Movement and Spacing of Singing *Amblycorypha parvipennis* Males[1,2]

KENNETH C. SHAW, ROBERT C. NORTH,[3] AND ANDREW J. MEIXNER[4]

Department of Zoology, Iowa State University, Ames, Iowa 50011

ABSTRACT

The nature of movement and spacing of flightless, singing *Amblycorypha parvipennis* Stål males was studied by marking and relocating singing males. Aggregation is, at least in part, passive because males preferentially select certain tall forbs, bushes, and trees as singing sites. Results of acoustical interaction of a pair of males at varying distances and distribution of nearest-neighbor distances were used to operationally define choruses—within which males proved to be uniformly distributed. Uniform distribution suggests territoriality, and the rarity of overt threat and fighting suggests that males space themselves by the sounds of other males. Although most males occupied a singing site for at least several hours an evening, males moved an average of 12.0 m in 24 h, a greater distance than other katydids studied. Movement was variable, with males moving within choruses, moving to smaller or larger choruses, or becoming solo males. Movement into and out of various resource patches suggests that males may monitor density of males and move away from or toward them. Extensive movement also may be a result of males moving to the sounds of females, which produce short ticks in response to male phrases, and males searching for females under conditions of high density. We speculate about the evolution of male acoustical interaction and the means by which females choose mates within a chorus.

Insect choruses[5] are aggregations; i.e., the individuals are not distributed randomly or uniformly throughout all available habitats. Aggregation of singing insects has been statistically confirmed for two species, *Gryllus integer* (Scudder) (Cade 1976) and *Teleogryllus commodus* (Walker) (Campbell and Clarke 1971, Campbell and Shipp 1979). Males may aggregate because they are attracted to the sounds of other males (i.e., active aggregation) (Alexander and Moore 1958, Morris 1972, Ulagaraj and Walker 1973, 1975, Cade 1979) or because they are attracted to feeding or oviposition sites of females (i.e., passive aggregation) (Spooner 1968, Feaver 1977).

Alexander (1960) suggested that, within male aggregations of singing crickets and katydids, males are probably repelled by sounds of adjacent males. Such repulsion has been supported by observations of Feaver (1977) and experimental studies by Campbell and Shipp (1979) and Thiele and Bailey (1980). Repulsion should result in uniform spacing within aggregations, and this has been confirmed statistically for *Orchelimum gladiator* Bruner and *Conocephalus nigropleurum* Bruner (Morris 1967), *Ligurotettix coquilleti* McNeill (Otte and Joern 1975), *Teleogryllus commodus* (Campbell and Shipp 1979), *Neoconocephalus nebrascensis* (Bruner) (Meixner and Shaw 1979), *Gampsocleis glabra* (Herbst) (Latimer 1980), and *Mygalopsis marki* Bailey (Thiele and Bailey 1980).

Little is known about the mobility and spacing dynamics of individual males within orthopteran choruses. Based on laboratory studies and field records of unmarked males, Alexander (1960, 1961) suggested that chorusing crickets and katydids are territorial, usually singing from the same perches or burrows each night. However, more recent studies have suggested that singing males·of a number of species are much more mobile and, although they may remain in restricted localities, almost all males change singing sites within 24 to 48 h (Morris 1967: *Conocephalus nigropleurum, Orchelimum gladiator,* and *Metrioptera roeseli* Hagenbach; Cade 1976: *Gryllus integer;* Feaver 1977: *Orchelimum nigripes* Scudder, *O. vulgare* Harris, and *O. gladiator;* Kleyla and Dodson 1978: *Scapteriscus aeletus* Rehn and Hebard, *S. vicinus* Scudder; Campbell and Shipp 1979: *Teleogryllus commodus;* Meixner and Shaw 1979: *Neoconocephalus nebrascensis;* Walker 1980: *Anurugryllus arboreus* Walker).

Males of *Amblycorypha parvipennis* Stål are slow moving and flightless. Adjacent males alternate production of 4- to 5-sec (23° C) phrases, and a male frequently initiates his phrase before the termination of a neighbor's phrase. Phonatomes (phonatome = sound produced by one cycle of wing movement) within overlapped phrases are synchronized (Fulton 1928). This study analyzes the nature of spacing and movement of individually marked, singing *A. parvipennis* males and shows that (1) aggregation is, at least in part, passive because of preference for singing from certain plants, (2) aggregations are subdivided into groups or choruses within which males are uniformly distributed, and (3) most males change perches within 24 h, frequently moving remarkably long distances for such slow-moving and flightless insects.

