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USING INSECT SOUNDS TO ESTIMATE AND MONITOR THEIR POPULATIONS

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ABSTRACT

Accurate estimates of population size are needed to understand the population dynamics of any species. They are also needed to determine when to implement a specific control tactic, and to measure whether that control tactic has been effective. This paper discusses the use of acoustic signals produced by insects and the feasibility of using these signals to census populations.

Insect sounds are either incidental (produced as a by-product of some activity) or non-incidental (produced to cause a response in some other animal). Incidental sounds differ from non-incidental sounds with respect to several features that are important to using sound to census populations. These features include species specificity, frequency content, ease of localization, distance traveled, and the duration and timing of sound production.

Studies of crickets show that information about which individuals in a population are producing sound, when the individuals produce sound (seasonally and daily), and the probability that individuals produce sound during census periods must be known to accurately estimate the size of a population.

RESUMEN

Se necesitan estimados precisos del tamaño de la población para entender el dinamismo de la población de cualquier especie. También se necesitan para determinar

cuándo es necesario implementar una táctica específica de control, y para medir la efectividad de dicha táctica. Se discute el uso de señales acústicas producidas por insectos y la posibilidad de usarlas en censos de poblaciones.

Los sonidos producidos por insectos son incidentales (producidos como producto secundario de otra actividad) o no incidentales (producidos para inducir una respuesta en otro animal) Los sonidos incidentales difieren de los no incidentales con respecto a algunas características que son importantes en el uso del sonido en el censo de poblaciones. Estas características incluyen especificidad de las especies, el contenido de la frecuencia, la facilidad en localizarla, distancia cubierta, y la duración y lo oportuno del sonido producido.

Estudios hechos con grillos muestran oue se debe de tener información sobre aquellos individuos que producen sonidos en la población, cuándo producen los sonidos (diariamente y estacionalmente), y la probabilidad que los individuos produzcan sonidos durante el censo para poder estimar con exactitud el tamaño de la población.

An often asked question of animal populations is 'Do individuals occur in a certain area?'. While knowing if they occur at a locality is necessary to study them, an even more important question is 'How many animals are there?' or 'What is the number of individuals in a certain area?'. One of the most important properties of any population is its size. Population size or density is information that is needed to understand the dynamics of a population, and it has import in all areas concerned with ecological modeling of populations.

Knowing the dynamics of pest populations is crucial in determining effective control tactics, when to initiate the tactics, and if the tactics, once implemented, are successful. Knowing how a population changes through time must be considered paramount in the management of a pest, and therefore, accurate and precise estimates of pest population density are needed.

For more than 20 years researchers have used sounds produced by insects to detect their presence (Adams et al. 1953, Wojcik 1968; see also Webb, Calkins, Wolfenbarger et al., Toba, Vick et al. this symposium). In contrast, few attempts have been made to use insect generated sound to estimate population size and density.

This paper will discuss the use of sounds produced by insects as a means of estimating their population size and in monitoring the population size over time.

CATEGORIES

In this paper the term "sound" is used in a broad sense: a vibration in some medium. By using this definition, all insects produce sounds during all stages of their lives. These sounds can be classified into two broad categories (Table 1). The first category contains sounds that are by-products of some activity of the animal. They are termed *incidental* sounds. In the second category are sounds that function to produce a particular response in another animal. These *non-incidental* sounds are termed *communication*. In most instances communication occurs between members of the same species, but interspecific communication also occurs, for instance in warning and anti-predator signals. Communication, as it is used here, includes deceptive or false signals (see Burk this symposium). An insect's activity can be monitored by listening for either incidental or non-incidental sounds, and therefore the sounds may be used to census insect populations.

Examples of the two categories of sounds produced by insects are shown in Table 1. The two categories differ in one fundamental aspect. Whereas, sounds used in communication are produced to be heard by another animal, incidental sounds are not.

TABLE 1. EXAMPLES OF SOUND GENERATED BY INSECTS AS BY-PRODUCTS OF SOME ACTIVITY (INCIDENTAL) OR DURING COMMUNICATION (NON-INCIDENTAL).

