ORIGINAL PAPER

# Wind-induced noise alters signaler and receiver behavior in vibrational communication

**Gabriel D. McNett · Lucia H. Luan ·
Reginald B. Cocroft**

**Abstract** Noise that masks communication signals can affect the evolution of signal form and decisions about when and where to communicate. For the many invertebrates that communicate using plant-borne vibrations, wind is considered to be the major source of environmental noise. However, the influence of wind-induced vibrations on signaling behavior has not been experimentally tested. We tested the hypothesis that wind-induced noise influences signaling behavior in a plant-feeding insect (the treehopper, *Enchenopa binotata* '*Ptelea*') in which mating is preceded by a vibrational duet between females and mate-searching males. We first characterized the diel signaling patterns of males in the field to identify the wind conditions under which signaling typically takes place. We then experimentally tested two predictions of the hypothesis: (1) that males use gap detection to initiate signaling during relatively wind-free periods; and (2) that females respond less to signals given in the presence of wind-induced vibrations. Both predictions were met, indicating that wind-induced noise is an important influence on the behavior of insects that use plant-borne vibrations.

Communicated by D. Gwynne

G. D. McNett · L. H. Luan · R. B. Cocroft
Division of Biological Sciences, University of Missouri,
105 Tucker Hall University of Missouri,
Columbia, MO 65211, USA

*Present Address:*
G. D. McNett (✉)
Department of Biology and Environmental Science,
Westminster College,
501 Westminster Avenue,
Fulton, MO 65251, USA
e-mail: gabe.mcnett@westminster-mo.edu

## Introduction

Natural environments are noisy for individuals communicating in any modality (Michelsen et al. 1982; Brenowitz 1986; Endler 1993; Forrest 1994; Atema 1995; Slabbekoorn and Smith 2002). Noise creates problems in detecting signals and deciphering the encoded information. Individuals are able to communicate more efficiently when they achieve spectral or temporal separation from noise, which often involve adaptive changes in senders and receivers (Römer 1993; Brumm and Slabbekoorn 2005). Enhancing signal detection may occur through changes in signal design (Slabbekoorn and Peet 2003; Foote et al. 2004) or through changes in signal timing (Greenfield 1988; Brown and Handford 2003). Which of these solutions is more efficient will depend on the relationship between the spectral and temporal properties of noise, the properties of the signal, and the behavior of sender and receiver.

Noise comes from both biotic and abiotic sources. The most common biotic source of noise is the presence of other signalers (e.g., Gerhardt and Klump 1987; Greenfield 1988; Aubin and Jouventin 1998), although human activity is also a significant noise source for urban species (Slabbekoorn and Ripmeester 2008; Parris et al. 2009). Abiotic sources, on the other hand, may vary depending on the dominant mode of communication. For birds and primates that rely on acoustic communication, wind or water can be a noise source (Waser and Waser 1977; Ryan and Brenowitz 1985; Douglas and Conner 1999). Fish or reptiles that communicate with chemical signals can be affected by pollutants (Fisher et al. 2005); those that

communicate with electric signals may be affected by lightning (Hopkins 1973), and those using visual signals can be affected by water turbidity (Seehausen et al. 1997), or wind-blown vegetation (Ord et al. 2007). For the vast number of small plant-dwelling arthropods that communicate using vibrations, abiotic noise comes predominantly from wind (Barth 1988; Cocroft and Rodríguez 2005; Tishechkin 2007).

Wind induces noisy vibrations throughout a plant when branches move and leaves flutter. These plant vibrations contain primarily low frequencies (<100 Hz), but may contain energy up to 20 kHz (Barth 1988; Casas et al. 1998; Cocroft and Rodríguez 2005; Tishechkin 2007). At a given location, wind velocity may show relatively predictable variation over the course of a day, and unpredictable variation on a scale of seconds or minutes (Tishechkin 2007). It is likely that both temporal scales of variation are important for communication and favor behavioral mechanisms that permit communication when noise levels are low. For example, diel variation in wind velocity may favor signaling during morning or evening lulls, as with species using acoustic communication (Andersson et al. 1998; Brown and Handford 2003). Short-term variation in wind velocity may favor signaling in silent gaps (Schwartz and Wells 1983; Douglas and Conner 1999) and "listening in the valleys" (Buus 1985). Such gap-detecting behaviors are found in a wide range of taxa, including humans (e.g., Schneider and Pichora-Fuller 1994), birds (e.g., Okanoya and Dooling 1990), and insects (Greenfield 1994). The use of gaps by vibrationally communicating insects is suggested by the field recordings of Tishechkin (2007), where communication signals are given in lulls between wind-induced vibrations. However, in spite of the prevalence of vibrational signaling and a general recognition of wind as a major noise source (Cocroft and Rodríguez 2005; Tishechkin 2007), the relationship between signal timing and wind-related noise in the vibrational modality has not been addressed experimentally.

In this study we test the hypothesis that wind noise alters signaler and receiver behavior over short time scales in a vibrationally communicating insect, the treehopper *Enchenopa binotata* 'Ptelea'. This is an undescribed species in the *E. binotata* complex of treehoppers (Cocroft et al. 2008), and is found only on one species of host plant (Rutaceae: *Ptelea trifoliata*). If wind-induced vibrations in plants affect communication efficiency—the ability to transmit information with minimal energy expenditure—males and females should reduce noise-related costs by signaling primarily during wind-free gaps. We first measured signaling behavior in relation to wind velocity in the field, to characterize the wind conditions experienced by signaling individuals. We then tested two predictions: (1) that males are more likely to initiate signaling during wind-free periods, and (2) that females are more likely to respond to signals that are not embedded in wind-induced noise.