Materials and Methods

The population of *A. parvipennis* we studied re-

sided in an old field (20,613 m²) on the north edge of Iowa State University. The dominant plant species were smooth brome, *Bromus inermis* Leyss, and bluegrass, *Poa pratensis* L., with a considerable amount of wild strawberry, *Fregaria virginia* Du chesne. In 1978 there were prominent patches of sweet clover, *Melilotus officinalis* (L.) Lam. and *Melilotus alba* Desr., horsemint, *Mentha longifolia* (L.), wild lettuce, *Lactuca canadensis* (L.), bull thistle, *Cirsium vulgare* (Savi) Tenove, and poison ivy, *Rhus radicans* L. The southern one-fourth of the field includes a 23-m, east-west strip of scattered Norway spruce, *Picea abies* (L.), 1.5 to 3.0 m in height. The northern three-eighths of the field was dominated by little ragweed, *Ambrosia artemisiifolia* (L.), some giant ragweed, *A. trifidium* (L.), and a prominent patch of horseweed, *Erigeron canadensis* (L.)

The field was bordered by fences on the east, south, and west. The field terminated to the north in land razed for construction. To the east, a woody hillside sloped gently to a small stream. A dense stand of honey locust, *Gleditsia triacanthos* L., and poison ivy lay south of the field, and the lawn of the university housing terminated the field on the west.

To identify movement and distribution of individual katydids, singing males were spotted with a flashlight, captured by hand, and coded with spots of various colors of Testor's® enamel paint on the tegmina and pronotum as well as with small cuts on the tegminal margins. Successive locations of marked males were indicated by metal stakes bearing numbered flags. Locations of singing males were plotted on graph paper by tape-measuring individual sites to north-south and east-west lines of metal stakes.

Male spatial distribution over the whole field and within selected areas was determined by using the nearest-neighbor method derived by Clark and Evans (1954). The statistic R is a measure of the degree to which the observed distribution departs from random expectations with respect to the distance to nearest neighbor. R is equal to the ratio of observed-to-expected mean nearest-neighbor distances (NND); i.e., $R = \bar{r}_A/\bar{r}_E$.

In a random distribution, R = 1. When individuals are maximally aggregated, R = 0; i.e., when all individuals occupy the same locus, distance to nearest neighbor is 0. In a perfectly uniform population, individuals will be distributed in hexagonal patterns with every individual (except those at the periphery) equidistant from six other individuals. In this case R = 2.1491.

The significance of the departure of $\bar{r}_A$ from $\bar{r}_E$ was tested by calculating c, the standard variate of the normal curve; c = 1.96 and 2.58 for 5 and 1% levels of significance, respectively.

Results

Males of *A. parvipennis* call after dark from herbaceous vegetation and occasionally from bushes or trees. Singing males were first heard on 21 June 1977

and 3 July 1978. In 1977, a dry summer, the population peaked at 16 to 20 males compared with approximately 80 singing males in 1978. Increased density in 1978 was associated with a smaller mean NND ($\bar{r}_A = 7.1 \pm 4.7$ m) than in 1977 ($\bar{r}_A = 12.2 \pm 9.4$ m). In 1977, the population rapidly declined and the last singing males (three) were recorded on the night of 7 July. In 1978, the last data were recorded on 7 August with 23 singing males; 1 male was heard singing on 11 September.

In 1977, the population had peaked by the time of the first census on 23 June. On this date males were distributed across the northern and central portions of the field. Several more males were singing in the ragweed but could not be located. By 28 June and thereafter, most identified males were near or on shrubs and vines along the southern fence line, and some unidentified males were in the ragweed.

In 1978, males first appeared in a narrow strip of brome and forbs along the northern roadway (group N) and within or near a dense patch of horsemint in the large patch of brome and forbs covering most of the southern portion of the field (group S) (Fig. 1). At peak density, males had spread throughout much of the brome-and-forbs areas, and some males had ventured into the ragweed-and-forbs areas (Fig. 2). Very few males moved into the area of smooth brome and bluegrass separating groups S and N (Fig. 2).

Concentration of males in the brome and forbs resulted in an aggregated population throughout the season; in other words, $\bar{r}_A$, observed mean NND, always significantly exceeded $\bar{r}_E$, expected NND, if population distributed randomly (Fig. 3) (area = 20,613 m²; N = 19 to 73; density = 9.2×10^{-4} to 37.8×10^{-4}; $\bar{r}_A = 5.30$ to 8.76; $\bar{r}_E = 8.12$ to 14.1; R = 0.452 to 0.878; c = −4.47 to −2.07; P < 0.05 to <0.01). An analysis of nightly distribution (12 nights for group S and 7 nights for group N) showed a wide range of variation in frequency of singing male occupancy of quadrats (15.2 by 15.2 m) (Fig. 4). The highest frequencies of quadrat occupancy for group N were in the narrow strip of tall herbs just south of the northern car pathway. This strip contained stands of wild lettuce, clover, and thistle. In group S, the two quadrats with the highest frequency of occupancy contained a dense stand of horsemint; smaller clumps of horsemint, clover, and some thistle were scattered throughout this brome-and-forbs area. One frequent singing site (quadrat with N = 26, Fig. 4) was a Norway spruce surrounded by clover.