INCIDENTAL	COMMUNICATION
walking	mating signals
flying (adults)	courtship signals
chewing	territorial displays
swimming	social & subsocial signals
breathing	anti-predator signals
heartbeats	warning signals

CATEGORY DIFFERENCES

Whenever an insect produces sound, that sound is a potential cue that predators and parasites might use in locating prey or hosts (Burk 1982 and refs.). Selection will favor the production of sounds that avoid the attention of predators and parasites. Because communication signals and incidental sounds differ in the function for which they are produced, it might be expected that differences in certain characteristics will be reflected between the categories. Understanding these differences will be important if we are to use insect sounds to monitor and census individuals within a population (Table 2).

Species Specificity: One of the major differences to be expected between the two categories is whether the sound is specific to a particular species. Sounds produced as by-products of certain activities should not be as species specific as those used in communication, especially when the communication mediates sexual pair formation. Specificity is important in whether sounds are suitable to monitor a particular species. When more than one species in an area produce the same or similar sounds it will be difficult to estimate population size for the species of interest. Likewise, it will be difficult to accurately estimate a population size if different members of same population produce different sounds.

Frequency Content: Generally incidental sounds have a broader frequency range than sounds used in communication, and a spectral 'signature' of the sound produced by an insect may be important in its detection and identification. However, the spectrum (relative power at different frequencies) of a sound changes with distance from the source, and is influenced by the particular habitat over which the sound propagates (Marten & Marler 1977, Wiley & Richards 1978). Thus, sounds with a narrow frequency range (non-incidental or communication signals) will be more convenient to use to locate and count individuals in a population.

TABLE 2. GENERALIZED COMPARISON OF CHARACTERISTICS BETWEEN INCIDENTAL SOUNDS AND THOSE PRODUCED DURING COMMUNICATION.

	INCIDENTAL	COMMUNICATION
Species Specificity	low	high
Frequency Range	broad	narrow
Localization	difficult	easy
Distance Traveled	short	long
Duration	short	long
Timing	unpredictable	predictable

Ease of Localization, Distance Traveled and Duration Produced: Because sound may attract the attention of predators and parasites, selection should favor incidental sounds that are not easy to localize, do not travel far, and are produced for short durations and/or at unpredictable times. While sounds used in communication can also be used by predators and parasites, they have evolved to be heard by another animal. Therefore they should be easily localized and produced at a level and for a duration that will allow the intended receiver to detect and locate the sender from some distance. Being able to localize a sound source from a distance is an important consideration when using sound produced by insects to census their populations.

Device Design: The ease and success with which sound can be used in monitoring and estimating populations will depend upon the above characteristics and understanding the contexts in which the sounds are produced. The differences in the two categories of sound will also influence the design of listening devices. Development of listening devices for specific incidental sounds will be difficult and will require in-depth analysis of the sounds (Webb et al. 1988). One potential advantage to sounds that are produced for communication is that an efficient and effective device for listening to the particular sound in the specific environment in which it is produced has already been developed. Natural selection has shaped and modified the ears of the receiving animals to be effective in detecting the sounds. Investigating the properties of the ears of receiving animals may help develop transducers with similar properties. Perhaps the animals' own ear can be used as a 'biological microphone' or transducer (Rheinlaender & Romer 1986, Romer & Bailey 1986).

MONITORING POPULATIONS

Sexual and Life-Stage Differences in Sound Production: To accurately census populations it is necessary to know what individuals in the population are producing sound and how these relate numerically to the rest of the population. In insects that communicate via sound usually only one sex produces the sound. For crickets it is usually the adult male, and to estimate a population size by counting calling males one must know the proportion of adults in the population and the sex ratio of the adults.

Another important consideration for sound censusing is whether different individuals of a population produce different sounds. For example, the characteristics of the sounds produced by insects often depend upon the size of the structures that produce the sound. During the growth of an insect the size of the structures change, and thus, the characteristics of the sound change with the life stage of the insect.

Different life-stages of an insect often occur at the same time of the year. If only one stage produces a particular sound, then information about the life history and the proportion of individuals in each age class must be considered. When certain sounds are characteristic of each stage then the sounds can be used to estimate the number of individuals in each life stage class and will provide information about the distribution of age classes of a population.

