



Bug talk trends & biases: literature survey and meta-analyses of vibratory sensing and communication in insects

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Abstract: Research on insect biotremology has resulted in a burgeoning body of literature over the past few decades. Despite this, several biases and knowledge gaps have been proposed, but not quantified. Therefore, a systematic literature review and meta-analyses were carried out to summarize the temporal trends and test for biases regarding taxa, developmental stages, and research topics reported in scientific papers spanning 75 years. The survey tracked 831 papers, which exhibited exponential growth since the 1990s and covered 17 insect orders. Among these studies, 70.4% were associated with adaptive behaviors, while the remaining (29.6%) focused on applied entomology and sensory organs. Three main biases were detected: (i) a prevalence of studies on Hemiptera, Hymenoptera, and Coleoptera, (ii) a focus on adults, and (iii) a preponderance of studies on reproductive behaviors. Considering only adaptive behaviors, the likelihood of studies with adults was 3× higher than for juveniles. Studies documenting receiver response were 2× higher than not. Still, few insect orders (9 of 17) included reports on vibrations used in an adaptive context, while studies reported in the remaining orders focused on mechanisms of vibration production or vibration characteristics. The results of this study highlight knowledge gaps worthy of future investigations. In particular, further research is necessary on the role of vibratory sensing and communication in juveniles (eggs, larvae, pupae, and nymphs), testing hypotheses on the adaptive roles of vibrations in a broader range of taxa, characterization of vibratory landscapes, and research on sensory receptors.

Keywords: biotremology, development, substrate-borne vibrations, vibroacoustic, behaviour, Insecta

1 Introduction

Vibratory sensing and communication are considered to be the most ubiquitous and ancient sensory modalities in insects (Hill 2009; Endler 2014). By vibration, we refer to mechanical waves transmitted through solids (e.g., soil, plant material, silk, wax), in contrast to those transmitted through air or water and commonly referred to as “sounds” (see Hill 2008; Hill & Wessel 2016). Solid-borne vibrations are widely available to insects in the environment and originate from both abiotic (e.g., rain, wind) and biotic (e.g., conspecifics, predators) sources. Vibrations arising from biotic sources can be produced incidentally as cues, such as when an insect walks, or directly as signals, such as when an insect communicates to a mate (Maynard-Smith & Harper 2003; Yack 2016; Giunti et al. 2018). Vibratory sensing and communication (or biotremology, a recently coined term) in

insects has received increasing research attention over the past few decades and this field of study has been variously described as a ‘gold mine’ with ‘unsurpassed opportunities’ (Cocroft et al. 2014a), and an ‘unchartered territory’ (Yack 2016), with ‘many opportunities for ground-breaking study’ (Cocroft & Rodríguez 2005). Despite the progress of this field, there are questions unanswered and gaps in our knowledge that deserve scrutiny.

A number of reviews have covered the topic of vibratory sensing and communication in insects to varying degrees. These include comprehensive reviews that focus on the distribution of taxa and contexts in general (e.g., Virant-Doberlet & Čokl 2004; Cocroft & Rodríguez 2005), or specific taxonomic groups (e.g., Plecoptera [Stewart 1997], Neuroptera [Devetak 1998; Henry et al. 2012; 2013], Hemiptera [Gogala et al. 1974; Claridge 1985; Čokl & Virant-Doberlet 2003; Cocroft & Mcnett 2006], Hymenoptera [Schneider & Lewis

2004; De-Luca & Vallejo-Marin 2013]; Mantophasmatodea [Eberhard & Eberhard 2013]). Others focus on the role of vibrations mediating specific types of interactions such as group-living (e.g., Coccoft 2001; Hunt & Richard 2013), prey-predator (e.g., Casas & Magal 2006; Virant-Doberlet et al. 2019), and myrmecophily (e.g. Casacci et al. 2019). Others address practical applications for insect monitoring and control (e.g., Rajendran 1999; Polajnar et al. 2015; Liu et al. 2017; Banga et al. 2018; Takanashi et al. 2019; Adedeji et al. 2020; Lima et al. 2020).

Based on the literature reviewed to date, a number of potential shortcomings and biases have been noted. The first relates to which insects detect and generate vibration. It has been stated that we are in the process of “identifying the players” including taxa never considered before (Hill 2008; 2009; Yack 2016). To the best of our knowledge, eighteen insect orders have been qualitatively recognized as using vibratory communication and sensing (Virant-Doberlet & Čokl 2004; Coccoft & Rodriguez 2005), but without a more in depth analysis and quantitative assessment. However, this number has been estimated as being low, leaving out some of the small-bodied orders (e.g., fleas, twisted wing parasites, jumping bristletails, and thrips). Second, it is proposed that research has focused on adult insects (Virant-Doberlet & Čokl 2004; Coccoft et al. 2014b; Yack 2016), which is a conundrum because juveniles are generally more substrate-bound than their adult counterparts, given that they are less likely to jump and do not fly. Third, it has been proposed that topics covered are biased towards some subjects, such as reproduction (see Virant-Doberlet & Čokl 2004; Coccoft et al. 2014b; Hill et al. 2019), but lacking in others, such as sensory organs (Yack 2016) and evolution (Hill et al. 2019). Finally, while there are many reports of proposed vibration sensing and communication, for example, based on morphology alone or recorded vibrations (e.g., Low 2008; Quiroga et al. 2019), it is not always clear whether these examples constitute adaptive usage of vibrations, as experimental evidence for information transfer is lacking. The above-mentioned concerns led to the present attempt to understand how vibratory sensing and communication has been studied in insects.

The purpose of this review is to survey the literature over a period of 75 years, from 1945 to 2020, to obtain an overview of strengths and weaknesses in the field. This study had two primary goals. First, to conduct a systematic literature survey to qualitatively describe the temporal trends in publications, the taxonomic groups, and developmental stages, and to identify the main topics studied. This was done using the Web of Science and Scopus databases. The second goal was to conduct meta-analyses to synthesize, quantify and test the investigation trends, with the purpose of testing specifically: (i) whether there is a prevailing bias on the development stages studied, and (ii) whether there was evidence for receiving vibrations (cues or signal) in an adaptive context. Note that our intention was not to conduct a complete

and global survey of all literature covering the topic of insect vibratory sensing and communication, but rather to carry out a comprehensive survey of a subset of the literature within our search constraints to identify trends. The results allow for the recognition of knowledge gaps and provide directions for further investigation.

2 Materials and methods

The procedures for the systematic literature survey and subsequent meta-analyses followed the guidelines of “Preferred Reporting Items for Systematic Reviews and Meta-Analyses” (PRISMA) (Moher et al. 2009), which are briefly described below.

2.1 Initial data collection, screening, and literature review

An overview of the process of data collection and screening is described in Fig. 1. First, a literature search was performed on the topic of vibratory sensing and communication among insects. We used combinations of keywords in two databases (Web of Science and Scopus), including literature published over a 75-year period, between January 1945 and December 2020. The search was carried out with general keywords to identify a broad initial dataset, and included the following terms: “bioacoustics,” “acoustic,” “vibratory,” “vibration,” “vibroacoustic,” “substrate-borne,” “solid-borne,” “vibrational,” “seismic,” or “biotremology,” in mandatory combination with “herbivore,” “insect,” “arthropod,” “Insecta” or “phytophagous.” Afterward, we included the references from the book by Coccoft et al. (2014b), which contains a comprehensive review on vibratory communication with an emphasis on arthropods. Duplicate papers were removed from the dataset, and the remaining were further screened for inclusion in the qualitative analysis by including in our dataset only studies that met the following criteria: (i) were published in English in a peer-reviewed journal; (ii) contained the target organism (i.e., insect) and solid-borne vibrations, and iii) reported the developmental stage of the organism studied (adults or juveniles). We excluded any narrative review, case report, protocol, editorial, book, book chapter, thesis, dissertation, and proceedings of meetings or conferences.

2.2 Qualitative analyses

The selected papers were used to recognize overall temporal trends in publishing, and to identify taxonomic groups (i.e., insect orders), developmental stages (i.e., egg, larva, pupa, or adult), and topics studied. Additionally, we compartmentalized the papers within eight subject categories, following the guidelines in Box 1 to recognize the major focus of attention. This information was compiled and summarized (Table S1) and used for building the interaction matrixes,

