
6 Size–Frequency Relationships in Insect Vibratory Signals

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INTRODUCTION

For insects that communicate using airborne sound, physical constraints on sound production and transmission lead to a relationship between body size and signal frequency. The efficiency with which sound is radiated depends on the size of the sound-producing structure. The lower the frequency, the larger the structure needed for efficient sound radiation (Michelsen and Nocke, 1974; Bennet-Clark, 1998a). This constraint places a lower limit, but not an upper limit, on the frequency of sounds used in communication. Once a sound has been radiated into the air, absorption of sound energy and scattering by objects in the sound path are both frequency-dependent, favouring lower frequency sounds for long-distance communication (Bradbury and Vehrencamp, 1998). As a compromise between these two constraints, animals often produce sounds whose frequencies are near the lower limit of efficient sound radiation (Bennet-Clark, 1998a).

The link between size and signal frequency has important evolutionary consequences. Because the size of the sound-producing structure is often closely related to overall body size, comparative studies usually reveal a negative relationship between body size and sound frequency among insects and other animals which use sound for long-distance communication (Ryan and Brenowitz, 1985; Bennet-Clark, 1998a; Gerhardt and Huber, 2002). Within species, ecological sources of selection on body size can influence the evolution of communication systems through their correlated effect on signal frequency (Ryan and Wilczynski, 1991). Social sources of selection may target frequency directly as a result of its reliable association with body size (Morton, 1977; Gerhardt and Huber, 2002).

In contrast to species which communicate using airborne sound, the relationship of body size to signal frequency has not been systematically investigated for species which communicate using substrate vibrations. Use of the vibratory channel is far more prevalent in insects than the use of airborne sound (Michelsen *et al.*, 1982; Markl, 1983; Claridge, 1985b; Gogala, 1985a; Henry, 1994; Stewart, 1997; Virant-Doberlet and Čokl, 2004), which probably occurs in hundreds of thousands

of species (Cocroft and Rodríguez, 2005). One of the most striking differences between the signals of species communicating with vibrations and those communicating with sound is that the vibratory signals, on the whole, have much lower carrier frequencies (Cocroft and Rodríguez, 2005). It is unclear whether body size plays as important a role in the evolution of vibratory signals as it does in the evolution of airborne signals. There is recent evidence for the importance of frequency differences for mate recognition in species using pure tone signals for vibratory communication (Rodríguez *et al.*, 2004). If divergence in signal frequency is decoupled from divergence in body size in such species, then vibratory signal frequency may be an evolutionarily labile trait, and one that could contribute to the rapid evolution of reproductive isolation among diverging populations.

Plant stems and leaves are among the most widely used substrates for insect communication. Plant borne vibratory signals are transmitted in the form of bending waves (Michelsen *et al.*, 1982; Gogala, 1985a; Barth, 1997). As with sound waves, absorption of energy during propagation of bending waves is frequency-dependent, with greater losses at higher frequencies (Greenfield, 2002). Therefore, as with airborne sound, frequency-dependent attenuation should favour lower frequency signals for longer range communication. A second, less predictable influence on vibration transmission arises from the frequency filtering properties of plant stems and leaves. Although such filtering can favour lower frequency signals, it does not always do so, and there are too few studies of the vibration transmitting properties of plant tissue to permit broad generalisations (Michelsen *et al.*, 1982; Čokl and Virant-Doberlet, 2003; Cocroft and Rodríguez, 2005).

The question is whether the mechanics of vibratory signal production impose a relationship between body size and signal frequency as with airborne sounds. Although use of substrate vibrations releases animals from some constraints on signal frequency, such as the acoustic short-circuit which makes radiation of low frequency sounds by small dipole sources inefficient (Gerhardt and Huber, 2002), the potential for other size-related constraints on signal frequency has not been explored. Little is known about the coupling of a vibratory signal between an insect and a plant stem (Michelsen *et al.*, 1982). The details of vibratory signal production are also unknown in most cases, apart from observations of which body parts are involved (Virant-Doberlet and Čokl, 2004). Our lack of knowledge of the details of vibratory signal production and transmission prevent us from making specific predictions about the relationship of body size to frequency.

Here we take an empirical approach to the question of size–frequency relationships in vibratory signals. Comparing the spectral features of vibratory signals across different individuals and species, or using data drawn from different studies, presents two challenges. First, the distribution of energy across the different frequencies in a signal will be influenced by the properties of the substrate on which a signal is recorded (Michelsen *et al.*, 1982). For signals using a narrow band of frequencies, the influence of substrate may be small or absent (Sattman and Cocroft, 2003). For signals containing a wider range of frequencies, differences in substrate filtering properties may introduce a significant amount of variation into a comparative dataset. Second, different investigators may use transducers which measure different components of a vibratory signal, and this will be reflected in the amplitude spectrum of the signal. For example, in a signal with a range of frequencies, acceleration amplitude will increase by 6 dB/octave relative to velocity amplitude. In this study we use methods which minimise substrate- and transducer-induced variation in signal amplitude spectra; or, for comparisons in which these sources of variation cannot be eliminated, we discuss their implications for interpretation of the results.

