

Vibrations in hemipteran and coleopteran insects: behaviors and application in pest management

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1 **Vibrations in hemipteran and coleopteran insects: behaviors and application in**
2 **pest management**

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16

17 **Abstract**

18 Many groups of insects utilize substrate-borne vibrations for communication. They
19 display various behaviors in response to vibrations in sexual and social communication
20 and in predator–prey interactions. Although the number of reports on communication
21 and behaviors using vibrations has continued to increase across various insect orders,
22 there are several studies of the exploitation of vibrations for pest management in
23 Hemiptera and Coleoptera. Here, we review studies of behaviors and communication
24 using vibrations in hemipteran and coleopteran insects. For instance, pentatomid bugs
25 display species- and sex-specific vibrational signals during courtship, whereas
26 cerambycid beetles show startle responses to vibrations in the context of predator–prey
27 interactions. Concepts and case studies in pest management using
28 vibrations—especially regarding the disruption of communication and behavior—are
29 also presented.

30

31 **Key words** vibrational signals, communication, pest control, behavioral disruption,
32 sense organ

33

34 **Introduction**

35 Many insect species utilize mechanical information from substrate-borne vibrations or
36 airborne sounds, or both, for various behaviors (Cocroft and Rodríguez 2005;
37 Greenfield 2002; Hill 2008). Vibrations account for the majority of mechanical
38 communications, and the number of species that use vibrations is estimated as 195,000
39 or more (Cocroft and Rodríguez 2005). Vibrations travel well through plants or other
40 substrates, allowing conspecifics and/or predators to detect the vibrations (Michelsen et
41 al. 1982).

42 Insects display various behaviors in response to vibrations. The functional
43 significance of vibration-mediated interactions can be classified into i) sexual
44 communication; ii) social communication; and iii) predator-prey interactions (e.g. Hill
45 2008; Takanashi et al. 2016). Sexual communication is mediated by vibrational sexual
46 signals or aggressive signals (Hill 2008). For instance, males of the brown planthopper
47 *Nilaparvata lugens* Stål (Delphacidae) locate females that produce vibrations by
48 drumming their abdomens on the rice plant (Ichikawa and Ishii 1974). In prairie mole
49 cricket *Gryllotalpa major* Saussure (Gryllotalpidae), males use the vibrations of rivals'
50 calls transmitted via the ground, instead of the sounds of their calls through the air, to
51 maintain space each other in a lek (Hill 2008; Hill and Shadley 2001). With regard to

52 social communication, synchronous hatching of the brown marmorated stink bug
53 *Halyomorpha halys* (Stål) (Pentatomidae) is induced by single eggshell-cracking
54 vibration over a short period in a clutch of eggs in contact with each other (Endo et al.
55 2018). Mutualism between *Iridomyrmex* ants (Formicidae) and lycaenid butterflies is
56 engaged by vibrational signals emitted by larvae and pupae of the butterfly (Travassos
57 and Pierce 2000). Predator–prey interactions include prey localization and antipredatory
58 behavior using vibrational cues (Hill 2008). The parasitoid wasp *Sympiesis sericeicornis*
59 Nees (Eulophidae) perceives the exact locations of its lepidopteran host in leaf mines by
60 eavesdropping on vibrations (Djemai et al. 2004). The red flour beetle *Tribolium*
61 *castaneum* (Herbst) (Tenebrionidae) shows tonic immovability (death-feigning) in
62 response to vibrations as a defense against predators (Kiyotake et al. 2014).

63 Although the number of reports of communication and behaviors using vibrations
64 has continued to increase across various insect orders (Greenfield 2002; Hill 2008;
65 Virant-Doberlet and Čokl 2004), studies of pest species damaging plants remain limited
66 in Hemiptera, Coleoptera and a few other orders (e.g., Endo et al. 2018; Ichikawa and
67 Ishii 1974; Polajnar et al. 2015). In particular, pest control by exploiting such signals
68 has been studied in Hemiptera and Coleoptera alone (Eriksson et al. 2012; Hosomi
69 1996; Lujo et al. 2016; Polajnar et al. 2015). Indeed, hemipteran and coleopteran insects

70 exhibit a variety of vibrational communications and behaviors. In this review, we focus
71 on Hemiptera and Coleoptera in studies of both behavior and pest management using
72 vibrations. We also review vibrational senses, behaviors, and communication in
73 Hemiptera and Coleoptera, and we discuss the effectiveness of vibrations in pest
74 management.

