Effects of group density on call rate, phonokinesis, and mating success in *Palmacorixa nana* (Heteroptera: Corixidae)

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**Introduction**

One important function of insect song is the attraction of potential mates. Experimentally the degree to which any acoustic signal will attract an animal is determined by playing the signal output of a single animal to a test animal and noting the response (e.g., Bailey and Robinson 1971; Morris 1972; Walker 1957). An assumption inherent in this type of experiment that output of a single animal is the only biologically important parameter has been shown to need some modification. Morris *et al.* (1978) found that female onoccephaline katydids prefer acoustic models representing two males over one.

Aggregation of singing insects presents a theoretical enigma. Males singing near each other must inevitably apportion matings with those females attracted to them while isolated males can monopolize matings. Alexander (1975) theorized that preferential mating by females with grouped males exerts a selection pressure for males to remain grouped.

The importance of grouped singers can be expected to increase with density. If female preference of grouped males exists in insects whose intermale distances are relatively large, then for insects that can tolerate much smaller intermale distances, such preferences may be very important.

Corixids have small intermale distances. Dense clumping of these bugs, especially in the mating season, has been noted for several species (Aiken 1980; Ekblom 1928; Kirkaldy 1898; Savage 1971a, 1971b). Densities of up to 2000 adults/m² have been recorded (Kelts 1979; Tones 1977).

Adults of *Palmacorixa nana* are 4 to 5 mm long and live in dense aggregations along stream margins (Aiken 1980). Since both sound production (Aiken 1982) and formation of dense aggregations are prominent features of activity of these animals, I investigated effects of density on singing and mating behaviour. Specifically I tested the following set of hypotheses. Male *P. nana*
form groups and there is some measurable acoustic correlation of density that can be used by females in assessing male density. Females should prefer grouped males and, consequently, such males should have more mating success.

**Materials and methods**

**Collecting and rearing**

Second and third instar nymphs of *P. nana* were collected in late March, 1978, in Black Creek, Ont. (Peel Co.). Nymphs were transported to the laboratory in insulated coolers and placed in 57-L glass aquaria at 5°C. These aquaria were then placed in an environmental chamber at 20°C and a 16 h light : 8 h dark cycle. Bugs were fed frozen brine shrimp daily. Adults began emerging in 4 weeks and were separated by sex and placed in separate aquaria.

**Sex ratio and density**

To quantify density and sex ratio in the field, a copper screen cylinder (15 cm diameter × 45 cm high) was dropped into the stream so that it was imbedded 5–10 cm into the substrate. A D-frame aquatic net was slipped into the substrate under the cylinder and raised, trapping all animals inside. Bugs were preserved in 70% ethanol and later counted and sexed.

Twenty-five stations were sampled, each sample covering 77 cm². All sampling stations were within 1 m of the shore and had the same soft detrital substrate, little prominent vegetation, and water depth between 10 and 30 cm. Stations were approximately 2 m apart except where the stream was inaccessible. At these points, samples were taken as close to 2-m intervals as possible.

Second and third instar nymphs were collected in November and March to determine sex ratio of emerging adults. Those collected in November were incubated in total darkness at 5°C and fed weekly. After 10 weeks, a stock population of nymphs was transferred to 20°C and a 16 h light : 8 h dark cycle until the water had warmed to 18 to 25°C. Nymphs were preserved and marked in 50% formaldehyde. Nymphs were then added to the cage and acclimation and recording procedures were repeated. This protocol was followed to obtain call rates from groups of 10 and 25 males. There were six replicates at each density and no individual was used in more than one replicate.

Mean call rates (number of calls per male per minute) were calculated for each of the four densities of males.

**Playback experiments**

Once the means for call rates were determined for each of the four male densities, a tape loop with calls delivered at these rates was prepared. One call rate was reproduced on each of the first, third, fifth, and seventh tracks of a Philips Ana-Log 7 seven-track instrumentation recorder permitting continuous and simultaneous playback of any two call rates. The same male call was reproduced the requisite number of times and the silent intervals throughout the tape were of equal duration.

Responses of males and females to different call rates were tested in the plastic wading pool. The pool was fitted with two University Sound MM-2 underwater speakers connected to the Philips Ana-Log 7 recorder through a Heathkit AA-14 amplifier. Speakers were partially buried in the sand substrate facing each other, 70 cm apart. The instrumentation recorder was in an adjoining room and was activated by a remote control switch.

