genotypically (pleiotropic) correlated traits can be separated and the adaptive significance of each trait ascertained.

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APPENDIX

Table I

The mean ($\bar{x}$ ± SD) number of crickets per night in the outdoor arena for each species and each density. Males (M) and females (F) are indicated along with the number of nights observed.

Species	Density	Sex	$\bar{x}$ ± SD	Nights Observed
G. veletis	High	M	21.3 ± 1.7	10
		F	18.8 ± 1.2	
	Low A	M	5.0 ± 0.0	10
		F	4.9 ± 0.3	
	Low B	M	4.4 ± 0.5	10
		F	3.1 ± 0.3	
G. pennsylvanicus	High 83	M	19.8 ± 1.4	19
		F	17.4 ± 6.1	
	High	M	20.2 ± 1.6	10
		F	20.0 ± 1.1	
	Low	M	4.9 ± 0.8	9
		F	5.8 ± 1.3	

Table II

The reliability in determining calling males and assigning matings to individuals. Confirmed instances divided by the total number produced the reliability values.

Variable	Confirmed	Unconfirmed	Reliability
Calling	227	20	0.92
Mating	111	16	0.87

Table III

The number of non-normal and normal distributions before and after transformation to natural logarithms for male variables of *Gryllus veletis* and *G. pennsylvanicus*. Also, the effects of transformation on skewness and kurtosis are given.

	Non-transformed		Transformed		Increase in	Increase in
Variable	Non-Normal	Normal	Non-Normal	Normal	Skewness	Kurtosis
Calling	2	4	2	4	1 : 6	2 : 6
Movement	1	5	0	6	4 : 6	4 : 6
Weight	1	5	0	6	4 : 6	3 : 6
Matings	1	5	1	5	4 : 6	4 : 6
Total	5	19	3	21	13 : 24	13 : 24

Table IV

The number of non-normal and normal distributions before and after transformation to natural logarithms for female variables of *Gryllus veletis* and *G. pennsylvanicus* . Also, the effects of transformation on skewness and kurtosis are given

	Non-transformed		Transformed		Increase in	Increase in
Variable	Non-Normal	Normal	Non-Normal	Normal	Skewness	Kurtosis
Movement	0	6	0	6	1 : 5	5 : 5
Weight	1	5	1	5	1 : 5	2 : 5
Matings	1	5	2	4	1 : 5	3 : 5
Total	2	16	3	15	3 : 15	10 : 15

Table V

Analysis for serial randomness of the nightly calling schedules for *Gryllus veletis* and *G. pennsylvanicus*. (Sp.) at each density (Den.). N is the sample size; LT is the number of values less than the mean number of callers; GT is the number of values greater than the mean number of callers; Z is the test statistic; and P is the probability value.

Sp.	Den.	Mean Number of Callers	N	Runs	LT	GT	Z	P
G.v.	High	5.28	100	27	55	45	- 4.77	< 0.01
	Low A	1.96	100	26	38	62	- 4.72	< 0.01
	Low B	1.48	100	22	45	55	- 5.79	< 0.01
G.p.	High 83	6.52	190	42	100	90	- 7.84	< 0.01
	High 84	5.81	100	28	45	55	- 4.57	< 0.01
	Low 84	1.16	90	27	60	30	- 3.34	< 0.01

Table VI

Analysis for serial randomness of the nightly mating schedules for *Gryllus veletis* and *G. pennsylvanicus*. (Sp.) at each density (Den.). N is the sample size; LT is the number of values less than the mean number of matings; GT is the number of values greater than the mean number of matings; Z is the test statistic; and P is the probability value (NS = not significant).

Sp.	Den.	Mean Number of Matings	N	Runs	LT	GT	Z	P
G.v.	High	0.58	100	44	62	38	- 0.88	NS
	Low A	0.14	100	25	86	14	- 0.03	NS
	Low B	0.07	100	13	94	6	0.67	NS
G.p.	High 83	0.56	190	83	126	64	- 0.47	NS
	High 84	0.46	100	47	64	36	- 0.02	NS
	Low 84	0.26	90	31	71	19	0.01	NS

Table VII

Analysis for serial randomness of the nightly movement schedules for *Gryllus veletis* and *G. pennsylvanicus.* (Sp.) males (M) and females (F) at each density (Den.). N is the sample size; LT is the number of values less than the mean number of males and females (see text for explanation); GT is the number of values greater than the mean number of males and females; Z is the test statistic; and P is the probability value.