75

76 **Vibrational senses**

77 In insects, the sense organs involved with vibrations are internal mechanoreceptors,
78 called chordotonal organs, which are located in the legs and other body parts (Field and
79 Matheson 1998; Hill 2008). Two chordotonal organs in the legs—the femoral
80 chordotonal organs and subgenual organs—play an important role in vibrational
81 reception (Field and Matheson 1998). The chordotonal organs, within which the neurons
82 are clustered into scoloparia, consist of multiple sensory neurons and attachment cells;
83 for example, there are 24 sensory neurons in the brown-winged green bug *Plautia stali*
84 Scott (Pentatomidae) and 70 sensory neurons in the Japanese pine sawyer beetle
85 *Monochamus alternatus* Hope (Cerambycidae) (Fig. 1) (Nishino et al. 2016; Takanashi
86 et al. 2016). The sensory neurons respond with high sensitivity to vibrations via the
87 attachment cells (Field and Matheson 1998). The femoral chordotonal organ of *M.*

88 *alternatus* is attached to the tibia via a cuticular apodeme, whereas that of *P. stali* is
89 attached to the tibia via attachment cells, without the apodeme (Fig. 1b, e). In both
90 species, vibrations are transmitted from substrates via the tibia to the femoral
91 chordotonal organs. The subgenual organs in the tibia possess air sacs for transmission
92 of vibrations in orthopteran insects, but not in *P. stali* (Field and Matheson 1998;
93 Nishino et al. 2016). Coleopteran insects including *M. alternatus* do not have subgenual
94 organs (Takanashi et al. 2016). There are other mechanoreceptors, such as external ones
95 for detecting strain on cuticular surfaces (Čokl and Virant-Doberlet 2003; Keil 1997).

96

97 **Vibrational communications and behaviors**

98 *Hemiptera*

99 Heteroptera, the so-called stink bugs or true bugs, are large group in the order
100 Hemiptera. Pheromones are well-known communication signals in this order. Male
101 adults attract adults and nymphs of both sexes by using pheromones (e.g., Mizutani
102 2006). Vibrations are also widely used among stink bugs. Chemical signals such as
103 pheromones are used for long-distance communication, whereas physical signals such
104 as vibrations and visual signals are used mainly for close-range communication on
105 plants (Sakakibara 2016). Among the Heteroptera, 16 families of land bugs are listed as

106 using vibrations as communication signals and to have mechanisms for producing
107 vibrations (Virant-Doberlet and Čokl 2004; for examples of these families, see Table 1).

108 In many cases, vibrations are used for male courtship and for communication between
109 sexes [e.g., Čokl et al. 1978 for the southern stink bug, *Nezara viridula* (Linnaeus)
110 (Pentatomidae); Kon et al. 1988 for the eastern green stink bug, *Nezara antennata* Scott
111 and *N. viridula* (Pentatomidae); Numata et al. 1989 for the bean bug, *Riptortus pedestris*
112 (Fabricius) (Alydidae); Polajnar et al. 2016b for *H. halys* (Pentatomidae)]. Adults of *N.*
113 *viridula* produce several stereotyped species- and sex-specific vibrational signals in the
114 course of their courtship. The signals, called songs, are often exchanged in a duet (Čokl
115 et al. 2000). Most of the Pentatominae species studied so far show similar behavioral
116 sequences and vibrational repertoires and syntax (Virant-Doberlet and Čokl 2004).
117 However, some songs might be missing from some repertoires, and different repertoires
118 might be added (Virant-Doberlet and Čokl 2004).

119 Vibrations are also used as signals for parent–embryo communication. In the
120 subsocial burrower bugs *Adomerus rotundus* (Hsiao) (Cydnidae) and *Parastrachia*
121 *japonensis* Scott (Parastrachiidae), mothers produce vibrations by shaking their bodies
122 rhythmically while maintaining an egg-guarding posture. The vibrations promote
123 synchronous hatching (Mukai 2016; Mukai et al. 2012, 2014), which decreases the

124 frequency of sibling cannibalism (Mukai et al. 2018). Unlike the subsocial burrower
125 bugs, *H. halys* does not guard its eggs, but it does synchronize hatching (Endo and
126 Numata 2017). Synchronous hatching of *H. halys* is induced by single eggshell-cracking
127 vibration in a clutch of eggs (Endo et al. 2018). Hemipteran embryos generally may
128 have an ability of responses to vibrations. A mother of *P. japonensis* vibrates her
129 abdomen and produces a low-pitched fluttering sound when she serves food (drupes) to
130 her nymphs in their nest. This provisioning call is considered to be a type of
131 parent-offspring communication (Nomakuchi et al. 2012). By using the provisioning
132 call as a cue, nymphs are likely to be able to distinguish between mother and predators
133 when the female enters the nest (Nomakuchi et al. 2012).

