

The Social Environment of an Aggregating, Ant-Attended Treehopper (Hemiptera: Membracidae: *Vanduzea arquata*)

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Many membracid treehoppers are attended by honeydew-harvesting ants. Ant mutualism often favors group living, which will in turn influence social interactions and communication. I investigated aspects of life history that underlie the social behavior of an aggregating, ant-attended treehopper. The number of adults, and their patterns of distribution, changes dramatically over the course of a season. Despite the relatively low vagility and high persistence in the same clump of host plants, individuals encounter a wide range of social environments. This aggregating species differs from solitary species in the clumped distribution of females, and possibly in the intensity of acoustic competition among males, but both aggregating and solitary species exhibit large temporal changes in density. A high degree of temporal and spatial variation in the social environment is probably characteristic of many insects and may be an important source of selection on insect communication.

KEY WORDS: *Vanduzea arquata*; mutualism; social behavior; *Formica*; *Crematogaster*; vibrational communication.

INTRODUCTION

Many species of membracid treehoppers are mutualists with ants, and this relationship can have far-reaching effects on their biology. Ant mutualism is especially influential on patterns of dispersion, favoring aggregation of

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membracids within patches of host plants and within individual plants (Wood, 1977, 1979; McEvoy, 1979). Accordingly, many species of ant-attended membracids spend much of their lives in groups (Funkhouser, 1917; Haviland, 1925; Wood, 1977, 1979, 1984; McEvoy, 1979). Although it is ultimately ecological factors such as predation that favor mutualism and group living (McEvoy, 1979; Wood, 1979; Fritz, 1982), this pattern of dispersion will have important consequences for social interactions (Wilson, 1975), mating systems (Emlen and Oring, 1977; Vehrencamp and Bradbury, 1984; Davies, 1991; Ott, 1994), and communication (Bradbury and Vehrencamp, 1998). Mating systems are unknown for most membracids (Wood *et al.*, 1984; Wood and Dowell, 1985; Masters, 1997), and systems of substrate-borne vibrational communication have only recently been documented (Strubing and Rollenbach, 1992; Hunt, 1993, 1994; Cocroft, 1996; also see Ossiannilsson, 1949). It is thus not clear what consequences ant mutualism has for the evolution of mating systems, social interactions, and communication in membracids.

Vanduzee arquata is an ant-attended treehopper that occurs on *Robinia pseudoacacia* (black locust) in the eastern United States. Its life history was first described by Funkhouser (1915), who noted that *V. arquata* forms dense groups on host-plant stems. Attending ants harvest the honeydew produced by adults and nymphs (Funkhouser, 1915; Fritz, 1982). As with other ant-attended species, the presence of ants greatly increases the survivorship of nymphs (Wood, 1977; McEvoy, 1979), probably by reducing predation (Fritz, 1982, 1983). Like other Auchenorrhyncha (reviewed by Claridge, 1985; Claridge and de Vrijer 1994), adult *V. arquata* communicate using substrate-borne vibrational signals (see below).

I conducted a field study of aspects of the life history of *V. arquata* that underlie their social interactions. I first characterized temporal and spatial variation in the number and distribution of adults, to establish the context in which communication takes place. I then examined persistence within a patch of host plants, as well as patterns of interplant movement within that patch, to determine the range of social environments encountered by individuals. I documented mating and male signaling behavior as indicators of social interactions. Finally, I observed female oviposition behavior, to determine the likely extent of relatedness among individuals in a single aggregation. The goals of the study were to set the stage for further investigation of communication in this species and contribute to an understanding of the effect of ant mutualism on social interactions.

METHODS

The study was conducted from August 7 through November 9, 1992, at the edge of a cemetery near Coy Glen in Ithaca, New York. Regular censuses

were begun on August 28, to encompass the second adult generation of *V. arquata* that year. Additional observations were made at the site in the summer of 1993. The study area was at the edge of second-growth forest and contained numerous *Robinia pseudoacacia* ranging in age from saplings to mature trees.