We investigated the relationship between body size and frequency at three levels: within a population; between closely related species; and across a wide range of species in different insect orders. For our investigations of size–frequency relationships within populations, we recorded a sample of individuals on a common substrate. For comparisons among closely related species, we use our own library of recordings of the signals of membracid treehoppers, and for the broader comparison we have drawn information from the literature.

METHODS

WITHIN-POPULATION VARIATION IN SIZE AND SIGNAL FREQUENCY

To investigate the relationship of body size to signal frequency within a population, mate advertisement signals were recorded from a sample of 35 males of the Neotropical treehopper *Umbonia crassicornis* (Hemiptera: Membracidae). Males were drawn from a greenhouse colony at the University of Missouri established with periodic collections from populations in southern Florida, USA, where this species has been naturalised. Signals were transduced using a laser vibrometer (Polytec CLV 1000 with CLV M030 decoder modules) at 5 mm/sec/V sensitivity. The laser head was positioned on a tripod approximately 10 to 15 cm from the stem and a small (~1 mm²) piece of reflective tape was attached to the stem at the recording location to increase reflectance of the laser signal. Signals were digitised at 44.1 kHz using a National Instruments data acquisition board and a custom written data acquisition program in LabVIEW v. 7.0.

Substrate related variation was minimised by recording each male at the same location (± 2 cm) on a 1 m tall potted host plant (Mimosaceae: *Albizia julibrissin*). Males were positioned with their dorso-ventral axis in the plane of the laser. A recorded male–female duet was played through a loudspeaker to induce signalling once a male was placed on the stem. Recordings were made with the host plant on a Kinetic Systems Vibraplane isolation table in a temperature-controlled room maintained at (23 ± 1)°C. After each male was recorded, its mass was measured using a Mettler Toledo AB545 balance, and its body length (front of vertex to tip of abdomen) was measured with an ocular micrometer using a Leica MZ75 microscope.

Signal frequency was measured for one signal from each male using a custom written program in MATLAB v. 6.5, with an FFT size of 8192 points. In *U. crassicornis* signals, the dominant frequency was typically the second harmonic; however, for some signals it was the fundamental. Accordingly, the principal energy in the second harmonic was measured for each signal to provide a more consistent measure across individuals.

The males recorded in this study were drawn from seven family groups. Families remain together through nymphal and early adult development, and thus siblings are similar in both genetic and environmental contributions to the phenotype. Accordingly, we used multiple regression, with family included as a nominal variable. The analysis was conducted using JMP IN 5.1, with size and frequency measurements log-transformed for statistical analysis.

We also provide data drawn from a study of size–frequency relationships in a species in the *Enchenopa binotata* species complex (Sattman and Cocroft, 2003). As in the present study, a sample of males was recorded with laser vibrometry. Males were recorded on more than one host plant stem. However, as shown in that study, the differences among individual host plants did not influence measurements of signal dominant frequency.

BETWEEN-SPECIES VARIATION IN SIZE AND SIGNAL FREQUENCY IN THE MEMBRACIDAE

To examine the relationship between body size and signal frequency among a set of closely related species, we used our own library of recordings of temperate and tropical species of Membracidae (see Table 6.1 for a list of species). We included one aetalionid, *Aetalion reticulatum*, which was placed within the Membracidae in the phylogenetic tree we used. Recordings of male mate advertisement signals were made on cut host plant stems, usually about 0.25 m in length, with the base placed in a florist's water tube held in a clamp. The transducer was placed within 5 to 10 cm of the signalling insect, reducing the changes in signal spectra imposed by transmission through a stem. In order to allow for use of phylogenetic comparative methods (see below), we included only those species in our recording library which were also present in an unpublished molecular phylogeny of membracids made available to us by C.P. Lin and R.L. Snyder (personal communication).