134 Vibrations are also used as information for defense or predation against different
135 species. In Cydnidae and Reduviidae, in which the nymphs constitute a colony,
136 individuals in the same colony vibrate together as a collective defense against predators
137 (Čokl and Virant-Doberlet 2003). Adults of some species of Triatominae, a subfamily of
138 Reduviidae, produce defensive vibrations using a stridulatory organ when disturbed or
139 handled. In addition, female adults stridulate to reject copulatory attempts made by
140 males (Lazzari et al. 2006; Schilman et al. 2001). Some predacious reduviid species
141 detect the vibrations of caterpillar prey (Čokl and Virant-Doberlet 2003).

142 Among the suborder Auchenorrhyncha, vibrational communications are spread
143 across several families (Table 1). Ichikawa and Ishii (1974) discovered that males of the
144 brown planthopper *N. lugens* (Delphacidae: Fulgoromorpha) use females vibrations for
145 mate location on the rice plant. In response to the female vibrations, the males also
146 produce vibrations with abdominal tymbals, which exist in Auchenorrhyncha and
147 Heteroptera (Hoch et al. 2006; Ichikawa 1976; Mitomi et al. 1984). Similarly, both
148 sexes use vibrations for mate location in Cicadomorpha [e.g., the American grapevine
149 leafhopper, *Scaphoideus titanus* Ball (Cicadellidae) and some species of treehoppers
150 (Membracidae); Cocroft and Rodríguez 2005; Mazzoni et al. 2009]. Furthermore, males
151 of *S. titanus* produce disturbance vibrations against rival males (Mazzoni et al. 2009).
152 Mothers of the thorn bug treehopper *Umbonia crassicornis* (Amyot and Serville) defend
153 their offspring against attacking predators after they produce vibrations for the purposes
154 of aggregation (Cocroft 1996).

155 Among Sternorrhyncha, both sexes of whiteflies (Aleyrodidae) produce vibrations
156 by drumming the abdomen for communication on the leaf of a host plant [e.g., the
157 greenhouse whitefly *Trialeurodes vaporariorum* (Westwood), the sweet potato whitefly
158 *Bemisia tabaci* (Gennadius) and the woolly whitefly *Aleurothrixus floccosus* Maskell;
159 Kanmiya 1996, 2006; Kanmiya and Sonobe 2002]. Male vibrations are species-specific

160 in terms of temporal and spectral characteristics, suggesting that vibrational signals are
161 used for species recognition (Kanmiya 2006). Males of the Asian citrus psyllid,
162 *Diaphorina citri* Kuwayama (Liviidae), locate females that are producing vibrations; the
163 males intermittently produce vibrational replies as a duet (Lujo et al. 2016; Wenninger
164 et al. 2009). In the sweet pepper aphid, *Aphis nerii* Boyer de Fonscolombe (Aphididae),
165 and the large cat's ear aphid *Uroleucon hypochoeridis* (Fabricius) (Aphididae), visual
166 signals in combination with twitching-related vibrations on the plant constitute a
167 synchronizing defense against insect predators (Hartbauer 2010). Nymphs of the pea
168 aphid, *Acyrtosiphon pisum* Harris (Aphididae), drop off the host plant in response to
169 vibrations and other stimuli, such as the humid breath of mammalian herbivores (Gish et
170 al. 2012).

171

172 *Coleoptera*

173 Coleoptera is the largest insect order and includes many pest species. Although there are
174 numerous reports of sound production by stridulatory organs across various coleopteran
175 families (Wessel 2006), most of these reports concern vibrational communication or
176 interactions (Table 2). In the mountain pine beetle *Dendroctonus ponderosae* (Hopkins)
177 (Curculionidae), stridulation generates vibrations on the host tree as well as airborne

178 sounds, presumably for sexual communication at close range (Flemming et al. 2013).