Adult treehoppers of each sex were marked, either individually or in batches (in which case all individuals first observed on a given date were given the same identifying mark). Marks consisted of a series of one to four small dots of colored enamel paint applied to the pronotum. Most individuals were stationary and were marked without removing them from the plant. Moving individuals were caught, marked, and replaced. Marking was done every day for 3 weeks beginning on August 28 and every fourth day thereafter. Immatures continued to eclose throughout the season, and these new adults represented the majority of new, unmarked individuals during censuses early in the season. However, because teneral adults rapidly converged on the color of older adults, it was not possible to determine whether new, unmarked individuals during censuses later in the season were teneral adults, immigrants from outside the study site, or adults that had been overlooked in a previous census.

Censuses were conducted approximately every fourth day. A census consisted of an inspection of all branches on the trees that contained *V. arquata* aggregations or were adjacent to trees with aggregations. The position of each adult was recorded to the nearest 5 cm, measuring from the base of the branch. The behavior of each individual was scored as stationary, signaling (males), mating, or ovipositing (females). The extent of interplant movement within the patch of host plants was calculated for individually marked males and females: for a given census date, an individual was scored as having moved if it was on a different tree than the one it was observed on in the previous census.

Vibrational signaling by males was monitored during regular censuses and recorded opportunistically throughout the study, using a Knowles BU 1771 accelerometer, a custom-built operational amplifier, and a Sony Professional Walkman cassette recorder. Males commonly produce three signal types (Fig. 1). I consider the signal in Fig. 1a to be a long-range sexual advertisement signal (Claridge, 1985), because it is given by mate-searching males and because playback of this signal elicits response signals from virgin females (Cocroft, unpublished data). The second signal type is apparently a close-range courtship signal (Fig. 1b) and is produced by males while standing on a female's pronotum. These two signal types can be detected visually because parts of the signal involve a large-scale rocking of the male from back to front. This rocking is correlated with the percussive taps present in the signal, which appear to be caused by some part of the body (presumably the head) striking the substrate (Figs. 1a and b). During other parts of the

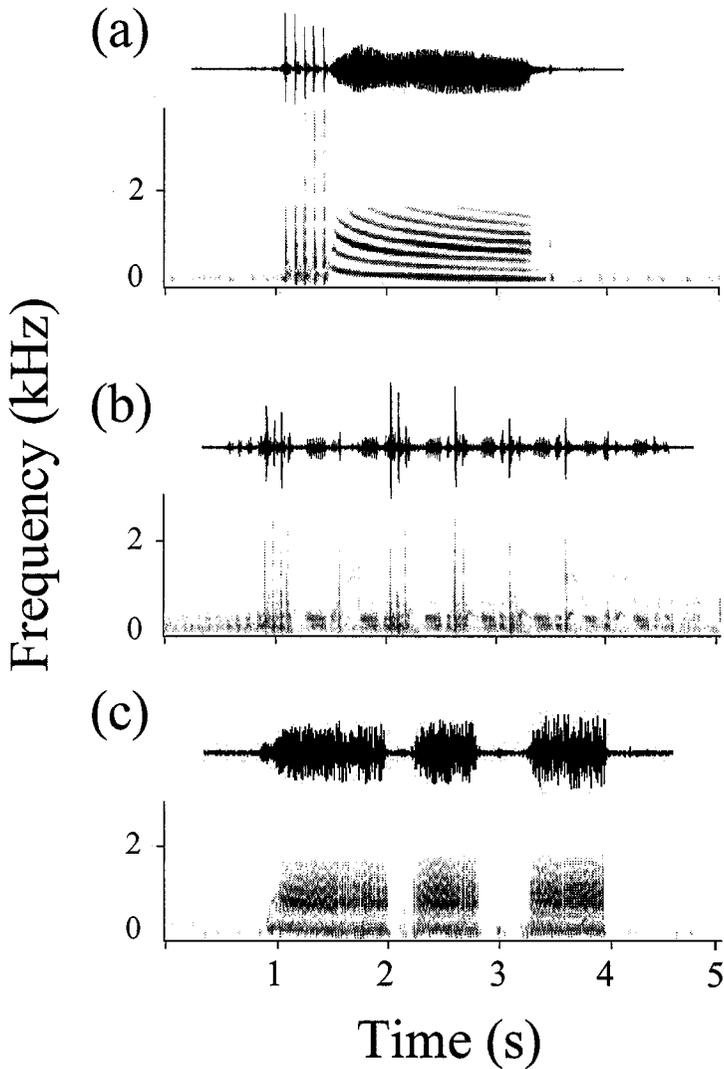


Fig. 1. Vibrational signals of *Vanduzee arquata* males; each panel contains an oscillogram (above) and a spectrogram (below). (a) Advertisement signal produced while mate-searching along host plant stem; (b) courtship signal produced while on the pronotum of a female; (c) signal produced while interacting with another male. Signals were recorded in the field at approximately 25°C.