## Material and methods

### Male signaling response

#### Experimental animals

The study was conducted in Boone County, Missouri, USA. Males and females used in the experiments were lab-reared offspring of adults collected the previous mating season from host plants on the University of Missouri campus. Experimental individuals were separated by sex prior to sexual maturation (5–7 weeks), maintained in sleeve cages on separate potted host plants and kept in a greenhouse under natural light during the breeding season.

The male *E. binotata* 'Ptelea' produces bouts of two or more signals, each consisting of a whine followed by a series of pulses (see Fig. 1). The signal is a frequency-modulated tone (sometimes with harmonics present), and for the local Columbia, Missouri population the average
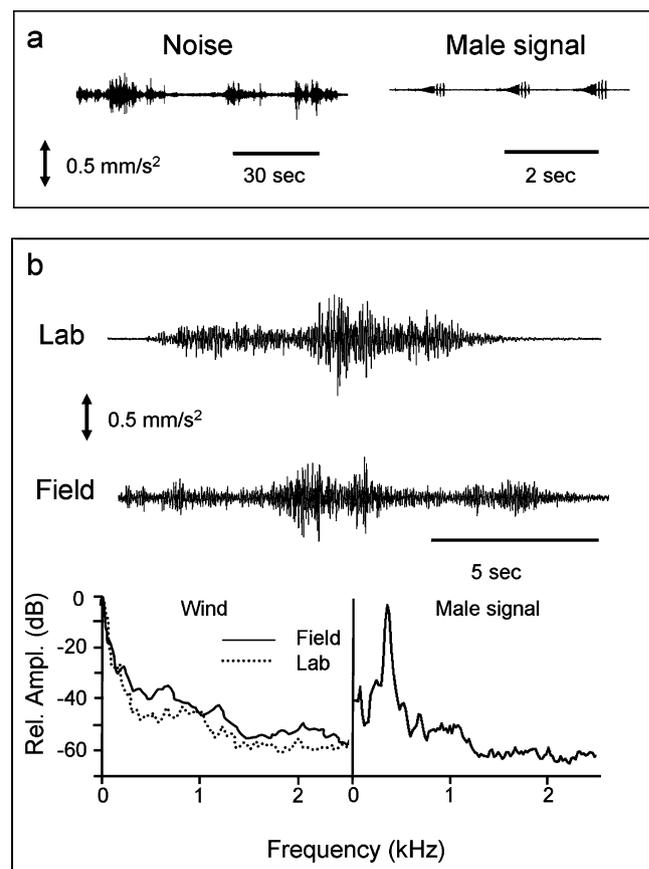
Fig. 1 Wind-induced vibrational noise recorded from leaf petioles of *P. trifoliata*. **a** Field recording of vibrations produced by a light breeze (peak wind velocity=1.1 m/s) and of three male advertisement signals. **b** Waveforms and amplitude spectra of vibrational noise recorded in the field and in the laboratory (peak wind velocity=1.5 m/s for both) and amplitude spectrum of a male signal

(±SD) frequency is 333±10 Hz [$N$=51 males; data drawn from Cocroft et al. (2010)].

Mate searching males produce advertisement signals to which receptive females respond, forming a vibrational duet (Hunt 1994; Rodríguez and Cocroft 2006). Duetting is an important component of mate choice because female responses function as localization beacons for males. In response to a duet, solitary males also initiate signaling. The duetting response of both sexes thus provides an assay for playback experiments. Males also form small choruses during the day, and we use this chorusing behavior to characterize diel patterns of signaling.

## Diel variation in wind speed and natural signaling behavior

Diel variation in male signaling behavior and wind speed was measured during the mating season in July 2005 to determine: (1) when communication takes place during the day and (2) what wind velocities would be appropriate for experimental tests. Four host plants were measured at each of three field sites ($n$=12 host plants) located within a 15-km$^2$ area of Boone County, Missouri, USA. To observe the insects' behavior at a range of wind speeds, host plants monitored at each site were chosen from both open and sheltered locations.

To determine the conditions under which communication takes place in *E. binotata* 'Ptelea', small aggregations of individuals were monitored in the field. During the breeding season, persistent groups of 2–12 individuals form on leaf petioles at the distal branch tips of their host plant. Groups may contain only males or, more commonly, both males and females. Males signal in choruses for extended periods. Female signaling was not measured, as females signal only during a short period of receptivity and thus is rarely heard. For each aggregation, male signaling behavior and local wind speed were monitored for 12 h (0800–2000 hours). Signaling in *E. binotata* 'Ptelea' ceases after 2000 hours (L.E. Sullivan-Beckers, unpublished data). Behavior and wind speed were sampled for 2 min every 30 min. The largest male-biased aggregation on each host plant was chosen for monitoring since these are most likely to engage in persistent signaling bouts (GDM, personal observation). Signaling was monitored by attaching a Signal Flex SF30 Universal Tuner Pickup to each host plant. Although attaching a pickup to the plant never appeared to disturb an aggregation, to eliminate potential disturbance during the sample period, pickups were placed within 10 cm of the focal aggregation at 0730 hours and were left throughout the day as long as two or more individuals remained. A single aggregation was monitored throughout the day at ten of the 12 host plants. For two host plants, the individuals in the initial focal aggregation dispersed and a second aggregation on the same host plant was monitored. For these two host plants the pickups were moved between sample periods. During each 2-min sample period, the pickup was connected to a battery-powered Johnson JA-004 Mini-amp/speaker at a distance of 2–3 m from the plant, and the total number of signals was counted by a field assistant using a hand-held tally meter (see below for a test of the accuracy of this method). We then calculated the proportion of signals for each sample period relative to the total number of signals detected.