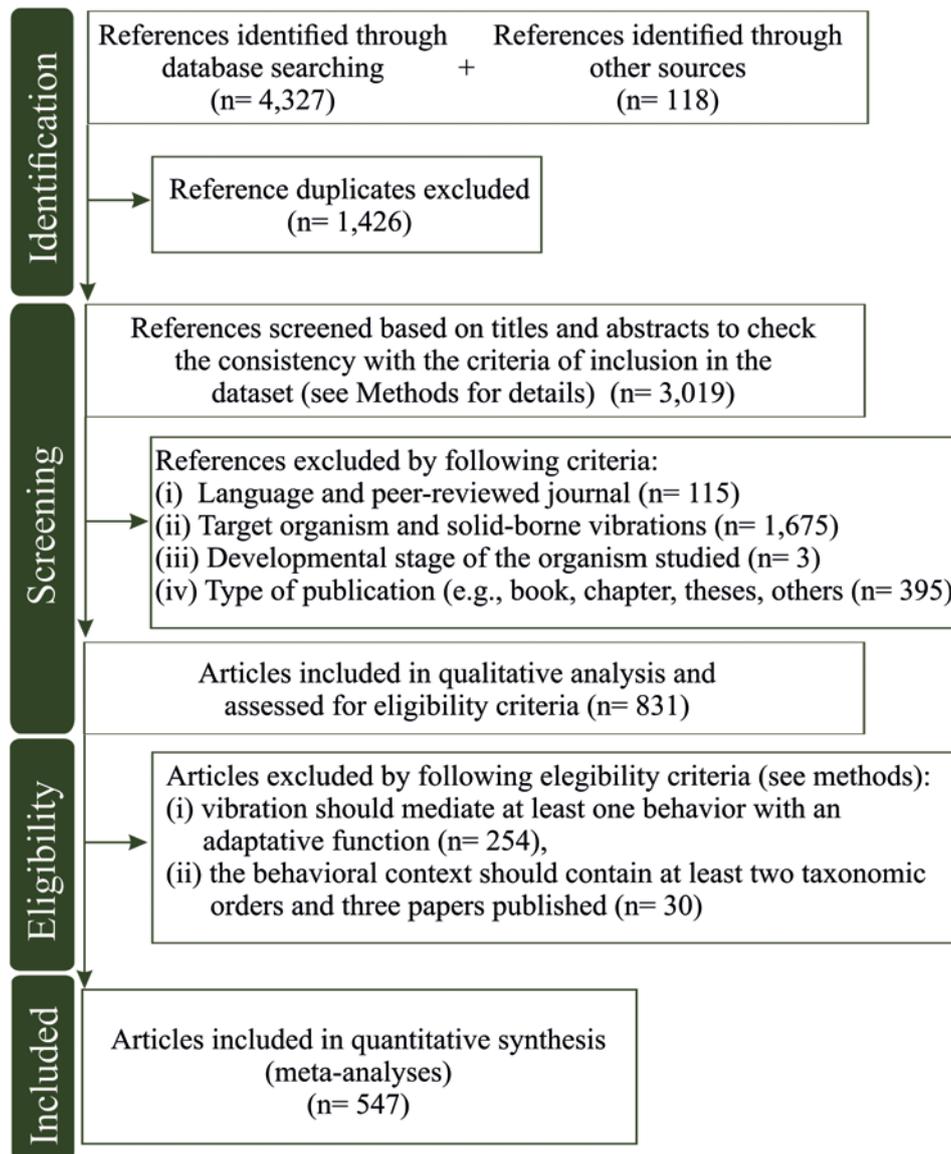


Fig. 1. Flowchart describing how scientific articles were step by step included/excluded in the literature dataset at the four stages of the systematic review process ('Identification', 'Screening', 'Eligibility', and 'Included'). Refer to the Materials and Methods for details on screening and eligibility criteria.

which identified the relationship among subject categories and insect orders tested.

2.3 Quantitative analyses

To establish the dataset for the quantitative analyses, papers were selected for inclusion based on two eligibility criteria: (i) the vibration should mediate at least one behavior with an adaptive role, according to the subject categories established in the [Box 1](#), and (ii) each behavioral context should contain at least two taxonomic orders and three papers published, which is an assumption to proceed with meta-analyses. This dataset was subjected to meta-analyses with binary out-

comes to test specifically whether the publications favored a particular developmental stage and whether there was evidence for vibration reception in an adaptive context, considering as evidence a change in behavior of the receiving organism. In all cases, the taxonomic groups and the adaptive behaviors were used as moderators. The risk ratio and 95% confidence intervals were used to determine the overall effect measured, where the former (i.e., risk ratio, RR) is the likelihood of an outcome between two alternatives (RR=1 means a similar outcome among two possibilities or lack of bias). The random-effect model was used because the individual studies differ, and their effects are usually assumed

Box1 - Subject categories ****a) Adaptive behaviors**

- 1. Reproductive behavior** – those articles where the insects utilize vibrations in the context of mating and reproduction, including attraction, locating a mate or rival, species recognition, courtship, competition between rivals, and pair maintenance.
- 2. Group-living** – those articles where the vibratory resource is used among group members for coordination or mediation in:
 - 2.1 *Group defense* – includes articles that describe alarm signaling, avoiding predation, territorial and spacing behavior, offspring-parent signaling, stop signaling, eavesdropping, aphids dropping.
 - 2.2 *Cooperative foraging* – includes articles where vibration is used in the location and assessment of food resources; recruitment for foraging, mediating food exchange between larvae and adult.
 - 2.3 *Synchronize other activities* – includes articles on sustaining cohesion, stimulating egg hatching, molting, group movement, swarming and processionary behavior.
 - 2.4 *Other social interactions* – includes articles where the vibrational resource is used in communicating social status, caste determination, and recruitment to nesting sites.
- 3. Foraging** – those articles that report on individual foraging by:
 - 3.1 *Herbivores* – includes articles that describe passive vibration cues produced by an insect during feeding behavior.
 - 3.2 *Pollinators* – includes articles where vibrations are generated when foraging for pollen (buzz pollination).
 - 3.3 *Predators or parasitoids* – includes articles where vibration cues (e.g. from crawling, chewing) facilitate prey/host capture.
- 4. Individual defense** – those articles that describe strategies by an individual in the context of defense from an intraspecific (conspecific) or interspecific (predator) by *stopping an attack, avoiding detection or capture, or defending a territory*.
- 5. Monitoring of abiotic factors** – those articles where the insects utilize vibrations from abiotic sources to gain information about the environment (wind, rain).
- 6. Myrmecophiles** – those articles where the vibratory resource is used in mutualistic or parasitic relationships with ants (mimicking queen, recruiting ants, elevating social status).

b) Other topics

- 7. Applied entomology or substrate feature** – those papers in which vibration cues or signals are used for the detection of insects by a device, as a trap for attraction or capture, or as an agent to disrupt activities (e.g. mating disruption). Or, papers describing how the vibrations are propagated in the solid-substrate.
- 8. Sensory receptors** – those papers in which the focus is to describe morphology and/or physiology of vibration receptors.

** All subject categories are not mutually exclusive.

Box 1. Definitions of subject categories used to systematize papers about vibratory sensing and communication in insects.

to be heterogeneous. The quantification and heterogeneity-test (i.e., Q, H, and I²) were conducted, and the inverse variance and DerSimonian–Laird methods were used to estimate the between-study variance (τ^2). Studies with $n \leq 1$ event in both groups were excluded from the meta-analyses. All analyses were performed using the R-software version 3.5.1 (R Development Core, Vienna, Austria), with the packages “meta”, “metafor” and “stats” (R Development Core Team 2020; Schwarzer et al. 2015). The graphical illustrations were produced with Wacom creative table (Intuos S,

Tokyo, Japan) using Corel Painter (Essential 6, Ottawa, ON, Canada).

3 Results

3.1 Summary of the literature

A summary flowchart showing the results of the article selection procedure is shown in Fig. 1. The original literature search resulted in 4,327 papers from Web of Science

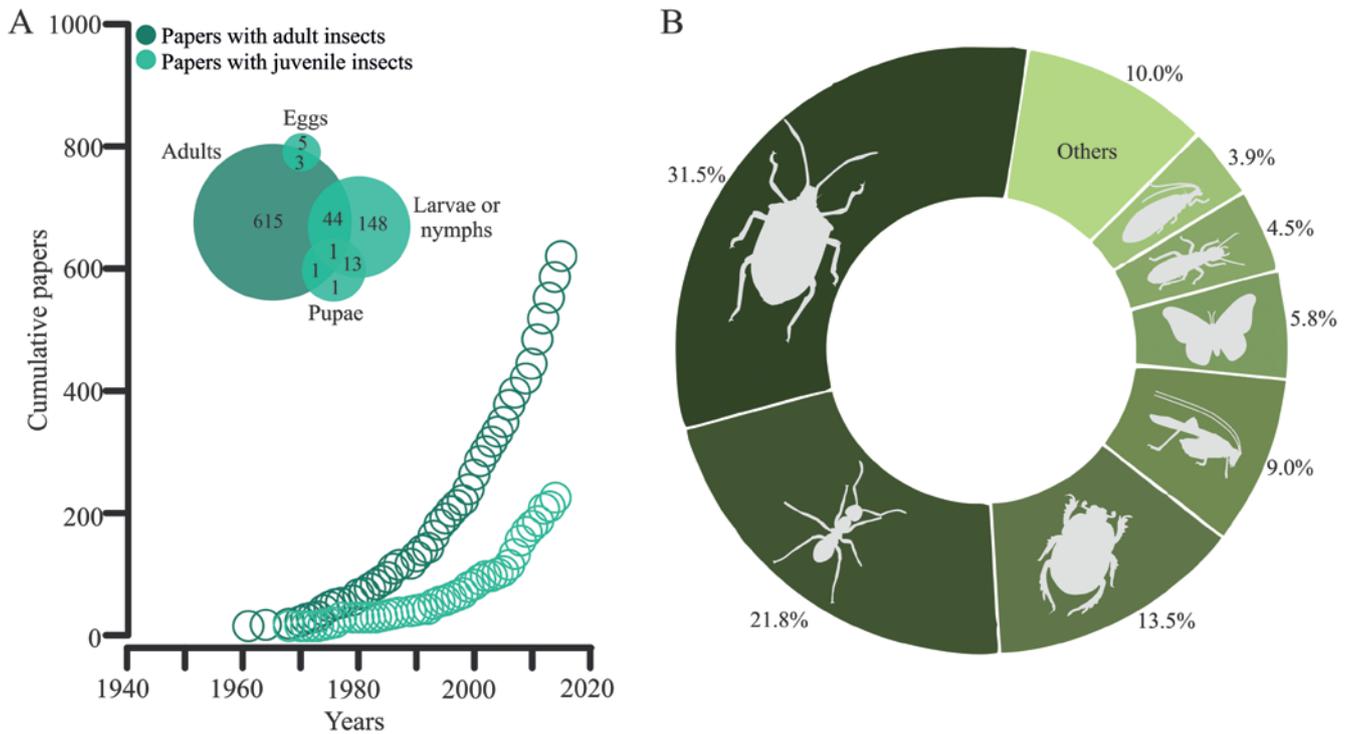


Fig. 2. (A) Scatterplot of the cumulative papers published on solid-borne vibrations of adult (dark green circle) and juvenile (light green circle) insects between 1945–2020. The inner diagram indicates the number of published papers on each specific developmental stage. The overlapping circles in the upper left of the figure indicate papers that include more than one developmental stage. (B) Distribution of the studies on insect solid-borne vibrations among taxonomic insect orders compiled for qualitative analysis (n=831 papers).

and Scopus. Additionally, 118 papers were incorporated from a comprehensive book on the topic with emphasis on arthropods (Cocroft et al. 2014b), totaling 4,445; 3,019 papers remained after removing duplicates. These 3,019 papers were screened based on titles and abstracts to check for consistency with the criteria of inclusion in the dataset (see Materials and methods for details). This resulted in 831 papers that were used in the qualitative analyses to describe the temporal trends, taxonomic groups, developmental stage, and main subjects explored. To conduct the meta-analyses, two additional eligibility criteria were applied to the 831 papers (see Materials and methods for details) resulting in 547 papers.