Singing males were found on a variety of plants, usually at a height of 0.2 to 1.2 m from the ground. Smooth brome and sweet clover were the predominant singing sites, with thistle, wild lettuce, and a variety of trees, shrubs, and tall weeds also relatively common (Table 1). During the summer of 1980, estimates of plant species' frequencies were made by randomly dropping a quadrat (25 by 25 cm) within 85 quadrats (15.2 by 15.2 m or equivalent) of the study area. These data suggest that *A. paravipennis*
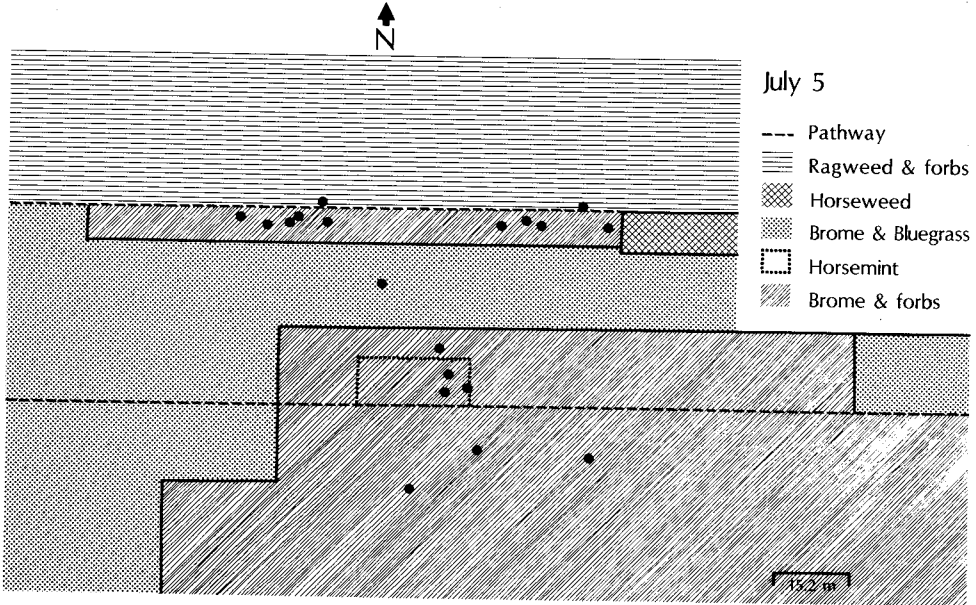
FIG. 1.—Distribution of *A. parvipennis* males in an old field on 5 July 1978.
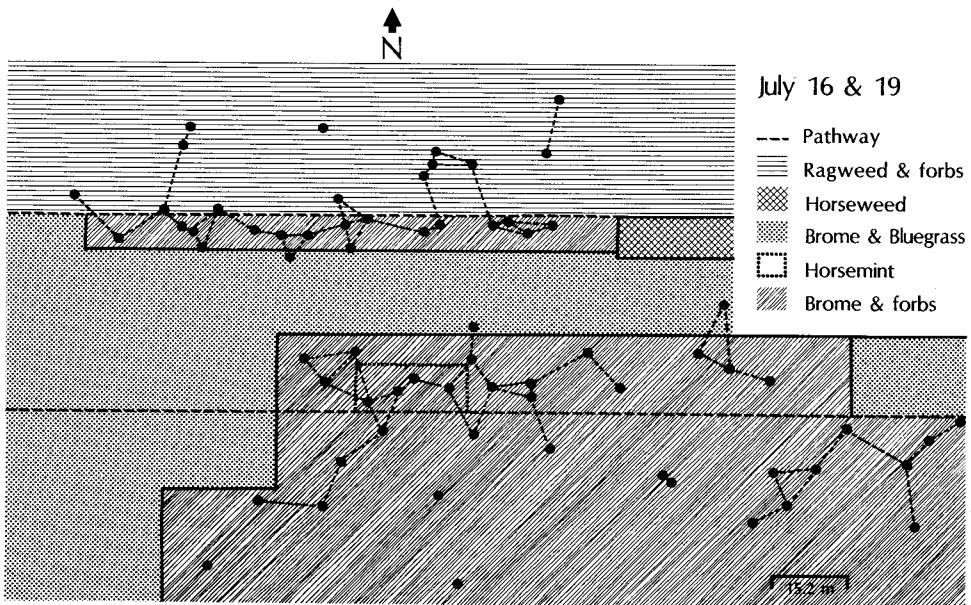