Wind speed was monitored within 1 m of the focal aggregation using a WindSonic ultrasonic anemometer (Gill Instruments, Hampshire, UK) mounted on a tripod. The anemometer was connected to a Dell 700m Inspiron laptop computer. The wind speed was sampled four times per second using WindCom software (Gill Instruments, Hampshire, UK). Peak and average velocity (m/s) was recorded for each of the 2-min sample periods throughout the 12-h monitoring period, yielding 25 recordings of wind speed per day per host plant.

## Detection by investigators of signals in noise

To address the potential for missed signals during the field monitoring of signaling behavior, a hearing test was given to the field assistant. For the hearing test, wind was produced using a computer fan mounted onto a tripod (Fig. 1b), and wind speed was maintained at a velocity of 1.5 m/s, the upper range of that commonly experienced by natural populations (see results). Stimuli consisted of three 2-min series, each containing 20 natural male signals arranged in random order and separated by randomly determined time intervals of 1–10 s. All three series were conducted at the same wind speed, but each differed with respect to male signal amplitude. The highest signal amplitude was equivalent to an average male signal measured within 2 cm of the male on a leaf petiole (peak amplitude=0.14 mm/s$^2$). The other two series attenuated the male signals by −6 dB and −12 dB, respectively. Signals were monitored using the same pickup and battery-powered mini-amp/speaker used for monitoring signals in the field and counted using a hand-held tally meter. The pickup was placed 50 cm from the playback location. The combined conditions of the hearing test likely produced signal-to-noise ratios that were substantially lower than those experienced in the field: the wind velocity (1.5 m/s) was greater than most field conditions, male signal amplitudes at the source (magnet) were either equal to or less than that of the average male, and the distance from the signal source to the pickup (50 cm) was five times greater than the distance to the focal aggregations in the field.

All signals were detected during tests conducted at the amplitude of signals of nearby males and when these were attenuated by 6 dB, suggesting that all males from the focal aggregation signaling at average amplitude would be detected even with wind velocities at the high end of the range. There were no false positives. Only when male signals were attenuated by 12 dB (simulating the signals of a distant aggregation on the same plant) did the hearing test reveal a large number of missed signals and false positives (14 out of 20 signals missed, two false positives). These results indicate that there will be little error in our observations of signaling from the focal aggregation. If signals of more distant males were detectable at the location of the focal aggregation, these could contribute to error because they would only be audible during wind-free periods. However, quiet and seemingly distant signals were rarely detected during wind-free periods.

*Testing male response*

Playback experiments were conducted with laboratory-reared males in July 2005 to test the hypothesis that males use gap detection to take advantage of short-term fluctuations in wind-induced noise. Males were tested in the laboratory and their signals were recorded, which allowed signals to be readily identified in spectrograms (Fig. 2).

Males were first stimulated to signal using playback of a recorded male–female duet (Fig. 3); this priming playback
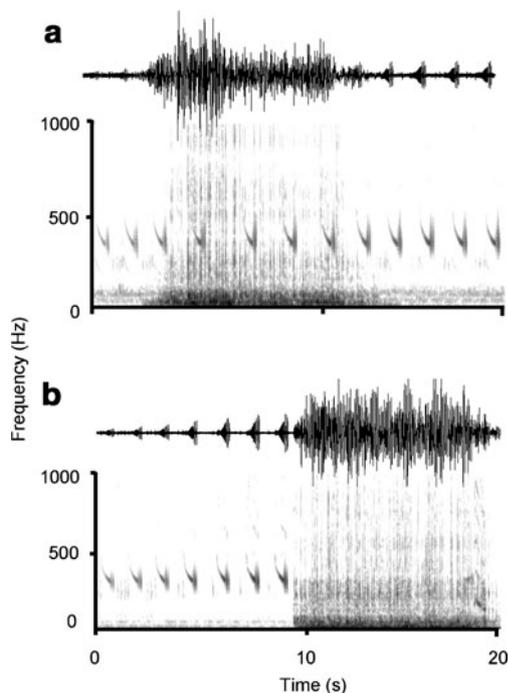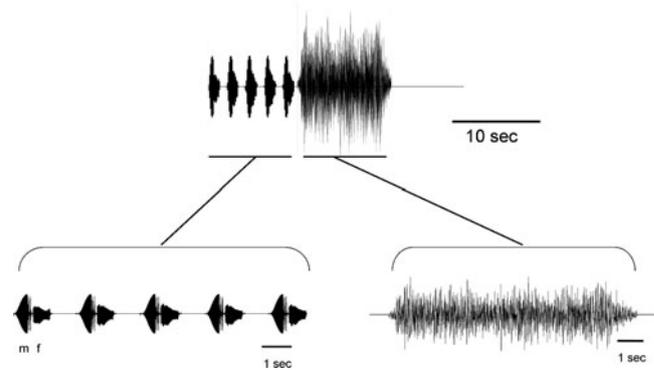