179 Males of the deathwatch beetle *Xestobium rufovillosum* (De Geer) (Anobiidae) tap their

180 heads on the substrate; this enables them to locate females emitting vibrational replies at

181 long range (Goulson et al. 1994). Among tenebrionid species, males of *Psammodes*

182 *striatus* (Fabricius) tap their abdomens on the substrate for sexual communication, with

183 a range of >50 cm (Lighton 1987). *Onymacris plana plana* Péringuey (Tenebrionidae)

184 is sensitive to vibrations between 100 and 5000 Hz, presumably for detecting food

185 through vibrations generated by the wind on the surface of the sand (Hanrahan and

186 Kirchner 1994). As a defense against predators, the red flour beetle *T. castaneum*

187 (Tenebrionidae) shows tonic immovability (death-feigning) in response to vibrations

188 (Kiyotake et al. 2014). Vibration-induced tonic immovability is also found in the

189 Colorado potato beetle, *Leptinotarsa decemlineata* Say (Chrysomelidae) (Acheampong

190 and Mitchell 1997), and the sap beetle, *Phenolia (Lasiodites) picta* (MacLeay)

191 (Nitidulidae) (Kishi and Takanashi 2019). In cerambycids, startle and freezing responses

192 are induced by vibrations in *M. alternatus*, *Paraglenea fortunei* (Saunders), and the

193 house longhorn beetle, *Hylotrupes bajulus* (Linnaeus) (Breidbach 1986; Takanashi et al.

194 2016; Tsubaki et al. 2014). The responses seem to serve as recognition of approaching

195 conspecifics or predators.

196 Vibrations mediate communication or interactions among adults, larvae, and pupae.
197 Group-living larvae of *Trypoxylus dichotomus* (Linnaeus) (Scarabaeidae) freeze in
198 response to vibrations produced by drumming pupae, thereby protecting the pupal cells
199 in the soil (Kojima et al. 2012c). The freezing response to pupae of *T. dichotomus* is
200 likely to have evolved from the response to predators because larvae also show freezing
201 to vibrations produced by moles (Kojima et al. 2012a, b). Females of the cowpea beetle
202 *Callosobruchus maculatus* (Fabricius) (Chrysomelidae) use vibrations from feeding
203 larvae within a host bean for the purpose of oviposition (Guedes and Yack 2016).

204

205 **Pest control using vibrations**

206 The importance of physical pest control by using lights or other non-chemical methods
207 has been increasing in response to societal needs for environmentally friendly
208 alternatives to synthetic pesticides (Polajnar et al. 2015; Shimoda and Honda 2013).
209 Knowledge of sensitivities and behaviors in response to vibrations is applicable to pest
210 management for behavioral manipulation and disruption. To apply artificial vibrations to
211 insect pests, vibration exciters (as hardware) and the temporal and spectral characters of
212 the vibrations (as software) are of great importance. In addition, the possible side-effects
213 of vibrations on plants and non-target insects need to be assessed carefully (for a review,

214 see Polajnar et al. 2015). Below, we present in detail some examples of disruption of
215 vibrational communication or behavior.

216

217 *Disruption of vibrational communication*

218 In pest species that use vibrational communication between sexes, it is a rational
219 strategy to disrupt this communication with artificial vibrations. Here, we review two
220 successful cases. Males of *S. titanus*, a vector of the lethal grapevine disease
221 Flavescence dorée, produce male-disturbance vibrations as well as sexual signals
222 (Mazzoni et al. 2009). Eriksson et al. (2012) demonstrated vibrational disruption of this
223 species by using mimic disturbance vibrations from an electromagnetic shaker. When
224 the disturbance vibrations were transmitted to grapevines through a supporting wire, the
225 mating frequency in field cages of the species decreased significantly. The amplitude
226 threshold for efficacy in mating disruption was determined in the laboratory and
227 validated in the field (Polajnar et al. 2016a). The other example is communication
228 disruption in *D. citri*, which is a vector of citrus greening disease, one of the most
229 destructive citrus disease worldwide (Hall et al. 2013). The two sexes of this species
230 exchange vibrational communication to locate each other (Wenninger et al. 2009).

231 Application of female vibrational mimics generated by a piezoelectric buzzer led to a

232 significant decrease in the mating percentage on a citrus tree (Lujo et al. 2016).