signals, the male's abdomen can be observed vibrating, although this can be detected only from close range. The third signal (Fig. 1c) may be involved in male–male competition because it is given by two mate-searching males that encounter each other. However, this signal does not involve the large-scale

movements associated with the previous two signal types and, thus, cannot be easily monitored during visual inspections. Consequently, only the first two signal types were scored during visual censuses in this study. On 1 day near the peak of abundance, the proportion of males on the study site signaling or moving within the plant was quantified throughout the day. Beginning each hour (from 800 to 1600 EDT), each male was observed individually for 20 s and scored as stationary, walking, signaling on the host plant stem, or signaling on a female.

RESULTS

Within the study area, almost all *V. arquata* were found on a cluster of five *R. pseudoacacia* saplings ranging from 1 to 2 m in height. Regular censuses were therefore limited to this area, which is referred to as the study site. Most aggregations were attended by *Formica* sp., but some were attended by *Crematogaster* sp.

The number of adults on the study site changed rapidly over the course of one generation (Fig. 2a). Observations of the first generation at the study site the following summer revealed a qualitatively similar pattern: the number of adults peaked 3–4 weeks after the first individuals eclosed, and adult numbers were low again before the second generation of adults began to eclose.

The number of adults per aggregation changed continuously throughout the season (Fig 2b). The distribution of aggregation sizes is shown for 1 day at the peak of abundance (Fig. 3). At this point, 93.2% of individuals (315/338) on the study site were in aggregations (defined as the presence of at least one other individual within 5 cm; in most cases individuals were densely packed within aggregations). Each tree had one to three relatively large aggregations ($N > 10$ individuals), and these tended to persist in the same location over repeated censuses. Aggregation contained both nymphs and adults. Fifth-instar nymphs left the aggregation to molt on the underside of nearby leaflets, then returned to the aggregation as teneral adults.

In all, 144 females and 139 males were individually marked; 86 females and 108 males were batch-marked (by date of first observation). During regular censuses, 82.6% of marked females and 76.1% of marked males were resighted. Females spent ($X \pm SD$) 19.2 ± 15.8 (range, 1–59) days on the study site, while males spent 11.3 ± 9.9 (range, 1–47) days on the study site (Fig. 4). The medians of these distributions (16 for females, 9 for males) are significantly different (Mann–Whitney U test, $U = 35956$, $P < 0.001$).

The number of individuals differed from tree; Fig. 5 shows the results of censuses of five trees during the period of peak abundance. Both sexes moved between trees throughout the time they were on the study site