FIG. 2.—Distribution of *A. parvipennis* males in an old field on 16 and 19 July 1978. Closed circles connected by dashed lines represent interanimal distances of 13.7 m or less.
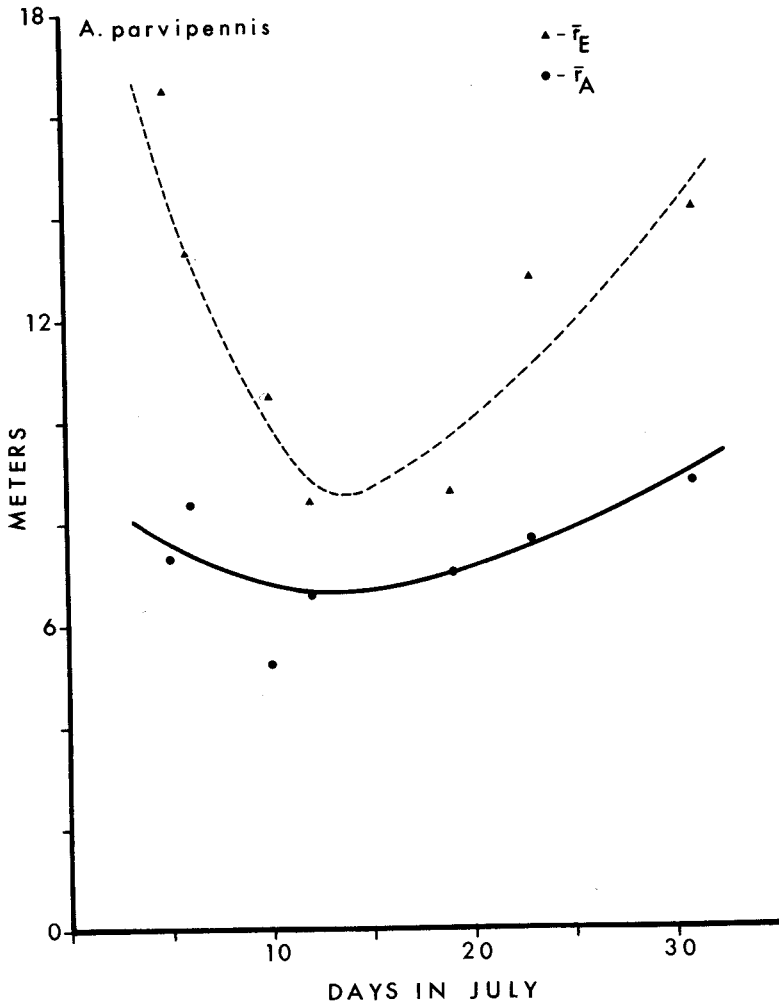
FIG. 3.—Comparison of $\bar{r}_A$ and $\bar{r}_E$ for total population of *A. parvipennis* in old field during summer of 1978.

males preferentially selected sweet clover, trees and shrubs, and wild lettuce as singing sites (Table 1). We also believe that males also preferred horsemint and thistle. Horsemint is lost in the category of tall herbs because it was unidentified in 1978. Thistle was much more widespread in 1980 than in 1978. In contrast, singing males occurred much less frequently than expected on smooth brome, wild strawberry, bluegrass, and poison ivy if singing sites were selected randomly (Table 1).

Using two areas whose perimeters were determined by quadrats (7.6 by 7.6 m) of peripheral singing males of groups S and N, distributions were analyzed for nights of peak density. Group S showed uniform distribution on 2 nights (13 July, area = 7141.9 m², N = 46, R = 1.223, P < 0.01; 16 July, area = 7141.9 m², N = 41, R = 1.251, P < 0.01) and random distribution on 2 other nights; group N showed random distribution on 2 nights of peak density. Random distributions probably were the result

of smaller NNDs in areas of high concentration of preferred plants (Fig. 2). Thiele and Bailey (1980) point out that open spaces and associated clumping within aggregations result in an underestimation of R.