Life table data for a hypothetical cricket population, *Gryllus hypotheticus* are shown in Table 3. This species has six life stages from egg to adult. The individuals in the population are distributed amongst the different age classes as shown in column p_x. During a census period 100 calling males are counted. Counting calling males gives a minimum size of the population, however this is far from a more accurate estimate ($N = 166$) calculated using life table statistics of the population. The number of individuals in each age class, n_x, can be estimated using the following equation:

$$n_x = (N \cdot p_x) / p_c \qquad \text{Eq. 1}$$

where n_x is the estimate of the number of individuals in the x age class, N ($=100$) is

TABLE 3. LIFE TABLE STATISTICS AND POPULATION ESTIMATION BASED ON MALE CALLING IN A HYPOTHETICAL CRICKET, *GRYLLUS HYPOTHETICUS*.

Life Stage x	Prop. of Population p_x	Number Counted N	Estimate[1] n_x
1	0.00		0
2	0.05		8
3	0.05		8
4	0.10		17
5	0.20		33
adult	0.60	100	100
TOTAL	1.00		166

[1]The estimate for each age class, n_x, is calculated from Eq. 1 (see text).

the number of individuals counted producing sound, p_x is the proportion of the population in the x age class, and p_c ($=0.60$) is the proportion of individuals in the counted age class. This assumes that all individuals in the age class being counted are producing sound during the census. To make the equation more general the number counted must be divided by the proportion of individuals of the age clas that are calling at the time of the census, r_c. The equation then becomes

$$n_x = (N \cdot p_x) / (p_c \cdot r_c).$$ Eq. 2

For instance, if all adult males are calling during the census and the adult population has a sex ratio of 50:50 (ie. $r_c = 0.50$), then the estimates of each class increase by a factor of 2. The total population is 332. As will be seen below, all males are not always calling during a census, and it becomes necessary to find out what proportion of the individuals are producing sound during a particular time to estimate the population.

Daily Periods of Sound Production: One of the problems with using sound to census populations is the lack of information about when to monitor. If reliable estimates of populations are to be made using the sound produced by insects, then all individuals in the population, or a constant proportion of those individuals, must produce sound at the time of censusing. Almost all activities of animals, especially those of insects, follow a circadian rhythm (Brady 1982). Much has been learned about physiological and environmental influences on these animal rhythms in the laboratory, but only recently have researchers looked at such rhythms with the animal's ecology in mind (Walker 1983). If insect sounds are to be used in estimation of population size, understanding these rhythms becomes necessary.

Species Differences in Rhythms: The periods of sound production are often very specific to a species and may be very different between closely related species. For a particular species these activities can be brief, lasting only a few minutes, or they may be spread throughout the day. For instance, each evening male mole crickets, *Scapteriscus acletus* and *S. vicinus*, begin calling shortly after sunset and continue to call for about an hour (Forrest 1983). This period also corresponds to female flight activity. Similarly, male *Anurogryllus arboreus*, a short-tailed cricket, call for about an hour shortly after sunset (Walker 1980a).

Males of other crickets call throughout the night and these species differ in the proportions of individuals calling at any one time. During an evening, about 25% of the *Anurogryllus muticus* in the population call at the same time (Walker & Whitesell 1982,

Walker 1983). About 50% of the total population of *Gryllodes supplicans* call simultaneously during an evening (Sakaluk 1987). The proportion of male field crickets (*Gryllus integer*, *G. veletis*, and *G. pennsylvanicus*) that call during an evening varies throughout the night and is dependent upon population density. Just after sunset 25-80% of the male population is calling, and there is an increase in calling activity at sunrise when almost 100% of the males are calling (Cade 1979, French & Cade 1987).

These daily calling periods may be changed by several environmental factors. For instance, calling may shift from predominantly nighttime to mostly daytime calling if nighttime temperatures are below those suitable for calling (Alexander & Meral 1967). Rain may also cause shifts in the calling period (Alexander & Meral 1967, Forrest 1983, Walker 1983, Walker & Whitesell 1982). Interaction with other species has also been found to cause shifts in the calling period of some katydids (Greenfield 1988, Latimer & Broughton 1984).