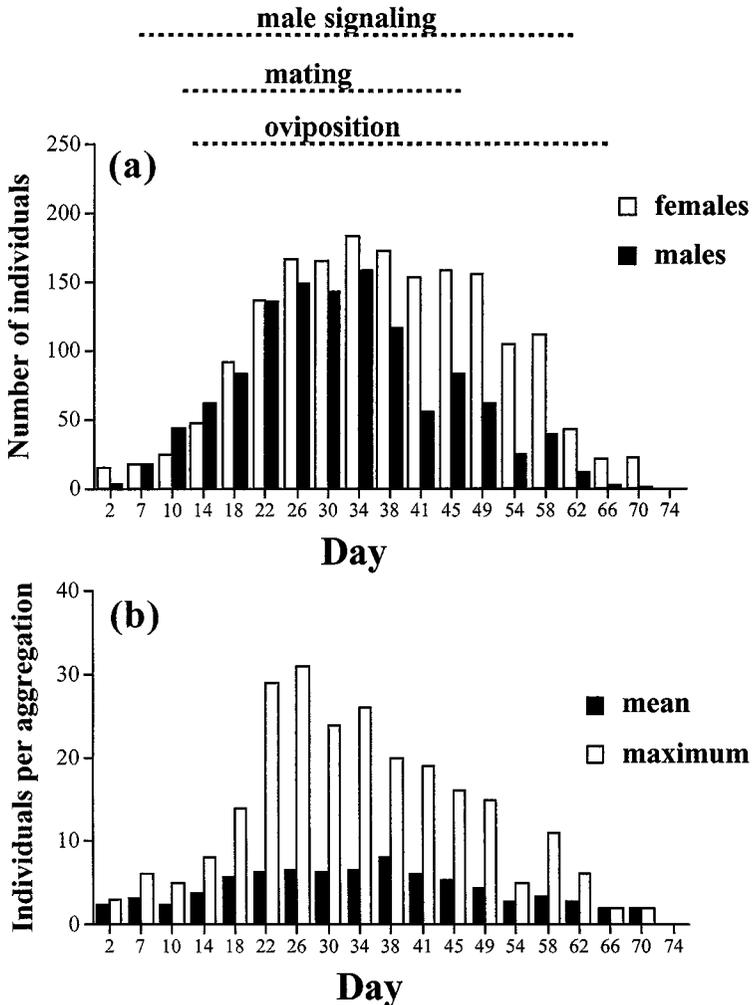


Fig. 2. (a) The number of adult *Vanduzee arquata* on the study site during the second annual generation. Shown above the graph are the periods during which signaling by males, mating, and oviposition were observed. Day 1 was August 29. (b) Average and maximum number of individuals per aggregation during the same period.

(Fig. 6). Observations of males suggested that they did not change locations until about 6 days after eclosion, a tendency reflected in Fig. 6 (note that some proportion of newly marked individuals may have immigrated as adults from other areas). Comparison of male and female movements

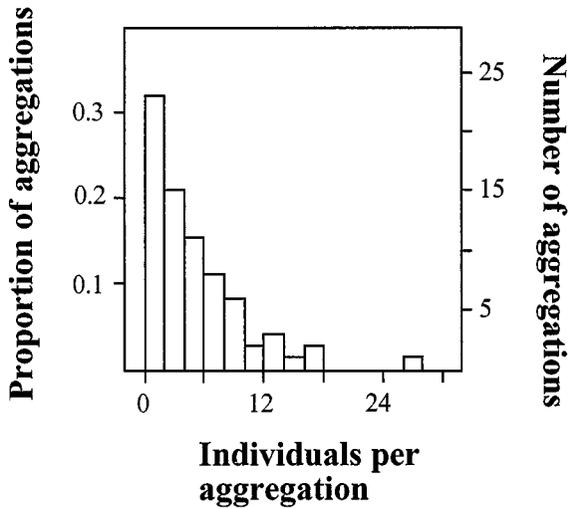


Fig. 3. Distribution of aggregation sizes on the date of peak abundance (day 34).

revealed differences among sampling periods (heterogeneity $\chi^2 = 32.3$, $df = 6$, $P < 0.001$). Results from each sampling period analyzed separately (using a chi-square test with Yates' correction and adjusted for multiple comparisons) showed that males moved significantly more than females, but only in the last two sampling periods (day 24, $\chi^2 = 17.4$; day 28, $\chi^2 = 8.9$; $df = 1$; $P < 0.05$).

Male Signaling Behavior

Males signaled in two contexts. In the first, males produced a substrate-born signal (cf. Fig. 1a) while standing on the plant stem ($N = 93$ observations; because some males were batch-marked or unmarked, the minimum number of males observed is 53). A male then typically remained motionless for a few seconds, then either walked rapidly to another location on the plant and called again or flew to another host plant. On small stems and leaf rachises, males typically signaled a few centimeters distal to the base of the stem (or leaf rachis) and then returned to the main stem, often repeating this pattern on each side stem or compound leaf rachis along a central trunk. Males seldom signaled on stems more than 1 cm in diameter, instead concentrating their activity on the distal portion of the branches where most other individuals occurred.