Sp.	Den.	Sex	Mean Number of Crickets	N	Runs	LT	GT	Z	P
G.v.	High	M	8.42	100	20	57	43	- 6.16	< 0.01
		F	7.43	100	25	51	49	- 5.22	< 0.01
	Low A	M	1.85	100	29	39	61	- 4.14	< 0.01
		F	1.81	100	25	47	53	- 5.21	< 0.01
	Low B	M	2.14	100	31	65	35	- 3.42	< 0.01
		F	1.05	100	21	67	33	- 5.51	< 0.01
G.p.	High 83	M	3.99	190	65	93	97	- 4.51	< 0.01
		F	5.29	190	42	90	100	- 7.84	< 0.01
	High 84	M	7.54	100	29	46	54	- 4.39	< 0.01
		F	4.29	100	20	57	43	- 6.16	< 0.01
	Low 84	M	2.29	90	29	53	37	- 3.41	< 0.01
		F	1.70	90	19	51	39	- 5.16	< 0.01

Table VIII

Transformed male sample means and standard deviations ( ), of calling score, nightly movement (m), individual weight (mg), and matings for *Gryllus veletis* and *G. pennsylvanicus* at different levels of population density.

	Gryllus veletis			*Gryllus pennsylvanicus*		
Variable	High	Low A	Low B	High 83	High	Low
Calling	0.12 (0.10)	0.18 (0.11)	0.15 (0.09)	0.09 (0.08)	0.13 (0.09)	0.08 (0.08)
Movement	4.01 (1.55)	4.02 (1.82)	4.56 (2.83)	3.97 (1.83)	3.17 (1.49)	4.77 (2.06)
Matings	0.18 (0.12)	0.19 (0.11)	0.10 (0.11)	0.17 (0.14)	0.16 (0.18)	0.27 (0.29)

Table IX

Transformed female sample means and standard deviations ( ) of nightly movement (m), and matings for *Gryllus veletis* and *G. pennsylvanicus* at different levels of population density.

	Gryllus veletis			*Gryllus pennsylvanicus*		
Variable	High	Low A	Low B	High 83	High	Low
Movement	4.05 (1.40)	2.72 (1.16)	2.75 (0.77)	2.73 (1.69)	1.28 (0.82)	2.64 (0.97)
Mating	0.21 (0.15)	0.20 (0.15)	0.15 (0.09)	0.21 (0.12)	0.16 (0.15)	0.33 (0.28)

Table X

Individual measures used in statistical analysis for *Gryllus veletis* and *G. pennsylvanicus* males. Species (Sp.), Density (Den.), Displacement (Displ.).

Sp.	Den.	Male Number	Weight (mg)	Number of Matings	Number of Mates	Arena Nights	Mean Calling Score	Mean Displ. (m)	Mean Matings
G. v.	High	00	415.1	1	1	10	0.09	07.53	0.1000
		01	480.8	1	1	05	0.15	06.20	0.2000
		03	393.7	1	1	10	0.14	08.80	0.1000
		05	502.9	0	0	04	0.00	00.34	0.0000
		07	385.0	0	0	10	0.02	03.63	0.0000
		09	457.4	5	4	10	0.11	06.18	0.5000
		21	429.2	1	1	10	0.08	10.45	0.1000
		23	331.8	4	3	10	0.16	07.93	0.4000
		25	428.7	2	2	06	0.03	08.92	0.3333
		37	525.0	3	3	10	0.07	07.99	0.3000
		41	417.8	2	2	09	0.04	07.00	0.2222
		43	317.3	1	1	10	0.03	04.70	0.1000
		45	447.4	5	3	10	0.23	08.70	0.5000
		55	491.6	6	5	10	0.35	10.21	0.6000
		67	467.9	2	2	10	0.01	11.69	0.2000
		69	468.6	0	0	02	0.01	15.39	0.0000
		71	458.6	5	4	10	0.07	15.68	0.5000
		73	376.3	4	4	10	0.02	09.98	0.4000
		75	385.0	3	3	10	0.15	11.93	0.3000
		77	519.6	3	2	10	0.43	02.68	0.3000
		81	324.1	2	2	06	0.23	11.15	0.3333
		83	461.1	3	1	06	0.17	11.82	0.5000
		89	439.1	1	1	06	0.44	12.12	0.1667
		91	372.3	0	0	06	0.23	14.76	0.0000
		95	355.5	1	1	06	0.26	10.70	0.1667
		99	304.4	2	2	06	0.16	19.85	0.3333
	Low A	11	485.2	4	2	10	0.45	01.92	0.4000
		33	456.3	2	2	10	0.19	14.74	0.2000
		55	347.4	2	2	10	0.15	09.88	0.2000
		77	440.2	5	1	10	0.06	15.13	0.5000
		99	502.7	1	1	10	0.26	10.38	0.1000
	Low B	01	483.4	0	0	07	0.14	05.91	0.0000
		03	422.4	0	0	03	0.15	20.50	0.0000
		05	542.7	0	0	10	0.42	03.40	0.0000
		11	383.9	2	2	09	0.13	20.12	0.2222
		13	379.3	2	1	07	0.09	06.50	0.2857
		23	305.0	2	1	05	0.12	03.36	0.4000
G. p.	High	00	434.8	0	0	05	0.03	02.81	0.0000
		02	667.0	7	4	10	0.36	05.00	0.7000
		04	503.0	3	2	10	0.27	05.17	0.3000
		06	616.3	4	4	10	0.14	09.17	0.4000
		10	511.0	1	1	10	0.12	08.14	0.1000
		12	563.0	2	2	10	0.09	14.29	0.2000
		14	416.6	0	0	10	0.25	10.15	0.0000