Characterizing the periods of sound production is useful in determining the proper times to census an insect population. Once this characterization has been made it becomes necessary to understand what the individuals in that population are doing during the periods of sound production. However, few data are available on sound production by individual insects under natural conditions.

Individual Differences in Rhythms Within Days: Calling periods sometimes vary between individuals within a population. Individual male mole crickets, *Scapteriscus acletus* and *S. vicinus*, have significantly different times that they begin their evening calling (Forrest 1983). Walker & Whitesell (1982) studied calling of individual male *A. muticus*. They found males that called near burrows generally called during the same period and for the same duration from night to night, but individuals differed in both respects. Some males were early evening callers while others called late in the evening. Other males that were not associated with burrows were more variable in their calling times and durations, often moving between census periods. One male moved more than 50 m during a night of singing.

Individuals Differences in Rhythms Between Days: Another important aspect of sound production is the variability in sound production from one day to the next. To reliably quantify population density using the sounds that are made by individuals in the population, the variation in sound production by individuals must be known. The probability of calling from night to night varied among individual male mole crickets monitored for periods of as long as a month (Fig. 1). One *S. vicinus* male called only 26% of the nights compared with other males that called as much as 79% of the nights during the same period. For all males combined, *S. acletus* males called an average of 78% of the suitable nights (>16°C and no rain) and *S. vicinus* males averaged 76%. All males were kept outdoors in 19-liter buckets of soil and were provided with enough food so as not to limit energy needed for calling (see below).

