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The adaptive significance of acoustic spacing in male bushcrickets *Tettigonia viridissima*: a perturbation experiment

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Summary. A perturbation experiment was carried out in which the spacing between singing male bushcrickets, *Tettigonia viridissima,* was artificially manipulated. The experiment entailed releasing virgin females into an area in which caged males were either spaced evenly or in which a proportion of the males were clumped. There was large variation among males in the proportion of time spent singing (range 39–91% of total singing time). Singing activity was correlated with male body weight, but was not influenced by male spacing. Out of a total of 108 females released during the experiment, the majority ($N = 90$) moved from their release points onto the cage of one of the closest singing males. More distant signalers sometimes attracted females when one of the closest males did not sing, or sang very little, during the period in which females were moving. When clumped, males were less successful in attracting females than when regularly spaced within the experimental area. Therefore, within a homogeneous habitat in which females are randomly distributed, male mating success will be maximized when males space out as far as possible from their competitors. As predicted, a regular dispersion of signaling males is the pattern observed in the preferred microhabitats of this species in nature.

Introduction

Choruses of sound-producing insects and anuran amphibians have received considerable attention from behavioral ecologists in recent years. These choruses consist of aggregations of males producing signals that attract sexually receptive, conspecific females.

The large scale spatial distribution of signaling males may, in many species, reflect the distribution of preferred resources such as foodplants (e.g., grasshoppers: Greenfield and Shelly 1985), oviposition sites (e.g., anurans: Wells 1977), or signaling sites (e.g., bushcrickets: Arak and Eiriksson, submitted). Alternatively, aggregations of males may form at arbitrary places in the habitat, called "leks" (reviewed by Bradbury and Gibson 1983), if clustering per se enhances an individual male's prospects of mating. Two suggestions have been made as to why males that join aggregations might experience increased mating success. Firstly, the combined effect of signaling by many males may increase the broadcast range of signal so that proportionally more females are attracted to larger choruses (Otte 1974; Alexander 1975). We refer to this as the "signal enhancement hypothesis". Secondly, it has been suggested that females may force males to aggregate in order to facilitate mate choice, and as a corollary, refuse to mate with isolated males (Alexander 1975; Bradbury and Gibson 1983). We refer to the latter hypothesis as the "female preference model."

On a smaller scale, it has been frequently found that signaling males maintain some minimum distance from each other by means of acoustic and physical interactions. This may sometimes result in a regular distribution of males within aggregations (e.g., bushcrickets: Bailey and Thiele 1983, Schatral et al. 1984; anurans: Arak 1983, Robertson 1984). The simplest interpretation of such "acoustic spacing" is that it allows males to broadcast their songs to females within a zone that is free from competitors (Arak 1983).

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The overall spatial distribution of signaling males in a habitat may, therefore, reflect a compromise between selective pressures favoring aggregation, which ensures a greater number of available females, and selective pressures to space out, which ensures successful courtship and mating once females have arrived at the aggregation (Doolan 1981). Given that there are many differences in population demography, habitat structure, and display behavior between signaling species, it seems likely that the balance of selective forces favoring either aggregation or dispersal will also vary. It is surprising, therefore, that few studies have been carried out with the aim of discriminating between different hypotheses for male spacing.

In this paper we investigate the optimal spacing pattern in bushcrickets, *Tettigonia viridissima,* by means of perturbation experiments. We have previously shown that the males prefer microhabitats that allow them to broadcast their songs from perches elevated above the dominant layer of vegetation. However, within aggregations, males are spaced evenly and maintain a minimum distance from their competitors both by acoustical and physical interactions (Arak and Eiriksson, submitted). Here we demonstrate that this spacing pattern is optimal for attracting females over short distances. Artificially increasing the degree of aggregation within clumps was found to decrease the ability of individual males to attract females, thus refuting the suggested advantages of signalling in groups.

Methods

All bushcrickets used in the experiments were collected in the field as final instar nymphs and reared to sexual maturity in the laboratory. Males and females were kept individually in well-ventilated plastic boxes (15 × 10 × 10 cm) and were fed daily with fresh grass and dried pellets of dog food. A few days after the final moult, 19 males were taken from the laboratory stock and each placed in a tubular cage (100 × 50 cm) made by suspending a black nylon net between two wire hoops. At each end of the cage, the net was gathered and tied firmly to a central wooden pole, approximately 2 m long, which supported the cage and provided a convenient singing perch for the captive male. The base of the pole was pushed firmly into the ground so that the lower end of the cage came to rest 30–40 cm above ground level. A small amount of fresh grass, a few sprigs of meadow-sweet *Filipendula ulmaria,* and dog food pellets were placed in each cage at 2-day intervals to provide food and cover. Males began singing in the cages within a few hours of acclimatization and sang regularly for several hours each day as long as the shade temperature exceeded 13° C.