Could clumps within aggregations be choruses? Choruses of synchronizing species are obvious (e.g., *Neoconocephalus nebrascensis* Meixner and Shaw [1979]), but what about alternating species where individuals are alternating with one or a few nearest neighbors? In preliminary experiments with a single pair of *A. parvipennis* males, the males were recorded singing at intermale distances of 3.0, 9.1, 12.2, and 15.2 m. At 3.0, 9.1, and 12.2 m, the two males reciprocally initiated their phrases before their partner terminated his phrase 41 to 50% of the time; at 15.2 m this occurred only 6% of the time. Also, both katydids shortened their phrases at intermale distances of 15.2 m (katydid A, mean phrase length was 5.1 sec; katydid B, 4.4 sec) compared with 9.1
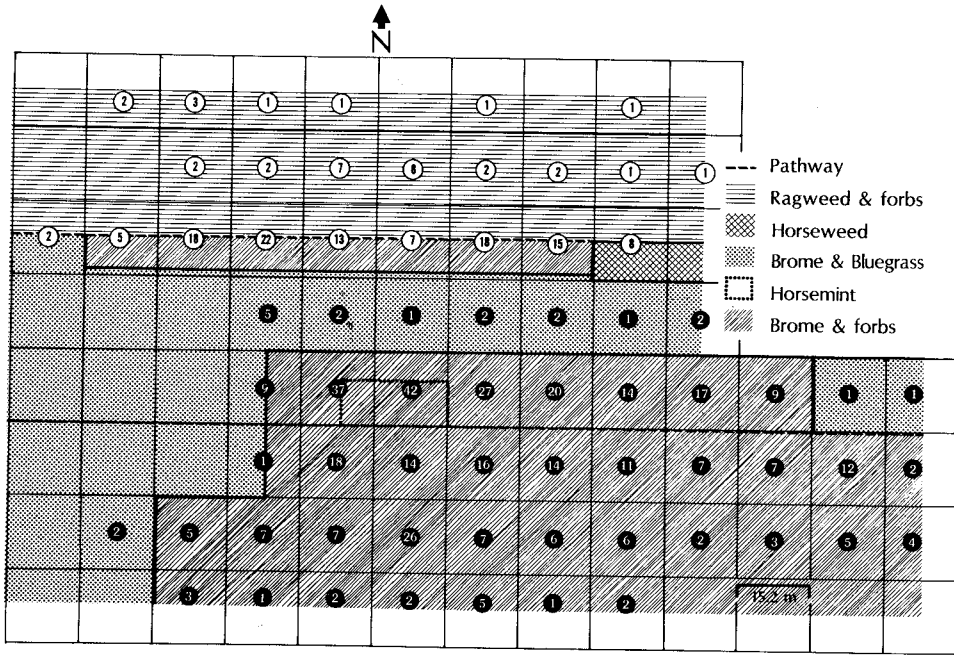
Fig. 4.—Quadrat (15.2 by 15.2 m) distribution of singing *A. parvipennis* males during summer of 1978. White-in-black numbers indicate total number of group S males in each quadrat for 11 nights. Black-in-white numbers indicate total number of group N males in each quadrat for 7 nights.

Table 1.—Frequency of plants in old field and as singing sites

Plant species	Singing sites (%) (n = 3,880)	Plants sampled (%) (n = 2,315)	Quadrats containing plants (%) (n = 85)
Smooth brome	21.1	44.1	76.5
Sweet clover	20.6	0.1	2.4
Tall forbs	14.4	5.2	61.2
Trees and shrubs	13.9	0.6	4.7
Wild lettuce	9.5	0.1	3.5
Bull thistle	7.0	0.4	9.4
Wild strawberry	4.9	5.5	44.7
Ragweed	4.6	12.7	24.7
Bluegrass	1.3	27.2	64.7
Poison ivy	1.0	1.0	25.9
Miscellaneous (small forbs, grape, *Rubus*)	1.5	2.2	20.6

to 12.2 m (katydid A, mean phrase length 6.1 to 6.4 sec; katydid B, 5.0 to 5.6 sec).

At present we have no data for interanimal distances between 12.2 m and beyond 15.2 m. However, because the frequency of NNDs between 10.7 and 12.2 m is equivalent to that between 12.2 and 13.7 m, after which there is a marked drop off (Fig. 5), we suggest that two *A. parvipennis* males may acoustically interact up to maximum interanimal distances of 13.7 m.[6] When all males with NNDs of 13.7 m or less were connected, most males (93%)

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[6] Actual distance between acoustically interacting individuals would be dependent upon a number of factors including variation in environmental sound attenuation and acoustical output by individual katydids.

were within choruses of 2 to 27 males (Fig. 2). Perimeters were drawn around choruses as around groups, and analysis of distribution of singing males within the six largest choruses (N = 11 to 27) showed uniform distribution (population S: 13 July, N = 12, area = 871.0 m^2, R = 1.853, P < 0.01; 13 July, N = 21, area = 1567.7 m^2, R = 1.411, P < 0.01; 16 July, area = 1451.6^2, R = 1.598, P < 0.01; 17 July, N = 11, area = 580.6 m^2, R = 1.835, P < 0.01; 17 July, N = 19, area = 1393.5 m^2, R = 1.262, P < 0.05; population N: 19 July, N = 27, area = 1219.4 m^2, R = 1.405, P < 0.01).

Although males usually remained at singing sites during the time we marked and staked (2000 to 2300 h, CST), most males had moved a considerable distance by the time they began singing 24 h later or on a subsequent night. Males averaged 7.1 m/24 h in 1977 and 12.0 m/24 h in 1978 while moving from 0 to 86 m between singing sites in 24 h (Table 2). On several occasions, males were observed walking through the grass, silent or singing, between 2100 and 2300 h (CST). Nine animals relocated within 2 to 3 h after marking moved from 0 to 10.7 m, averaging 4.9 m. Assuming a maximum rate of 5 m/h, it would take a continuously moving male, moving in a straight line, more than 17 h to walk 86 m.