233

234 *Disruption of behavior with vibrations*

235 Cerambycids—the so-called longicorn beetles—include many pests, and their larvae

236 damage fruit and ornamental trees. These beetles include serious pests known to be

237 invasive species and vectors of tree diseases (Kobayashi et al. 1984; Wang 2017). In

238 cerambycids, although vibrational communication for mate localization over long

239 ranges has not yet been found, a series of behaviors is displayed in response to

240 vibrations (Breidbach 1986; Takanashi et al. 2016; Tsubaki et al. 2014). This means that

241 various cerambycid behaviors can be disrupted by artificial vibrations for pest control.

242 Indeed, Hosomi (1996) investigated vibrational disruption by using mechanical knocker

243 on fig trees against adults of *Apriona japonica* Thomson. Intermittent vibrations at 5 to

244 40 Hz disrupt feeding to some extent, but not oviposition. No fatal negative effects of

245 the vibrations on fruit and shoot growth have been detected (Hosomi 1996).

246 *Monochamus alternatus*, the vector of the pine wilt nematodes that kill pine trees

247 (Kobayashi et al. 1984), demonstrates freezing and startle responses when exposed to

248 vibrations below 1 kHz (Fig. 2) (Takanashi et al. 2016). The freezing is mediated by

249 femoral chordotonal organs (Fig. 1b, c) that detect low-frequency vibrations (Takanashi

250 et al. 2016). Also, *P. fortunei* dwelling on herbaceous plants shows freezing and startle
251 responses when exposed to low-frequency vibrations (Fig. 2) (Takanashi et al. 2016;
252 Tsubaki et al. 2014). Thus, these two cerambycid beetles show high sensitivity to
253 frequencies of 100 to 500 Hz (Fig. 2). Because freezing means cessation of walk and
254 other behavior, low-frequency vibrations are assumed to disrupt the feeding, oviposition,
255 and residence of cerambycids on host trees. Also, it is possible that vibrations enhance
256 repellency, that is, escape from the host tree. Preliminary experiments have shown that
257 feeding and other behaviors in *M. alternatus* are disrupted by low-frequency vibrations
258 (T. Takanashi et al. unpublished data). Low-frequency vibrations might therefore be also
259 useful for pest control in cerambycids.

260 On the basis of our findings of vibrational sensitivity in cerambycid beetles, we are
261 currently developing a new procedure for pest management by using vibrations as an
262 environmentally friendly alternative to synthetic pesticides. To generate vibrations at
263 large amplitudes on trees, a prototype of a vibration exciter was made by using a giant
264 magnetostrictive material (GMM) as a new technology (Fig. 3). GMM, an alloy
265 comprised of iron and rare metals, exhibits a large magnetostrain, namely a strain
266 caused by a magnetic field (Söderberg et al. 2005). This exciter generates low-frequency
267 vibrations at high acceleration, and these vibrations are expected to manifest enough

268 power to disrupt the behaviors of target pests (Takanashi et al. 2016). In addition,
269 intermittent application of vibrations can help avoid the problem of habituations to
270 vibrations. Our pilot experiments demonstrated disruption of behavior in *M. alternatus*
271 by a GMM vibration exciter attached to a tree (H. Sakamoto, T. Koike, N. Fukaya, T.
272 Takanashi in preparation); this was also shown in the brown-winged green bug, *P. stali*
273 (N. Uechi and T. Takanashi in preparation). Future studies are essential to explore and
274 resolve several issues, including installation of the exciter and jigs for vibrational
275 transmission, reduction of the cost of the exciter, and the possibility of side-effects on
276 plants and other organisms.

277

278 **Conclusion**

279 Because many insects in a variety of taxa exhibit sensitivity to vibrations (Cocroft and
280 Rodríguez 2005; Greenfield 2002; Hill 2008), artificial vibrations are applicable to the
281 disruption of behaviors or communication. Furthermore, a vibration exciter that uses
282 GMM technology is able to generate vibration on various substrates (e.g., crops in
283 greenhouses). Such new pest control technologies will help to reduce the need to apply
284 synthetic pesticides and will become part of integrated pest management (IPM) in the
285 future (Polajnar et al. 2015). Potential negative side effects of the vibrations on plants

286 and non-target beneficial insects will need to be minimized (Polajnar et al. 2015). We
287 should be able to find the most appropriate procedures to use against various pests, and
288 we will be able to promote IPM by combining several existing procedures with newly
289 developed technologies, including vibration.