3.2 Qualitative literature trends

The temporal trend in publishing over a period of 75 years, from January 1945 to December 2020, was followed (Fig. 2A). However, the milestone of the first manuscript published occurred only in the early 1960s, when Moore in 1961, identified vibrations by hemipteran adults (Moore 1961; Table S1). Overall, the trajectory of the field during its two first decades following the first publication in 1961 exhibited a slow linear growth, with studies remaining scarce until the late 1980s and 2000s for adults and juveniles

respectively. Afterwards, there was an exponential growth in publication output extending to the present (Fig. 2A).

A diversity of taxonomic groups (17 of the 30 recognized orders [Gullan & Cranston 2014, considering Isoptera, Blattodea, Psocoptera, and Phthiraptera as different orders]) was identified in the scientific papers on vibratory sensing and communication. The most representative groups were Hemiptera (31.5%), Hymenoptera (21.8%), Coleoptera (13.5%), Orthoptera (9.0%), Lepidoptera (5.8%), Isoptera (4.5%), and Neuroptera (3.9%), while the ten insect orders remaining encompassed only 10% of papers (Fig. 2B). Orders that were not reported included Archaeognatha, Zygentoma, Ephemeroptera, Zoraptera, Grylloblattodea, Mantodea, Psocoptera, Phthiraptera, Thysanoptera, Raphidioptera, Megaloptera, Strepsiptera, and Siphonaptera.

There was an apparent bias in the developmental stages being studied, with the vast majority of studies focusing on adults (Fig. 2A). Indeed, of 831 papers identified, 74% focused only on adults (n=615 papers), 20.1% only on juveniles (n=167 papers), and 5.9% covered both juveniles and adults (n=49 papers). Among juveniles, the vibration was more frequently investigated on larvae or nymphs (n=206 papers), while pupae (n=16 papers) and eggs (n=8 papers) were least represented (Fig. 2A).

Of the 831 papers, a wide range of topics was identified, extending from adaptive behaviors to applied entomology (see Table S1). Such topics were herein compartmentalized within eight broad subject categories (Box 1) in order to examine the most commonly explored subjects, and the main taxonomic groups studied within each (Fig. 3). Overall, the interaction among taxonomic groups and subject categories showed that about 70.4% of papers focused on understanding the role of vibration in an adaptive context (Fig. 3). These articles were clustered into six subject categories of which the main one is reproductive behavior (36.2% of papers; 12 orders), followed by the moderately represented group-living (17.3% of papers; 6 orders), foraging (9.2% of papers; 7 orders), and individual defense (5.5% of papers; 9 orders); and then the least represented, monitoring abiotic factors (1% of papers; 5 orders) and myrmecophilic interactions (1.2% of papers; 2 orders) (Fig. 3). The remaining 29.6% of the literature did not relate directly to adaptive

functions, and these included papers on applied entomology (16.5% of papers; 9 orders) and sensory organs (13.1% of papers; 12 orders) (Fig. 3).

In summary, a total of 831 papers were selected for qualitative analysis. This qualitative description of the literature showed an increase in studies on vibratory sensing and communication in insects during the last 75 years. Reports included 17 insect orders, with a heavy focus on the adult stage. The papers focused mainly on adaptive behaviors, with reproductive behaviors representing the topic most commonly studied among subject categories.

3.3 Meta-analyses and overall trends

Of the 831 studies, 547 met the two eligibility criteria for meta-analyses (see Materials and methods). These 547 papers covered four subjects related to adaptive behavior: reproductive behavior (7 orders), group-living (3 orders), foraging

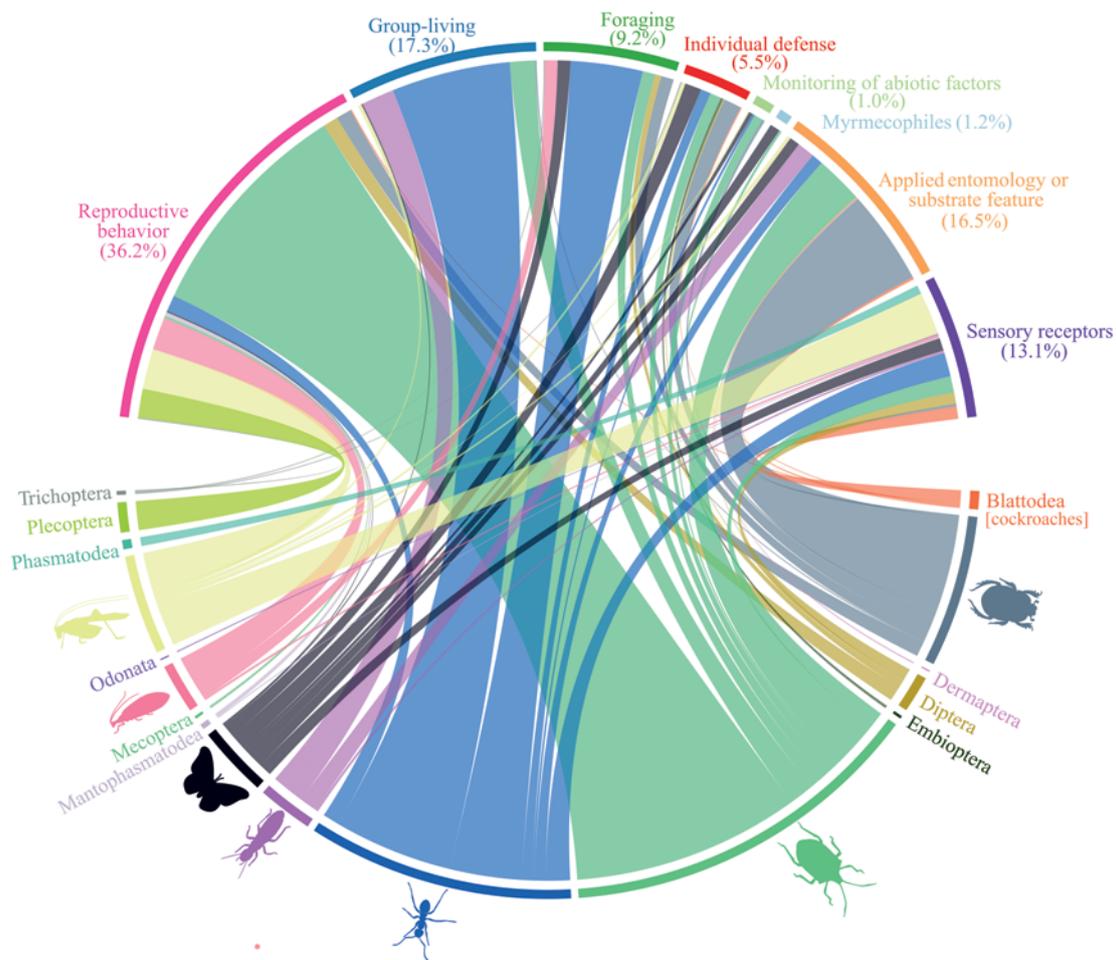


Fig. 3. Interaction diagram between insect orders and subject categories included in the current systematic review from studies documenting vibratory sensing and communication in insects ($n=831$ papers). Connections between insect orders and subject categories represent the interaction. The thickness of arcs represents the number of times that interactions were studied.

(6 orders), and individual defense (4 orders). These papers were subjected to meta-analyses to test two main questions.

The first question was if there is a bias towards a developmental stage. The meta-analysis model indicated that indeed the likelihood of studies with adults is about 3× higher than with juveniles (RR=3.01; $z=2.54$; $P<0.01$; orange diamond) (Fig. 4), reinforcing the trends previously suggested in the qualitative analysis. However, the dataset indicates that the likelihood of studies in favor of a specific developmental stage is strongly related to the taxonomic group and adaptive behavior, reflected in high and significant heterogeneity among studies, which deserves scrutiny (Fig. 4). Studies on reproductive behavior are highly associated with adults regardless of the taxonomic group (RR=50.16; $I^2=0\%$; $P=0.84$; pink diamond), which is expected. On the other hand, group-living (RR=0.73; $I^2=93\%$; $P<0.01$; blue diamond), individual foraging (RR=0.84; $I^2=79\%$; $P<0.01$; green diamond) and individual defense (RR=1.44; $I^2=70\%$; $P<0.01$; red diamond) do not exhibit bias towards any specific developmental stage. In these cases, the developmental stage studied is strongly associated with the insect orders; for instance, Isoptera, Lepidoptera, and Neuroptera are more commonly studied as juveniles, whereas the remaining orders are predominantly studied as adults (Fig. 4).