TABLE 6.1
Membracid Species Included in the Comparative Analysis

<i>Acutalis tartarea</i>	<i>Heteronotus trinodosus</i>	<i>Potnia brevicornis</i>
<i>Aetalion reticulatum</i>	<i>Hypsoprora coronata</i>	<i>Potnia dubia</i>
<i>Alchisme apicalis</i>	<i>Ischnocentrus inconspicua</i>	<i>Publilia concava</i>
<i>Aphetea inconspicua</i>	<i>Lycoderes</i> sp. Panama	<i>Smilia camelus</i>
<i>Atyma querci</i>	<i>Metheisa lucillodes</i>	<i>Stictocephala diceros</i>
<i>Bajulata bajula</i>	<i>Microcentrus perditus</i>	<i>Stictocephala lutea</i>
<i>Bolbonota</i> sp. Panama	<i>Micrutalis calva</i>	<i>Stylocentrus championi</i>
<i>Campylenchia latipes</i>	<i>Micrutalis</i> sp. Panama	<i>Thelia bimaculata</i>
<i>Campylocentrus brunneus</i>	<i>Nassunia bipunctata</i>	<i>Tolania</i> sp. Panama
<i>Cladonota apicalis</i>	<i>Nassunia</i> sp. Panama	<i>Trinarea sallei</i>
<i>Cymbomorpha prasina</i>	<i>Notocera bituberculata</i>	<i>Tropidaspis affinis</i>
<i>Cyphonia clavata</i>	<i>Ophiderma definita</i>	<i>Tylopelta americana</i>
<i>Cyrtolobus vau</i>	<i>Ophiderma salamandra</i>	<i>Umbonia crassicornis</i>
<i>Darnis latior</i>	<i>Oxyrachis tarandus</i>	<i>Umbonia spinosa</i>
<i>Enchenopa binotata</i> Panama	<i>Platycotis</i> sp. Panama	<i>Vanduzee arquata</i>
<i>Enchophyllum melaleucum</i>	<i>Polyglypta costata</i>	<i>Vanduzee mayana</i>
<i>Glossonotus crataegi</i>	<i>Poppea capricornis</i>	<i>Vanduzee segmentata</i>

Our recordings of membracid signals were made with three different transducers. In addition to the laser vibrometer described above, we used a Knowles BU-1771 accelerometer and an Astatic 91T ceramic phonograph cartridge. Different transducers measure different components of a vibratory signal, accelerometers measure its acceleration; laser vibrometers measure its velocity; and ceramic phonograph cartridges measure its displacement. To compare, measurements made with different transducers we converted all signal spectra to velocity units. We first played band-limited noise (80 Hz to 5 kHz) through a shaker and measured it simultaneously with the three transducers. We then used the ratios between the relevant amplitude spectra to adjust the spectrum of signals recorded with the accelerometer or phonograph cartridge. As a result, all of our measurements of the amplitude spectra of membracid signals are directly comparable.

For many of the membracids we have recorded, and especially for rarely encountered tropical species, signals are available for only one or a few individuals. Our measurement of signal frequency was therefore made from measurement of one individual per species. For purposes of this analysis, we assumed that between-species variation was greater than within-species variation. In species for which we have many recordings, this assumption appears to be met as frequency has a low coefficient of variation within populations (unpublished data). Size was likewise measured for one individual per species, where possible from the voucher specimen from which the signal was recorded. As an index of body size, the total length was measured from the front of the vertex to the tip of the folded wing as in McKamey and Deitz (1996), using either an ocular micrometer (as above) or digital photos with a scale included. Size measurements for a few species for which specimens were not available were obtained from Funkhouser (1917).

We measured the dominant frequency using MATLAB as above. Because every individual was recorded on a different substrate, these dominant frequency measurements are subject to substrate-induced variation. Accordingly, we also measured the lowest frequency in the signal containing appreciable energy (20 dB below the amplitude of the dominant frequency). We anticipated that a measurement reflecting the overall bandwidth of the signal would be less

substrate-dependent than measurements reflecting the relative amplitude of different frequencies within that frequency band. All variables (body length, dominant frequency, low frequency) were log-transformed for statistical analysis.

Before proceeding with a statistical analysis of the correlation of size and frequency, we assessed the degree of phylogenetic autocorrelation in the data using the test for serial independence in PI (Phylogenetic Independence) v. 2.0 (Reeve and Abouheif, 2003). The molecular phylogenetic tree provided by C.P. Lin and R.L. Snyder (personal communication) was pruned to exclude species not used in our analysis. The test for serial independence revealed the presence of significant phylogenetic signal in dominant frequency ($p < .01$), but not in size ($p = .35$) or in the lowest frequency ($p = .31$). To adjust for the phylogenetic component of variation in dominant frequency, we used the CAIC program v. 2.0.0 (Purvis and Rambaut, 1995) to calculate phylogenetically independent contrasts between size and dominant frequency. Below we present the original data and the independent contrasts.

BETWEEN-SPECIES VARIATION IN SIZE AND SIGNAL FREQUENCY IN THE INSECTA

We examined the relationship of body size and signal frequency on a broad scale across several insect orders using data drawn from the literature (see Table 6.2 for a list of species and references). We obtained measures of dominant frequency and the lowest frequency present in the signal (20 dB below peak, as above) either from the measurements reported in the paper or from estimates based on amplitude spectra or spectrograms. Only one of the papers on insect vibratory communication that we examined included information on the size of the insects. For the rest of the species, we used approximate size information by obtaining a measurement of total length from values reported in the literature for the same sex and species recorded. Information was also obtained from the investigators who published the signal analyses; from values reported on websites; or from our measurements of museum specimens. Because there is no species-level phylogeny available for the Insecta as a whole, our examination of size-frequency relationships at this scale did not incorporate information on phylogenetic relationships.