290

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301

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- 509

510 **Table 1** Vibrational communications and interactions in Hemiptera. Families reviewed

511 by Virant-Doberlet and Čokl (2004) are included

512

Family	Species	Intra-species communication	Inter-species interaction	References
Heteroptera				
Alydidae	<i>Riptortus pedestris</i>	male courtship, communication between male and female		Numata et al. 1989
Coreidae	<i>Coreus marginartus</i>	courtship		Gogala 1990
Cydnidae	<i>Adomerus rotundus</i> , <i>Tritomegas bicolor</i>	male copulatory attempts, parent–embryo communication (synchronous hatching)		Gogala 1984; Mukai et al. 2012, 2018
Miridae	<i>Lygus rugulipennis</i>	courtship		Koczor and Čokl 2015
Parastrachiidae	<i>Parastrachia japonensis</i>	parent–embryo/offspring communication (synchronous hatching, provisioning call)		Mukai et al. 2014; Nomakuchi et al. 2012
Pentatomidae	<i>Halyomorpha halys</i> , <i>Nezara viridula</i> , <i>Nezara antennata</i>	male courtship, communication between male and female, embryo interaction (synchronous hatching)		Čokl et al. 1978, 1999, 2000; Endo and Numata 2017; Endo et al. 2018; Kon et al. 1988; Polajnar et al. 2016b
Reduviidae	<i>Rhodnius</i>	male copulatory	defense	Čokl and

<i>prolixus</i> , <i>Triatoma</i> <i>infestance</i>	attempts	against predators or disturbance, detection of food	Virant-Doberlet 2003; Lazzari et al. 2006; Schilman et al. 2001
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Auchenorrhyncha

Aphrophoridae	<i>Aphrophora</i> <i>alni</i>	calling, male territorial and rivalry signals	Tishechkin 2003; Virant-Doberlet and Čokl 2004
Caliscelidae	<i>Acromega</i> <i>scurrilis</i> , <i>Peltonotellus</i> <i>turgidus</i>	calling	Tishechkin 2003, 2016
Cercopidae	<i>Cercopis</i> <i>vulnerata</i>	calling, territorial signals	Tishechkin 2003
Cicadellidae	<i>Scaphoideus</i> <i>titanus</i>	mate location, disturbance of rival males	Mazzoni et al. 2009
Cicadidae	<i>Cicada orni</i> , <i>Okanagana</i> <i>rimosa</i>	mate location (vibrational component of air-borne calling signal)	Stölting et al. 2002; Virant-Doberlet and Čokl 2004
Cixiidae	<i>Celebenna</i> <i>thomarosa</i> , <i>Cixius</i> <i>nervosus</i>	mating behavior	Hoch et al. 2011; Tishechkin 2003, 2008
Delphacidae	<i>Laodelphax</i> <i>striatellus</i> , <i>Nilaparvata</i> <i>lugens</i> , <i>Sogatella</i> <i>furcifera</i>	communication between males and females	Ichikawa 1976; Ichikawa and Ishii 1974; Tishechkin 2008
Derbidae	<i>Cedusa</i>	calling	Tishechkin 2008

	<i>sarmatica</i>			
Dictyopharidae	<i>Dictyophara</i>	mating behavior,		Tishechkin 2003,
	<i>pannonica</i>	calling		2016
Flatidae	<i>Metcalfa</i>	mating behavior		Virant-Doberlet
	<i>pruinosa</i>			and Žežlina 2014
Issidae	<i>Alloscelis</i>	calling		Tishechkin 2003,
	<i>vittifrons,</i>			2008
	<i>Scorlupella</i>			
	<i>discolor</i>			
Machaerotidae	<i>Taichorina</i>	calling		Tishechkin 2003
	<i>geisha</i>			
Meenoplidae	<i>Eponisiella</i>	calling		Tishechkin 2016
	<i>paludicola</i>			
Membracidae	<i>Unbonia</i>	mate location,	defense	Cocroft 1996;
	<i>crassicornis</i>	mating	against	Cocroft and
			predators	Rodríguez 2005
Tettigarctidae	<i>Tettigarcta</i>	courtship		Claridge et al. 1999
	<i>crinita</i>			
Tropiduchidae	<i>Trypetimorpha</i>	calling, competition		Tishechkin 2003
	<i>occidentalis</i>	between males		