Average movement between capture and recapture dates separated by 1 to 21 days ranged from 7.1 m for 24 h to 28.7 m for 3 to 7 days in 1977, and from 12.0 m for 24 h to 70.8 m in 15 to 21 days in 1978 (Table 2). For 1977, a regression analysis showed that total distance of movement significantly
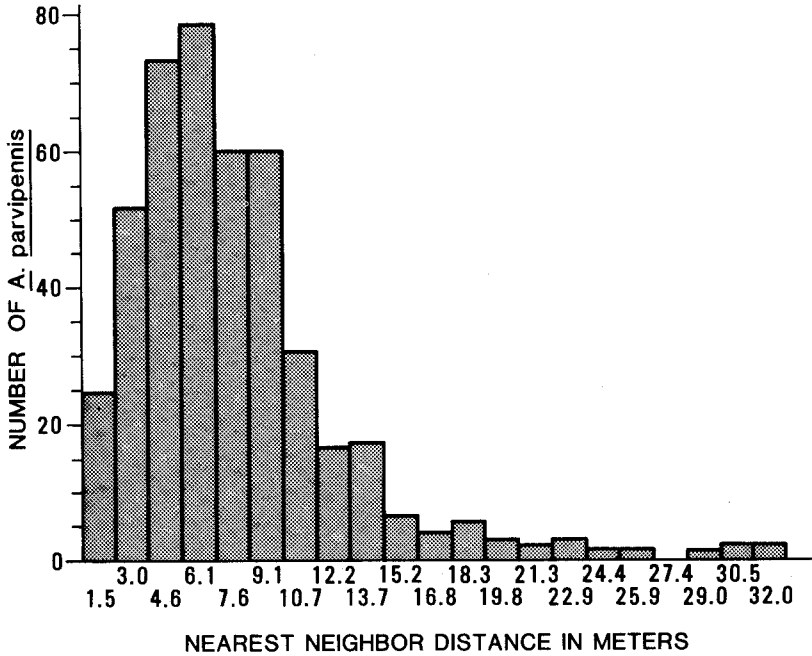
FIG. 5.—Distribution of NNDs of singing *A. parvipennis* males for summer of 1978.

Table 2.—Distance between successive locations of marked katydids for 1977 and 1978

| Year | Time lapse (days) | n | Distance (m) between successive locations | |
			Range	Mean
1977	1	8	1.1–18.3	7.1 ± 5.8
	2	4	1.8–31.4	17.5 ± 12.9
	3–7	6	7.9–47.6	28.7 ± 17.8
1978	1	65	0–86.0	12.0 ± 13.1
	2	27	3.5–79.3	22.2 ± 21.8
	3	38	1.1–84.1	18.1 ± 19.9
	4	10	3.5–70.4	24.9 ± 19.9
	5	7	4.9–39.6	23.7 ± 12.5
	6	21	0.4–70.4	18.1 ± 15.9
	7	24	1.2–73.6	23.8 ± 19.2
	8	9	4.9–106.4	36.0 ± 32.8
	10	7	8.5–24.8	18.0 ± 5.5
	11	5	6.1–50.0	17.3 ± 18.5
	12	6	32.3–81.7	48.2 ± 19.1
	14	8	3.8–92.1	35.5 ± 27.2
	15–21	5	39.6–93.0	70.9 ± 26.0

increased with time (m = 5.756, b = 2.309, r = 0.745, P < 0.01). Males moved to the edge of the field, and the southern movement was most apparent. Singing males were first heard between the middle and northern pathways on 21 June. No males were heard in the southern one-third of the field until 28 June. By 31 June, one-half (8 to 10) of the males singing in the old field were along the fence on the southern edge of the field.

The regression of distance on time was not sig-nificant in 1978. Movement was predominantly across and along or parallel to the northern and middle pathways (Fig. 6–7), resulting in many ka-tydids being closer to the marking site on some nights and further away on others. Only 7 of 85 katydids recaptured one or more times after marking moved from one group to another (e.g., katydids no. 19, 84, 67, Fig. 7). However, there was expansion of the groups from early in the season to time of peak population. Group S expanded east, west, and south, whereas group N expanded mostly north into the ragweed and forbs (cf. Fig. 1 and 2).