Song sections were recorded at a distance of 50 cm above the sound-producing mirror of each male, using an ultrasound detector Model D-960, (frequency range 10–150 kHz, Lars Petterson, Vretgränd 9D, S-753 22 Uppsala, Sweden) on time-expansion mode, linked to a Sony TC-D5M cassette recorder. The time-expanded signals (frequency-reduced 10 times) were analyzed on a Uniscan 4500 sonagraph to determine frequency characteristics of songs. Sound pressure levels of songs were measured 50 cm above the mirror, using a Brüel and Kjær 2221 precision sound level meter on peak-recording mode. In this mode, the meter has a linear frequency response from 0.2 Hz to 20 kHz. The peak measurement of the signal, therefore, corresponds to the peak amplitude of the emphasized fundamental frequency of the song (approximately 10 kHz). All males were weighed to the nearest 0.01 g before each experiment began. After completing all experiments, the males were killed, and pronotum length, hind tibia length, and mean diameter of the sound-producing mirror were measured using a Wild binocular microscope with graticule eyepiece.

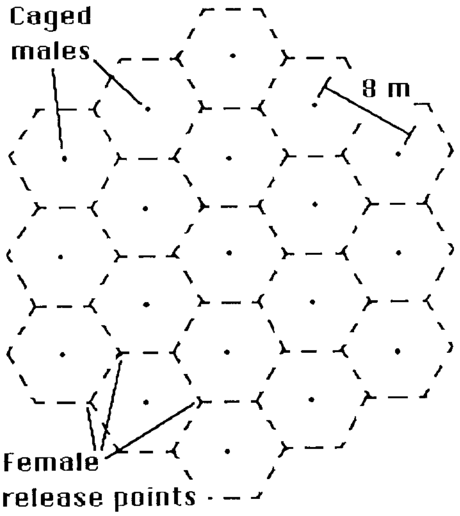

Fig. 1. The experimental design showing how positions of caged males and female release points were determined. Only 3 of the 36 female release points are indicated

In preliminary trials, virgin females readily approached singing males 1 week after their final molt. At this time, the 19 caged males were arranged in a field adjacent to the Tovetorp Research Station, 90 km south of Stockholm. This site was chosen because it consisted of fairly homogeneous vegetation, mainly long grasses and clover, and was not colonized by wild *T. viridissima* (the nearest singing males were found approximately 100 m away, beyond the hearing range of the animals used in the experiment; see Rheinlaender and Römer 1986). The experimental area was first mapped out into a honeycomb pattern of 19 perfectly fitted hexagons of equal size (Fig. 1). In Experiment 1, a randomly chosen cage was placed at the center of each hexagon (Fig. 2a). For a fixed number of males in a given area, this arrangement maximizes the distance between adjacent males, each individual having six equidistant nearest-neighbors. The distance between consecutive cages was fixed at 8 m, slightly greater than the mean nearest-neighbor distance of 6 m between regularly-spaced singing males observed in thicker vegetation in the field (Arak and Eiriksson, submitted).

In Experiment 2, we simulated a situation in which a proportion of the males cluster within the habitat. The six cages in closest proximity to the central cage were moved 6 m directly towards the latter. The arrangement (Fig. 2b) then consisted of a central group of seven cages spaced 2 m apart (denoted 'C'), surrounded by an outer group of 12 cages spaced 8 m apart (denoted 'O').