Effects of Density and Nutrition on Sound Production: If sounds are to be used to measure population size and density, the influence of population size or density on the production of sound must be known. This too will depend upon the context in which the sound is produced. For incidental sounds, the number of sounds detected should increase linearly with increasing density. In other contexts (eg. aggressive sounds), the proportion of the population producing sounds may be low under low density situations and may then increase dramatically (exponentially) as the population density increases. The reverse may be true for sounds such as the calling songs of crickets. In this case, the proportion of the population calling may decrease as the density increases because of an increase in attacks from neighbors (see Burk 1983 and this symposium), or because the sounds are energetically expensive to produce and the high density situation makes another strategy of finding mates more profitable.
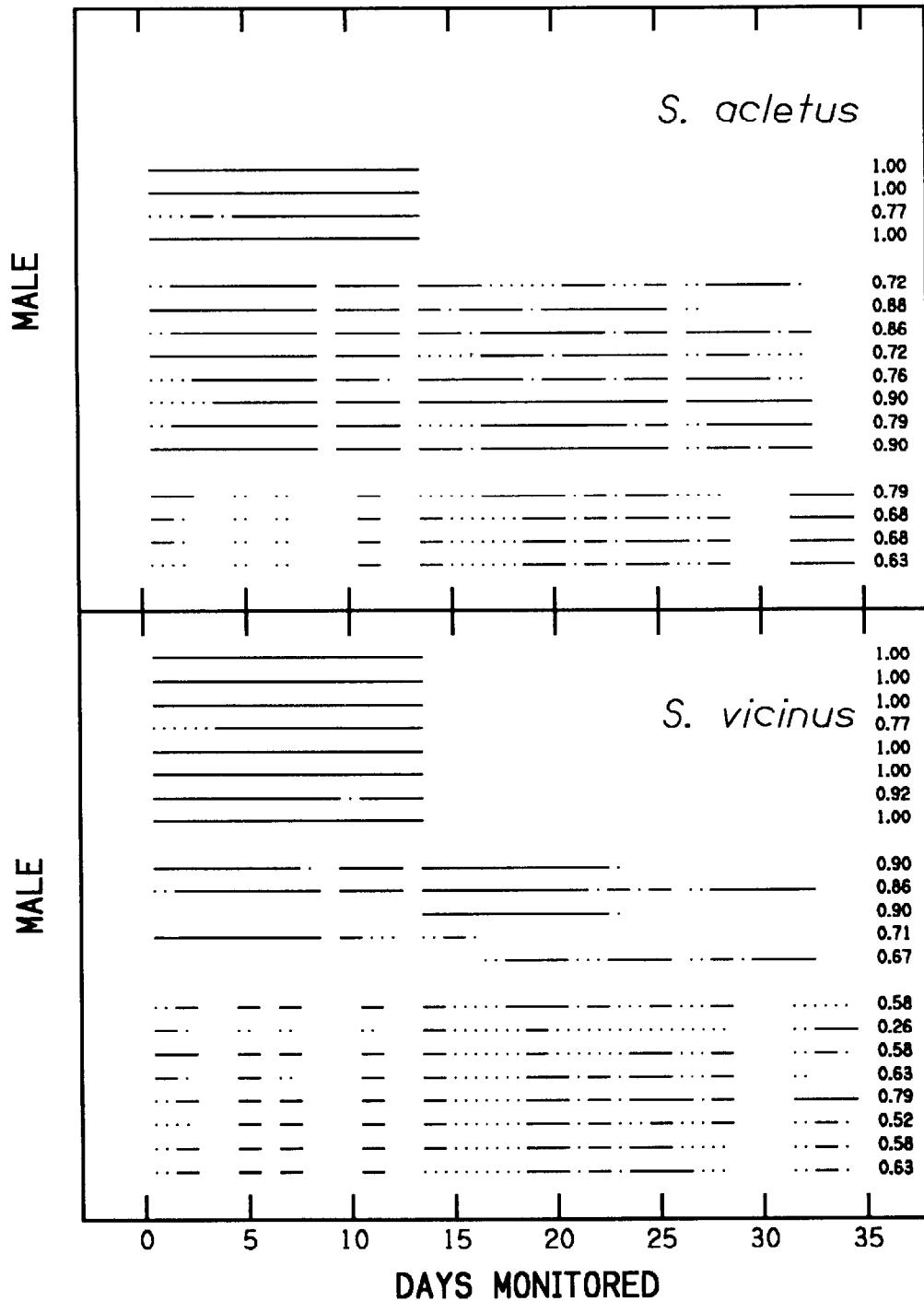
Fig. 1. Daily calling probabilities of individual male *Scapteriscus acletus* and *S. vicinus*. Each horizontal line represents data from a single male (N = 16 *S. acletus* = 21 *S. vicinus*). Solid lines are days males called, dotted lines represent days males did not call, and open area show days males were not monitored. Males are grouped according to dates monitored. Top 4 *S. acletus* and 8 *S. vicinus* were monitored 10-22 Apr 1979, middle 8 *S. acletus* and 5 *S. vicinus* were monitored 18 May-18 Jun 1979, and bottom 4 *S. acletus* and 8 *S. vicinus* were monitored 7 Mar-9 Apr 1980. Numbers at the right are the proportion of suitable (>16°C and no rain) nights that each individual called.

Data for calling in two mole crickets as a function of male density (Shaw 1981, personal communication) are shown in Figure 2. Male mole crickets were place at various densities in 10 m² outdoor arenas. The number of individuals calling in the arenas was monitored on successive nights. The maximum percentage of males calling decreases exponentially with increasing density and reaches a constant level of about 10% calling at high densities (Fig. 2). These data can be fit with an exponential decay function of the form

$$P(x) = \alpha / (1\text{-}e^{(-x/\tau)}),$$ Eq. 3

where P(x) is the proportion of the total calling at density x, α is the asymptotic value of the function as x becomes large, and τ is the function's rate of decay. The dotted line in Figure 2 is the least-squares fit to all data using the above equation (α = 0.11 and τ = 2.00). Walker (1980b, personal communication) has shown that the presence of conspecific male and female mole crickets will decrease the proportion of nights individual males call by as much as 70%.