The sample drawn from the literature includes signals with a variety of functions, including mate attraction, solicitation of maternal care and attraction of ant mutualists. We first examined the relationship of body size to frequency for all signals regardless of function using log-transformed variables. Then, because the above investigations of size-frequency relationships within populations and among closely related species were based on male mate advertisement signals, we conducted a second analysis based only on mating signals.

RESULTS

WITHIN-POPULATION VARIATION IN SIZE AND SIGNAL FREQUENCY

There was no relationship between body length and signal frequency (measured as the principal energy in the second harmonic) for a sample of 35 *U. crassicornis* males (Figure 6.1a; $F = 1.33$, $p > .25$); the same was true for body mass ($F = .04$, $p > .8$). There also was no effect of family on signal frequency (for length and mass $p > .3$). Analyses using dominant frequency, which for some individuals was the fundamental rather than the second harmonic, yielded similar results (e.g. for mass, $F = .001$, $p > .9$).

We also provide data from a previous study examining the relationship of size and mating signal frequency in a second species of membracid, the *E. binotata* complex member which uses *Ptelea trifoliata* host plants (Sattman and Coccoft, 2003). In that dataset there was no relationship between body length and the dominant frequency of the signal (Figure 6.1b; $N = 24$).

TABLE 6.2
Insect Species Used in the Comparative Analysis with References for Signal Descriptions

Coleoptera	Curculionidae	<i>Hylobius abietis</i>	Selander and Jansson (1977)
Diptera	Chloropidae	<i>Lipara lucens</i>	Ewing (1977)
—	Psychodidae	<i>Lutzomyia longipalpis</i>	Ward <i>et al.</i> (1988)
Hemiptera	Aleyrodidae	<i>Trialeurodes vaporariorum</i>	Kanmiya (1996a, 1996b, 1996c)
—	Alydidae	<i>Alydus calcaratus</i>	Gogala (1990)
—	—	<i>Riptortus clavatus</i>	Numata <i>et al.</i> (1989)
—	Aphodidae	<i>Aphodius ater</i>	Hirschberger and Rohrseitz (1995)
—	Cicadellidae	<i>Dalbulus</i> sp.	Heady <i>et al.</i> (1986)
—	—	<i>Empoasca fabae</i>	Shaw <i>et al.</i> (1974)
—	—	<i>Graminella nigrifrons</i>	Heady and Nault (1991)
—	—	<i>Macrostelus fascifrons</i>	Purcell and Loher (1975)
—	Cydnidae	<i>Sehirus bicolor</i>	Michelsen <i>et al.</i> (1982)
—	Membracidae	<i>Enchenopa binotata</i>	Sattman and Cocroft (2003)
—	—	<i>Spissistilus festinus</i>	Hunt (1993)
—	—	<i>Umbonia crassicornis</i>	Cocroft (1999)
—	Pentatomidae	<i>Acrosternum hilare</i>	Čokl <i>et al.</i> (2001)
—	—	<i>Nezara viridula</i>	Čokl <i>et al.</i> (2000)
—	—	<i>Thyanta custator</i>	McBrien <i>et al.</i> (2002)
—	—	<i>Thyanta pallidovirens</i>	McBrien <i>et al.</i> (2002)
—	Plataspidae	<i>Coptosoma scutellatum</i>	Gogala (1990)
—	Reduviidae	<i>Triatoma infestans</i>	Roces and Manrique (1996)
—	Rhopalidae	<i>Corizus hyoscyami</i>	Gogala (1990)
—	Tettigarctidae	<i>Tettigarctia crinita</i>	M.F. Claridge, personal communication
Hymenoptera	Apidae	<i>Apis mellifera</i>	Michelsen <i>et al.</i> (1986a, 1986b)
—	Formicidae	<i>Atta sexdens</i>	Masters <i>et al.</i> (1983)
Lepidoptera	Lycaenidae	<i>Arawacus lincoides</i>	DeVries (1991)
—	—	<i>Chlorostrymon simaethis</i>	DeVries (1991)
—	—	<i>Jalmenus evagoras</i>	DeVries (1991)
—	—	<i>Leptotes cassius</i>	DeVries (1991)
—	—	<i>Lysandra bellargus</i>	DeVries (1991)
—	—	<i>Maculinea alcon</i>	DeVries (1991)
—	—	<i>Panthiades bitias</i>	DeVries (1991)
—	—	<i>Polyommatus icarus</i>	DeVries (1991)
—	—	<i>Rekoa palegon</i>	DeVries (1991)
—	—	<i>Strymon yojoa</i>	DeVries (1991)
—	—	<i>Thereus pedusa</i>	DeVries (1991)
—	Riodinidae	<i>Calospila cilissa</i>	DeVries (1991)
—	—	<i>Calospila emylius</i>	DeVries (1991)
—	—	<i>Juditha molpe</i>	DeVries (1991)
—	—	<i>Nymphidium mantus</i>	DeVries (1991)
—	—	<i>Synargis gela</i>	DeVries (1991)
—	—	<i>Synargis mycone</i>	DeVries (1991)
—	—	<i>Theope maiuta</i>	DeVries (1991)
—	—	<i>Theope thestias</i>	DeVries (1991)
—	—	<i>Theope virgilius</i>	DeVries (1991)
—	—	<i>Thisbe irenea</i>	DeVries (1991)
Mecoptera	Panorpidae	<i>Panorpa</i> sp.	Rupprecht (1975)
Neuroptera	Chrysoperlidae	<i>Chrysoperla plorabunda</i>	Henry and Wells (1990)
—	Sialidae	<i>Sialis</i> sp.	Gogala (1985a)