Fig. 3 Example stimulus used to test male responses to wind. A duet consisting of four alternating male and female signals was used to elicit male signaling. Plant vibrations were induced using a fan

was then followed by a short period of wind and silence. The duet was recorded on the stem of a potted host plant using similar recording methods to those used here. Wind was generated using a computer fan wired to a switch. Two wind speeds at the location of the male were used, low (0.75 m/s) and high (1.50 m/s), and were achieved by adjusting the distance between the test plant and the fan. Twenty five males were tested at each wind speed (n=50) using a 2-min test series. The duets were played from a Dell 700m Inspiron laptop running Raven software (v. 1.2; Cornell Bioacoustics Laboratory, USA), amplified (Radioshack MPA-250), and transduced into the stem of a potted *P. trifoliata* ~1 m tall using a magnet attached to the stem with wax and driven by an electromagnet (see Cocroft and Rodríguez 2005). The test stimulus contained a 10-s wind burst and a 10-s silent gap.

Individual males were transferred to the testing plant and allowed to settle for 2–3 min prior to the playback. Males remained within 10 cm of the transducer. Signals were recorded using a PCB 352A24 accelerometer (weight, 0.8 g; attached using mounting wax) connected to a PCB 480E09 ICP Sensor Signal Conditioner (PCB Piezotronics, NY, USA), amplified using an M-Audio Mobile USB Pre amp (Avid Technology, Tewksbury, MA, USA), and acquired on a Dell 700 m Inspiron laptop running Raven software (v. 1.2; Cornell Bioacoustics Laboratory, USA). The number of signals during wind and during wind-free periods was counted. A logistic regression was used to determine whether the probability of male signaling depended on the presence/absence of wind, wind level, or a wind presence–wind level interaction.

Female signaling response

*Stimulus design*

We tested whether females preferentially produce signaling responses to male signals during wind-free gaps. Female



Fig. 2 *E. binotata* (*Ptelea*) males that **a** continued signaling or **b** stopped signaling during bouts of fan-generated wind

responses were measured in late May/early June 2006. We used naturally recorded wind-induced vibrations to further isolate the effects of this type of noise on communication. The vibrations ("wind bursts," details given below) were recorded in the field using a PCB 352A24 accelerometer (weight, 0.8 g) attached with wax to a host plant petiole (average wind speed=0.83 m/s; range, 0.52–2.52 m/s). Fan-generated wind noise, as was used with the male experiments, simultaneously introduces two variables that a plant-feeding insect will detect: air movement and the induced vibrations. Using naturally recorded wind-induced vibrations removes the former. The two recordings, male signals and wind-induced vibrations, were played from separate transducers separated by 10 cm. Overall, four stimuli were used. First, a control stimulus (a bout of four male signals) was used to test whether a female was responsive. Second, three test stimuli combined male signal bouts in one channel with one of three wind conditions in the other channel (no wind, low wind, and high wind). The male signal bouts of each test stimulus contained six separate signal bouts (four signals per bout). The sequence of the three test stimuli was randomized for each female, and the control stimulus preceded and followed the three test stimuli. With two control stimuli and three test stimuli, each with six signal bouts, each female received 20 total signal bouts.

Male signals in the control stimulus were naturally recorded signals, but those in the test stimuli were computer-generated using signal parameters set to local population averages using a custom-made program in MATLAB (v. 6.5, Mathworks, Natick, MA) (Rodriguez et al. 2006). The computer-generated signals used a constant frequency of 330 Hz, the average frequency in the local population of *E. binotata* 'Ptelea' (Cocroft et al. 2008), rather than the frequency sweep found in natural male signals. Constant frequency signals are nearly as effective in eliciting female response (Rodriguez et al. 2006; see also Fig. 6) and ensure that each female received the same frequency, and any variation in female signaling response is not due to variation in plant frequency filtering. Peak amplitude was equalized for all male signals within a bout, but was varied between bouts. Signal amplitude was measured and adjusted at the point on the stem at which females were released. Amplitude for the six bouts was relative to that of a male at 1 cm and dropped in steps of 6 dB (0 dB, −6 dB, −12 dB, −18 dB, −24 dB, and −30 dB peak amplitude).

The six recorded wind bursts of the test stimuli overlapped the six bouts of male signals. Recorded wind bursts were drawn from field recordings of natural wind-induced vibrations in leaf petioles of 19 different *P. trifoliata* host plants. The root mean square (RMS) amplitude of each wind burst was calculated using Raven (v. 1.2, Cornell Bioacoustics Laboratory, USA). RMS amplitude was used instead of peak amplitude since the latter would have been less reliable as an indicator of overall noise intensity due to the rapid amplitude fluctuations inherent in wind-induced vibrations (Figs. 1 and 2). Six exemplars of recorded wind bursts were chosen for the low-wind and high-wind levels. Those chosen represented ±1 SD of the average RMS amplitude of all recorded wind bursts. These RMS amplitude levels corresponded to an approximate peak wind speed of 1.0 m/s (low wind) and 2.0 m/s (high wind). With an equal number of exemplars and signal bouts (six), a single female never experienced the same wind exemplar more than once.