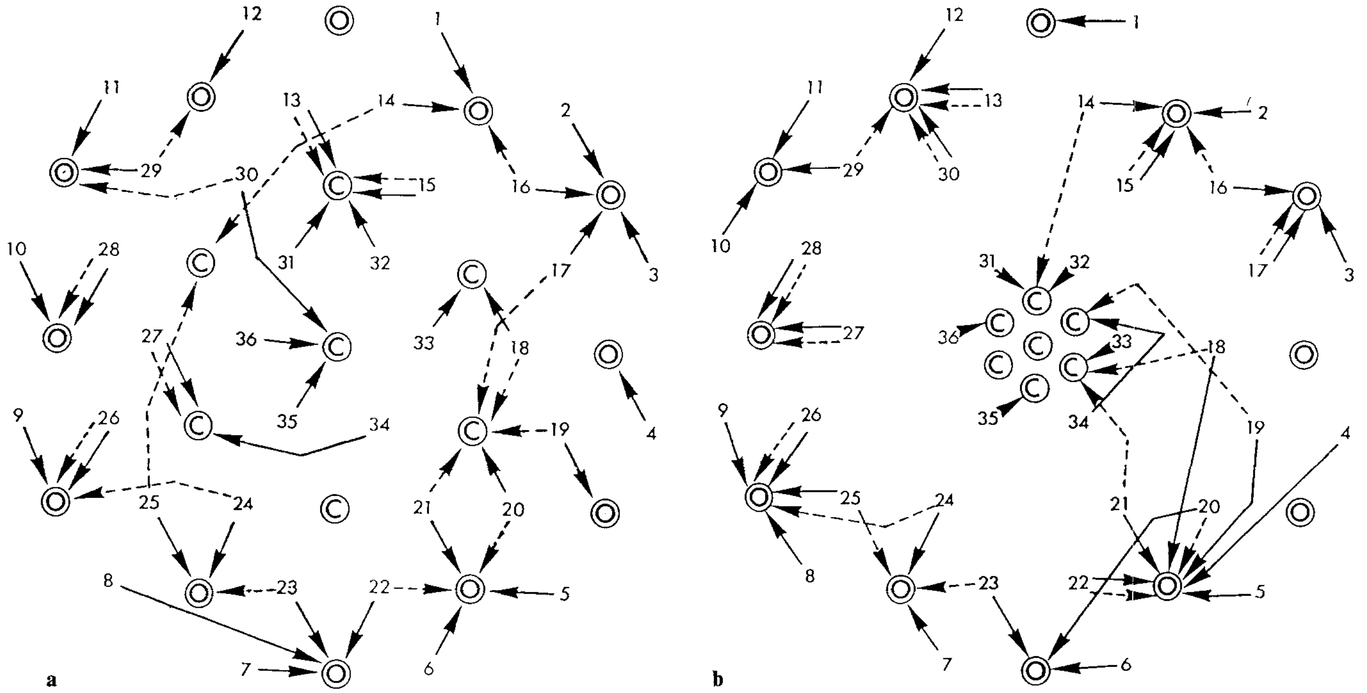

Fig. 2. The arrangement of caged singing males in (**a**) Experiment 1 and (**b**) Experiment 2. The letters C and O indicate "central" and "outer" males. The solid arrows show the movements of females from their realease points during the first series of experiments; dashed arrows show their movements in the second series. Females were released only from intermediate positions 13–30 in the second series. The position of males was randomized between the two experimental series

In each experiment, 36 virgin females, individually color-coded with paint spots on the pronotum, were placed in plastic rearing boxes and randomly assigned to release points situated at all points of intersection between the corners of adjacent hexagons (see Fig. 1). The experiments took place between 1400 hours and 2300 hours during the last week of August and the first week of September 1987. When all males had been singing for at least 30 min, the lids were carefully removed from the boxes containing the females. Three observers then noted whether or not each male sang for a period of 5 s in successive 3-min intervals. Our observations did not seem to disturb the males. Since males typically produce trills of almost continuous song, interspersed with short, 1–2 s periods of silence, we believe that our point samples of singing activity provide a reliable estimate of the overall singing activity of individual males. Song activity was sampled during at least two periods, each of 30 min duration, within an experimental trial, giving a minimum of 20 point samples of singing activity per male. Females were recovered and placed in plastic bags as soon as they had climbed onto a cage in which a male was singing; their identity and choice of male was noted at the same time. Removal of females from cages occasionally caused the male to stop singing, but in all cases the male began singing again within a few seconds. The experimental trial was terminated when all males had stopped singing for the day, usually when the temperature had dropped below 13° C. Females that had not made choices at this time were sometimes discovered in their release boxes, or quite close to the release point, sitting still or feeding. The experiment was repeated on successive days until a choice had been made by a female from every release point.

The same females were used in Experiments 1 and 2, and as far as possible, they were assigned to the same release points. (This was not always possible since some females released in Experiment 1 were not recovered.) Thus, the conditions in Experiments 1 and 2 were closely matched, except that the dispersion of the central group of seven males had changed. The whole series of experiments was repeated a second time, but the positions of males were randomized between each series. In the second series, however, females were in short supply, therefore they were released only from positions 13–30, intermediate between the central and outer groups of males. To test for an effect of clumping on female attraction, the relative success of central and outer groups of males were compared between Experiments 1 and 2.