Meta-analysis was also used to ask whether there is supporting evidence for vibration being confirmed to serve an adaptive function. The likelihood of studies documenting a receiver response was 2× higher (RR=2.13; $z=2.47$; $P=0.01$; orange diamond) than not. Nonetheless, the dataset exhibits high heterogeneity among insect orders and behavioral contexts, which invites further scrutiny within each behavioral context (Fig. 5). Reproductive behavior (RR=5.44; $I^2=82\%$; $P=0.01$; pink diamond) and group-living (RR=2.80; $I^2=76\%$; $P=0.01$; blue diamond) are prevalent among the receiver responses recorded, regardless of insect order. In contrast, individual foraging (RR=0.54; $I^2=71\%$; $P<0.01$; green diamond) and individual defense (RR=1.34; $I^2=81\%$; $P<0.01$; red diamond) do not exhibit significant trends (RR around 1), and thus show similar likelihood in reporting adaptive consequences of the response. Besides, the assessment of response is strongly related to the insect order investigated (Fig. 5).

In summary, the quantitative analyses of the literature confirmed bias in the developmental stage, revealing a likelihood of studies 3× higher with adults than with juveniles. Also, scientific papers often document a response or change in behavior in the receiving organism, supporting the conclusion that the studies provided experimental evidence for the function of vibration in adaptive contexts. However, these studies are mainly related to reproduction and group living. It is also important to note that only a limited number of insect orders (9 of 17 orders identified to be associated with vibrations) have been studied experimentally in the context of adaptive function.

4 Discussion

In rapidly growing subjects some aspects of research are more extensively explored than others. This study provides a systematic review and meta-analyses of published literature on vibratory sensing and communication in insects with the goals to summarize the growth of this topic over the past 75 years, and to identify and quantify the trends and biases within the field that will help to guide future research.

Our results showed that there was an exponential growth in the field beginning in the late 1980s through to the present. The earliest reports related to substrate-borne vibrations in insects were published a century ago, in the 1920s (e.g., booklice: Pearman 1928; termites: Emerson & Simpson 1929). However, such reports are not included in our literature review, which extended from 1945 to 2020 due to limitations on the time period covered by the databases. The scientific publication output on vibratory sensing and communication in insects began modestly in the early 1960s, with studies remaining scarce until the late 1980s. The low publication rate during this early period was expected, as the scientific community had limited access to technologies necessary to detect vibrations, relying primarily on phonograph cartridges (Muraoka et al. 1974; Watanabe 1978). In the late 1980s technological advances increased the availability of equipment (e.g., accelerometers, laser doppler vibrometers) and consequently, the awareness of this sensory modality (Cocroft & Rodríguez 2005; Elias and Mason 2014). Such advances allowed for a rapid expansion of research on the subject of insect biotremology, resulting in a total of 831 papers included in our literature survey. The exponential trend currently persists, as 96 new papers were identified in the Web of Science database subsequent to our search (i.e. between December 2020 and August 2021). This ongoing publication output likely reflects the increase of researcher networks around the world, the broadening of topics addressed in the research field, and the increasing accessibility to instrumentation.

In our survey, we identified which insect orders included species that detect or generate vibration. The number of 17 insect orders recorded (see Fig. 3) was lower than the 18 orders previously reported by Cocroft & Rodríguez (2005), a likely consequence of our more restrictive criteria of assessment. Curiously, the orders identified did not overlap entirely between the two studies. For example, Raphidioptera, Megaloptera, Psocoptera, Thysanoptera, and Zoraptera, were reported by Cocroft & Rodríguez (2005), but not identified herein. In contrast, Odonata, Dermaptera, Phasmatodea, and Mantophasmatodea, identified in our survey, were not identified by Cocroft & Rodríguez (2005). This discrepancy is likely due to the different methodological approaches used to identify the literature (i.e., narrative review vs systematic reviews [see Uman 2011; Gurevitch et al. 2018]) and the ~15-year gap between the two studies. Regardless, our

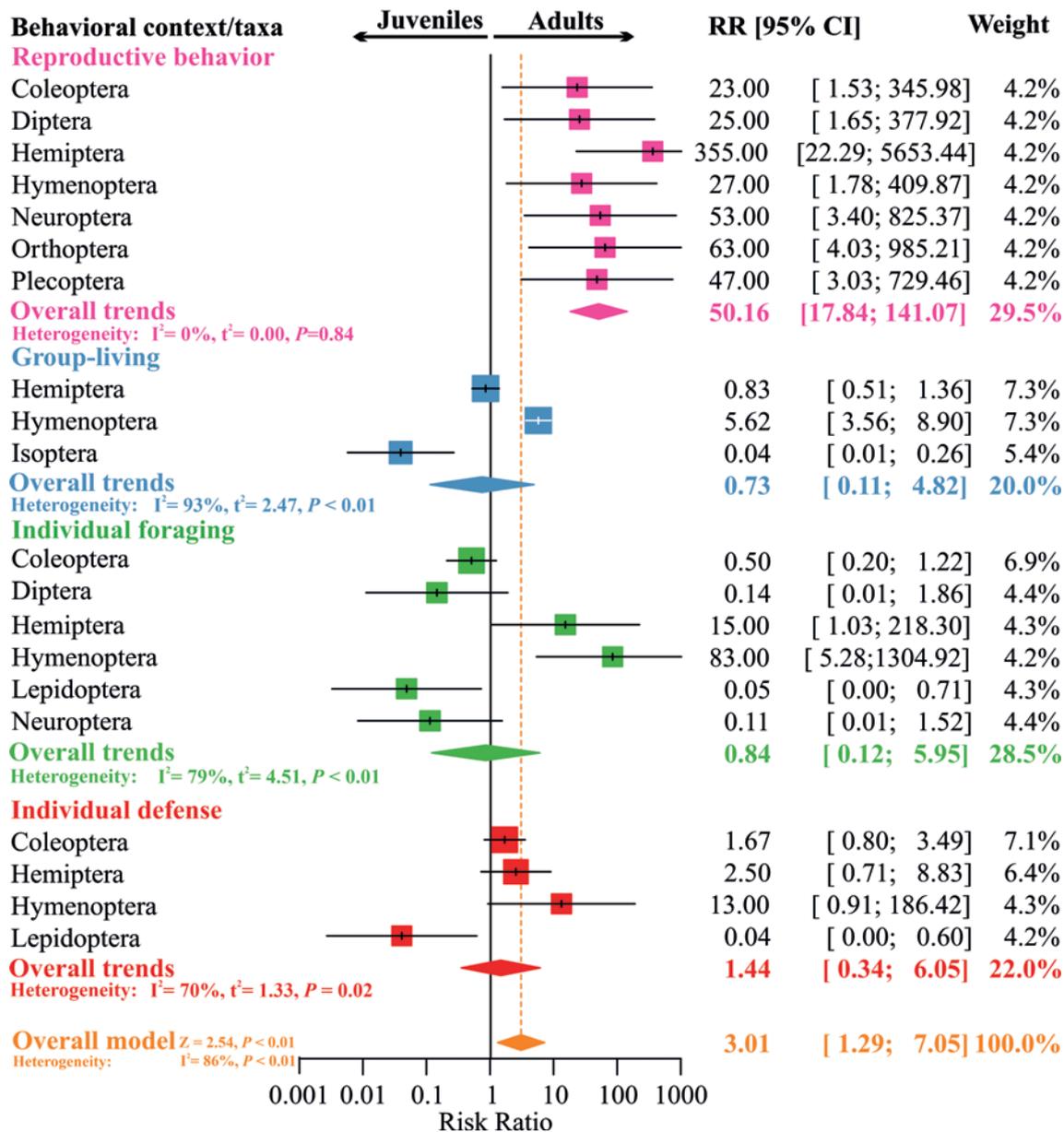


Fig. 4. Forest plot summarizing the results from the frequency of studies by developmental stages, considering the insect orders and behavioral contexts, as moderators. The risk ratios (95% CIs) are denoted by colored boxes (horizontal black lines). The combined RR estimate for overall trends is represented by a colored diamond, where diamond width corresponds to 95% CI bounds. The black vertical solid-line represents lack of effect, whereas the vertical orange dashed line shows the overall estimated effect resulting from all studies. The P-values for heterogeneity test of risk ratios are indicated.

results reinforce the statement that we remain in the process of “identifying the players”, including taxa never considered before (Hill 2008; Yack 2016), as at least 13 orders (our study), or 8 if we include those additional orders identified by Cocroft & Rodrigues (2005), remain unreported in the literature.

Among the 17 insect orders we identified, the seven with most published papers were Hemiptera, Hymenoptera,

Coleoptera, Orthoptera, Lepidoptera, Isoptera, and Neuroptera, respectively (Fig. 2B). This bias was expected, as these orders also have a large number of species described, and are also well-studied for other reasons (Gullan & Cranston 2014), thereby increasing the likelihood of researchers noticing vibratory behaviors. In contrast, the other 10 orders identified were only sparsely represented (Fig. 3). Future studies should focus on the orders not well-represented in the litera-