### Testing female response

Each female was placed on a leaf petiole of the same potted *P. trifoliata* host plant (0.5-m tall) equidistant between the two transducers (magnet/electromagnet pairs). The stimuli were played to the transducers using Audacity (v.1.2.4). The amplitude spectrum of each wind burst was adjusted to compensate for plant-filtering properties using a procedure described in Cocroft and Rodríguez (2005); briefly, the filter imposed by the playback setup and plant stem was calculated then used to generate a digital filter to apply to the experimental stimuli to compensate for that filtering. The RMS amplitude was calibrated to the low and high levels before the female was placed on the plant. The highest peak amplitude of the male signal bouts (defined as 0 dB) was 0.14 mm/s$^2$, equivalent to an average male at <2 cm on a leaf petiole. The amplitude levels of wind and male signals were calibrated at the point on the leaf petiole where the females would be released for testing (i.e., at the accelerometer). All females remained within 2.5 cm of the accelerometer except for one that settled 4 cm away. The signaling responses of 25 females were recorded using the same computer, accelerometer, pre-amp, and software described above for males (*Testing male response*). Female response was recorded as a binary variable with a positive response indicating a female responded to at least one of the four male signals in a bout. A logistic regression was used to test whether the probability of a female's response (i.e., a signal produced immediately after a male advertisement signal) was predicted by male signal amplitude, wind level, or signal amplitude–wind level interaction.

## Results

### Male signaling response

#### Diel variation in wind speed and natural signaling behavior

In the field, most signaling occurred during the morning and evening when wind velocity was lowest (Fig. 4). The
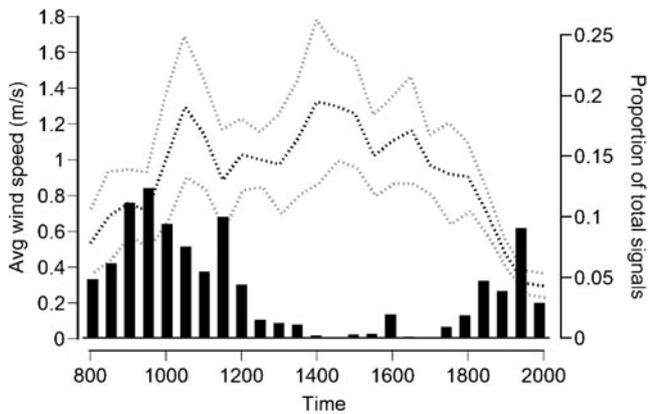
**Fig. 4** Diel variation in wind velocity and male signaling behavior. Average wind velocity (*dotted line*, ±95% confidence interval) measured within 1 m of focal aggregation of signaling individuals. Male signaling behavior (*bars*) peaked in the morning and evening when wind was low

**Table 1** Males signaled less during wind than during gaps especially for high-velocity wind (logistic regression)

| Source | df | Chi-square | P value |
|---|---|---|---|
| Wind vs. gap | 1 | 85.2 | <0.001 |
| Wind level | 1 | 4.9 | <0.05 |
| Wind presence*Level | 1 | 0.3 | 0.57 |

*df* degrees of freedom

detected signals were almost exclusively produced by the focal aggregation: faint signals that may have come from more distant males were rarely heard during wind-free periods. Based on these field observations wind speeds of 0.75 m/s (low) and 1.5 m/s (high) were chosen for the lab-based experiments. The low wind speed represents a velocity at which communication frequently occurred (see Fig. 4, 09:30). The high wind speed represents a velocity above which communication seldom occurred (Fig. 4; 1400–1600 hours).

*Male response*

In response to wind generated in the laboratory, males signaled significantly more during wind-free gaps than during wind bursts (Fig. 5; Table 1). Signaling was inhibited more by higher-velocity wind (Table 1), and this inhibition continued into the wind-free gaps as evidenced by the lower rate of signaling during gaps in the 'high wind' stimulus (Fig. 5). The lack of a significant interaction
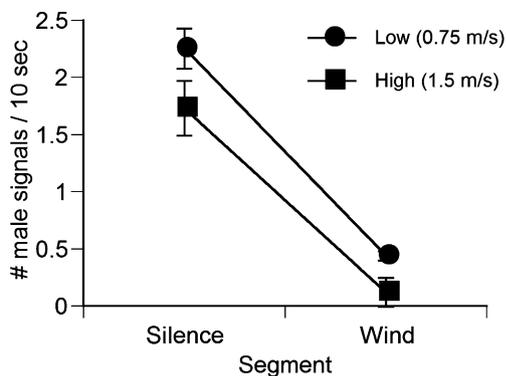


**Fig. 5** Inhibition of signaling by wind-induced noise, males signaled in the gaps after wind bursts and their signaling rate was lower after high-velocity wind bursts

term reflects the inhibition of signaling at both wind levels (there might have been a significant interaction if, for example, signaling was only inhibited during the higher-velocity wind).

Female signaling response

*Female response*

Females showed no evidence of habituation or decreased motivation during presentation of 20 signal bouts (Fig. 6), including six computer-generated bouts for each of three different wind levels and a control bout from a natural male before and after the 18 test bouts.

The females' probability of signaling in response to male signals was influenced by male signal amplitude, wind level, and their interaction (Table 2). The patterns of responses shown in Fig. 7 indicate that for male signals of high amplitude (i.e., simulating a male within several centimeters), females responded just as frequently when wind noise was present. However, for low-amplitude male signals (simulating a more distant male), female response dropped substantially when wind was present. Indeed, during the control treatments (no wind), the greatest proportion of females responded to the quietest signals (Fig. 7). All females responded to the male signals at −30 dB (re: average male signal at <2 cm); and all but one female responded to −24 dB. In contrast, female response never reached 100% when wind-induced noise was present regardless of wind level. During low-wind and high-wind response to the quietest male signals dropped to 50% or less (Fig. 7).