Nutrition will also influence sound production. If the sounds to be monitored are produced because of feeding activity, then abundant food supplies could cause a decrease in movement associated with acquiring food. Sound production caused by the movement of the insect would decrease. However, if the food has little nutritional value, then the individual must consume more and feed more often to make up for the low nutritional intake (Slansky 982). Sound production would increase. If the sounds are energetically expensive to produce, poor nutrition may decrease the production of such sounds. Cal-
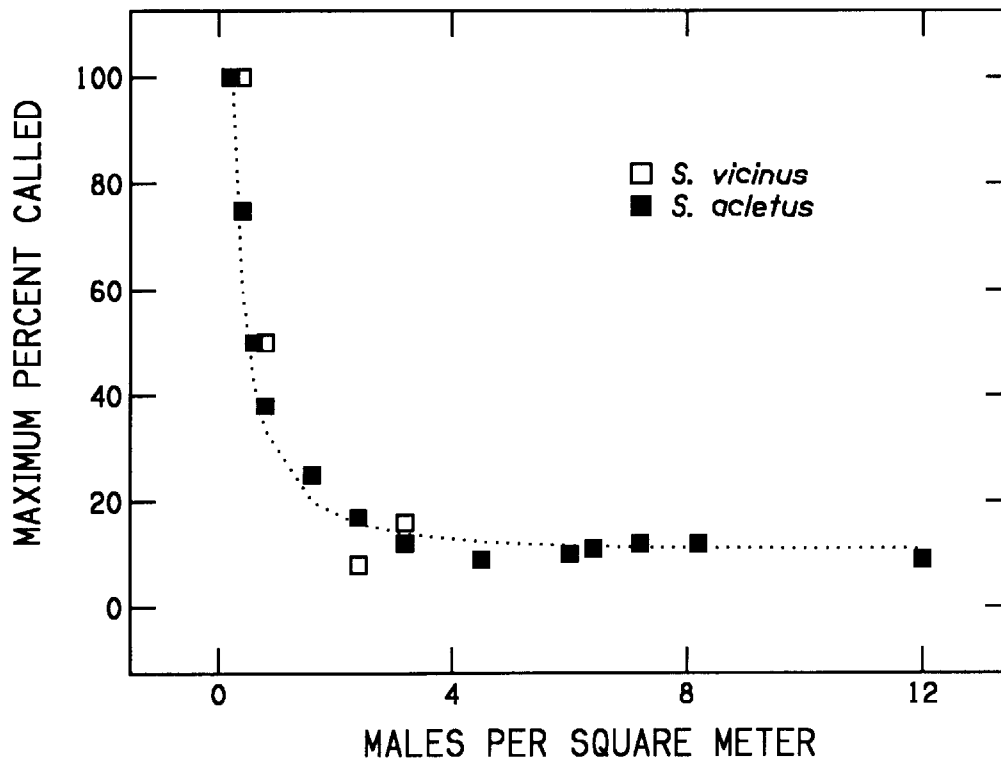

Fig. 2. Maximum percent of male mole crickets calling in 10 m² outdoor arenas plotted as a function of male density in the arena. Dotted line is a least-square fit to the data using α = 0.11 and τ = 2.00 as parameters of Eq. 3 (see text, Shaw 1981, personal communication).

ling male crickets use more than 10 times the energy used during resting (Prestwich & Walker 1981, Kavanagh 1987). Walker (1980b, personal communication) found that the proportion of nights that male mole crickets called decreased from about 80 to 30% when they were deprived of food (Fig. 3).

Seasonal Periods of Sound Production: Besides daily periods of sound production, animals very often have specific seasonal periods. This is especially true of insects where certain life stages are only present during specific times of the year. Crickets are a good example. It has become common practice to use counts of calling crickets to determine life cycles, seasonal maturation, and adult activity periods of crickets (Alexander 1962, Alexander & Meral 1967, Walker 1983). Because adult males are the only part of the population that produce calling songs, the season of sound production generally corresponds to the adult activity of the species. However, in some species males are rarely heard at certain times of the year even though adult males are abundant in the population. This may be caused by the abundance of acoustically orienting parasitoid flies present at this time of the year (Burk 1982 and refs.). The seasonal activity of sound production must be considered if acoustic signals are to be used to monitor populations.