Only 4 of 66 males, resighted in 24 h, stayed within 1 m of their singing site on 2 successive nights. How-ever, if $\bar{r}_A$ is taken as a measure of territory size (Feaver 1977), then one-half of these 66 males moved a distance equal to less than the $\bar{r}_A$ of 7.1 for 1978. Some males did stay for several days in rela-tively restricted areas (e.g., katydid no. 19, Fig. 7). However almost all males monitored for more than a few nights moved relatively long distances (i.e., greater than 7.1 m). Males moved into and out of preferred areas. Males in preferred areas moved out to join small choruses (e.g., katydid no. 66, Fig. 6) or to become solo males (e.g., katydid no. 3, Fig. 6). Solo males (e.g., katydid no. 67, Fig. 7) or males from outlying small choruses (e.g., katydid no. 80, Fig. 6) moved into preferred areas. Extensive move-ment of males resulted in continual change of indi-vidual males and positions of males within choruses as well as in the shape of choruses.
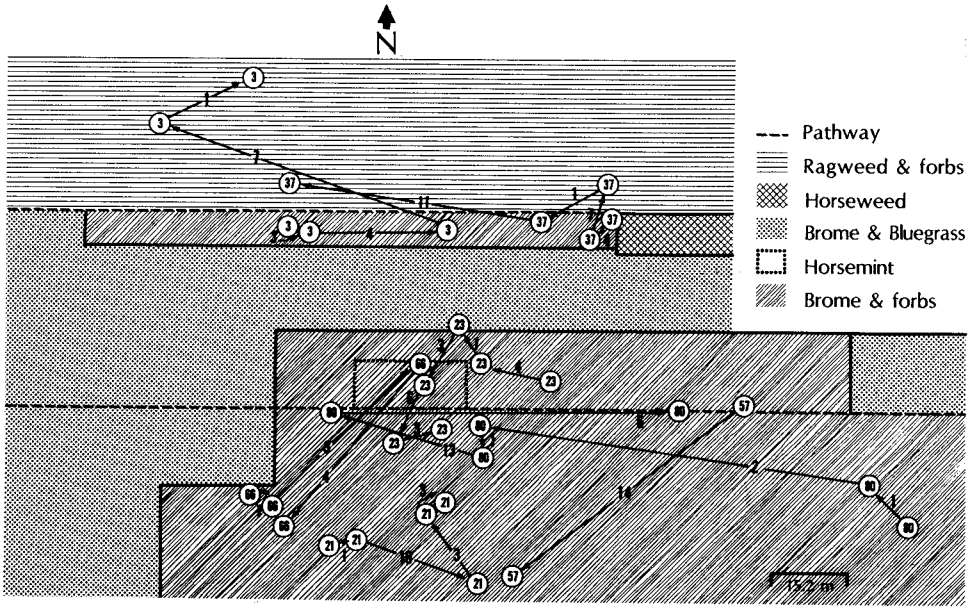
FIG. 6.—Selected examples of changes in singing sites chosen from 85 *A. parvipennis* males captured one or more times after marking during summer 1978. Numbers on arrows indicate days between successive singing sites.
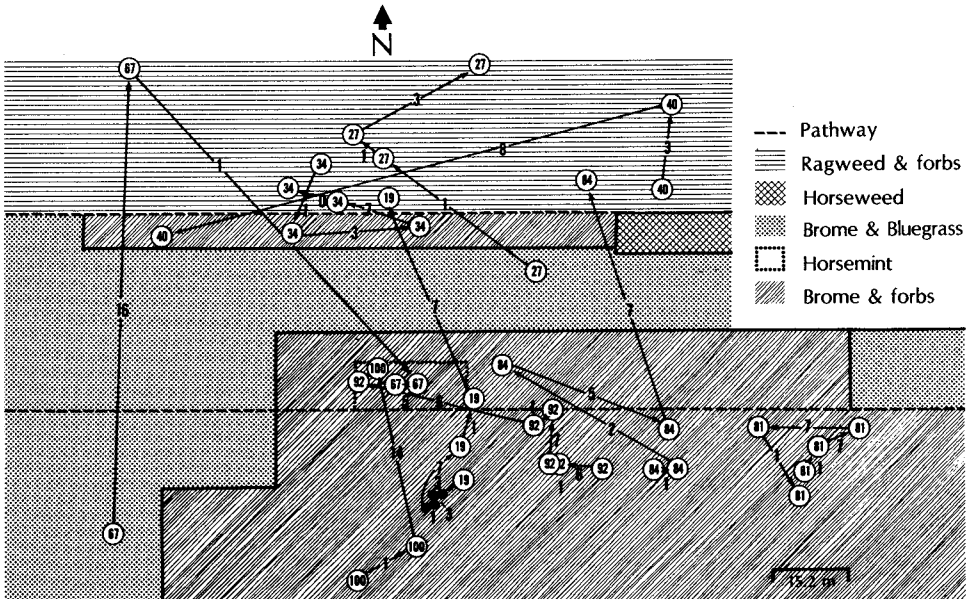

FIG. 7.—See legend to Fig. 6.