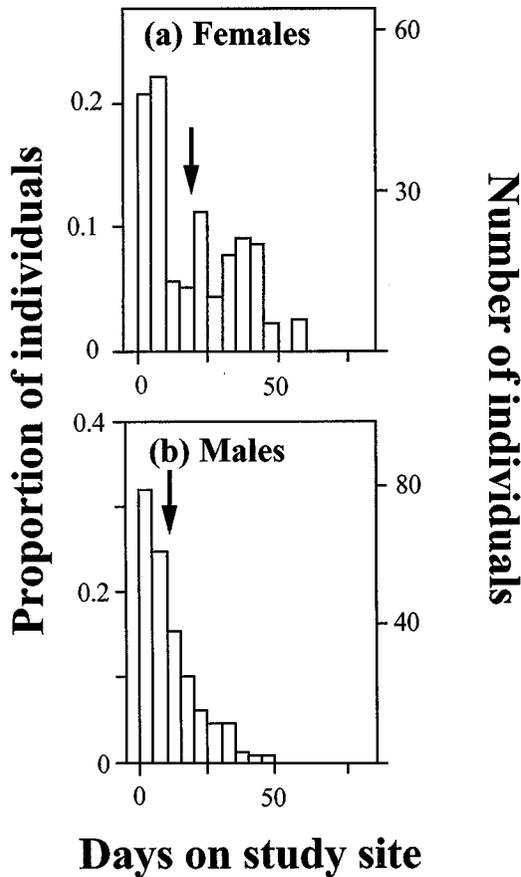


Fig. 4. Persistence of marked individuals on the study site. **(a)** Females; **(b)** males. Arrows indicate means.

Males also signaled while in contact with females in aggregations. After climbing onto a female's pronotum, a male produced a series of signals (cf. Fig. 1b) for several minutes, then moved back onto the stem ($N = 206$ observations, $N > 88$ males). As with signals produced on the host-plant stem, males rocked and produced percussive taps, although when on females these taps were produced in repeated series. These signals were lower in intensity when recorded on the plant stem than were advertisement signals, either because they were attenuated by transmission through the female's body or because they were less intense at the source. Within adult aggregations, there often were several males signaling on different females (typically one

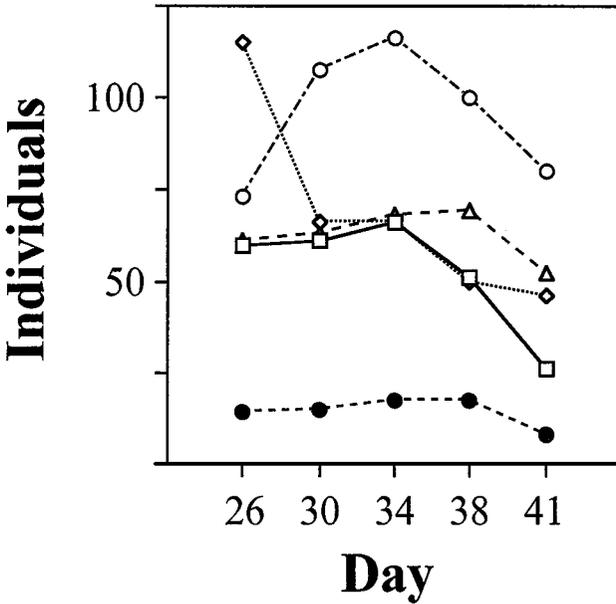


Fig. 5. Numbers of adults on neighboring host plants on 5 days around the peak of abundance. Each tree is represented by a different symbol.

male per female, but occasionally two). For 18 individually marked females, males were observed signaling on them on two to four occasions up to 33 days apart. Some males remained in aggregations for extended periods, occasionally signaling on one or more females, then once again taking a stationary place within the aggregation. Individual males signaled in both contexts: 29 males were seen signaling both on the stem and on females, often in close succession. The behavior of the male was observed in two cases prior to copulation. In both cases the male signaled on the female's pronotum before copulation, and in one case the male signaled on the female, then on the branch in front of the female.

Males were observed signaling throughout most of the study period, from September 4 to October 28 (day 7 to day 62; see Fig. 2a). Twenty-six individually marked males were observed signaling on at least 2 days, from 4 to 32 days apart ($X + SD = 12.1 \pm 7.5$).

On 1 day (September 13; day 16 in fig. 2a) the number of males signaling was quantified throughout the day. The number of males signaling (see Figs. 1a and b) changed during the day, reaching a peak at about midday (Fig. 7). At that time, about one in four males (24.6%) was signaling when observed.