Table X (cont'd)

Sp.	Den.	Male Number	Weight (mg)	Number of Matings	Number of Mates	Arena Nights	Mean Calling Score	Mean Displ. (m)	Mean Matings
G.p.	High	18	415.4	1	1	10	0.38	08.92	0.1000
		20	441.2	1	1	05	0.14	05.84	0.2000
		30	615.0	6	3	09	0.11	01.75	0.6667
		34	451.0	2	1	02	0.05	06.53	1.0000
		36	329.0	1	1	04	0.21	07.00	0.2500
		40	325.6	0	0	10	0.03	04.06	0.0000
		42	592.0	4	2	09	0.33	06.55	0.4444
		44	390.8	1	1	07	0.10	12.17	0.1429
		52	431.0	2	1	03	0.01	00.25	0.6667
		56	454.6	0	0	02	0.22	02.55	0.0000
		58	356.7	0	0	03	0.05	06.21	0.0000
		60	467.8	2	2	10	0.34	07.49	0.2000
		62	432.0	1	1	08	0.08	00.13	0.1250
		70	688.4	2	2	10	0.02	07.63	0.2000
		74	374.3	1	1	08	0.24	10.65	0.1250
		80	421.0	3	2	08	0.07	06.60	0.3750
		86	377.0	1	1	08	0.07	08.63	0.1250
		90	328.7	0	0	02	0.00	00.00	0.0000
		96	733.5	1	1	10	0.17	05.39	0.1000
		98	384.8	0	0	05	0.17	07.57	0.0000
	Low	04	415.0	11	3	09	0.26	16.68	1.2222
		06	446.5	0	0	02	0.00	07.66	0.0000
		08	564.5	4	3	09	0.14	16.72	0.4444
		10	442.7	0	0	03	0.00	01.40	0.0000
		12	573.5	5	3	08	0.12	11.59	0.6250
		14	637.0	1	1	05	0.12	09.07	0.2000
		16	577.5	2	2	06	0.04	11.69	0.4183
	High 83	01	500.6	0	0	09	0.10	09.18	0.0000
		02	434.6	3	3	19	0.08	10.40	0.1600
		03	517.0	0	0	05	0.07	02.26	0.0000
		04	451.1	3	3	19	0.06	14.43	0.1600
		05	471.5	7	5	19	0.11	08.10	0.3700
		06	430.1	10	2	19	0.01	03.44	0.5300
		07	495.0	3	2	19	0.11	18.64	0.1600
		08	469.0	1	1	19	0.05	14.14	0.0500
		10	399.7	0	0	04	0.04	13.98	0.0000
		11	379.6	12	4	19	0.06	09.22	0.6300
		23	483.1	6	5	19	0.12	13.26	0.3200
		24	402.7	11	6	15	0.09	26.87	0.6700
		25	432.4	6	5	19	0.21	05.45	0.3200
		30	481.4	9	9	19	0.57	09.10	0.4500
		31	427.1	7	4	19	0.12	10.90	0.3700
		32	494.1	3	1	19	0.05	14.14	0.1600
		33	465.3	4	3	19	0.12	10.07	0.2100
		34	366.8	11	5	19	0.03	10.24	0.5800
		35	500.8	1	1	12	0.14	23.02	0.0800
		41	401.4	3	2	14	0.08	06.96	0.2100

Table X(cont'd)

Sp.	Den.	Male Number	Weight (mg)	Number of Matings	Number of Mates	Arena Nights	Mean Calling Score	Mean Displ. (m)	Mean Matings
		42	349.2	0	0	14	0.03	05.42	0.0000
		44	. . . .	2	2	12	0.08	10.28	0.1700
		45	. . . .	1	1	12	0.09	02.88	0.0800
		55	. . . .	4	2	12	0.03	08.36	0.3300

Table XI

Individual measures used in statistical analysis for *Gryllus veletis* and *G. pennsylvanicus* females. Species (Sp.), Density (Den.), Displacement (Displ.)