**Discussion**

Studies in the vibrational modality have suggested that wind-induced noise is an important feature of the communication environment (Barth 1988; Cokl and Doberlet 2003; Cocroft and Rodríguez 2005; Tishechkin 2007). Our monitoring of natural populations of male *E. binotata* 'Ptelea' revealed that most signaling occurred during the morning and evening hours when wind velocity was low
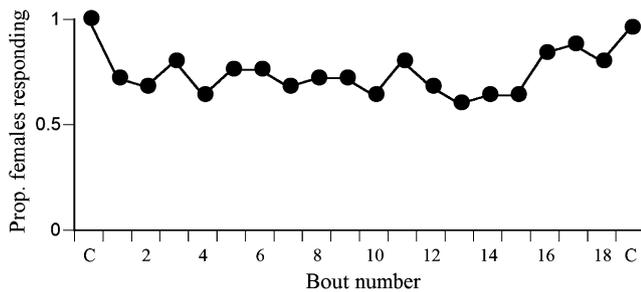
**Fig. 6** Females showed no evidence of habituation or decreasing motivation during the presentation of 20 signal bouts. A comparison of the proportion of females responding to the first and last artificial stimulus revealed no significant difference (two-sided Z test; H$_0$, $p_1=p_2$; $Z=0.6623$, $p=0.5078$; $N_1=N_2=25$)
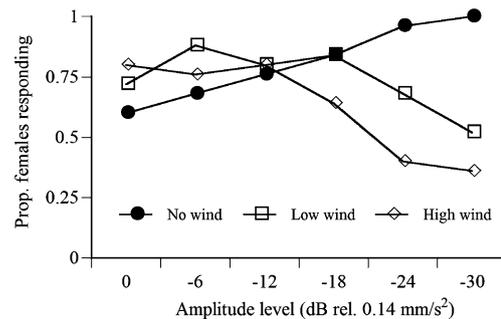


**Fig. 7** Females were less likely to duet with male signals in the presence of wind-induced vibrations especially for male signals of low amplitude. Male-signal amplitude was relative to an average male at a 2-cm distance on a leaf petiole. Note that only in the absence of noise did all females respond

(see Fig. 4). Light levels and temperature were changing in parallel with wind speed so although this diel pattern of signaling is consistent with the noise-avoidance behavior seen in other taxa (Saxena and Kumar 1980; Greenfield 1988; Douglas and Conner 1999; Lengagne and Slater 2002; Sun and Narins 2005; Patricelli and Blickley 2006; Fuller et al. 2007) we have no evidence for a causal relationship. However, over a shorter time scale, laboratory experiments revealed a clear cause-and-effect relationship between wind noise and reduced signaling (see Table 1). Males avoided producing advertisement signals during wind gusts (see Fig. 5), and females often failed to reply to advertisement signals played back during wind gusts (see Fig. 7). Reduced signaling during wind-induced noise was suggested by the field recordings of Tishechkin (2007), but this is the first study to experimentally demonstrate an influence of wind on vibrational communication for both signalers and receivers.

In the absence of wind-induced noise, females signaled more consistently in response to low-amplitude male signals than to high-amplitude signals (see Fig. 7). Although female preference curves have been characterized for several signal traits (Rodriguez et al. 2006), these data provide the first characterization of female responses as a function of signal

**Table 2** Female duetting responses were influenced by the amplitude of the male signal, wind speed, and their interaction (logistic regression)

| Source | df | LR Chi-square | P value |
|---|---|---|---|
| Amplitude level | 5 | 13.3 | <0.05 |
| Wind level | 2 | 71.8 | <0.0001 |
| Amplitude level*Wind level | 10 | 90.7 | <0.0001 |
| Female | 24 | 218.3 | <0.0001 |

Wind (especially higher-velocity wind) inhibited responses to low-amplitude signals to which females, otherwise, were the most responsive. However, wind had little effect on female responses to high-amplitude signals

*df* degrees of freedom, *LR* likelihood ratio

amplitude. The pattern of female responses suggests that female signals function as localization beacons; the highest playback signal amplitude corresponded to that of a male in the immediate vicinity, a situation in which females need not provide locational information. During mate-choice experiments, female *E. binotata* 'Ptelea' invest hours or days in mate assessment when there is more than one male (Sullivan Beckers 2008). The consistent female response to low-amplitude male signals, therefore, might function to recruit multiple males to her vicinity, providing a larger selection of mates. However, this long-range function of male–female duets is clearly inhibited by wind; in the presence of wind noise, females largely ceased responding to the lowest-amplitude signals (see Fig. 7), suggesting that wind decreases signal detection.

Insects on a plant stem might detect wind through the noise it generates in the substrate or through direct perception of air movement. With male responses to laboratory-generated air currents (see Fig. 5), either aspect of the stimulus may have caused the changes in male behavior. However, female responses to vibrational playback (see Fig. 7) reveal that the substrate-borne component is at least sufficient to cause changes in signaling behavior. In that experiment, male signals were played back from one location and wind from another with the female in the center. It is thus possible that females experienced spatial release from masking (Schwartz and Gerhardt 1989; Bee 2008), in which case the effect of masking might sometimes be stronger than that detected here. In the field, however, it is not clear what directional information wind-borne vibrations may contain as this will depend on the location at which the frequencies originate that mask the treehopper signals.