Discussion

Preferential selection of certain plant species for singing sites suggests that at least some males of *A. parvipennis* passively aggregate around and within resources valuable to females. Feaver (1977) found that males of the genus *Orchelimum* congregate in areas where females are most likely to occur, i.e., in or near areas where females feed and oviposit. Males of *Inscudderia strigita* (Scudder) also sing from plants used by females for food and oviposition sites (Spooner 1968). We have observed *A. parvipennis* males and females feeding on flowers of sweet clover and horsemint, favorite singing sites of males. These forbs are considerably taller than the predominant brome and bluegrass and may be more efficient signal broadcasting sites. Efficient broadcasting may be the basis for males moving into and singing from trees and bushes. Active aggregation cannot be dismissed without experimental studies.

Although some *Orchelimum vulgare* males move into resource patches before other males begin to sing (Feaver 1977), *O. vulgare* males also are attracted to sounds of other males (Morris 1972). It is possible that *A. parvipennis* males locate likely areas to encounter females by moving to the sounds of calling males. If active aggregation does occur, then aggregates of *A. parvipennis* males would qualify as "resource-based leks" (Alexander 1975).

Uniform distribution within choruses suggests that males are territorial (Davies 1978), as does the production of conspicuous signals (Fretwell 1972) which probably serve to repel conspecific males (Alexander 1960, Campbell and Shipp 1979, Thiele and Bailey 1980). Other definitions (e.g., Brown 1975) stress occupation of fixed areas and conspicuous signals combined with threat and attack. In four summers of field observations, we have observed what appears to be threat and fighting on only one occasion. Males grappled with cerci and fore- and hindlegs, and one male bit the other on cerci and abdomen. This interaction was probably precipitated by the proximity of a female which one of the combatants eventually courted. Thiele and Bailey (1980) have not observed physical contact between males of the conocephaline *Mygalopsis marki* Bailey. Failure to defend and occupy sites for more than 24 to 48 h suggests that female oviposition or feeding sites or both are abundant and therefore uneconomical for males to defend (see similar arguments for *Orchelimum* spp. [Feaver 1977] and some species of dragonflies [Campanella 1975]).

Males also may move in response to increasing density of competing conspecific males. Singing males first appeared in the most suitable habitats, i.e., those with the highest density of plants which serve as feeding and probably oviposition sites for females (Fig. 1). However, as density increased, the suitability of the initially preferred habitats may have decreased making other resource patches equally suitable (Fretwell 1972, Otte and Joern 1975). With changing population density and a corresponding change in suitability of various resource patches, males may monitor density of males in various resource patches moving into or out of them.

Alexander (1975) and Otte (1977) have suggested that at high densities males may benefit more by searching than by calling. During 1978, we observed at least nine moving silent or calling males. Singing males were considerably more dense and NNDs were significantly less in 1978 than in 1977. This increased density and competition may have effected searching for females and contributed to change in location of singing sites.

However, other species of singing Orthoptera also may move in response to density changes in choruses. The mean change of 12 m/24 h between singing sites for *A. parvipennis* males was nearly twice that of *Neoconocephalus nebrascensis* males that fly (6.8 m [Meixner and Shaw 1979]) and three times that of *Orchlimum* spp. males that fly and are much more active than *A. parvipennis* (3.0 m [Morris 1967]). Much of this difference may be the result of males moving toward females that answer male calls. Phaneroptine females normally respond acoustically to male calls and males move toward the females (Spooner 1968). We have observed three male-female interactions in the field, and males did move toward acoustically responding females. Although in our observations responding females were ≤ 1 m from a calling male, Spooner (1968) has observed flying male phaneropts moving 23 to 30 m to natural or imitation female calls. Males other than the male of an acoustically interacting pair sometimes move to the sound of a female (Spooner 1968). In one field observation, three males and one female were on a single clover plant and another male eventually moved in.

It appears that where an *A. parvipennis* male spends most of his time during a given evening is conditional upon a number of factors which may include: (1) location of host plants or other plants suitable for calling, (2) density of such plants, (3) number of singing males in a given resource area, and (4) location of female sounds and possibly other female-emitted stimuli. Aggregation in areas of host plants suggests that the proximity of other loud, sound-producing, polygamous conspecifics has resulted in the evolution of overlapping of phrases by adjacent competitors. Such aggregations should be advantageous to females giving them a number of males from which to select a mate (Alexander 1975, Otte 1977).

If groups of singing *A. parvipennis* males are leks, how might a female choose a mate? Several investigations have suggested that females might choose the male singing the most intense song (Morris et al. 1978, Cade 1979, Forrest 1979). Greenfield (personal communication) suggests that females of *Neoconocephalus affinis* (Beauvois) may choose males (*N. affinis* males overlap buzzes of irregular lengths) who end their song when adjacent males are silent. The tendency for an *A. parvipennis* male to begin his phrase before the end of an adjacent male's phrase may reduce the ability of a female to move

toward his competitor and reduce the ability of the competing male to perceive the female tick(s) which follow a male's phrase.

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