Four experimental treatments were used. (1) Males responding to different call rates at equal intensity. (2) Females responding to different call rates at equal intensity. (3) Both sexes responding to courtship calls versus different spontaneous call rates at equal intensity. (4) Females responding to call rates preferred in treatments 2 and 3, reduced in intensity by 5 dB.

**Equal intensity trials (treatments 1 and 2)**

Trials were arranged such that mean call rates for any two densities were played simultaneously. In each trial, the side of the arena from which the higher call rate was broadcast was...
TABLE 1. Percent time spent by females in either half of the arena for all experiments involving response to courtship (C) and spontaneous (S) calls presented together (n = 20)

<table>
<thead>
<tr>
<th>Sex</th>
<th>Courtship call dB</th>
<th>Call rate at 20 dB compared with courtship calls</th>
<th>% time spent in arena half broadcasting:</th>
<th>( \chi^2 )</th>
<th>( p )</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>C</td>
<td>S</td>
<td></td>
</tr>
<tr>
<td>Male</td>
<td>20</td>
<td>16.5</td>
<td>65.2</td>
<td>34.8</td>
<td>12.58</td>
</tr>
<tr>
<td>Female</td>
<td>20</td>
<td>16.5</td>
<td>80.5</td>
<td>19.5</td>
<td>52.30</td>
</tr>
<tr>
<td>Female</td>
<td>15</td>
<td>16.5</td>
<td>16.4</td>
<td>83.6</td>
<td>82.2</td>
</tr>
<tr>
<td>Female</td>
<td>15</td>
<td>2.5</td>
<td>82.8</td>
<td>17.2</td>
<td>61.9</td>
</tr>
<tr>
<td>Female</td>
<td>15</td>
<td>1.5</td>
<td>87.7</td>
<td>12.3</td>
<td>113.9</td>
</tr>
</tbody>
</table>

For a trial, a 2.5-cm diameter clear Plexiglas cylinder was labelled the “active half” signifying that the speaker was broadcasting a greater number of calls. For each trial, a speaker broadcasting a specific call rate was selected using a random number table with the restriction that, of the 20 trials for each call rate pairing, 10 were from each speaker. Call level was adjusted to an intensity of 20 dB (re 1 \( \mu \)bar) at the arena centre.

For a trial, a 2.5-cm diameter clear Plexiglas cylinder was set in the arena centre. A corixid was introduced into the cylinder and when it had come to rest on the bottom, not touching the cylinder walls (usually taking less than 30 s), the cylinder was immediately removed and playback initiated. The time each animal spent in each half of the arena and the time spent swimming were recorded on a Rustrak 292-8 event recorder. Trials lasted 10 min or until the animal exited the arena. An exit occurred when an animal crossed a circular line with a radius of 35 cm from the arena centre. A silent control experiment was conducted on both sexes in which no sound was broadcast through the speakers although they were turned on. No animal was used more than once.

**Responses of both sexes to spontaneous call rates versus courtship calls (treatment 3)**

Responses of males and females to the simultaneous broadcast of male courtship and spontaneous calls were investigated. If the courtship call were an obligatory part of the mating behaviour, females, at least, should prefer this call and spend more time in the half of the arena with the speaker broadcasting it.

Courtship calls were repeated at a rate of 2.2 calls/min at an intensity of 20 dB and tested against the mean spontaneous call rate of 25 males.

**Response of females in unequal intensity trials (treatment 4)**

This experiment was identical to the equal intensity trials except that the previously preferred of any two call rates was decreased in intensity from 20 to 15 dB. Various call rate pairings and their respective intensities appear in Table 1. In unequal intensity trials, the courtship call was broadcast at 15 dB and the various spontaneous call rates at 20 dB.

**Acoustic power as a response criterion**

Power ratios, a measure of the amount of energy delivered per unit time for any sound level, were determined for each intensity (Peterson and Gross 1972, Table 1, p. 248). These values were then used to solve the equation, total energy = (pulse trains/call) \times (number of calls/minute) \times duration of a pulse \times power ratio for \( x \) dB. Results of this calculation are presented in Table 2. This calculation accounts for the periods of silence interspersed between pulse trains (Aiken 1980). Simply calculating the duration of a call would result in an overestimate of total energy.