Sp.	Den.	Female Number	Weight (mg)	Number of Matings	Number of Mates	Arena Nights	Mean Displ. (m)	Mean Matings
G. v.	High	02	502.6	1	1	06	09.35	0.1667
		04	475.0	1	1	10	07.10	0.1000
		06	603.9	2	2	10	15.13	0.2000
		08	615.6	1	1	10	15.85	0.1000
		10	570.8	1	1	10	10.04	0.1000
		12	528.1	2	1	10	10.40	0.2000
		14	488.0	3	3	10	05.46	0.3000
		16	409.7	0	0	02	00.00	0.0000
		18	501.8	0	0	02	10.20	0.0000
		20	541.2	5	3	10	08.90	0.5000
		22	442.4	4	4	10	08.59	0.4000
		24	471.6	2	2	05	10.47	0.4000
		36	429.6	5	4	10	13.45	0.5000
		38	424.1	1	1	10	16.36	0.1000
		40	407.0	4	3	10	05.38	0.4000
		44	428.0	1	1	10	07.64	0.1000
		60	393.8	4	4	08	14.18	0.5000
		66	405.3	3	2	10	08.54	0.3000
		70	437.9	7	5	10	11.89	0.7000
		72	. . . .	3	2	06	07.49	0.5000
		74	. . . .	2	2	06	16.93	0.3333
		76	561.0	2	2	05	07.18	0.4000
		80	512.0	4	4	05	09.68	0.8000
	Low A	00	481.8	6	2	09	03.35	0.6667
		10	570.8	2	2	10	03.91	0.2000
		22	442.4	1	1	10	02.96	0.1000
		38	424.1	3	1	10	17.13	0.3000
		44	428.0	2	2	10	09.03	0.2000
	Low B	00	481.8	2	1	10	06.94	0.2000
		10	570.8	1	1	10	04.88	0.1000
		38	424.1	3	2	10	03.62	0.3000
G. p.	High	01	645.4	0	0	05	02.82	0.0000
		03	256.4	1	1	06	01.27	0.1667
		05	375.4	4	3	10	04.32	0.4000
		07	685.5	1	1	10	09.33	0.1000
		11	528.7	8	4	10	05.07	0.8000
		13	345.1	0	0	10	00.30	0.0000
		15	426.5	1	1	07	00.00	0.1429
		17	441.7	1	1	10	05.67	0.1000
		19	360.0	3	3	10	03.41	0.3000
		23	324.2	1	1	10	09.52	0.1000
		25	362.7	0	0	05	01.10	0.0000
		39	415.0	1	1	10	01.46	0.1000
		47	530.0	0	0	03	06.33	0.0000

Table XI (cont'd)