TABLE 6.2
Continued

Orthoptera	Tettigoniidae	<i>Choeroparnops gigliotosi</i>	Morris <i>et al.</i> (1994)
—	—	<i>Conocephalus nigropleurum</i>	De Luca and Morris (1998)
—	—	<i>Copiphora brevirostris</i>	Morris <i>et al.</i> (1994)
—	—	<i>Docidocercus gigliotosi</i>	Morris <i>et al.</i> (1994)

BETWEEN-SPECIES VARIATION IN SIZE AND SIGNAL FREQUENCY IN THE MEMBRACIDAE

If we first examine the data using species as independent data points in a linear regression, there is a significant negative relationship between size (body length) and dominant frequency (Figure 6.2a; $N = 51$, $r^2 = .09$, slope = $-.60$; $p < .05$). There is also a significant negative relationship between size and the lowest frequency in the signal (Figure 6.2b; $N = 51$, $r^2 = .17$, slope = $-.69$, $p < .01$). Although there is considerable scatter in both figures, there were no small species that produced low frequency signals. Dominant frequency was the only variable

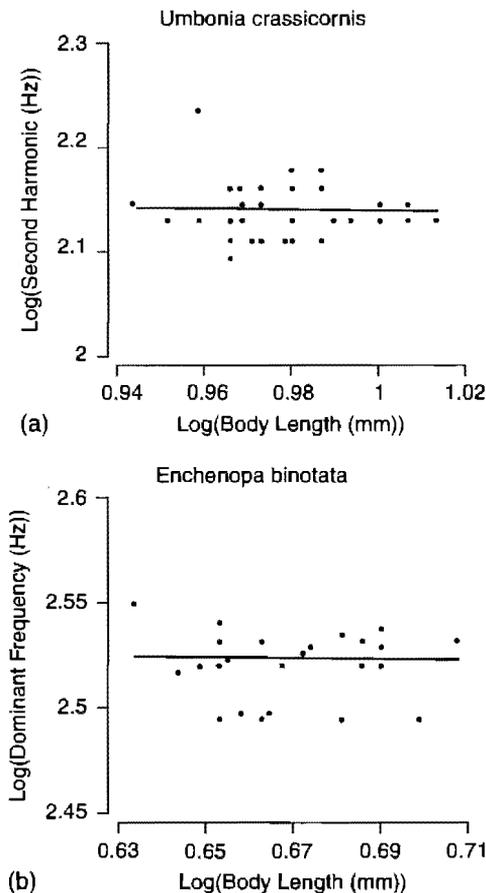


FIGURE 6.1 The relationship of body size and frequency in the vibratory mating signals of two species in the family Membracidae. (a) *U. crassicornis*; (b) *E. binotata* from *P. trifoliata*.