**Mating success and density**

Field-collected bugs were isolated by sex and kept at 20°C with a 16 h light : 8 h dark cycle. All animals were used in experiments after isolation by sex for a maximum of 48 h.

Groups of 5, 10, and 25 males were selected from the stock culture and placed in a foam-lined section of aquarium and allowed to acclimate for 24 h. Females were then added to the chamber at a ratio of one per five males. At higher densities, this ratio resulted in the maximum number of bugs that could be observed accurately. Females were added using a siphon tube and allowed 30 min with no behaviour patterns being tallied to adjust to the novelty of the surroundings and to the act...
of being transferred. Occurrence of all behaviour patterns was recorded on a Rustrak 292-8 event recorder for at least eight 15-min observation sessions at each density. No more than four observation sessions were conducted in the same day and no animal was used in more than one group.

The various patterns observed were the following. (a) Nudge, (striking of the head of an approaching animal against any part of the approached animal’s body). Nudges result in displacement of the nudged animal. (b) Homosexual mounting attempt, (mounting of a male onto the dorsum of another male with simultaneous aedeagal extrusion and probing (Aiken 1981)). (c) Heterosexual mounting attempt (mounting of a female by a male with simultaneous aedeagal extrusion and probing). (d) Copulation (mating of a male and female (Aiken 1982)). (e) Interference (any contact by a third animal with a mating pair after approach). Interference usually consists of nudging or mounting the mating pair.

Results

Field densities
Densities of P. nana varied from 1 to 50 adults/sample. Differences in density were observed in areas that were apparently similar in bottom type and vegetation. In experiments to follow, call incidence of males at densities of 1, 5, 10, and 25 males/150 cm² was determined. Converting field densities to number of males/150 cm² yielded densities of 0.85 to 21.3 males/150 cm², indicating that densities used in these experiments were realistic in terms of the field data.

Sex ratio in the field
Ratio of males/females in the field varied markedly from a minimum of 0.25 to a maximum of 3.0. There was no correlation between sex ratio and density \( (r = 0.29, 0.2 > p > 0.1) \). There was a significant correlation, however, between number of males and number of females at any site \( (r = 0.71, p < 0.001) \).

Animals that overwintered in the laboratory (collected in November) and those overwintered in the field (collected in March) showed similar sex ratios on emergence. For both groups, sex ratio favours males through the entire emergence period and correlation of number of males and females is highly significant for both \( (r = 0.99, p < 0.001) \). Sex ratio for both groups is more male biased at the beginning of the emergence period.

Male aggregation
Males show a tendency to group around each other. In 15 of 24 observation periods, analysis of distances to nearest neighbour (Clark and Evans 1954) indicated a clumped distribution \( (p = 0.05) \).

The second experiment also indicated that males form groups. Frequency of males per section was tested against a Poisson distribution and differed significantly from random \( (\chi^2 = 325.1, p < 0.001) \) and showed males to be highly clumped \( (s^2/u \gg 1) \).

Call rate and density of males
In 90 min of recording, no signals were detected from single males \( (n = 6, \text{ Fig. 1}) \). As density increased, number of calls per 15 min increased up to the density of 10 males/150 cm². When 25 males were in the recording cage, however, call rate increased dramatically: call rate increased by a factor of eight for a 2.5 times increase in male density (Fig. 1). Attempts were made to determine the call rates for higher male densities (i.e., 40 and 50 males), but calls were overlapped to such an extent that they were impossible to count. Mean call rates, calculated as number of calls per male per minute, for densities of 1, 5, 10, and 25 males/150 cm² were 0, 1.5, 2.5, and 16.5, respectively (Fig. 1). Increase in call rate with density was exponential \( (p < 0.001) \).

Playback experiments
Responses of males to different call rates at equal intensity (treatment 1)
In control experiments, males showed no differences in the amount of time spent in either half of the pool.