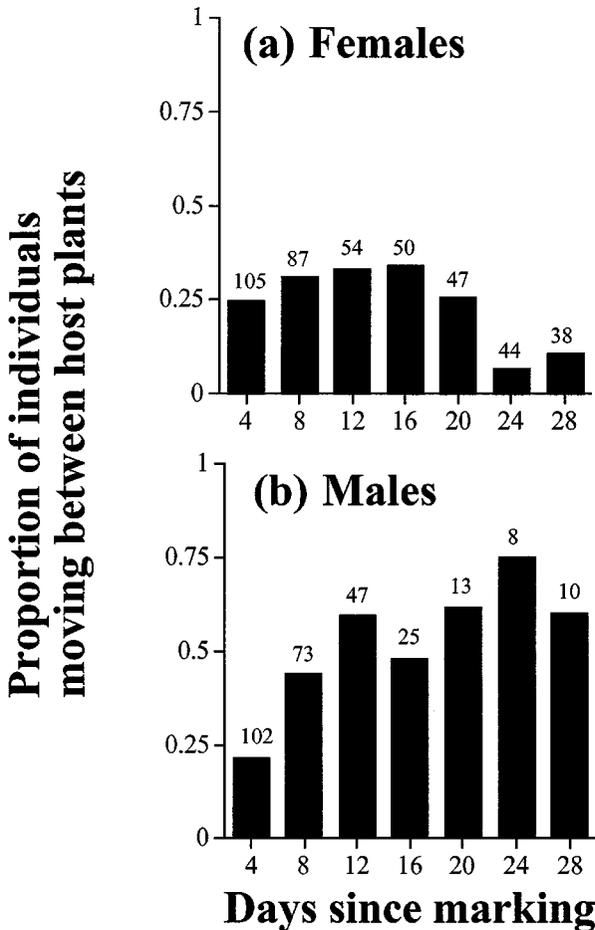


Fig. 6. Proportion of (a) females and (b) males that moved between host plants, calculated for 4-day periods after they were first marked. Total numbers of individuals used to calculate proportions are shown above bars.

Mating and Oviposition

Mating was observed between September 8 and October 12 (days 11 through 46; see Fig. 2a). Of 10 mated pairs observed, only 1 pair was within an aggregation; the other 9 were on stems or leaves 10 to 40 cm away from the nearest aggregation. Copulation lasted 1–2 h in three pairs in which it was timed. In two cases a second male was associated with a copulating pair,

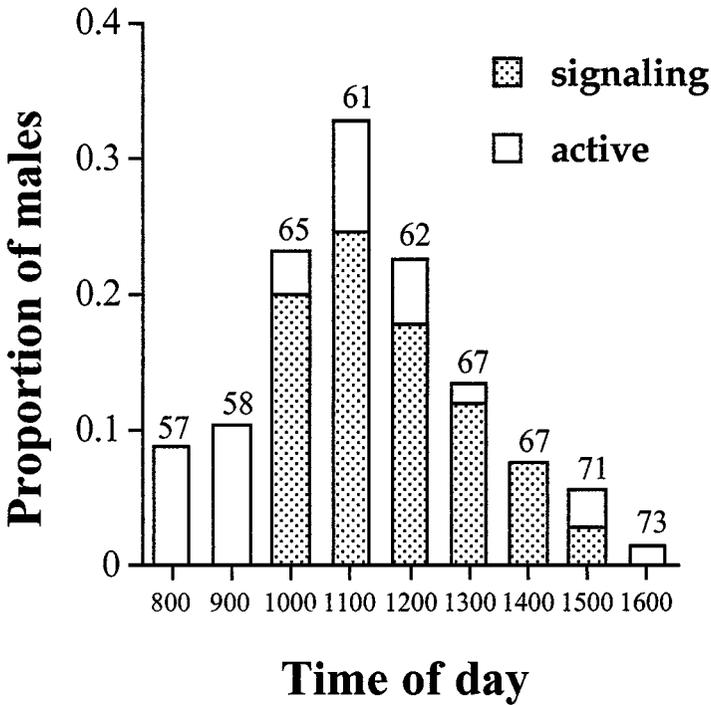


Fig. 7. Proportion of males on the study site walking and signaling during the course of a day, as determined by hourly scan samples. The number of males observed per hourly sample is shown above the bars.

moving between the pronota of the mated male and the female. In one of these cases, the female also copulated with the second male.