How important is wind as a source of background noise for vibrational communication on plants? For *E. binotata* 'Ptelea', whose host plant occurs on edges and in disturbed habitats, wind dominates the vibrational environment. A wind velocity of 0.75 m/s was sufficient to evoke gap

detection (see Fig. 5). On average, the wind velocity measured in this study was at least that high for 75% of daylight hours. We can speculate that higher wind velocities may inhibit communication altogether especially during periods when wind speed never drops to zero. In open habitats such as grasslands, wind may be even more significant as a source of selection on vibrational communication. In closed, forested habitats, wind speed will be lower in the herbaceous layer and the understory and higher in the canopy (Wiley and Richards 1982) where many vibrationally communicating insect taxa (such as leafhoppers) are especially abundant.

In addition to abiotic noise from wind, the presence of other signaling individuals is likely a significant source of noise for many vibrationally communicating animals (Cocroft and Rodríguez 2005). When multiple signalers are present, males in some species form alternating choruses (Hunt and Morton 2001), including males of the species studied here (Sullivan Beckers 2008). However, in the green stink bug, for which the temporal pattern of signal repetition is important for mate recognition, males do not form choruses. In the presence of computer-generated stimuli that simulated the presence of many signaling conspecifics, males were less likely to respond to female signals (Polajnar and Čokl 2008). In contrast to *E. binotata* 'Ptelea' males and females in the presence of wind, signaling by green stink bug females was not inhibited by continuous pure-tone stimuli. Instead, many females changed the frequency of their signals possibly enhancing detection by males.

A wealth of questions remains about the influence of wind on vibrational communication. At the most basic level, wind-induced vibrations result from the interaction between two components: wind and plant structures. How does variation in wind speed affect the vibration of a given plant structure? Do higher wind speeds increase the bandwidth of the induced noise along with its amplitude, masking the signals of a broader range of species? The spectral shape of wind-induced noise can vary between two structurally different plant species (Barth 1988) and between plant stems and leaf petioles of a single species (McNett and Cocroft 2008). Within- and between-plant variation in noise may provide another strategy to communicate during noise. Do windy environments place a premium on communicating in specific locations where the effects of wind are less, such as hollows (Tishechkin 2007) or the 'leeward side' of larger plants? Addressing these questions will bring us closer to understanding the natural vibrational environments in which communication takes place.

## References

Andersson S, Rydell J, Svensson MGE (1998) Light, predation and the lekking behaviour of the ghost swift *Hepialus humuli* (L.) (Lepidoptera: Hepialidae). Proc R Soc Lond B Biol Sci 264:1345–1351

Atema J (1995) Chemical signals in the marine environment: dispersal, detection, and temporal signal analysis. Proc Natl Acad Sci USA 92:62–66

Aubin T, Jouventin P (1998) Cocktail-party effect in king penguin colonies. Proc R Soc Lond B Biol Sci 265:1665–1673

Barth FG (1988) Spiders of the genus *Cupiennius* Simon 1891 (Araneae, Ctenidae) II. On the vibratory environment of a wandering spider. Oecologia 77:194–201

Bee MA (2008) Finding a mate at a cocktail party: spatial release from masking improves acoustic mate recognition in grey treefrogs. Anim Behav 75:1781–1791

Brenowitz EA (1986) Environmental influences on acoustic and electrical animal communication. Brain Behav Evol 28:32–42

Brown TJ, Handford P (2003) Why birds sing at dawn: the role of consistent song transmission. Ibis 145:120–129

Brumm H, Slabbekoorn H (2005) Acoustic communication in noise. Adv Study Behav 35:151–209

Buus S (1985) Release from masking caused by envelope fluctuations. J Acoust Soc Am 78:1958–65

Casas J, Bacher S, Tautz J, Meyhöfer R, Pierre D (1998) Leaf vibrations and air movements in a leafminer-parasitoid system. Biol Control 11:147–153

Cocroft RB, Rodríguez RL (2005) The behavioral ecology of insect vibrational communication. Bioscience 55:323–334

Cocroft RB, Rodríguez RL, Hunt RE (2008) Host shifts, the evolution of communication, and speciation in the *Enchenopa binotata* species complex of treehoppers. In: Tilmon KJ (ed) Specialization, speciation, and radiation: the evolutionary biology of herbivorous insects. University of California Press, Berkeley, CA, pp 88–100

Cocroft RB, Rodríguez RL, Hunt RE (2010) Host shifts and signal divergence: mating signals covary with host use in a complex of specialized plant-feeding insects. Biol J Linn Soc 99:60–72

Cokl A, Doberlet MV (2003) Communication with substrate-borne signals in small plant-dwelling insects. Annu Rev Entomol 48:29–50

Douglas HD III, Conner WE (1999) Is there a sound reception window in coastal environments? Evidence from shorebird communication systems. Naturwissenschaften 86:228–230

Endler JA (1993) The color of light in forests and its implications. Ecol Monogr 63:1–27

Fisher HS, Wong BBM, Rosenthal GG (2005) Alteration of the chemical environment disrupts communication in a freshwater fish. Proc R Soc Lond B Biol Sci 273:1187–1193

Foote AD, Osborne RW, Hoezel AR (2004) Whale-call response to masking boat noise. Nature 428:910