Play 1

![Fig. 1. Number of spontaneous calls per male per minute for increasing male density. Open circles represent call rates for each of six 15-min replicates at each density. Closed circles represent mean call rates at each density.](https://www.nrcresearchpress.com/doi/10.1139/z82-166)
(Table 3). When only one speaker was broadcasting, males spent more time in the active half of the pool (Table 3). Differences between amount of time spent in either half of the pool were only significant for the 16.5:0 and 2.5:0 comparisons (Table 3).

When both speakers were broadcasting, males showed marked differences from females. In the 16.5:1.5 and 2.5:1.5 comparisons, males preferred the higher call rate (Table 3). When call rates of 16.5 and 2.5 calls/min were compared, however, males showed a significant preference (Table 3) for lower call rate and thus lower density of males. Although males showed a preference for the call rate of 16.5 over 1.5 calls/min, the preference was not as strong as that of females (Table 3).

Males spent less time swimming when sound was broadcast than when the pool was silent (Fig. 2) and showed no significant differences in the proportion of time spent swimming between the various treatments (Mann–Whitney U–test, $p > 0.05$).

**Response of females to different call rates at equal intensity (treatment 2)**

In the control experiments, females showed no significant preference for either half of the pool ($\chi^2 = 0.2$, $p > 0.02$ (Table 2)). When presented with call rates for each density of males from one speaker at a time (16.5:0, 2.5:0, and 1.5:0 comparisons), females spent more time in the active half of the arena (Table 3). At lower call rates (i.e., male densities), females spent less time in the active half of the arena. In all three combinations, proportion of time spent in the active half of the arena was significantly higher ($p < 0.05$, Table 3).

When confronted with two sound sources, females spent more time in the active half of the arena (Table 3). In all trials, the amount of time spent in the half of the pool, with the speaker broadcasting the higher call rate, was significantly higher (Table 3).

When in a silent arena, females swam for an average of 3% of the time they spent in the arena (Fig. 2). In the presence of any sound, females swam less (Fig. 2). Swimming incidence in all trials was significantly less than in a silent arena (Mann–Whitney U–test, $p < 0.001$). In determining effect of call rate on swimming behaviour, only those call rate comparisons with one speaker silent were used. This was to avoid confusion of the effect of different call rates played simultaneously. Swimming behaviour, when two call rates (i.e., two speakers broadcasting) are presented simultaneously, is dealt with in the discussion of acoustic power as a response criterion.
Responses of both sexes to spontaneous call rates versus courtship calls (treatment 3)
Females spent more time ($\chi^2 = 52.3, p < 0.001$, Table 1) in the half of the pool from which the courtship call was broadcast. Since the courtship call was preferred over the call rate of 16.5 calls/min and, from previous experiments, the call rate of 16.5 calls/min was preferred over all others, call rates of 2.5 and 1.5 calls/min were not tested against the courtship call.
Males spent significantly more time in the half of the pool from which courtship calls were broadcast (Table 1).

Responses of females in unequal intensity trials (treatment 4)
Preferences of females in this experiment were not as clear as in equal intensity trials. In the 16.5:2.5 and 16.5:1.5 comparisons, females preferred the higher call rate even though it was at a lower intensity ($p < 0.005$ for both, Table 4). Response to either call rate did not differ in the 2.5:1.5 comparison ($0.1 > p > 0.05$, Table 4). Response of females to unequal intensity trials involving courtship and spontaneous calls is inconsistent. Females preferred courtship calls over spontaneous call rates of 2.5 and 1.5 calls/min even though this stimulus was less intense ($p < 0.001$, Table 1).

Acoustic power as a response criterion
The results of all playback experiments were analysed with respect to the energy delivered in the preferred call rate or call. For every comparison, the call rate or call preferred was the one with the higher power (Table 2). This analysis with respect to total energy present also yielded interesting results when applied to mean proportion of time spent swimming by females. For this analysis, energy levels for both call rates (or calls) being compared were added to give total energy present.
There was a significant correlation between mean proportion of time spent swimming and total energy present ($r = 0.693, t = 3.32, p < 0.01$) indicating that as total energy present increased, proportion of time spent swimming decreased.

Mating success and density: patterns observed

Nudge
The rate of nudging increased from 0.47 to 1.46 acts per male (Table 5).

Homosexual mounting attempts
Homosexual mounting attempts decreased in frequency as density increased (Table 5). The number of homosexual mounting attempts was less when there were females present.