Results

Male singing activity

On average, males were observed singing during 66% of the point samples (range 39–91%, $sd = 13.7\%$, $N = 19$). Male singing activity was highly correlated with body weight ($r = 0.60$, $P < 0.001$, $N = 18$), but not with pronotum length ($r = 0.12$, $P > 0.9$) or femur length ($r = 0.22$, $P > 0.7$). In both Experiments 1 and 2, there was no significant difference between the median singing activity of males in the central and outer groups ($P > 0.4$; Mann Whitney test for difference in median song activity).

We tested the possibility that the cluster of central males in Experiment 2 coordinated their

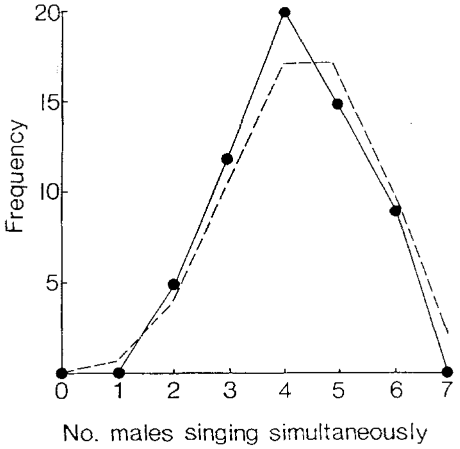

Fig. 3. The frequency at which different numbers of males within the central cluster (C males, Experiment 2) were singing simultaneously within a given song sampling period. The solid line joins the observed frequencies, and the dashed line shows the frequencies expected by chance if males sing independently of each other

singing activity in such a way that might increase their ability to attract females. Potentially they might achieve this by singing strictly in unison to augment the total intensity of the combined signal, or by alternating song bouts with each other to maximize the total time that a signal is being emitted (see Alexander 1975). During each consecutive 3-min sampling interval, we counted the number of males in the central group of seven that were recorded as singing. The frequencies of sampling intervals in which a given number of males were singing simultaneously is shown in Fig. 3. The observed frequencies at which different numbers of males sang simultaneously did not differ significantly from the frequencies expected by chance if each male sings independently of others in the group ($\chi^2 = 4.05$, $P = 0.54$, $df = 5$). We conclude, therefore, that the males within the central cluster timed the emission of their songs at random. However, it should be noted that during all sampling intervals there were never fewer than two of the seven central males singing at the same time. Thus, when singing alone, even the most persistent signaler (which sang in 91% of all sampling intervals) could not match the combined output of the central cluster of seven males.

Female choice

Out of a total of 108 females that were recaptured on cages in which males were singing, 90 (83.3%) were attracted to one of the closest singing males (i.e., at a distance of 4.6 m from the release point of the female). The furthest distance travelled by a female to a singing male was 12.3 m, bypassing one other male on the way.

Table 1. Observed and expected number of females choosing equidistant males ranked according to morphological and song characters

Character	No. of comparisons	Observed (expected) number of females choosing male			*P*
		Rank 1	Rank 2	Rank 3	
Body weight	81	44 (34.7)	31 (34.7)	6 (11.7)	0.02
Pronotum length	69	35 (30)	23 (30)	11 (9)	0.20
Femur length	60	22 (25.7)	30 (25.7)	8 (8.7)	0.52
Mirror diameter	69	34 (30)	28 (30)	7 (9)	0.55
Song frequency	62	29 (27.7)	26 (27.7)	7 (6.7)	0.91
Peak SPL of song	49	22 (21.7)	21 (21.7)	6 (5.7)	0.97
Singing activity	81	60 (34.7)	18 (34.7)	3 (11.7)	0.0001

For those females attracted to one of the closest males, we compared several characteristics of the successful male with those of the equidistant unsuccessful males. The males equidistant from each female's release point were ranked according to the following criteria: body weight, pronotum length, femur length, mean diameter of the sound-producing mirror, fundamental frequency of song, sound pressure level of song, and overall singing activity during the period when the female was making a choice. The male with the highest value of each character was ranked as 1, and the male with the lowest value was ranked 2 or 3 (depending on whether there were 2 or 3 males equidistant from the female's release point). Since we do not have complete data on all males, a maximum of 81 comparisons were possible. The number of females attracted to males of given character rank is shown in Table 1, along with the numbers expected by chance if females are attracted to one of the equidistant males at random with respect to male characters. The only significant departures from random were male weight and male singing activity. Seventy-four percent of all females attracted to one of the closest males chose the male with the highest singing activity ($P < 0.0001$), and 54% chose the heaviest male ($P < 0.05$). The heaviest males were most likely to be successful only because body weight and singing activity are highly