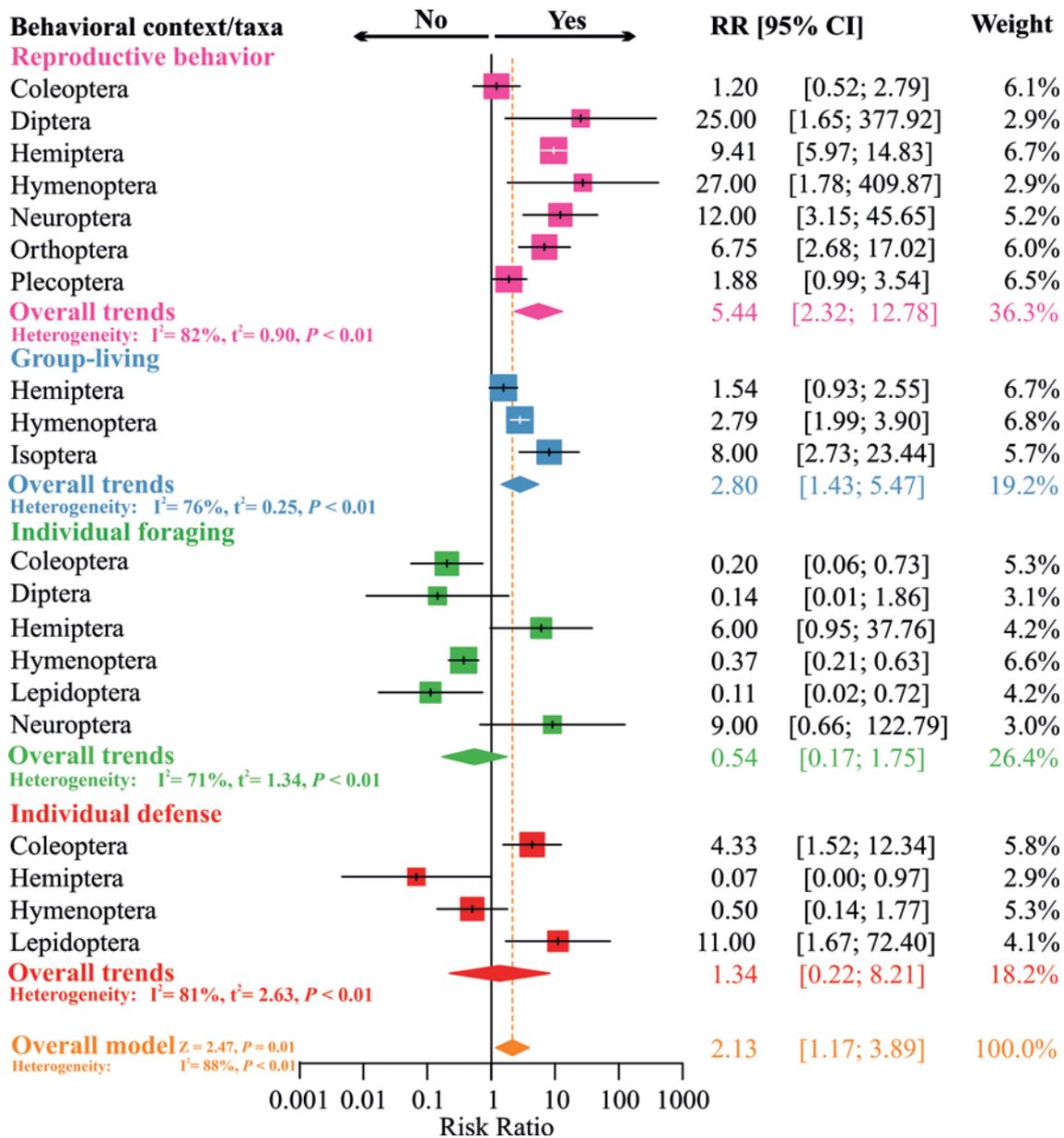


Fig. 5. Forest plot summarizing the results from the frequency of studies documenting a response to vibration by the receiving organism, considering the insect order and behavioral contexts as moderators. The risk ratios (95% CIs) are denoted by colored boxes (horizontal black lines). The combined RR estimate for overall trends is represented by a colored diamond, where diamond width corresponds to 95% CI bounds. The black vertical solid-line represents lack of effect, whereas the orange vertical dashed line shows the overall estimated effect resulting from all studies. The P-values for the heterogeneity test of risk ratios are indicated.

ture, and also should explore sparsely represented genera, families, and species from all orders. This will reveal a wider use of vibration within the Class Insecta, and allow for comparative studies to test hypotheses on function and evolution.

Our results confirmed that there is a research bias towards adults rather than juveniles (Fig. 4). This result reinforces the trends of our own qualitative analysis, as well as previous narrative reviews (e.g. Virant-Doberlet & Čokl 2004; Hill

& Wessel 2016; Yack 2016). Possible explanations for this bias may be the relatively smaller size of juveniles, making vibrations less easily detectable, as well as the general research interest on reproduction in many orders (Fig. 4 – pink diamond), which of course is absent in juveniles. The bias in favor of adults was not generalized among all behavioral contexts. A similar likelihood of studies with adults and juveniles (or lack of bias, RR=1) exists for group-living

(Fig. 4 – blue diamond), foraging (Fig. 4 – green diamond), and individual defense contexts (Fig. 4 – red diamond) showing that studies with juveniles, although smaller in number, are better distributed among these behavioral contexts. This result is likely associated with a growing number of reports that juveniles (particularly from Isoptera, Lepidoptera, Neuroptera, and Hemiptera) use vibrations in a variety of contexts, including egg hatching synchronization (Mukai et al. 2014; Nishide & Tanaka 2016; Endo et al. 2019), coordination of social group activities and recruitment (Fletcher 2007; 2008; Hamel & Coccoft 2012; Yadav et al. 2017), foraging (Suryanarayanan & Jeanne 2008; Suryanarayanan et al. 2011), territorial and spacing behavior (Yack et al. 2001; 2014; Fletcher et al. 2006; Scott et al. 2010; Guedes et al. 2012), and predator avoidance (Castellanos & Barbosa 2006; Low 2008; Gish et al. 2012; Kojima et al. 2012a). This result highlights the potential of juveniles as experimental models in biotremology. Juveniles also comprise a remarkably large portion of agricultural pests, making them conspicuous research models for basic and applied entomology.

Our survey identified a diversity of topics related to insects and vibration, ranging from communication to pest management applications. There was a prevalence of papers focusing on reproductive behaviors, group living, and applied entomology, and a strong interaction between these topics and Hemiptera, Hymenoptera, and Coleoptera, respectively, which suggested that topic and taxonomic biases are related (Fig. 3). The hemipterans, for instance, were important experimental models since the pioneering works of Ossiannilsson (1949), Strübing (1958), Gogala et al. (1974), and Ichikawa & Ishii (1974), leading to a historical series of publications on behaviors associated with reproduction such as species recognition, attraction, mate finding, courtship, and rivalry. The hymenopterans are also conspicuous models in studies of group activities mediated by vibration, such as when eusocial bees signal the location and profitability of a food source (e.g., Hrnčir et al. 2004a; 2004b), or when sawfly larvae use vibrations for recruitment and group cohesion (e.g., Fletcher 2007; 2008). Coleopterans have commonly been used as models for applied entomology from 1965 to the present (Bailey & McCabe 1965; Mankin et al. 2021), with a focus on the detection and monitoring of concealed insects through vibroacoustic cues (e.g., stored product weevils [Njoroge et al. 2016] and wood-boring beetles [Mankin et al. 2016; Jalinias et al. 2019]) (see TableS1).

We assessed whether studies provided evidence for adaptive significance, based on whether there was evidence for a receiver response to a vibrational cue or signal. Our findings revealed that the likelihood of studies documenting a receiver response was 2× higher than not (Fig. 5). Such results were more prominent in reproductive behaviors and group living. This likely reflects the easier assessment of these behaviors, such as when stinkbugs move towards a signalling mate (Čokl & Virant-Doberlet 2003) or when termites respond to

an alarm call (Rosengaus et al. 1999; Delattre et al. 2019). In contrast, studies of foraging and individual defense showed no bias in documenting an adaptive behavior (i.e. they were equally likely to report an adaptive behavior or not).

The lack of bias in foraging likely reflects the fact that, while in some cases a receiver response is relatively easy to document, such as when a predator detects and responds to vibration cues of a prey (e.g., walking or chewing), or by detecting its own signals (e.g., vibrational sounding/echolocation) (Devetak 1985; Pfannenstiel et al. 1995; Meyhöfer et al. 1997; Al-Wahaibi & Walker 2000; Broad & Quicke 2000; Devetak et al. 2007; Fertin & Casas 2007), in other cases a change in behavior of the receiver was not always evident. For example, evidence for a response of the receiver is not always reported in examples of foraging activities such as in buzz pollination, when bees actively vibrate a flower's anthers to release pollen (King 1993; De-Luca et al. 2019; Rosi-Denadai et al. 2020) or when ants create a “vibratome” to facilitate leaf cutting (Tautz et al. 1995). While such examples still constitute adaptive behaviors, they were not scored as such based on our criteria. Similarly, in examples of individual defense, in some cases evidence for vibration reception is easier to document, such as when an insect responds to an attack or threat (Kojima et al. 2012a; 2012b, 2012c; Ichikawa & Sakamoto 2013; Ben-Ari et al. 2014), defends a territory (Yack et al. 2001; 2014; Fletcher et al. 2006; Bowen et al. 2008; Scott et al. 2010; Scott & Yack 2012), or avoids detection by freezing or thanatosis (Acheampong & Mitchell 1997; Djemai et al. 2004; Castellanos & Barbosa 2006; Lee & Jabłoński 2006; Takanashi et al. 2016; Miyatake et al. 2019). On the other hand, many other articles commonly reporting a defensive behavior do not provide evidence of information transfer (Masters 1979; 1980; Puranik et al. 1981; Masters et al. 1983; Tschuch & Brothers 1999; Quiroga et al. 2019), and thus do not test for potential adaptive roles.

In conclusion, our literature survey recognized 17 insect orders associated with vibratory events that are used in a wide diversity of contexts. In these studies, three prominent biases were detected: i) prevalence of studies on Hemiptera, Hymenoptera, and Coleoptera; and ii) a focus on adults, with far less attention to juveniles; and iii) on reproductive behaviors, with less attention to other behavioral contexts. Future studies should focus on a broader range of orders and higher taxa (i.e., genera, families, species). Documentation of the role of vibration in different adaptive contexts is also necessary in exploring how both adults and juveniles (i.e., eggs, larvae/nymphs, and, pupae) use vibrations. A lack of research on the vibratory landscapes of most insects remains noticeable, and also importantly, how many insects sense and process vibrations. Such studies will no doubt lead to novel and intriguing insights into the complex vibratory environments of substrate-bound insects, and may have practical applications for monitoring and managing pests, and inspiring biomimetic devices.