Oviposition was observed between September 9 and November 1 ($N = 29$ individually marked females and ≥ 6 batch-marked females; oviposition period shown in Fig. 2a). Oviposition sites were in leaf scars on stems of the previous year's growth. Females oviposited at multiple sites: 10 individually marked females inserted their ovipositors in two to seven leaf scars ranging from 5 to 100 cm apart. Five individually marked females were seen ovipositing on more than 1 day, from 1 to 22 days apart. Up to 13 females deposited eggs in leaf scars along the same stem.

Sources of Mortality

Five marked females were found with their ovipositors stuck in the branch, and these females subsequently died without moving away. Four

other detached ovipositors were found in stems. Near the end of the season, 10 females and 6 males were found dead on stems.

One male was eaten by a salticid, and one female was found dead in a spider web (two attending ants, a *Formica* sp., and a *Crematogaster* sp. were also seen being eaten by spiders). Attending *Formica* ants attacked two males; one was carried down the trunk by the ant, both escaped. Other predators observed eating *V. arquata* adults or nymphs in upstate New York in a subsequent summer include a pentatomid (*Podisus* sp.), spiders, and a coccinellid larva.

DISCUSSION

The distribution of *Vanduzeeae arquata* is highly clumped, as in many other anttended membracids (McEvoy, 1979; Wood, 1979). Most of the population is concentrated on a subset of available host plants, and within a single plant individuals occur in dense aggregations (Funkhouser, 1915; Fritz, 1982). In this study, at the time of peak abundance more than 90% of adults were found in groups. The density of adults also varies dramatically in time: during the course of one generation the number of adults rapidly increased, peaked, and then decreased, a pattern characteristic of *V. arquata* at another locality (Fritz, 1982).

Adult *V. arquata* will experience a range of social environments, given the changes in numbers of individuals and sizes of aggregations that occurred over the course of the season. Some variation occurs over a short time scale: within 1 day the proportion of active, signaling males varied from zero to one-fourth of the adult male population (similar diel patterns of activity may occur in other membracids [Johnson and Mueller, 1990]). Changes in the number of adults on the study site occur on a scale of days to weeks, and these can also fall within the experience of single individuals (see also Denno and Roderick, 1991; Ott, 1994). Marked males persisted on the study site for an average of 11 days (and up to 6 weeks), and marked females persisted for an average of 19 days (and up to 8 weeks). Individually marked males signaled on occasions up to 32 days apart, and individually marked females were courted by males on occasions up to 33 days apart. These observations suggest that single individuals can encounter very different social environments over time. On a longer time scale (beyond the experience of a single individual), numbers of adults can also vary between first and second summer generations (Fritz, 1982) and between years (Cocroft, personal observation).

Individuals will encounter spatial as well as temporal variation. Adults moved between and within host plants, with males moving more frequently

than females. Mate-searching males can travel quickly from branch to branch and from tree to tree, using a call-fly or call-walk strategy (Gwynne, 1987; Hunt and Nault, 1991) that increases the overall active space of their signaling effort. This movement of males may have the effect of “averaging” the spatial variation, such that a male’s social environment may include a patch of nearby host plants. If so, then temporal variation in the number of adults in the entire patch may be more important for male and female mating strategies than local spatial variation within the patch. Spatial variation may be more important on a broader scale, where different patches of host plants can vary greatly in the density of *V. arquata* (Cocroft, personal, observation): at that scale, individuals in different patches of host plants may spend their lives in very different social environments.

Adult *V. arquata* show relatively low vagility, in spite of their interplant movement. The high mark-resighting frequencies in this study suggest that many individuals spend their adult lives in the same small patch of host plants. Other membracids in which dispersal has been quantified also show relatively low vagility (Wood and Guttman, 1982; Wood and Dowell, 1985).

As with the overall number of adults, the size of aggregations changed during the season. All but the smallest aggregations (two or three individuals) contained both males and females. At least some females mate within aggregations: Funkhouser (1915) reported that most mating pairs were found within aggregations, and in this study 1 of 10 mating pairs was found within an aggregation. There was no indication that males physically defended aggregated females, although this observation does not rule out the possibility of aggressive interactions mediated by signals (see Ichikawa, 1982). Indeed, males within an aggregation often began signaling (with the signal shown in Fig. 1c) when a mate-searching male approached. However, it is not clear how this signaling may influence the behavior of an approaching male. In any case, the interpretation of male behavior is currently limited by a lack of knowledge of how the operational sex ratio varies spatially and temporally, which will be influenced by how often females mate, at what ages, and in what locations.