Sternorrhyncha**ha**

Aleyrodidae	<i>Aleurothrixus floccosus</i> , <i>Bemisia tabaci</i> , <i>Siphoninus phillyreae</i> , <i>Trialeurodes vaporariorum</i>	communication between males and females		Kanmiya 1996, 2006; Kanmiya and Sonobe 2002
Aphalaridae	<i>Aphalara affinis</i>	mate finding and courtship		Lubanga et al. 2014
Aphididae	<i>Aphis nerii</i> , <i>Toxoptera oadiiiae</i> , <i>Uroleucon hypochoeridis</i>		defense against predators	Gish et al. 2012; Hartbauer 2010
Carsidaridae	<i>Protyora sterculiae</i>	mate finding and courtship		Lubanga et al. 2014
Liviidae	<i>Diaphorina citri</i>	communication between males and females		Lubanga et al. 2014; Lujo et al. 2016; Wenninger et al. 2009
Psyllidae	<i>Cacopylla pyri</i> , <i>Macrohomonota gladiata</i>	mate finding and courtship		Eben et al. 2014; Liao and Yang 2017
Triozidae	<i>Aacanthocnema dobsoni</i> , <i>Schedotrioza apicobystra</i>	mate finding and courtship		Percy et al. 2006

515 **Table 2** Vibrational communication and interactions in Coleoptera. Proposed

516 mechanisms for vibrational generation and responses to vibration are shown in

517 parentheses.

518

Family	Species	Intra-species communication	Inter-species interaction	References
Anobiidae	<i>Xestobium rufovillosum</i>	male and female tapping (orientation)		Goulson et al. 1994
Tenebrionidae	<i>Onymacris plana plana</i> , <i>Psammodes striatus</i> , <i>Tribolium castaneum</i>	male tapping (orientation)	food movement by wind (orientation)	Hanrahan and Kirchner 1994; Kiyotake et al. 2014; Lighton 1987
Chrysomelidae	<i>Callosobruchus maculatus</i> , <i>Leptinotarsa decemlineata</i>	larval feeding (oviposition)	predator movement (tonic immobility)	Acheampong and Mitchell 1997; Guedes and Yack 2016
Cerambycidae	<i>Hylotrupes bajulus</i> , <i>Monochamus alternatus</i> , <i>Paraglenea fortunei</i>	male and female movement (startle, freezing)	predator movement (startle, freezing)	Breidbach 1986; Takanashi et al. 2016; Tsubaki et al. 2014
Scarabaeidae	<i>Trypoxylus dichotomus</i>	pupal tapping (freezing)	predator movement (freezing)	Kojima et al. 2012a, b, c
Nitidulidae	<i>Phenolia (Lasiodites) picta</i>		predator movement? (tonic immobility)	Kishi and Takanashi 2019
Curculionidae	<i>Dendroctonus ponderosae</i>	male stridulation (mating?)		Fleming et al. 2013

519 **Figure legends**

520

521 **Fig. 1** Leg chordotonal organs in *Monochamus alternatus* (**a–c**) and *Plautia stali* (**d–f**).

522 **a** Photograph of *M. alternatus* adult. **b** Diagram indicating the locations of femoral

523 chordotonal organ (FCO): sensory neurons (scoloparium) (*red arrow*) and cuticular

524 apodeme (*red line*) in prothoracic femur are shown. **c** Fluorescent retrograde labeling of

525 FCO scoloparium viewed posteriorly. **d** *P. stali* adult. **e** FCO scoloparium (*red arrow*) in

526 prothoracic femur and subgenual organ (*red arrowhead*) in prothoracic tibia are shown.

527 **f** Fluorescent retrograde labeling of FCO scoloparium viewed anteriorly. Scale bars = 4

528 mm (**a, d**), 500 μm (**b, e**), 50 μm (**c, f**). **c** and **f** are reproduced from the work of

529 Takanashi et al. (2016) and Nishino et al. (2016), respectively, with permission of the

530 publishers. **e** Courtesy of H. Nishino (redrawn from Nishino et al. 2016).

531

532 **Fig. 2** Thresholds of behavioral responses to vibrations in *Monochamus alternatus* and

533 *Paraglenea fortunei*. Startle responses from a standstill (*solid lines*) in both species and

534 freezing response during walk in *P. fortunei* (*dashed line*) are indicated. Adapted from

535 the work of Takanashi et al. (2016) and Tsubaki et al. (2014).

536

537 **Fig. 3** A vibration exciter made by using giant magnetostrictive materials, which
538 generates vibration to induce behavioral responses from insects on a tree. The exciter is
539 attached horizontally to the tree with black bands. Scale bar = 50 mm.
540