Heterosexual mounting attempts, interference in mating, and copulation
As density increases, there is no overall increase in mounting attempts per male (Table 5). There is a decrease in frequency of occurrence at a density of 10 males/150 cm$^2$. In denser groups, number of copulations per male is higher (Table 5). Males must, however, contend with a higher frequency of mating interference as density increases (Table 5). In terms of successes per unit effort, males do better at higher densities. At a density of 10 males/150 cm$^2$, each male can expect to copulate 1.8 times for every 100 heterosexual mounting attempts and 1.2 times for every 100 mating attempts irrespective of sex of the partner (Table 5). For 25 males/150 cm$^2$, there is a copulation rate of 23 per 100 heterosexual mounting attempts or 4.4 times per 100 mounting attempts. Clearly, males enjoy a greater mating success in denser aggregations. These data correspond well with success rate observed in other mating experiments (Aiken 1980). In those experiments, copulation rate was 27% for heterosexual mounting attempts.

| Table 4. Mean percent time spent by females in the respective halves of the arena: call rates preferred at equal intensities were decreased in intensity from 20 to 15 dB and paired with nonpreferred call rates at 20 dB
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Call rate</td>
<td>% time in 20 dB half</td>
<td>% time in 15 dB half</td>
<td>$\chi^2$</td>
</tr>
<tr>
<td>2.5:16.5</td>
<td>10.8</td>
<td>89.2</td>
<td>119.1</td>
</tr>
<tr>
<td>1.5:16.5</td>
<td>10.1</td>
<td>89.9</td>
<td>111.7</td>
</tr>
<tr>
<td>1.5:2.5</td>
<td>50.7</td>
<td>49.3</td>
<td>3.4</td>
</tr>
</tbody>
</table>

| Table 5. Number of acts for each observed behaviour pattern with increasing male density
<table>
<thead>
<tr>
<th>Behaviour pattern</th>
<th>Density (males/150 cm$^2$)</th>
<th>Number of acts/male in 15 min</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nudging</td>
<td>5</td>
<td>0.47</td>
</tr>
<tr>
<td></td>
<td>10</td>
<td>0.54</td>
</tr>
<tr>
<td></td>
<td>25</td>
<td>0.46</td>
</tr>
<tr>
<td>Homosexual mount</td>
<td>5</td>
<td>0.76</td>
</tr>
<tr>
<td></td>
<td>10</td>
<td>0.76</td>
</tr>
<tr>
<td></td>
<td>25</td>
<td>0.54</td>
</tr>
<tr>
<td>Heterosexual mount</td>
<td>5</td>
<td>0.11</td>
</tr>
<tr>
<td></td>
<td>10</td>
<td>0.05</td>
</tr>
<tr>
<td></td>
<td>25</td>
<td>0.13</td>
</tr>
<tr>
<td>Mating interference</td>
<td>5</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>10</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>25</td>
<td>0.06</td>
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<tr>
<td>Copulations</td>
<td>5</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>10</td>
<td>0.01</td>
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<td></td>
<td>25</td>
<td>0.03</td>
</tr>
<tr>
<td>Copulations/mount</td>
<td>5</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>10</td>
<td>0.18</td>
</tr>
<tr>
<td></td>
<td>25</td>
<td>0.24</td>
</tr>
</tbody>
</table>
Discussion

Possible relationships between aggregating and mating behaviour in corixids have been suggested (Ekblom 1928; Kirkaldy 1898; Savage 1971a, 1971b). Data presented here are the first experimental evidence of the connection between a behavioural response of females to song and enhanced mating success.

Alexander (1975) argued that aggregations of singing male insects result from females preferentially mating with grouped males. This sexual selection by females is especially strong in species with a paucity of females available for mating (Darwin 1871). In P. nana, sex ratio data show this condition to have been satisfied. Especially at the beginning of emergence, males predominate and, hence, compete for the less abundant females. Aiken (unpublished data), Applegate and Kieckhefer (1977), and Hungerford (1920) have found a numerical dominance of males in other Palmarcorixa species.

In addition, mated corixid females appear to be unreceptive for several days (Jansson 1973), whereas I have seen males attempt to mate within a few minutes of completing a copulation. The operational sex ratio, then based on the number of females actually available for mating, may then be much more skewed toward males.