Forrest TG (1994) From sender to receiver: propagation and environmental effects on acoustic signals. Am Zool 34:644–654

Fuller RA, Warren PH, Gaston KJ (2007) Daytime noise predicts nocturnal singing in urban robins. Biol Lett 3:368–370

Gerhardt HC, Klump GM (1987) Masking of acoustic signals by the chorus background noise in the green tree frog: a limitation on mate choice. Anim Behav 36:1247–1249

Greenfield MD (1988) Interspecific acoustic interactions among katydids *Neoconocephalus*: inhibition-induced shifts in diel periodicity. Anim Behav 36:684–695

Greenfield MD (1994) Synchronous and alternating choruses in insects and anurans: common mechanisms and diverse functions. Am Zool 34:605–615

Hopkins CD (1973) Lightning as background noise for communication among electric fish. Nature 242:268–270

Hunt RE (1994) Vibrational signals associated with mating behavior in the treehopper, *Enchenopa binotata* Say (Hemiptera: Homoptera: Membracidae). J N Y Entomol Soc 102:266–270

Hunt RE, Morton TL (2001) Regulation of chorusing in the vibrational communication system of the leafhopper *Graminella nigrifons*. Am Zool 41:1222–1228

Lengagne T, Slater PJB (2002) The effects of rain on acoustic communication: tawny owls have good reason for calling less in wet weather. Proc R Soc Lond B Biol Sci 269:2121–2125

McNett GD, Cocroft RB (2008) Host shifts favor vibrational signal divergence in *Enchenopa binotata* treehoppers. Behav Ecol 19:650–656

Michelsen A, Fink F, Gogala M, Traue D (1982) Plants as transmission channels for insect vibrational songs. Behav Ecol Sociobiol 11:269–281

Okanoya K, Dooling RJ (1990) Detection of gaps in noise by budgerigars (*Melopsittacus undulatus*) and zebra finches (*Peophila guttata*). Hear Res 50:185–192

Ord TJ, Peters RA, Clucas B, Stamps JA (2007) Lizards speed up visual displays in noisy motion habitats. Proc R Soc Lond B Biol Sci 274:1057–1062

Parris KM, Velik-Lord M, North JMA (2009) Frogs call at a higher pitch in traffic noise. Ecol Soc 14:25

Patricelli GL, Blickley JL (2006) Avian communication in urban noise: causes and consequences of vocal adjustment. Auk 123:639–649

Polajnar J, Čokl A (2008) The effect of vibratory disturbance on sexual behaviour of the southern green stink bug *Nezara viridula* (Heteroptera, Pentatomidae). Cent Eur J Biol 3:189–197

Rodríguez RL, Cocroft RB (2006) Divergence in female duetting signals in the *Enchenopa binotata* species complex of treehoppers (Hemiptera: Membracidae). Ethology 112:1231–1238

Rodriguez RL, Ramaswamy K, Cocroft RB (2006) Evidence that female preferences have shaped male signal evolution in a clade of specialized plant-feeding insects. Proc R Soc Lond B Biol Sci 273:2585–2593

Römer H (1993) Environmental and biological constraints for the evolution of long-range signalling and hearing in acoustic insects. Philos Trans R Soc Lond B Biol Sci 340:179–185

Ryan MJ, Brenowitz EA (1985) The role of body size, phylogeny, and ambient noise in the evolution of bird song. Am Nat 126:87–100

Saxena KN, Kumar H (1980) Interruption of acoustic communication and mating in a leafhopper and a planthopper by aerial sound vibrations picked up by plants. Experientia 36:933–936

Schneider BA, Pichora-Fuller MK (1994) Gap detection and the precedence effect in young and old adults. J Acoust Soc Am 95:980–991

Schwartz JJ, Gerhardt HC (1989) Spatially mediated release from auditory masking in an anuran amphibian. J Comp Physiol A Sens Neural Behav Physiol 166:37–41

Schwartz JJ, Wells KD (1983) The influence of background noise on the behavior of a Neotropical treefrog, *Hyla ebraccata*. Herpetologica 39:121–129

Seehausen O, Alphen JJMv, Witte F (1997) Cichled fish diversity threatened by eutrophication that curbs sexual selection. Science 277:1808–1811

Slabbekoorn H, Peet M (2003) Birds sing at a higher pitch in urban noise. Nature 424:267

Slabbekoorn H, Ripmeester EAP (2008) Birdsong and anthropogenic noise: implications and applications for conservation. Mol Ecol 17:72–83

Slabbekoorn H, Smith TB (2002) Bird song, ecology and speciation. Philos Trans R Soc Lond B Biol Sci 357:493–503

Sullivan Beckers LE (2008) The ecology of mate choice: identifying the agents of sexual selection on mating signals in *Enchenopa* treehoppers. University of Missouri, Dissertation

Sun JWC, Narins PM (2005) Anthropogenic sounds differentially affect amphibian call rate. Biol Conserv 121:419–427

Tishechkin DY (2007) Background noises in vibratory communication channels of Homoptera (Cicadinea and Psyllinea). Russ Entomol J 16:39–46

Waser PM, Waser MS (1977) Experimental studies of primate vocalization: specializations for long-distance propagation. Z Tierpsychol 43:239–263

Wiley RH, Richards DS (1982) Adaptations for acoustic communication in birds: sound transmission and signal detection. In: Kroodsma DE, Miller EH (eds) Acoustic communication in birds, vol I, Academic Press. New York, NY, pp 131–181