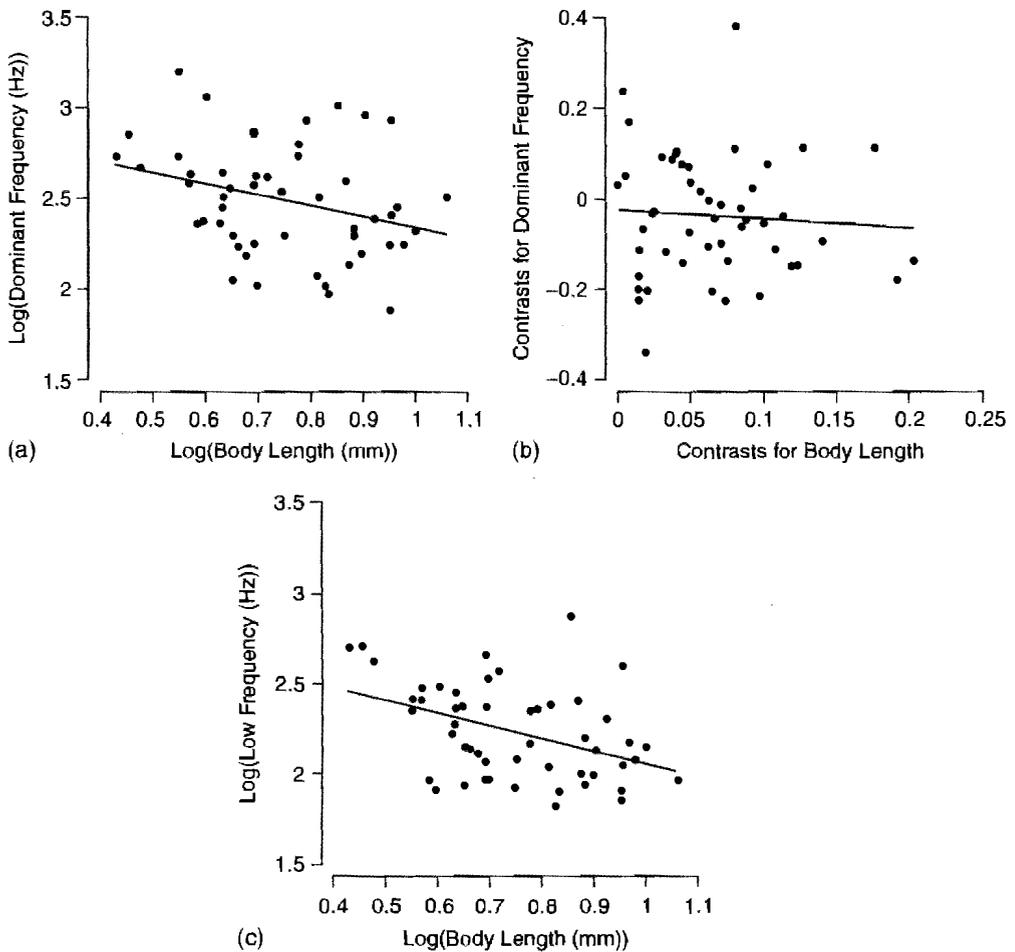


FIGURE 6.2 The relationship of body size and frequency among 51 species in the family Membracidae. (a) Relationship between size and dominant frequency; (b) phylogenetically independent contrasts between size and dominant frequency; (c) relationship between size and the lowest frequency in the signal.

which showed significant phylogenetic signal; if we examine the phylogenetically independent contrasts, the results are qualitatively similar with a marginally significant relationship between size and dominant frequency (Figure 6.2c; $N = 50$ contrasts, $r^2 = .07$, slope = $-.45$, $p = .06$).

BETWEEN-SPECIES VARIATION IN SIZE AND SIGNAL FREQUENCY IN THE INSECTA

If all of the signals from our literature survey are included regardless of signal function, linear regression reveals no relationship between body size and dominant frequency (Figure 6.3a; $N = 52$) or between body size and the lowest frequency in the signal (Figure 6.3b; $N = 53$). Note that these comparisons use species as data points in the absence of a species-level phylogeny for this broad comparison.

In contrast, if we consider only the species for which measurements were available for mate advertisement signals, there is a significant negative relationship between body size and dominant frequency (Figure 6.4a; $N = 28$, $r^2 = .28$, slope = $-.60$, $p < .01$) and between body size and the lowest frequency in the signal (Figure 6.4b; $N = 29$, $r^2 = .42$, slope = $-.71$, $p < .001$).