Sp.	Den.	Female Number	Weight (mg)	Number of Matings	Number of Mates	Arena Nights	Mean Displ. (m)	Mean Matings
		49	843.0	1	1	03	07.67	0.3333
		55	493.5	4	4	10	01.90	0.4000
		57	472.7	1	1	10	01.35	0.1000
		69	598.7	1	1	06	01.68	0.1667
		71	529.0	3	2	10	02.29	0.3000
		73	376.2	2	2	10	03.34	0.2000
		75	498.4	0	0	08	01.78	0.0000
		81	321.0	3	1	08	01.41	0.3750
		83	508.6	6	3	08	03.21	0.7500
		89	500.0	2	1	05	04.09	0.4000
		93	657.6	1	1	05	02.38	0.2000
		95	528.2	1	1	05	01.22	0.2000
	Low	01	645.4	10	2	09	07.54	1.1111
		03	256.4	1	1	09	02.58	0.1111
		05	375.4	6	4	09	04.09	0.6667
		07	695.5	2	1	09	04.68	0.2222
		09	477.9	1	1	09	06.49	0.1111
		13	345.1	3	2	05	09.39	0.6000
	High 83	12	440.5	10	2	18	02.45	0.5556
		13	441.8	5	5	07	10.45	0.7143
		14	419.6	3	3	19	08.92	0.1579
		15	500.1	3	1	17	04.98	0.1765
		16	403.8	4	2	18	05.02	0.2222
		17	301.6	4	2	18	02.28	0.2222
		18	487.8	0	0	03	07.40	0.0000
		19	407.6	2	1	16	14.47	0.1250
		20	....	6	4	14	01.45	0.4286
		26	....	8	7	16	11.14	0.5000
		27	....	6	3	16	16.60	0.3750
		28	....	1	1	09	09.33	0.1111
		29	....	4	3	16	05.84	0.2500
		50	....	6	4	12	01.12	0.5000
		51	....	5	4	08	08.82	0.6250
		52	....	0	0	14	07.46	0.0000
		53	....	5	3	14	01.73	0.3571
		54	....	3	1	13	05.30	0.2308
		60	....	4	3	13	04.14	0.3077
		62	....	7	4	12	06.64	0.5833
		63	....	4	4	12	07.34	0.3333
		70	....	1	1	07	03.71	0.1429
		71	....	5	3	08	02.04	0.6250
		72	....	1	1	08	09.11	0.1250
		73	....	3	2	08	00.34	0.5000
		74	....	6	1	08	01.66	0.6250
		75	....	1	1	08	02.33	0.1250

Differences in mean calling score were tested between species at the same density. The 1983 *G. pennsylvanicus* data were not included in the between species analyses since there were no comparable data on *G. veletis* for 1983. At high density there was no significant difference in mean calling score between *G. veletis* and *G. pennsylvanicus* males ($t = -0.27$, $df = 51$, $P > 0.05$). Similarly, no significant differences in mean calling scores were observed between *G. pennsylvanicus* low density and *G. veletis* low density A or low density B ($t = 1.83$, $df = 10$, $P > 0.05$; $t = 1.35$, $df = 11$, $P > 0.05$).

The mean displacement between species at high density was not significantly different for males, but *G. veletis* females moved significantly more than *G. pennsylvanicus* females ($t = 2.00$, $df = 51$, $P > 0.05$; $t = 8.92$, $df = 35.1$, $P < 0.001$). No significant differences were found between mean displacements for *G. pennsylvanicus* low density males and *G. veletis* low density A or B males ($t = -0.65$, $df = 10$; $t = -0.15$, $df = 11$, $P > 0.05$). No significant differences were found between mean displacements for *G. pennsylvanicus* low density females and *G. veletis* low density A or B females ($t = 0.13$, $df = 9$; $t = 0.17$, $df = 7$, $P > 0.05$).

The mean number of matings were not significantly different between *G. veletis* high density males and *G. pennsylvanicus* high density males ($t = -0.27$, $df = 51$, $P < 0.05$). Similarly, the mean number of matings were not significantly different between *G. pennsylvanicus* low density males and *G. veletis* low density A or low density B males ($t = 0.58$, $df = 10$; $t = -1.51$, $df = 7.8$, $P > 0.05$). The mean number of matings were not significantly different between *G. veletis* high density females or *G. pennsylvanicus* high density females ($t = 1.34$, $df = 46$, $P > 0.05$). Similarly, the mean number of matings were not significantly different between *G. pennsylvanicus* low density females and *G. veletis* low density A or low density B females ($t = -0.89$, $df = 9$; $t = 1.04$, $df = 7$; $P > 0.05$).

Table XII

The mean ages ($\bar{x} \pm SD$) of crickets entering the outdoor arena for each species and each density. Males (M) and females (F) are indicated along with the number of crickets (N) and the number of crickets captured as adults (CA). Those crickets captured as adults were assumed to be sexually mature (6 days old).

Species	Density	Sex	$\bar{x} \pm SD$	N	CA
G. veletis	High	M	13.0 ± 7.4	26	7
		F	7.9 ± 5.4	23	2
	Low A	M	11.6 ± 0.9	5	0
		F	18.4 ± 7.5	5	0
	Low B	M	47.7 ± 2.3	6	0
		F	43.3 ± 9.8	3	0
G. pennsylvanicus	High 83	M	7.0 ± 2.2	24	14
		F	3.4 ± 2.2	27	6
	High	M	11.7 ± 2.4	27	24
		F	6.0 ± 2.8	25	15
	Low	M	9.0 ± 2.6	7	5
		F	7.3 ± 1.0	6	0