Table 2. Total number of females attracted to central and outer males (both experimental series combined)

	Number of females attracted to:	
	Central males	Edge males
Experiment 1 (central males spaced)	21	33
Experiment 2 (central males clumped)	10	44

$\chi^2 = 6.07$, $P = 0.1$, $df = 3$

correlated (see preceding section). This explanation is supported by 20 comparisons in which the most active singer was not the heaviest male: In 19 of these cases the most active singer was chosen.

Further evidence of the importance of male singing activity comes from an analysis of those cases in which females did not choose one of the closest males. In 12 out of 18 cases, the female by-passed a male that did not sing at all during the period when the female was moving ($N = 8$), or that sang very little (less than 30% of all observations, $N = 4$). Only six females passed by males that were singing persistently (during 80–100% of all observations).

Male success in relation to spatial dispersion

In this section we compare the relative success of the central and outer groups of males in both experiments. The combined results from both experimental series show that when all males were evenly distributed (Experiment 1), the central group of seven males attracted 38.8% of all females released during the experiment. When these central males were clumped (Experiment 2), they attracted only 18.5% of females. Although the central males had less success when clumped than when evenly distributed, the difference was not significant ($P = 0.1$, Table 2). This was due to the fact that the outer group of 12 females (release points 1–12) were consistently attracted to one of the outermost males, and the inner group of 6 females (release points 31–36) were consistently attracted to one of the centrally situated males in both experimental arrangements of males. Only the choices made by females in intermediate positions (release points 13–30) differed between the two experiments. When only this group of females is considered, 41.7% chose one of the central males in Experiment 1 (when they were evenly distributed), but only 11.1% chose a central male in Experiment 2 (when they were clumped). We conclude, therefore, that clumping significantly reduced the ability of the central group of males to attract females from intermediate positions (Table 3, $P = 0.007$).

Table 3. Number of females released from intermediate positions (13–30) attracted to central and outer males (both experimental series combined)

	Number of females attracted to:	
	Central males	Edge males
Experiment 1 (central males spaced)	15	21
Experiment 2 (central males clumped)	4	32

$\chi^2 = 11.96$, $P = 0.0075$, $df = 3$

Discussion

In the present study, we tested the effect of male spatial dispersion in *T. viridissima* on the ability of signalling males to attract females. The results show that males were less successful in attracting females when aggregated than when evenly distributed. This effect was primarily caused by the strong tendency of females to be attracted to the closest signaling male. Under these conditions, a male advertising to attract females will maximize his "zone of attraction" when spaced out as far apart as possible from his competitors. Thus, the only stable dispersion of signalling males will be one in which males are evenly spaced within the habitat: Any male who deviates from this pattern will be penalized by reduced mating success.

Alexander's (1975) hypothesis that females prefer to mate only where males are clustered in space, allowing maximum opportunity for mate choice, is not supported by the results of this study. Moreover, female *T. viridissima* showed little evidence of active sampling of several potential mates. On occasions when we observed female phonotaxis, the movements of females were nearly always unidirectional and apparently aimed at a particular signaler. Only six females (5.5%) by-passed a male that was actively singing at the time. The striking tendency of females to choose one of the nearest males is unlikely to be due to their inability to detect more distant signalers. Rheinlander and Römer (1986) and Arak and Eiriksson (submitted) have shown that females can detect male song from a distance of 40–60 m in a grassland habitat when the sound source is elevated above the surrounding vegetation. We conclude from this that all the caged males in our experiments were placed well within the hearing range of females. However, signals produced by the closest males suffer less attenuation, acoustical interference, and environmental degradation than signals emitted by more distant singers. Directional cues contained in the high frequency components of the song are also better preserved. Thus, closer males transmit their songs to the female with less ambiguity, facilitating species-specific pattern recognition and more accurate source location. Whatever the mechanism responsible, it can be argued from a functional point of view, that there may be an adaptive advantage of choosing the closest signaler if there are significant costs of movement for females (Searcy and Andersson 1986). Such costs might include an increased risk of predation due to conspicuous movements of the female during phonotaxis.