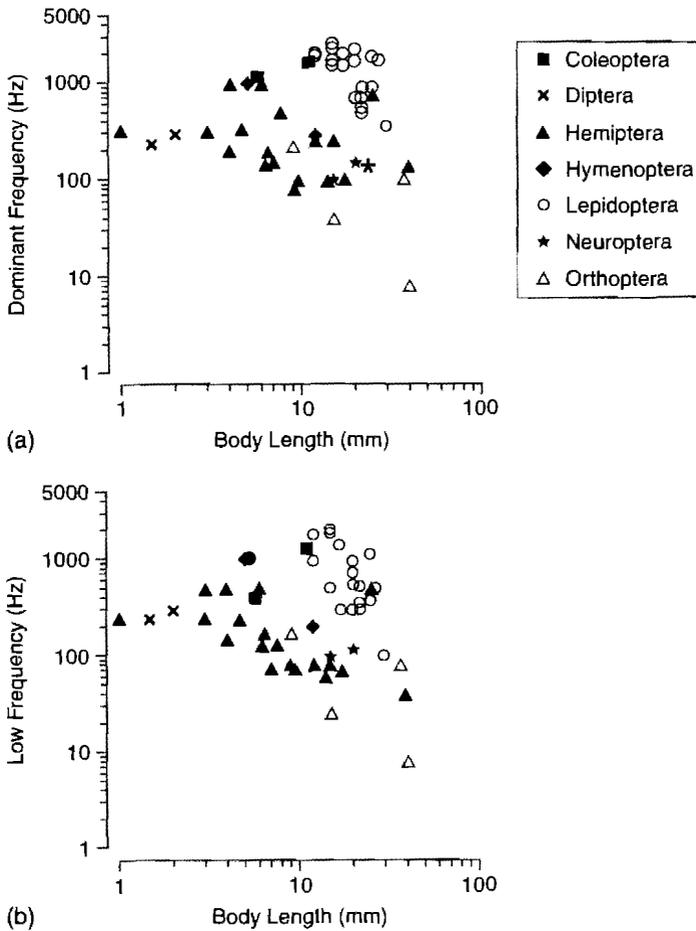


FIGURE 6.3 The relationship of body size and frequency in 53 species of insects from several orders using data drawn from the literature. (a) and (b) show the relationship of size and dominant and low frequency for all species, whether the signal described for a given species was used in mating, alarm or attraction of mutualists.

DISCUSSION

For communication systems using airborne sound, the close relationship between body size and frequency has shaped the evolution of signal function and diversity (Morton, 1977; Gerhardt and Huber, 2002). Here we asked if a similar relationship exists for the most widespread form of mechanical signalling, substrate-borne vibratory communication. We examined the relationship of body size to signal frequency within populations and across species.

We found rather different patterns in the within-population comparison than in the between-species comparisons. In the two species of insects for which we examined within-population variation (the membracid treehoppers *U. crassicornis* and *E. binotata*), there was no correlation between the size of the signaller and the frequency of the signal. In contrast, there was a negative relationship between body size and measurements of signal frequency among 51 species in the family Membracidae, when using species as independent data points and when using phylogenetically independent contrasts. When we expanded our comparison to variation in size and signal frequency across various insect orders, the results depended on whether or not we

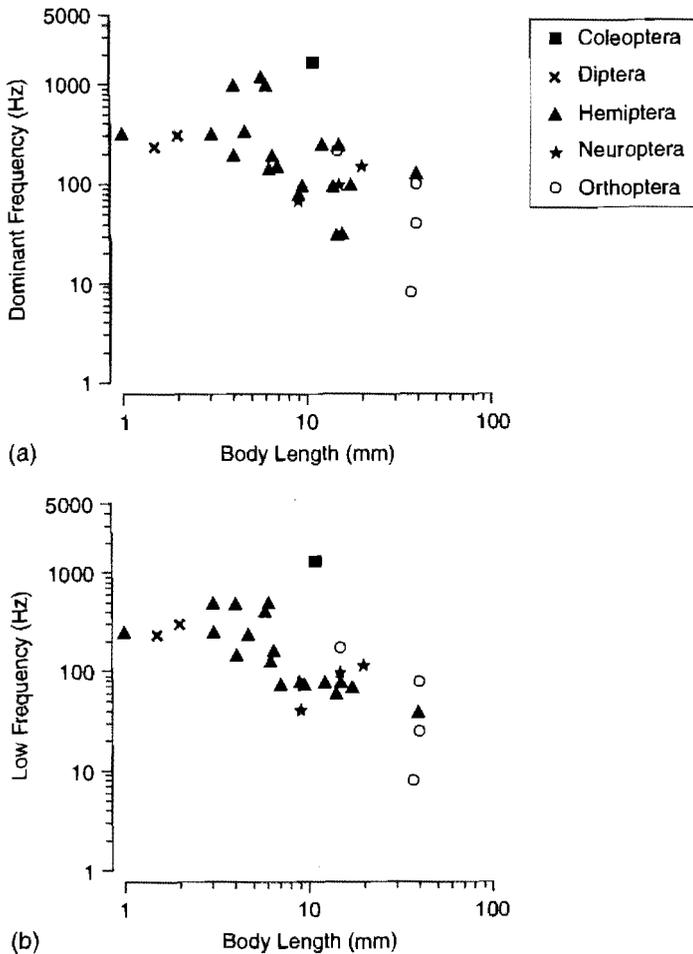


FIGURE 6.4 The relationship of size to dominant (a) and low (b) frequency in the insect vibratory signals shown in Figure 6.3, with the analysis restricted to the signals used in mating.

grouped together signals with different functions. Considering all signals together, including those used in mating, alarm communication and attracting ant mutualists, there was no relationship of size and frequency. However, if we restricted our analysis to mate advertisement signals, as we did for the signals of membracid treehoppers, there was a strong negative relationship between body size and both the dominant and the lowest frequency of the signal. Examination of Figures 6.2 to 6.4 reveals a lack of data points in the lower left-hand corner of the figure; although there is considerable variation in frequency for species of a similar size, there were no very small species which produced very low frequency signals.