Spatial and temporal variability in the density of breeding adults can have dramatic effects on mating behavior and communication. For example, in breeding choruses of toads (*Bufo calamita*), mating strategies of males are density dependent: at high densities some males switch from stationary advertisement calling to active searching (Arak, 1983). In other frog species, the local density of calling males can influence whether some males produce advertisement calls or become silent satellites of calling males (Perill *et al.*, 1982; Sullivan, 1982). Features of the advertisement signals themselves may also vary as a function of nearest-neighbor distance (reviewed by Wells, 1988). Although behavioral changes as a function of density were not

examined in this study, male advertisement signals (Fig. 1a) can vary in the number of percussive taps produced at the beginning of the signal and in the number of “whines” produced after the initial taps (Cocroft, unpublished data). Preliminary observations of individuals maintained in a greenhouse colony revealed that signals of males housed individually contained fewer taps and whines than those of males housed with other individuals (Cocroft, unpublished data), suggesting that there may be density-related changes in signaling behavior.

Adult groupings largely reflect maturation within groups of immatures. Although I have not considered nymphs as an important component of the social environment of adults, it is possible that they may be. For example, a mate-searching male might remain near groups of late-instar nymphs, if it would thereby increase its access to recently eclosed, receptive females (e.g., Deinert *et al.*, 1994).

The mating system of *V. arquata* is likely characterized by outbreeding (at least with respect to the individuals present in a patch), given the pattern of adult movement and female oviposition. Adult aggregations will include individuals of varying degrees of relatedness, because they are formed from a mix of individuals that eclosed on that stem as well as immigrants from other locations. Furthermore, because females oviposit at several locations within host plants, and because several females often oviposit in the same length of stem (Funkhouser, 1915; this study), the nymphs that develop on any one stem will often include offspring of multiple females. Nymphs also move between aggregations (Fritz, 1982). The composition of aggregations is thus very different from that of treehoppers with maternal care of nymphs, in which aggregations often consist of offspring from a single female (Wood, 1979; Masters, 1997).

Which of the patterns documented in *V. arquata* are influenced by their mutualism with ants, and which might be shared with solitary membracids? Some aspects of the social environment are likely to be shared between solitary and aggregated species, such as marked temporal variation in the number of adults (e.g., Funkhouser, 1917; also see Ott, 1994). However, because of the degree of clumping, local spatial variation in the number of adults is probably more extreme in this ant-attended species than in solitary species. This difference may lead to a difference in male mate-searching strategies. For example, allocation of effort by males in active mate searching versus short-range courtship of already-located females might differ, because the cost of locating additional females is probably lower in aggregated species. In many species of membracids, a mate-searching male that encounters a female will often climb onto her pronotum and remain for a long period, sometimes hours, and during this time may produce courtship signals (Wood, 1974; Cocroft, personal observation). In the highly aggregated *V. arquata*, males

only briefly court individual females, then move to a neighboring female, resume mate searching, or stop signaling and remain within the aggregation. Males in aggregated species have the opportunity to remain near a clump of females; some male *V. arquata* clearly did not do this, but some appeared to do so, as indicated by their presence in the same aggregation during repeated censuses.

The number, distribution, and behavior of conspecifics are important features of an individual's social environment. Because all of these can show marked spatial and temporal variation in *V. arquata*, studies of communication and mating behavior in this species should consider variation in the social environment as a potentially important source of selection. In particular, the behavior of males will be influenced by the availability and distribution of receptive females (Emlen and Oring, 1977; Bradbury and Vehrencamp, 1977). Potential sources of variation in male behavior include the proportion of time spent searching along plant stems versus calling on aggregated females, as well as characteristics of the signals themselves. In addition, if signal variation is correlated with variation in the social environment, then this must be controlled for in geographic or species-level comparative studies of signals. Because marked spatial and temporal variation characterizes many insect populations (e.g., Strong *et al.*, 1990; Wolda, 1979), variability in the social environment may be an important source of selection on insect communication systems.

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