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References

- Acheampong, S., & Mitchell, B. K. (1997). Quiescence in the Colorado potato beetle, *Leptinotarsa decemlineata*. *Entomologia Experimentalis et Applicata*, 82(1), 83–89. <https://doi.org/10.1046/j.1570-7458.1997.00116.x>
- Adedeji, A. A., Ekramirad, N., Rady, A., Hamidisepehr, A., Donohue, K. D., Villanueva, R. T., ... Li, M. (2020). Non-destructive technologies for detecting insect infestation in fruits and vegetables under postharvest conditions: A critical review. *Foods*, 9(7), 927. <https://doi.org/10.3390/foods9070927>
- Al-Wahaibi, A. K., & Walker, G. P. (2000). Oviposition behavior of *Anagrus nigriventris*, an egg parasitoid of beet leafhopper, *Circulifer tenellus*. *BioControl*, 45(2), 139–153. <https://doi.org/10.1023/A:1009994405237>
- Bailey, S. W., & McCabe, J. B. (1965). The detection of immature stages of insects within grains of wheat. *Journal of Stored Products Research*, 1(2), 201–202. [https://doi.org/10.1016/0022-474X\(65\)90022-6](https://doi.org/10.1016/0022-474X(65)90022-6)
- Banga, K. S., Kotwaliwale, N., Mohapatra, D., & Giri, S. K. (2018). Techniques for insect detection in stored food grains: An overview. *Food Control*, 94, 167–176. <https://doi.org/10.1016/j.foodcont.2018.07.008>
- Ben-Ari, M., Talal, S., & Inbar, M. (2014). Anticipatory and reactive crouching of pea aphids in response to environmental perturbations. *Environmental Entomology*, 43(5), 1319–1326. <https://doi.org/10.1603/EN14046>
- Bowen, J. L., Mahony, S. J., Mason, A. C., & Yack, J. E. (2008). Vibration-mediated territoriality in the warty birch caterpillar *Drepana bilineata*. *Physiological Entomology*, 33(3), 238–250. <https://doi.org/10.1111/j.1365-3032.2008.00627.x>
- Broad, G. R., & Quicke, D. L. (2000). The adaptive significance of host location by vibrational sounding in parasitoid wasps. *Proceedings. Biological Sciences*, 267(1460), 2403–2409. <https://doi.org/10.1098/rspb.2000.1298>
- Casacci, L. P., Bonelli, S., Balletto, E., & Barbero, F. (2019). Multimodal signaling in myrmecophilous butterflies. *Frontiers in Ecology and Evolution*, 7, 454. <https://doi.org/10.3389/fevo.2019.00454>
- Casas, J., & Magal, C. (2006). Mutual eavesdropping through vibrations in a host-parasitoid interaction: from plant biomechanics to behavioural ecology. In S. Drosopoulos & M. F. Claridge (Eds.), *Insect sounds and communication: Physiology, Behaviour, Ecology, and Evolution* (pp. 263–271). Boca Raton, Florida: CRC Press.
- Castellanos, I., & Barbosa, P. (2006). Evaluation of predation risk by a caterpillar using substrate-borne vibrations. *Animal Behaviour*, 72(2), 461–469. <https://doi.org/10.1016/j.anbehav.2006.02.005>
- Claridge, M. F. (1985). Acoustic signals in the Homoptera: Behavior, taxonomy, and evolution. *Annual Review of Entomology*, 30(1), 297–317. <https://doi.org/10.1146/annurev.en.30.010185.001501>
- Cocroft, R. B. (2001). Vibrational communication and the ecology of group-living, herbivorous insects. *American Zoologist*, 41(5), 1215–1221. <https://doi.org/10.1093/icb/41.5.1215>
- Cocroft, R. B., & Rodríguez, R. L. (2005). The behavioral ecology of insect vibrational communication. *Bioscience*, 55(4), 323–334. [https://doi.org/10.1641/0006-3568\(2005\)055\[0323:TBEO IV\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2005)055[0323:TBEO IV]2.0.CO;2)
- Cocroft, R. B., & McNett, G. D. (2006). Vibratory communication in treehoppers (Hemiptera: Membracidae). In S. Drosopoulos & M. F. Claridge (Eds.), *Insect sounds and communication: Physiology, Behaviour, Ecology, and Evolution* (pp. 305–318). Boca Raton, Florida: CRC Press.
- Cocroft, R. B., Gogala, M., Hill, P. S., & Wessel, A. (2014a). Fostering research progress in a rapidly growing field. In R. B. Cocroft, M. Gogala, P. S. M. Hill, & A. Wessel (Eds.), *Studying vibrational communication* (pp. 3–12). Heidelberg, Berlin: Springer; https://doi.org/10.1007/978-3-662-43607-3_1
- Cocroft, R. B., Gogala, M., Hill, P. S. M., & Wessel, A. (2014b). *Studying vibrational communication*. Springer; <https://doi.org/10.1007/978-3-662-43607-3>
- Čokl, A., & Virant-Doberlet, M. (2003). Communication with substrate-borne signals in small plant-dwelling insects. *Annual Review of Entomology*, 48(1), 29–50. <https://doi.org/10.1146/annurev.ento.48.091801.112605>
- Delattre, O., Šobotník, J., Jandák, V., Synek, J., Cvačka, J., Jiříček, O., ... Sillam-Dussès, D. (2019). Chemical and vibratory signals used in alarm communication in the termite *Reticulitermes flavipes* (Rhinotermitidae). *Insectes Sociaux*, 66(2), 265–272. <https://doi.org/10.1007/s00040-018-00682-9>
- De Luca, P. A., & Vallejo-Marin, M. (2013). What's the 'buzz' about? The ecology and evolutionary significance of buzz-pollination. *Current Opinion in Plant Biology*, 16(4), 429–435. <https://doi.org/10.1016/j.pbi.2013.05.002>
- De Luca, P. A., Buchmann, S., Galen, C., Mason, A. C., & Vallejo-Marin, M. (2019). Does body size predict the buzz-pollination frequencies used by bees? *Ecology and Evolution*, 9(8), 4875–4887. <https://doi.org/10.1002/ece3.5092>
- Devetak, D. (1985). Detection of substrate vibrations in the antlion larva, *Myrmeleon formicarius* (Neuroptera: Myrmeleonidae). *Bioložki vestnik*, 33(2), 11–22.
- Devetak, D. (1998). Detection of substrate vibration in Neuropteroidea: A review. *Acta Zoologica Fennica*, 209, 87–94.
- Devetak, D., Mencinger-Vračko, B., Devetak, M., Marhl, M., & Špernjak, A. (2007). Sand as a medium for transmission of vibratory signals of prey in antlions *Euroleon nostras* (Neuroptera: Myrmeleontidae). *Physiological Entomology*, 32(3), 268–274. <https://doi.org/10.1111/j.1365-3032.2007.00580.x>
- Djemei, I., Casas, J., & Magal, C. (2004). Parasitoid foraging decisions mediated by artificial vibrations. *Animal Behaviour*, 67(3), 567–571. <https://doi.org/10.1016/j.anbehav.2003.07.006>
- Eberhard, M. J., & Eberhard, S. H. (2013). Evolution and diversity of vibrational signals in Mantophasmatodea (Insecta). *Journal of Insect Behavior*, 26(3), 352–370. <https://doi.org/10.1007/s10905-012-9352-6>
- Elias, D. O., & Mason, A. C. (2014). The role of wave and substrate heterogeneity in vibratory communication: practical issues in studying the effect of vibratory environments in communication. In R. B. Cocroft, M. Gogala, P. S. M. Hill, & A. Wessel