The question is how should we interpret these results in terms of the reliability of spectral measurements of vibratory signals and in terms of the implications for vibratory signal production and evolution. For the within-species comparisons, the potential challenges for signal measurement were minimal or absent, maximising the probability of detecting a size–frequency relationship. However, we found no suggestion of such a relationship. For the two populations examined (one each for *U. crassicornis* and *E. binotata* from *Ptelea*), variation in signal frequency appears to be decoupled from variation in body size. Within-population variation in signal frequency can be important for female choice, where female preference may exert stabilising or

directional selection on male signal frequency (reviewed for insects and anurans in Gerhardt and Huber, 2002). For *E. binotata* from *P. trifoliata*, females prefer frequencies near the mean frequency of males in the population (Cocroft and Rodríguez, 2005). Signal frequency differs substantially among species in the *E. binotata* complex (Rodríguez *et al.*, 2004), and females of each species examined have preferences centred on the mean frequency of males in their population (Rodríguez, Ramaswamy and Cocroft, unpublished data). If *E. binotata* from *Ptelea* is representative, however, female preference based on signal frequency is unlikely to lead to correlated changes in male size.

For the broad between-species comparisons reported here, the potential to mask any relationship between size and frequency might exist for the following reasons:

- The sources of variation in measurements of vibratory signal spectra discussed above
- The differences among substrates and transducers
- The limited availability of accurate size measurements

However, for the membracid data set and the overall insect data set, there was a significant negative correlation between body size and dominant frequency and the lowest frequency in of male mating signals. The correlation was higher between size and the lowest frequency in the signal, possibly because the overall bandwidth of the signals was less substrate-dependent than the relative amplitude of different frequencies within that frequency band. The r^2 values (reflecting the proportion of variation explained) were higher at the broader level of comparison, suggesting that the relationship between size and frequency is relatively loose, and unlikely to be detected unless there is a large range of values for both variables. The lack of a relationship for the analysis which included signals other than those used in mating, is primarily accounted for by the lycaenid and riordinid caterpillars, which produce signals to attract ant mutualists (DeVries, 1991). These signals are typically broadband and relatively high in frequency, perhaps as a result of selection to produce vibratory signals similar to those of the ants with which they are communicating (DeVries *et al.*, 1993).

Two factors might explain why there is an inverse relationship between body size and frequency in insect vibratory signals. First, an insect resting on six legs can be modelled as a mass on a set of springs (Tieu, 1996; Cocroft *et al.*, 2000; also see Aicher *et al.*, 1983). Other things being equal, the greater the mass, the lower the resonant frequency of a mass-and-spring system. It is not known whether insects use this resonance in signal production (or signal reception; see Aicher *et al.*, 1983), but if they do this could explain why larger insects produce lower frequency vibratory signals. Second, it is likely that at least some species use the thoracic muscles to generate vibratory signals (Gogala, 1985a; Cocroft and McNett, Chapter 23). Wingbeat frequency is inversely correlated with mass in insects (Dudley, 2000), and if the wing muscles are used to produce vibratory signals, this could generate a negative correlation between signal frequency and mass.

In this study, we did not examine the relationship of size with temporal variables or overall signal amplitude. For vibratorily communicating katydids, size was tightly correlated with tremulation rate, larger males signalled at a faster rate (De Luca and Morris, 1998). In communication systems using airborne sound, size has been found to correlate with a variety of temporal signal traits (Gerhardt and Huber, 2002). In general, larger animals can produce higher amplitude signals (see Markl (1983) for vibratory signals). At a finer level (*e.g.* among individuals within a population or between closely related species), amplitude comparisons will be difficult to make for insects communicating with plant-borne vibrations because the amplitude of plant-borne signals is highly substrate dependent (Čokl and Virant-Doberlet, 2003). The same insect will produce a higher amplitude signal on a thin stem than on a thick stem, and the amplitude of a signal recorded at different distances from a signaller does not decrease monotonically (Michelsen *et al.*, 1982).

For the membracid data set, there was evidence that close relatives tend to be similar in dominant frequency, though not in size. Ecology and behaviour are also similar within many membracid clades (Wood, 1979, 1984; Dietrich and Deitz, 1991; McKamey and Deitz, 1996), and it would be worthwhile to investigate whether phylogenetic aspects of signal variation reflect adaptation to similar ecological conditions such as low population densities or use of herbaceous vs. woody plants.

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