Otte (1974) and Alexander (1975) suggested that larger choruses might attract proportionally more females due to combining signalling effort and thus promote male aggression (but see Bradbury 1981 for objections). However, the need to preserve the species-specific temporal pattern of signals might mitigate against any potential advantages of communal signalling in *T. viridissima.* Since males produce long trills that overlap almost entirely when signalling together, important temporal features of the signal such as rate of amplitude modulation, pulse shape, and pulse duration will become obscured within the combined signal. Hence, any increase in signal amplitude or total broadcasting time experienced by the aggregate of males may be insufficient to counter the effect of increased signal ambiguity. This explanation is supported by experimental work on another bushcricket, *Conocephalus nigropleurum,* with a similar amplitude-modulated song (Morris et al. 1978). When females were offered a choice between the combined, hence louder, sound output of a "group" of two males and the simultaneous broadcast of a single male's song, they significantly preferred the combined song. However, in another experiment, females received the combined two-male song at the same power as that of the single male song, simulating our experimental situation in which the female is closer to the single male than to the group. In this case, females strongly preferred the single male song over that of the group, suggesting that the least ambiguous signal is more attractive when presented at the same amplitude as the combined song.

Most females were attracted to one of the closest signalling males. Among these females, the majority showed a preference for the most active signaler. It is tempting to suggest that this preference has evolved by sexual selection. The most active signalers were among the heaviest males, and our laboratory studies have shown that there is a strong correlation between male body weight and spermatophore weight in this species ($r=0.81$, $P<0.001$, $N=17$). Further, Gwynne (1984, 1988) has demonstrated that the spermatophore of the bushcricket, *Requena verticalis,* which is consumed by the female after mating, causes a significant increase in the number and size of eggs laid by females and in the hatching success of offspring. The advantage to females of obtaining large spermatophores, though not universal among bushcrickets (Wedell and Arak 1989), may provide an adaptive basis for female discrimination between males observed in *T. viridissima* and other species (Gwynne 1982).

The results presented here differ with the findings of some previous studies. Studies on the prairie chicken leks (Hamerstrom and Hamerstrom 1960), frog choruses (Ryan et al. 1981), singing groups of cicadas (Doolan 1981), and grasshoppers (Shelly and Greenfield 1985) have all shown that larger aggregations of males attract more females per male than do smaller aggregations. However, Cade (1981) found that there was no significant difference between the number of females attracted to songs of male field crickets, *Gryllus integer,* broadcast through single, isolated loudspeaker and the mean numbers attracted to loudspeakers arranged in aggregations. He concluded that although males are aggregated in the field, this cannot be explained by female preference for aggregated males. As far as we know, our study is the first to demonstrate a negative effect of aggregation on the ability of males to attract females. Because our results were obtained in a controlled, experimental situation, we can be sure that this effect was not due to differences in the local densities of females.

Although we do not rule out the possibility of female preference for aggregated males on a larger scale (i.e., females choosing between different clumps of males), the only studies to date that support such an effect are confounded by alternative explanations. For example, in the desert grasshopper, *Ligurotettix coquilletti,* males clump on dispersed creosote bushes (*Larrea tridentata*), their host foodplant, and females congregate on those bushes that contain relatively low amounts of plant secondary compounds (Greenfield & Shelly 1985). In an elegant experiment, Shelly et al. (1987) showed that females whose chemosensory organs had been removed settled on bushes indiscriminately. Thus, variability among bushes in their plant chemistry alone appears to be sufficient to promote clustering of females on cresote bushes. However, additional observations suggest that females were less likely to leave bushes between successive days if groups of signalling males were present, suggesting that male epigamic displays may play some part in influencing female dispersion as well. In the tungara frog. *Physalaemus pustulosus,* larger choruses of males attract proportionally more females than do smaller choruses (Ryan et al. 1981). Although females do prefer certain males in this species (Ryan 1985), it is by no means certain that females prefer larger groups in order to facilitate mate choice. The effect could come about because individuals in larger groups are relatively safer from predators that are known to specialize on frogs.

In conclusion, we failed to find any evidence for signal enhancement by communal display in *T. viridissima* or for female preference for clustered males within artificial choruses. The results of this study suggest that the optimal spacing pattern is one in which signalling males are evenly dispersed within preferred habitats. This is precisely the distribution that is observed in nature for male *T. viridissima,* and, indeed, many other acoustically advertising animals. Although several authors have suggested that signaling males may benefit by maintaining a distance from their competitors, this is the first experimental demonstration that supports this suggestion.

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