- (Eds.), *Studying vibrational communication* (pp. 215–247). Heidelberg, Berlin: Springer; https://doi.org/10.1007/978-3-662-43607-3_12
- Emerson, A. E., & Simpson, R. C. (1929). Apparatus for the detection of substratum communication among termites. *Science*, 69(1799), 648–649. <https://doi.org/10.1126/science.69.1799.648>
- Endler, J. A. (2014). The emerging field of tremology. In R. B. Cocroft, M. Gogala, P. S. M. Hill, & A. Wessel (Eds.), *Studying vibrational communication* (pp. vii–x). Heidelberg, Berlin: Springer; <https://doi.org/10.1007/978-3-662-43607-3>
- Endo, J., Takanashi, T., Mukai, H., & Numata, H. (2019). Egg-cracking vibration as a cue for stink bug siblings to synchronize hatching. *Current Biology*, 29(1), 143–148. <https://doi.org/10.1016/j.cub.2018.11.024>
- Fertin, A., & Casas, J. (2007). Orientation towards prey in ants: Efficient use of wave propagation in sand. *The Journal of Experimental Biology*, 210(19), 3337–3343. <https://doi.org/10.1242/jeb.004473>
- Fletcher, L. E., Yack, J. E., Fitzgerald, T. D., & Hoy, R. R. (2006). Vibrational communication in the cherry leaf roller caterpillar *Caloptilia serotinnella* (Gracillarioidea: Gracillariidae). *Journal of Insect Behavior*, 19(1), 1–18. <https://doi.org/10.1007/s10905-005-9007-y>
- Fletcher, L. E. (2007). Vibrational signals in a gregarious sawfly larva (*Perga affinis*): Group coordination or competitive signaling? *Behavioral Ecology and Sociobiology*, 61(12), 1809–1821. <https://doi.org/10.1007/s00265-007-0414-2>
- Fletcher, L. E. (2008). Cooperative signaling as a potential mechanism for cohesion in a gregarious sawfly larva, *Perga affinis*. *Behavioral Ecology and Sociobiology*, 62(7), 1127–1138. <https://doi.org/10.1007/s00265-007-0541-9>
- Giunti, G., Campolo, O., Laudani, F., & Palmeri, V. (2018). Male courtship behaviour and potential for female mate choice in the black soldier fly *Hermetia illucens* L. (Diptera: Stratiomyidae). *Entomologia Generalis*, 38(1), 29–46. <https://doi.org/10.1127/entomologia/2018/0657>
- Gish, M., Dafni, A., & Inbar, M. (2012). Young aphids avoid erroneous dropping when evading mammalian herbivores by combining input from two sensory modalities. *PLoS One*, 7(4), e32706. <https://doi.org/10.1371/journal.pone.0032706>
- Gogala, M., Čokl, A., Drašlar, K., & Blažević, A. (1974). Substrate-borne sound communication in Cydnidae (Heteroptera). *Journal of Comparative Physiology. A, Neuroethology, Sensory, Neural, and Behavioral Physiology*, 94(1), 25–31. <https://doi.org/10.1007/BF00610155>
- Guedes, R. N. C., Matheson, S. M., Frei, B., Smith, M. L., & Yack, J. E. (2012). Vibration detection and discrimination in the masked birch caterpillar (*Drepana arcuata*). *Journal of Comparative Physiology. A, Neuroethology, Sensory, Neural, and Behavioral Physiology*, 198(5), 325–335. <https://doi.org/10.1007/s00359-012-0711-8>
- Gullan, P. J., & Cranston, P. S. (2014). *The insects: An outline of Entomology*. John Wiley & Sons Ltd.
- Gurevitch, J., Koricheva, J., Nakagawa, S., & Stewart, G. (2018). Meta-analysis and the science of research synthesis. *Nature*, 555(7695), 175–182. <https://doi.org/10.1038/nature25753>
- Hamel, J. A., & Cocroft, R. B. (2012). Negative feedback from maternal signals reduces false alarms by collectively signaling offspring. *Proceedings of the Royal Society B: Biological Sciences*, 279(1743), 3820–3826. <https://doi.org/10.1098/rspb.2012.1181>
- Henry, C. S., Brooks, S. J., Duelli, P., Johnson, J. B., Wells, M. M., & Mochizuki, A. (2012). Parallel evolution in courtship songs of North American and European green lacewings (Neuroptera: Chrysopidae). *Biological Journal of the Linnean Society. Linnean Society of London*, 105(4), 776–796. <https://doi.org/10.1111/j.1095-8312.2011.01845.x>
- Henry, C. S., Brooks, S. J., Duelli, P., Johnson, J. B., Wells, M. M., & Mochizuki, A. (2013). Obligatory duetting behaviour in the *Chrysoperla carnea*-group of cryptic species (Neuroptera: Chrysopidae): its role in shaping evolutionary history. *Biological Reviews of the Cambridge Philosophical Society*, 88(4), 787–808. <https://doi.org/10.1111/brv.12027>
- Hill, P. S. M. (2008). *Vibrational communication in animals*. Harvard University Press. <https://doi.org/10.2307/j.ctv22jnrn8>
- Hill, P. S. M. (2009). How do animals use substrate-borne vibrations as an information source? *Naturwissenschaften*, 96(12), 1355–1371. <https://doi.org/10.1007/s00114-009-0588-8>
- Hill, P. S., & Wessel, A. (2016). Biotremology. *Current Biology*, 26(5), R187–R191. <https://doi.org/10.1016/j.cub.2016.01.054>
- Hill, P. S. M., Lakes-Harlan, R., Mazzoni, V., Narins, P. M., Virant-Doberlet, M., & Wessel, A. (2019). *Biotremology: Studying vibrational behavior*. Springer; <https://doi.org/10.1007/978-3-030-22293-2>
- Hrcir, M., Jarau, S., Zucchi, R., & Barth, F. G. (2004a). Thorax vibrations of a stingless bee (*Melipona seminigra*). I. No influence of visual flow. *Journal of Comparative Physiology. A, Neuroethology, Sensory, Neural, and Behavioral Physiology*, 190(7), 539–548. <https://doi.org/10.1007/s00359-004-0514-7>
- Hrcir, M., Jarau, S., Zucchi, R., & Barth, F. G. (2004b). Thorax vibrations of a stingless bee (*Melipona seminigra*). II. Dependence on sugar concentration. *Journal of Comparative Physiology. A, Neuroethology, Sensory, Neural, and Behavioral Physiology*, 190(7), 549–560. <https://doi.org/10.1007/s00359-004-0515-6>
- Hunt, J. H., & Richard, F. J. (2013). Intracolony vibroacoustic communication in social insects. *Insectes Sociaux*, 60(4), 403–417. <https://doi.org/10.1007/s00040-013-0311-9>
- Ichikawa, T., & Ishii, S. (1974). Mating signal of the brown planthopper, *Nilaparvata lugens* Stål (Homoptera: Delphacidae): vibration of the substrate. *Applied Entomology and Zoology*, 9(3), 196–198. <https://doi.org/10.1303/aez.9.196>
- Ichikawa, T., & Sakamoto, H. (2013). A third type of defensive behavior in the tenebrionid beetle *Zophobas atratus* pupae. *Journal of Insect Science*, 13(1), 33. <https://doi.org/10.1673/031.013.3301>
- Jalinas, J., Güerri-Agulló, B., Dosunmu, O. G., Haseeb, M., Lopez-Llorca, L. V., & Mankin, R. W. (2019). Acoustic signal applications in detection and management of *Rhynchophorus* spp. in fruit-crops and ornamental palms. *The Florida Entomologist*, 102(3), 475–479. <https://doi.org/10.1653/024.102.0303>
- King, M. J. (1993). Buzz foraging mechanism of bumble bees. *Journal of Apicultural Research*, 32(1), 41–49. <https://doi.org/10.1080/00218839.1993.11101286>
- Kojima, W., Ishikawa, Y., & Takanashi, T. (2012a). Deceptive vibratory communication: Pupae of a beetle exploit the freeze response of larvae to protect themselves. *Biology Letters*, 8(5), 717–720. <https://doi.org/10.1098/rsbl.2012.0386>
- Kojima, W., Ishikawa, Y., & Takanashi, T. (2012b). Pupal vibratory signals of a group-living beetle that deter larvae: Are they mimics of predator cues? *Communicative & Integrative Biology*, 5(3), 262–264. <https://doi.org/10.4161/cib.19886>