Geographic Ranges and Population Spread: Two very practical uses of monitoring insect populations based upon the sounds produced are determining geographic ranges and measuring the spread of populations. The use of acoustic signals to determine population ranges and their spread have been used extensively in insects that use sound to com-
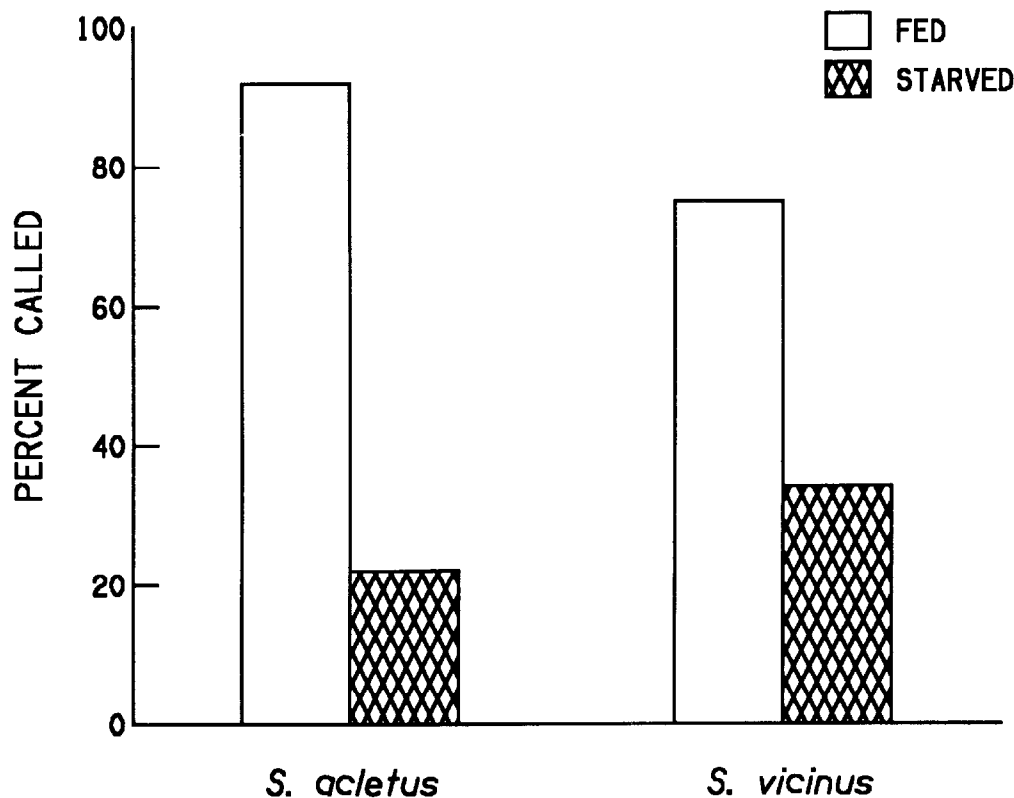

Fig. 3. Bars show how starving influences the nightly calling of male mole crickets. Percent of nights called is significantly decreased for males that are deprived of food (hatched bars) compared with males provided food (open bars) (Walker 1980b, personal communication.

municate over long distances (Alexander 1962). The signals of particular species are easily distinguished, and to determine a species geographic range it is a simple matter of cataloguing the localities where that species sound has been heard. This technique could also be used for incidental sounds, provided a suitable detection device can be produced. This application will increase our ability to monitor the spread of migratory species and pest species that have been introduced to new areas.

CONCLUSIONS

Monitoring and estimating populations is important in the management of any pest species. Because sound of one form or another is produced by all insects, a promising area of research is to use sound in detecting, censusing, and monitoring insect populations. An understanding of the sounds, knowing the contexts in which they are produced, and knowing how the production of sound relates to the ecology and biology of the animals will improve population estimation. In most instances, the population size will be underestimated. It is only when insects of different species produce indistinguishable sounds or when individuals are very mobile and are counted more than once that a population would be overestimated. Thus, the use of sound censusing provides baseline data for estimating population size. Where exact counts are not a necessity, monitoring the sounds of insects can provide much information about a species life history. Using sound should become an increasingly important tactic for monitoring population spread and has application in monitoring the movement of migratory pest species.

ACKNOWLEDGMENTS

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