In laboratory experiments, males aggregate in the absence of any salient physical features. They are, in fact, using each other as loci. In the field, aggregations of males are not discrete clumps or groups, but rather continuously vary in density. Finke (1968) speculated that aggregations of corixids were under the influence of environmental factors. P. nana is found only in a 1-m basin. They are probably attracted to these areas by environmental factors (e.g., higher temperature, slower current). Aggregations I am concerned with, however, are within this band along the shoreline. In this situation, several different concentrations of males can occur along any length of the stream.

When males are in denser aggregations, rate of spontaneous calling increases exponentially, allowing females to discriminate between relative densities of any aggregations. Wefelscheid (1912) also noted that below a certain minimum density Plea minutissima (Heteroptera: Pleidae) would not sing and speculated that the function of the call was to attract conspecifics to aggregations for mating. Smith (1973) found an exponential increase in call output of Rhantus gutticollis (Coleoptera: Dytiscidae) associated with increases in density, but related it to preemigration behaviour.

While females react to calls of aggregated males, it is not entirely accurate to label the spontaneous call a calling song. Calling songs function to attract females to signalling males and have been described as rhetorical (Morris 1980), since males have no immediate expectation of a response. If this were a calling signal, there should be both a linear increase in call rate simply from the addition of more calling males and some signal output from a single male. In these experiments, neither of these criteria was met. Although the spontaneous call is not a calling signal in the strictest sense, its use by females may impose this role upon it. Males probably signal agonistically and the signal is not rhetorical (Morris 1980). Females, however, are using the signal to find aggregations of males and are exploiting a signal that males are using in an entirely different context. Female choice of males that are in groups would exert a selection pressure on males to remain in groups.

Response of females to different call rates is not phonotactic but phonokinetic. Females do not exhibit directed swimming toward a source, but alter the proportion of time spent swimming in response to the intensity of stimulation (Frankel and Gunn 1960). In this comparison, the varying parameter of stimulation is acoustic power. Acoustic power is the only physical parameter of all testing situations that is consistently correlated with all female preferences (Table 2). Unfortunately, there are no data on output of a single male at a fixed distance from or orientation to the hydrophone. Morris et al. (1978) have examined power as a factor in katydid phonotaxis and found that differences in power of the signals were sufficient to account for most statistically significant choices by females.

Females, because of their tendency to spend less time swimming in areas of greater acoustic power, tend to associate with denser aggregations of males. Field collections confirm that where there are more males, there are more females. When among males in aggregations, females presumably choose males on other criteria beyond the scope of these experiments.

When given a choice between the densest (25 males, 16.5 calls/male per minute) and the next densest (10 males, 2.5 calls/male per minute) aggregation, males behaved in such a way as to associate with the less dense aggregation. The males’ preference for denser aggregations in the comparison of call rates 16.5:0 and 16.5:1.5 raises the question of whether males prefer a particular density or are simply avoiding the most dense aggregations. If all a male had to do was maximize his chances of encountering females, he should behave in such a way as to be where most females are. P. nana males should, therefore, respond in the same way as females. Clearly, they do not. Therefore, there may be costs to males associated with dense groups that alter their response to call rates and lead to the preferences exhibited here.

Alexander (1975) hypothesized that male acoustic insects should only sing in the vicinity of each other if there were some reproductive advantage to be gained from doing so. These data clearly support this hypothe-
sis and also give some indication of the costs as well as benefits accruing to males in dense groups. Each male *P. nana* increases his number of copulations and, perhaps more importantly, copulations per mount attempt indicating an increased copulatory efficiency. Males also benefit in denser groups in that they are involved in fewer homosexual mounting attempts. Such can account for half the mounting attempts (Aiken 1982) and, given that males discriminate sex on apparently unreliable criteria (Aiken 1981), any reduction represents a saving of both time and energy to any male. Finally, dense groups are where most females will be. It, therefore, would benefit any male to associate with a denser group.

Males, however, are confronted with costs as group density increases. Since call rate increases exponentially with density, each male is putting an increasing amount of energy into calling. Males also are involved in more aggressive interactions (nudging) and are interfered with more in mating as density increases (Table 5). Obviously, joining a dense aggregation is not simply a matter of increasing copulations.

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