- Kojima, W., Takanashi, T., & Ishikawa, Y. (2012c). Vibratory communication in the soil: Pupal signals deter larval intrusion in a group-living beetle *Trypoxylus dichotoma*. *Behavioral Ecology and Sociobiology*, *66*(2), 171–179. <https://doi.org/10.1007/s00265-011-1264-5>
- Lee, S. D. & Jabłoński, P. G. (2006). Effects of visual stimuli, substrate-borne vibrations and air current stimuli on escape reactions in insect prey of flush-pursuing birds and their implications for evolution of flush-pursuers. *Behaviour*, *143*(3), 303–324. <https://doi.org/10.1163/156853906775897860>
- Lima, M. C. F., de Almeida Leandro, M. E. D., Valero, C., Coronel, L. C. P., & Bazzo, C. O. G. (2020). Automatic detection and monitoring of insect pests – A review. *Agriculture*, *10*(5), 161. <https://doi.org/10.3390/agriculture10050161>
- Liu, H., Lee, S. H., & Chahl, J. S. (2017). A review of recent sensing technologies to detect invertebrates on crops. *Precision Agriculture*, *18*(4), 635–666. <https://doi.org/10.1007/s11119-016-9473-6>
- Low, C. (2008). Seismic behaviors of a leafminer, *Antispila nysae-foliella* (Lepidoptera: Heliozelidae). *The Florida Entomologist*, *91*(4), 604–609. <https://doi.org/10.1653/0015-4040-91.4.604>
- Mankin, R. W., Al-Ayedh, H. Y., Aldryhim, Y., & Rohde, B. (2016). Acoustic detection of *Rhynchophorus ferrugineus* (Coleoptera: Dryophthoridae) and *Oryctes elegans* (Coleoptera: Scarabaeidae) in *Phoenix dactylifera* (Arecaceae: Arecaceae) trees and offshoots in Saudi Arabian orchards. *Journal of Economic Entomology*, *109*(2), 622–628. <https://doi.org/10.1093/jee/tov398>
- Mankin, R., Hagstrum, D., Guo, M., Eliopoulos, P., & Njoroge, A. (2021). Automated applications of acoustics for stored product insect detection, monitoring, and management. *Insects*, *12*(3), 259. <https://doi.org/10.3390/insects12030259>
- Masters, W. M. (1979). Insect disturbance stridulation: Its defensive role. *Behavioral Ecology and Sociobiology*, *5*(2), 187–200. <https://doi.org/10.1007/BF00293305>
- Masters, W. M. (1980). Insect disturbance stridulation: Characterization of airborne and vibrational components of the sound. *Journal of Comparative Physiology. A, Neuroethology, Sensory, Neural, and Behavioral Physiology*, *135*(3), 259–268. <https://doi.org/10.1007/BF00657254>
- Masters, W. M., Tautz, J., Fletcher, N. H., & Markl, H. (1983). Body vibration and sound production in an insect (*Atta sexdens*) without specialized radiating structures. *Journal of Comparative Physiology. A, Neuroethology, Sensory, Neural, and Behavioral Physiology*, *150*(2), 239–249. <https://doi.org/10.1007/BF00606374>
- Maynard-Smith, J., & Harper, D. (2003). *Animal signals*. Oxford University Press.
- Meyhöfer, R., Casas, J., & Dorn, S. (1997). Vibration-mediated interactions in a host–parasitoid system. *Proceedings. Biological Sciences*, *264*(1379), 261–266. <https://doi.org/10.1098/rspb.1997.0037>
- Miyatake, T., Matsumura, K., Kitayama, R., Otsuki, K., Yuhao, J., Fujisawa, R., & Nagaya, N. (2019). Arousal from tonic immobility by vibration stimulus. *Behavior Genetics*, *49*(5), 478–483. <https://doi.org/10.1007/s10519-019-09962-x>
- Moher, D., Liberati, A., Tetzlaff, J., & Altman, D. G. (2009). Preferred reporting items for systematic reviews and meta-analyses: The PRISMA statement. *PLoS Medicine*, *6*(7), e1000097. <https://doi.org/10.1371/journal.pmed.1000097>
- Moore, T. E. (1961). Audiospectrographic analysis of sounds of Hemiptera and Homoptera. *Annals of the Entomological Society of America*, *54*(2), 273–291. <https://doi.org/10.1093/aesa/54.2.273>
- Mukai, H., Hironaka, M., Tojo, S., & Nomakuchi, S. (2014). Maternal vibration: An important cue for embryo hatching in a subsocial shield bug. *PLoS One*, *9*(1), e87932. <https://doi.org/10.1371/journal.pone.0087932>
- Muraoka, T., Onoye, H., & Takayanagi, A. (1974). Measurement of phonograph cartridges by the pulse-train method. *Journal of the Audio Engineering Society*, *22*(7), 502–510.
- Nishide, Y., & Tanaka, S. (2016). Desert locust, *Schistocerca gregaria*, eggs hatch in synchrony in a mass but not when separated. *Behavioral Ecology and Sociobiology*, *70*(9), 1507–1515. <https://doi.org/10.1007/s00265-016-2159-2>
- Njoroge, A. W., Affognon, H., Mutungi, C., Rohde, B., Richter, U., Hensel, O., & Mankin, R. W. (2016). Frequency and time pattern differences in acoustic signals produced by *Prostephanus truncatus* (Horn) (Coleoptera: Bostrichidae) and *Sitophilus zeamais* (Motschulsky) (Coleoptera: Curculionidae) in stored maize. *Journal of Stored Products Research*, *69*, 31–40. <https://doi.org/10.1016/j.jspr.2016.06.005>
- Ossiannilsson, F. (1949). Insect drummers. A study on the morphology and function of the sound producing organ of the Swedish Homoptera Auchenorrhyncha with notes on their sound production. *Opuscula Entomologia*, *1949*(10), 1–146.
- Pearman, J. V. (1928). On sound production in the Psocoptera and on a presumed stridulatory organ. *Entomologist's Monthly Magazine*, *64*(14), 179–186.
- Pfannenstiel, R. S., Hunt, R. E., & Yeagan, K. V. (1995). Orientation of a hemipteran predator to vibrations produced by feeding caterpillars. *Journal of Insect Behavior*, *8*(1), 1–9. <https://doi.org/10.1007/BF01990965>
- Polajnar, J., Eriksson, A., Lucchi, A., Anfora, G., Virant-Doberlet, M., & Mazzoni, V. (2015). Manipulating behaviour with substrate-borne vibrations—potential for insect pest control. *Pest Management Science*, *71*(1), 15–23. <https://doi.org/10.1002/ps.3848>
- Puranik, P. G., Ahmed, A., & Siddiqui, M. A. (1981). The mechanism of sound production in the pentatomid bug *Tessaratoma javanica* Thunberg. *Proceedings: Animal Sciences*, *90*(2), 173–186. <https://doi.org/10.1007/BF03185992>
- Quiroga, N., Muñoz, M. I., Pérez-Espinoza, S. A., Penna, M., & Botto-Mahan, C. (2019). Stridulation in the wild kissing bug *Mepraia spinolai*: Description of the stridulatory organ and vibratory disturbance signal. *Bioacoustics*, *29*(3), 266–279. <https://doi.org/10.1080/09524622.2019.1603120>
- R Development Core Team (2020). R: A Language and Environment for Statistical Computing. <http://www.R-project.org>
- Rajendran, S. (1999). Detection of insect infestation in stored food commodities. *Journal of Food Science and Technology*, *1999*(36), 283–300.
- Rosengaus, R. B., Jordan, C., Lefebvre, M. L., & Traniello, J. F. A. (1999). Pathogen alarm behavior in a termite: A new form of communication in social insects. *Naturwissenschaften*, *86*(11), 544–548. <https://doi.org/10.1007/s001140050672>
- Rosi-Denadai, C. A., Araújo, P. C. S., Campos, L. A. D. O., Cosme, L., Jr., & Guedes, R. N. C. (2020). Buzz-pollination in Neotropical bees: Genus-dependent frequencies and lack of optimal frequency for pollen release. *Insect Science*, *27*(1), 133–142. <https://doi.org/10.1111/1744-7917.12602>
- Schneider, S. S., & Lewis, L. A. (2004). The vibration signal, modulatory communication and the organization of labor in honey

- bees, *Apis mellifera*. *Apidologie*, 35(2), 117–131. <https://doi.org/10.1051/apido:2004006>
- Schwarzer, G., Carpenter, J. R., & Rucker, G. (2015). *Meta-analysis with R*. Springer; <https://doi.org/10.1007/978-3-319-21416-0>
- Scott, J. L., Matheson, S. M., & Yack, J. E. (2010). Variation on a theme: Vibrational signaling in caterpillars of the rose hook-tip moth, *Oreta rosea*. *Journal of Insect Science*, 10(1), 54. <https://doi.org/10.1673/031.010.5401>
- Scott, J. L., & Yack, J. E. (2012). Vibratory territorial signals in caterpillars of the poplar lutestring, *Tethea or* (Lepidoptera: Drepanidae). *European Journal of Entomology*, 109(3), 411–417. <https://doi.org/10.14411/eje.2012.053>
- Stewart, K. W. (1997). Insect Life: Vibrational Communication in Insects. *American Entomologist (Lanham, Md.)*, 43, 81–91. <https://doi.org/10.1093/ae/43.2.81>
- Strübing, H. (1958). Lautäußerung – der entscheidende Faktor für das Zusammenfinden der Geschlechter bei Kleinzikaden (Homoptera – Auchenorrhyncha) (Vorläufige Mitteilung). *Zoologische Beiträge*, 4(1), 15–21.
- Suryanarayanan, S., & Jeanne, R. L. (2008). Antennal drumming, trophallaxis, and colony development in the social wasp *Polistes fuscatus* (Hymenoptera: Vespidae). *Ethology*, 114(12), 1201–1209. <https://doi.org/10.1111/j.1439-0310.2008.01561.x>
- Suryanarayanan, S., Hermanson, J. C., & Jeanne, R. L. (2011). A mechanical signal biases caste development in a social wasp. *Current Biology*, 21(3), 231–235. <https://doi.org/10.1016/j.cub.2011.01.003>
- Takanashi, T., Fukaya, M., Nakamuta, K., Skals, N., & Nishino, H. (2016). Substrate vibrations mediate behavioral responses via femoral chordotonal organs in a cerambycid beetle. *Zoological Letters*, 2(1), 18. <https://doi.org/10.1186/s40851-016-0053-4>
- Takanashi, T., Uechi, N., & Tatsuta, H. (2019). Vibrations in hemipteran and coleopteran insects: Behaviors and application in pest management. *Applied Entomology and Zoology*, 54(1), 21–29. <https://doi.org/10.1007/s13355-018-00603-z>
- Tautz, J., Roces, F., & Hölldobler, B. (1995). Use of a sound-based vibratome by leaf-cutting ants. *Science*, 267(5194), 84–87. <https://doi.org/10.1126/science.267.5194.84>
- Tschuch, G., & Brothers, D. J. (1999). Modeling vibration and sound production in insects with nonresonant stridulatory organs. *The Journal of the Acoustical Society of America*, 106(6), 3706–3710. <https://doi.org/10.1121/1.428227>
- Uman, L. S. (2011). Systematic reviews and meta-analyses. *Journal of the Canadian Academy of Child and Adolescent Psychiatry*, 20(1), 57–59.
- Virant-Doberlet, M., & Čokl, A. (2004). Vibrational communication in insects. *Neotropical Entomology*, 33(2), 121–134. <https://doi.org/10.1590/S1519-566X2004000200001>
- Virant-Doberlet, M., Kuhelj, A., Polajnar, J., & Šturm, R. (2019). Predator-prey interactions and eavesdropping in vibrational communication networks. *Frontiers in Ecology and Evolution*, 7, 203. <https://doi.org/10.3389/fevo.2019.00203>
- Watanabe, K. (1978). Phonograph for use with record cartridges. U.S. Patent No. 4,123,065. Washington, DC: U.S. Patent and Trademark Office.
- Yack, J. E., Smith, M. L., & Weatherhead, P. J. (2001). Caterpillar talk: Acoustically mediated territoriality in larval Lepidoptera. *Proceedings of the National Academy of Sciences of the United States of America*, 98(20), 11371–11375. <https://doi.org/10.1073/pnas.191378898>
- Yack, J. E., Gill, S., Drummond-Main, C., & Sherratt, T. N. (2014). Residency duration and shelter quality influence vibratory signalling displays in a territorial caterpillar. *Ethology*, 120(4), 354–364. <https://doi.org/10.1111/eth.12210>
- Yack, J. E. (2016). Vibrational signaling. In G. S. Pollack, A. C. Mason, A. N. Popper, & R. R. Fay (Eds.), *Insect hearing* (pp. 99–123). Cham, Switzerland: Springer; https://doi.org/10.1007/978-3-319-28890-1_5
- Yadav, C., Guedes, R. N. C., Matheson, S. M., Timbers, T. A., & Yack, J. E. (2017). Invitation by vibration: Recruitment to feeding shelters in social caterpillars. *Behavioral Ecology and Sociobiology*, 71(3), 51. <https://doi.org/10.1007/s00265-017-2280-x>

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